MAIZE GENETICS COOPERATION

NEWSLETTER

70

March 15, 1996

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and
U.S. Department of Agriculture
University of Missouri
Columbia, Missouri

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CLONE INFORMATION SHEET

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Maize Genetics Cooperation Newsletter
Curtis Hall
University of Missouri
Columbia, MO 65211
phone 573-882-2768
fax 573-884-7850
email ed@teosinte.agron.missouri.edu

"The Barbara A. McClintock Graduate Fund in Plant Science has been established to encourage and support the work of promising graduate students in the field of plant biology, with preference given to women. We hope you will join campaign initiator Robert Rabson, Professor Ronnie Coffman, alumni, friends of the college, and those concerned with world agricultural development in support of this important and timely project. The Barbara A. McClintock Graduate Fund will provide much needed student support at Cornell, but it will do more than that. It will honor the career of one of the college's most outstanding alumnae and continue McClintock's remarkable legacy of research and mentorship, memorializing her spirit, her work, and her genius."

To contribute, or for more information on the Barbara A. McClintock Graduate Fund, please contact:

Maya L. Gasuk
Director of Development
Agriculture and Life Sciences
272 Roberts Hall
Ithaca, NY 14853

I. FOREWORD

The 'Cooperation' exists because you are a 'Cooperator' in keeping up the tradition of sharing information with colleagues, here and in many unheralded conversations, correspondence, and shared stocks and clones. The working research information here is shared with the understanding that each item is unpublished and is not to be cited in publications without specific consent of the authors. By sharing our research information, we contribute to the advancement of biology and to the power of shared technical knowledge.

Information here is in the form of "notes" and is not "published" in the sense of a refereed journal. Cooperators present brief technical notes, updates, mutants, segregation ratios, tables of mapping data, developmental and anatomical information and techniques, clones, biochemical functions, and the like. Comprehensive material and analyses are better directed to formal publication.

More and more cooperators supply notes, tables and figures in electronic form, and this greatly facilitates editing and compiling.

Following the interesting and valuable Reports, from individual Cooperators and laboratories, note the information sections, summaries, and compilations presented in this issue:

Address List
Maize Genetics Cooperation - Stock Center
Maize Genome Database
Maize Probe Bank
New Genes - Newly Mapped Genes - New Markers
Combined Table of SSR Loci
Working Maps
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Physical Maps of the Maize Mitochondrial Master Chromosomes (with thanks to Christiane Fauron)
Zealand 1996
Symbol and Author Indexes

Gifts to the Endowment Fund for support of the Newsletter now total about $100,000. Please see the listing, in the front of this issue, of donors whose generosity has made this total grow. We are all grateful for the support of our colleagues and of organizations with which we have common interests. Gifts to the Endowment Fund continue to be needed to assure that costs of production are met, and are very much appreciated.

The continuity and support necessary for collecting genetic and molecular information, evaluating it, and preparing gene lists, maps, and similar syntheses are made possible only by sustained and ongoing encouragement of this work within the Agricultural Research Service. The MaizeDB project advanced, through the efforts of Dr. Jerry Miksche, from a temporary to a regular, ongoing program provided by the Curator, Dr. Mary Polacco. We urge you with our strongest enthusiasm to use, assess, and contribute to the database.

Mary Polacco ingeniously contrived and "dumped" the supplemental Gene List (New Genes and Newly Mapped Genes); the list of New Markers; Zealand 95; reference links for ; the Stock List; and author and symbol indexes from MaizeDB, aided by the skillful savvy of Denis Hancock and Shirley Kowalewski. Help, advice and ideas also from my colleagues Mike McMullen, who reviewed and helped refine the whole, and Pat Byrne and Georgia Davis, who compiled, summarized, and evaluated contents, are warmly appreciated. Shirley Kowalewski skillfully made the contents into fine form, twisted diverse electronic sources to suit and interpreted exotic scripts, structured the year's literature and indexes, and questioned quality or content, or gave creative advice, at key moments. At University Printing Services, Yvonne Ball and the printshop staff again efficiently ensured the job was done promptly and well.

Details about the 1997 Maize Genetics Conference at Clearwater Beach, Florida, March 13-16, 1997, will be available on the MaizeDB Web at the earliest date, and information will be mailed to former attendees in November 1996; others may request the mailing by providing their address to Coe. The program and abstracts are provided by Bill Sheridan. The pilot trial for electronic submission and "Webification" of abstracts for the 1996 Maize Conference in parallel was largely successful, and will be enhanced for the 1997 Conference. The Steering Committee for the 1997 Maize Genetics Conference is:

Mary Alleman	Jeff Bennetzen	Paul Chomet
Curt Hannah, local coordinator	Barbara Kloeckener	Jane Langdale
Mike McMullen	Paul Sisco, Chair	Julie Vogel

For submission of notes for the next issue (Number 71, 1997), please see details inside the back cover.

If you wish to subscribe to this Newsletter please use the form in the back of this issue.

Editor Coe

ALBANY, CALIFORNIA
USDA Plant Gene Expression Center

Mapping of the *abphyl* locus which regulates phyllotaxy in maize

--Jackson, D and Hake, S

In last year's newsletter we described a new heritable *abphyl* mutation which causes an increase in the size of the shoot apical meristem in the coleoptilar stage embryo and a subsequent change in phyllotaxy from distichous to decussate in a large proportion of mutant individuals (MNL 69:2). We have continued to introgress this mutation into different genetic backgrounds, and it acts as a single recessive locus. We used bulked segregant analysis (Michelmore et al., PNAS 88:9828-9832) to map the locus, with much appreciated advice from Mike McMullen (USDA-ARS, University of Missouri, Columbia). Plants showing the *abphyl* phenotype were outcrossed to B73 (all of the F1 were normal) then backcrossed to *abphyl*, so the F2 segregated 1:1 mutant: normal (heterozygotes). Two pools of DNA from approximately 30 mutant and 30 normal individuals, respectively, as well as B73 DNA, were digested with *Sst*I, *Eco*RI, *Eco*RV or *Bam*HI and subjected to Southern analysis using core RFLP probes. No linkage was found with probes from chromosomes 1, 3, 6, 9 or 2L, however two probes from 2S, *umc6* and *umc131*, showed very clear differences in hybridization patterns between the mutant and normal pools with all of the enzymes used.

We prepared DNA from 30 individual mutant and 30 normal plants and used these to get a more accurate map position. Probes *umc6* and *umc131* detected 10 and 8 recombinants, respectively, from the 60 individuals tested, and since the current UMC maize RFLP map shows these RFLP loci to be 35 cM apart this is highly suggestive that the locus (symbol *abph1*) lies between them. To confirm this we used a probe, *umc34*, which lies between *umc6* and *umc131*, and failed to observe any recombinants in our population, suggesting that *abph1* probably lies within a couple of cM of *umc34*. We also used a probe from *b1* (kindly provided by Vicki Chandler, University of Oregon) and estimate that *abph1* is in the order of 8 cM from *b1*. We are in the process of refining these data by mapping relative to other mutants on 2S, as well as initiating tagging strategies using stocks carrying transposable elements at *b1* (kindly provided by Vicki Chandler), and a new *Ac* transposition onto 2S, from the Maize Genetics Coop Stock Center (originally from Hugo Dooner, MNL 69:115).

Identification of target genes of the KNOTTED1 homeodomain protein by subtractive hybridization

--Char, BR and Hake, S

To understand the role the homeobox gene *knotted1* (*kn1*) plays in development, we undertook to identify its downstream targets. A subtractive hybridization scheme to isolate up-regulated target genes was devised, taking advantage of the pattern of expression of *kn1* in the dominant *Kn1-N2* allele. In this allele, *kn1* is ectopically expressed in localized regions of the leaf, usually close to veins, whereas in wild-type plants *kn1* expression is undetectable in leaves. mRNA from unexpanded leaves of 10-day old *Kn1-N2* seedlings was isolated and converted into double-stranded cDNA. Some of this double-stranded cDNA was used to construct a cDNA library. First strand wild type leaf cDNA was synthesized on mRNA attached to magnetic beads and the resulting RNA:DNA hybrids denatured to remove the RNA strand. A large excess of wild type cDNA attached to the beads was then hybridized to a trace amount of denatured double-stranded cDNA made from *Kn1* leaves. After exhaustive hybridization the renatured cDNA left in solution was used to make a cDNA library, the wild-type cDNA population being removed along with the beads. The cDNAs in solution represented unique clones present in the *Kn1* leaf cDNA population. The subtracted library was screened with a subtracted probe, and in addition, fifty random clones were picked and analyzed.

A total of seven different genes were obtained from the two approaches. From the library screen, ABA-inducible glycine-rich

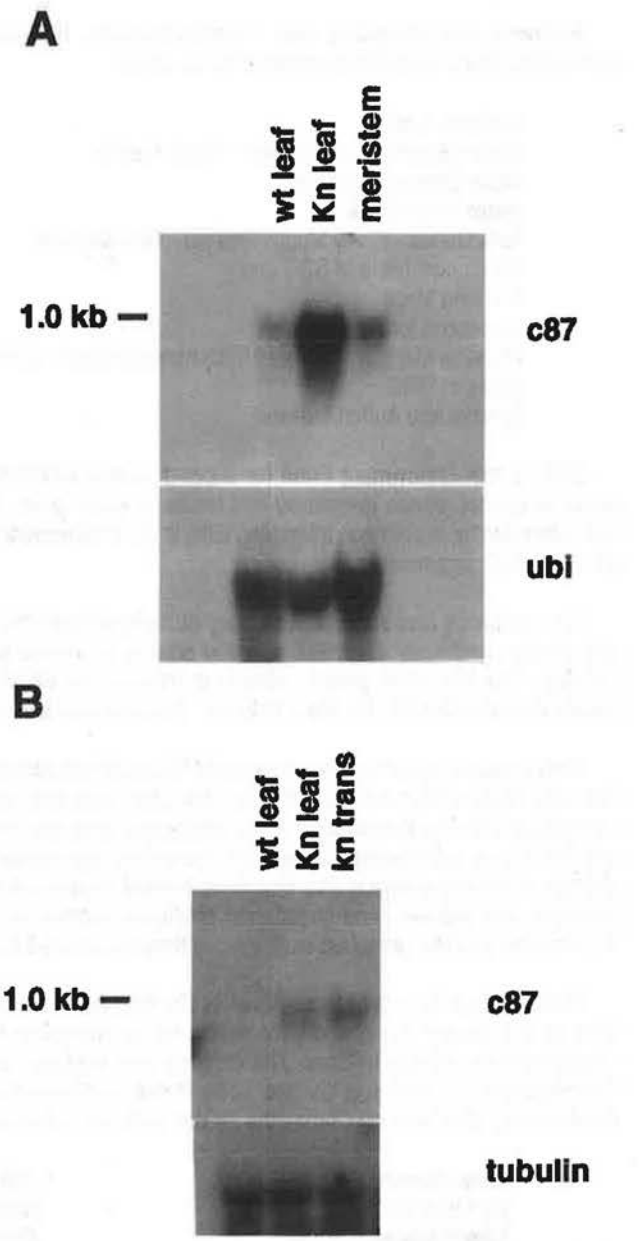


Figure 1. Expression levels of *c87* mRNA in wild-type, *Kn1* and 35S::*kn1* leaves. A. Northern blot showing the increase in expression of *c87* in *Kn1* leaves as compared to wild-type leaves. Expression is also detectable in meristem enriched tissue. 10 µg of total RNA was loaded in each lane. The blot was reprobed with a maize ubiquitin (*ubi*) probe as a loading control. B. Northern blot of leaf RNA from wild-type, *Kn1* and 35S::*kn1* plants probed with a *c87* cDNA probe. *Kn1* and 35S::*kn1* (*kn* trans) leaves show increased levels of *c87* mRNA. 10 µg of total RNA was loaded in each lane. The blot was reprobed with a maize tubulin probe as a loading control.

protein (GRP) and CHEM2, a stress-inducible GRP, were obtained. The ABA-inducible GRP, also known as MA16, contains a consensus RNA-binding motif. From the randomly picked clones, five additional groups of cDNAs were isolated, each group comprising 1 to 2 clones. These included *c87*, a cDNA showing some homology to plant S-like ribonucleases, a cDNA showing homology to *BnC24*, a *Brassica napus* gene homologous to a human tumour gene, breast basic conserved1 (*bbc1*), and 3 cDNA fragments which showed no significant homology to any sequences in the GenBank database. The two GRPs were also represented in the randomly picked clones.

On Northern blots, *c87* showed a substantial increase in expression in *Kn1* leaves over wild type leaves (Figure 1A), showing that the subtraction protocol enriched for cDNAs that are more abundant in *Kn1* leaves. ABA-inducible GRP and CHEM2 also showed increases in expression in *Kn1* leaf tissue, while the other genes did not show an increase or were not detectable on RNA blots. In addition, *c87* showed increased mRNA levels in leaves of transgenic maize plants constitutively expressing *kn1* (Figure 1B). Approximately 3 kb of *c87* genomic sequence upstream of the transcription start site was obtained. A KN1 homeodomain peptide bound with low affinity to fragments of the *c87* promoter in gel retardation assays. Full-length cDNAs for *c87* were obtained and used to generate probes for in situ hybridization on tissue from wild-type and *Kn1* seedlings. *c87* mRNA was detected in *Kn1* leaves but not in wild-type leaves. Localized expression of *c87* was detected in ears, in structures closely associated with stamen primordia, possibly lodicules. In tassels, *c87* is localized to the L1 and L2 cell layers on the abaxial side of developing flowers. Later in development *c87* expression appears as a ring at the base of the growing point of each floret. Determination of the map location of *c87* is in progress.

ALBANY, CALIFORNIA
Plant Gene Expression Center
BERKELEY, CALIFORNIA
University of California at Berkeley

Dosage analysis on the *teosinte branched1* mutation suggests it is an antimorphic dominant mutation

--Hubbard, L and Hake, S

Plants homozygous for the *teosinte branched1* mutation in maize exhibit a severe phenotype of extreme tillering and long lateral branches tipped by tassels in upper ear nodes. Previous observations suggest that *tb1-ref* has a semi-dominant effect on tiller number when heterozygous, displaying a mild tillered phenotype with no obvious effects on the female inflorescence (Schnable, MNL 66:5, 1992).

Dosage analysis of the *tb1* locus was begun to further investigate the *tb1-ref* allele. Crosses were carried out using a line of maize obtained from James Birchler (University of Missouri) that is carrying a transposition of 18% of the long arm of chromosome 1L within chromosome 3L, which we will designate as Tp(1-3). Tp(1-3) encompasses the *tb1* locus and thus can be used to generate stocks hyperploid for the normal or mutant alleles of *tb1* (Birchler and Levin, Genetics 127:609-618, 1991). A Tp(1-3) heterozygote was crossed by *tb1-ref* homozygotes and the F1 was backcrossed by *tb1-ref* homozygotes. The resulting material was assayed for the presence of *tb1-ref* or the normal *tb1* allele by linkage to different *adh1* alleles.

Results from the dosage analysis on plants carrying 1 or 2 doses of normal or mutant *tb1* alleles show that when *tb1-ref* allele is present at a higher dose than the normal allele, the severe tb1-ref phenotype is observed (Table 1). These results suggest that the *tb1-ref* allele actively interferes with functioning of the normal *tb1* allele and therefore, this mutation should be interpreted as antimorphic. These findings are consistent with the observation that this mutation may be semi-dominant. Analyses of the mild tillering phenotype in *tb/+* relative to +/+ and tb/+/+ (+ representing the normal allele and *tb* the mutant) are under investigation.

Table 1. Results from crosses in which the female parent is heterozygous for Tp(1-3) and *tb1-ref* and the male parent is homozygous for *tb1-ref*.

	Severe phenotype*	Normal phenotype
tb/tb	9	
tb/+		14
tb/+/+		13
tb/tb/+	9	

*Severe phenotype consists of long lateral branches tipped by tassels in the ear position and excessive tillering.

Note: The stock carrying *tb1-ref* allele was obtained from Bill Sheridan (University of North Dakota).

AMES, IOWA
Iowa State University

Anther color in BSSS–101 inbred line

—Zhang, XH and Hallauer, AR

BSSS–101 line was derived by single–seed descent from the Iowa Stiff Stalk Synthetic (BSSS) population after 10 generations of self–pollination. BSSS-101 was regarded as a homogeneous line for breeding purposes. Purple and green anther colored plants were observed within BSSS-101 in the breeding nursery in 1992. In 1992, plants with purple and green anthers were crossed to produce the F1 generation. The F2 generation was produced in the 1992–1993 winter nursery by self pollination. The backcrosses of F2 generation plants with purple and green anthers to the parents with purple and green anthers were produced in 1993. Purple and green anther plants within the F2 generation also were selfed in 1993 to produce the F3 generation. Purple and green anther color parents and the F1 and F2 generations were grown in the 1993 breeding nursery. Purple and green anther color parents, and F1, F2, F3, and backcross generations were grown in the 1994 breeding nursery. In each season, individual plants were classified for purple and green anther color. Plants that had slightly blotched anther color upon emergence from stamens were also recorded. The classification of plants with different anther color was recorded in each generation at the time of pollen shed.

When two plants of different anther color were crossed within the BSSS-101 line of maize in 1992, the F1 generation exhibited a 3:1 ratio of plants with purple and green colored anthers in 1993: 53 plants had purple anthers and 17 plants had green anthers. The F2 generation also exhibited a 3:1 ratio: 157 plants with purple anthers and 52 plants with green anther (Table 1). In 1994, the 3:1 ratio also was observed in F1 and F2 generations: F1 generation had 15 plants with purple anthers and 5 plants with green anthers, and F2 generation had 287 plants with purple anthers and 93 plants with green anthers. An 8:1 ratio was observed in

the F3 generation upon selfing F2 plants with purple anthers (160 plants with purple anthers and 20 plants with green anthers). For plants having green anthers, however, anther color did not segregate either in crosses made between plants with green anthers or in selfs of F2 plants with green anthers (Table 1). The backcrosses of F2 generation plants with purple anther color to the parent with purple anthers had only purple anthers. A 1:1 ratio was found in the backcrosses of F2 generation plants with purple anther color to the green anther color parent. When F2 generation green anther plants were crossed to the green anther parent, progeny of this backcross all had green anther color (Table 2). It was observed that plants with purple anthers had light–red silks, light purple color at base of stem, colorless aleurone, and red cobs. Plants with green anthers had green silks, green color at base of stem, colorless aleurone, and red cobs. Daily examination of the field plants indicated that the purple anthers were affected by sunlight. In general, if the anthers were slightly blotched purple upon emergence, the anthers later became completely purple after exposure to sunlight.

Table 1. Data for anther color obtained from crosses and selfs of BSSS–101 line in 1992, 1993, and 1994.

Year	Generation	Purple anther (no. plants)	Green anther (no. plants)	Total	Ratio
1992	BSSS–101	47	26	73	3:1
1993	Parent (purple in 1992)	73	0	73	—
	Parent (green in 1992)	0	74	74	—
	F1 (purple x green cross in 1992)	53	17	70	3:1
	F2 (self of cross in 1992–93)	157	52	209	3:1
1994	Parent (purple in 1993)	48	0	48	—
	Parent (green in 1993)	0	30	30	—
	F1 (purple x green cross in 1993)	15	5	20	3:1
	F2 (self of cross in 1993)	287	93	89	3:1
	F3 (purple anther F2 self)	160	20	80	8:1
	F3 (green anther F2 self)	0	96	96	—

Table 2. Data obtained for anther color of backcrosses of BSSS–101 line in 1994.

Cross[a]	Purple anther (no. plants)	Green anther (no. plants)	Total	Ratio
P x P	93	0	93	—
P x G	54	50	104	1:1
G x G	0	83	83	—

[a]P refers to plants with purple anthers. G refers to plants with green anthers.

Anthocyanin pigment is synthesized in the aleurone layer of the maize endosperm, in the embryo, and in many vegetative plant organs, including leaf, stem, anthers, glumes of the cob, tassel, and coleoptiles (Coe et al., Corn and Corn Improvement pp. 81–258, ASA, 1988). Genes that affected different plant tissues were determined and given gene designation. The *a1* allele causes colorless aleurone, green or brown plant, and brown pericarp with *p1–RP*. The *a2* allele is similar to *a1*, but *a2* gene has red pericarp with *p1–RP*. The *a3* allele is a recessive intensifier of expression of *R1* and *B1* in plant tissues. Some genes affect aleurone and embryo color; *beta* determines aleurone and plant color and red pericarp; *bz1* modifies purple aleurone and plant color to either pale or reddish brown, and anther color is yellow–fluorescent; *bz2* is like *bz1*, but has anthers that are not fluorescent; the *C1* gene determines colored aleurone, *c1* colorless, *C1–I* dominant colorless, *c1–p* pigment inducible by light; the *c2* gene has colorless aleurone, reduced plant color, and reduced chalcone synthase, and *c2– Idf* is a dominant inhibitor; the *p1* gene confers red pigment in cob and pericarp; *sm1*, salmon silk color with *P1-RR*, and brown with *P1-ww*; and the *r1* gene regulates the anthocyanin pathway, dominant *R1* (S element) confers function in aleurone; dominant represented by *R1-r* or *r1-r* (P element) confers function in anthers, leaf tip, and brace roots (Coe et al. ibid; Coe, MNL 68:157–184, 1994).

In this study, the F1 generation had a 3:1 ratio for purple and green anthers. Anther color could be due to one pair of allelic genes and a modifier gene. The allele that controls purple anthers is completely dominant to the allele that controls green anthers. The modifier gene plays a role in the heterozygous condition only, based on the data of the backcrosses and on effect of anthers under sunlight.

The purple anther color genotypes may be of three kinds; *c1-n, c1-p*, and *r-r*, according to phenotype of plants, in which it had purple anthers, yellow pollen, light red silks, colorless aleurone, and red cob. The green anther genotypes can be just one kind, *r-g*, according to effects on colorless aleurone, red cobs, yellow pollen, and green silks of plant (Coe et al., ibid). The gene controlling anther color could be at the *R* locus or in the *R* region. The four basic types, *R-r, R-g, r-r, r-g*, designated by Emerson (Cornell Univ. Agric. Exp. Stn. Mem. 39. 1921), are symbolized according to effect on aleurone color (R vs. r) and on anther color (r, red vs. g, green). Hence, we conclude that the purple anther genotypes could be *r-r*.

The purple anthers became darker after exposure to sunlight, based on the blotched purple anthers that emerged from the stamens. A modifier gene of anther pigment may be *pl-Bh*, which leads to variegated pigment in virtually all tissues of the plant, including the kernel, an organ not pigmented by other *pl* alleles (Cocciolone and Cone, Genet. 135:575–588, 1993). The color at the base of the stem and silks of plants could be a linkage effect with anther color in the BSSS-101 line.

One pair of alleles should have the same anther color in the F1 generation of the cross of homozygous plants. The F1 generation, however, had a 3:1 ratio for plants with purple and green anthers. Anther color did not segregate when the purple anther parent was selfed. This suggested that some traits related to anthocyanin pigment were not homozygous or were partially homozygous in some plants and that there was a modifier gene that had an interaction in the case of heterozygotes. Because of segregation within the F1 generation, larger population sizes will be needed.

Based on these ambiguous results, we will increase the population size of the F1 and the F2 generations and control the environment in the crossing and selfing of plants. The genotypes of each generation will be tested with appropriate genetic tester stocks and by using isolation to determine which genes controlled the anther color of BSSS-101 plants.

Genetic analysis of *su1-R2412*, an allele of *su1* with an intermediate phenotype

--James, M

Su1 codes for a starch debranching enzyme that is active during starch biosynthesis (James et al., Plant Cell 7:417-429, 1995). Mutant *su1-Ref* kernels accumulate sugars and the water-soluble polysaccharide phytoglycogen during development, and have a shrunken and overall translucent appearance in the mature dried state. Many *su1* alleles have been identified, including some that appear near-normal, or that have a phenotype intermediate to wild type and *su1-Ref*. I am investigating one of these intermediate alleles, *su1-R2412*, which arose in a *Mutator* background. When homozygous, *su1-R2412* results in a mildly wrinkled and translucent kernel crown, while the base of the kernel appears normal. This phenotype was observed in less than the expected

Mendelian ratios following the self-pollinations of heterozygotes. When *su1-R2412* is combined with *su1-Ref*, an intermediate phenotype results, in which the kernel is slightly shrunken and translucent on the periphery, especially in the crown. This suggests that *su1-R2412* has a modulating effect on *su1-Ref*.

Because *su1-R2412* was generated in a *Mutator* background, the mutation is likely due to the insertion of a *Mu* element at the *su1* locus. To test for the reversion of *su1-R2412* to wild type due to *Mu* element excision, approximately 700 *su1-R2412/su1-Ref* plants were pollinated by *su1-Ref* testers (Silver Queen) in an isolation plot in the 1994 summer nursery. Silver Queen also is homozygous for *y1*, which was used in subsequent analyses as a contamination marker. The resulting ears segregated for the standard sugary and intermediate sugary phenotypes, but also had many starchy kernels, suggesting a high rate of reversion of *su1-R2412* to wild type. The frequency of this putative reversion was calculated to be approximately 2.4%. This reversion frequency is higher than that calculated for another allele of *su1*, *su1-R4582::Mu1*, by approximately 10^4.

To test whether the starchy kernels represented stable reversion events, 36 starchy kernels were planted and self-pollinated in the 1995 summer nursery; in addition, 10 kernels that had an intermediate sugary phenotype also were planted. 25 plants derived from the starchy kernels produced ears that segregated for both *su1* and *y1*; however, these ears contained both the standard sugary and intermediate sugary phenotypes, indicating that *su1-R2412* was still present. This suggests that these 25 "revertant" kernels may have been starchy as a result of suppression of the mutant phenotype, as described by Barkan and Martienssen (PNAS 88:3502-3506, 1991), rather than as a result of the excision of a *Mu* element from the *su1* locus. The remaining 11 plants from starchy kernels produced ears that segregated for *su1*, but not *y1*, indicating that these starchy kernels most likely resulted from contaminating wild type pollen. All 10 plants derived from the intermediate sugary kernels (presumably *su1-R2412/su1-Ref*) produced ears that contained from 25% to 50% starchy kernels, in addition to both sugary phenotypes; as expected, each ear contained approximately 25% kernels with the standard *su1* phenotype (presumably *su1-Ref/su1-Ref*). Thus, one or two doses of *su1-R2412* were able to confer either an intermediate sugary or a normal kernel phenotype.

DNA gel blot analyses with *Eco*RI and *Bam*HI of populations segregating 1:1 for *su1-R2412* showed a RFLP of approximately 2 kb that cosegregated with the *su1-R2412* mutant allele. PCR and nucleotide sequence analyses localized this polymorphism to the 5' leader region of *su1*. Experiments are in progress to investigate 1) the presence and identity of a possible *Mu* element insertion in this 5' leader region; and 2) the molecular basis for the starchy "revertant" kernels, including possible correlations of the methylation status of this region or element with the mutant or wild type phenotype.

Three putative *Mutator*-induced alleles of *bm4*

--Robertson, DS

As a result of studies conducted on *Mutator*-induced *Bf1* mutants (*Bf1-Mu*), three *bm4* mutant alleles at the *bm4* locus were found. All *Bf1-Mu* mutants produced in these studies were selected against the *Bf1-R* allele (mutant phenotype - homozygous seedlings, and anthers of heterozygous or homozygous plants, fluoresce blue under U.V. light). Each of the original *Bf1-Mu* isolates was of the genotype *Bf1-Mu/Bf1-R*. These original isolates (214 total) were crossed as females to a standard line (*bf1+/bf1+*), resulting in progeny plants of the genotypes *Bf1-Mu/bf1+* and *Bf1-R/bf1+*. Plants from the progenies of thirty-eight of the isolates, which had been outcrossed to standard, were crossed reciprocally to *Bf1-R Bf1-R* stocks, as a first screen to determine if any of these isolates might involve deletions. If a deletion was involved, about half of the plants, when outcrossed as males, might have a reduced frequency of Bf seedlings in their outcross progenies. Whereas, these same plants, outcrossed as females, might have about 50% Bf seedlings or less in their outcross progenies. If less, however, the female outcross progenies should have more Bf seedlings than the male outcross progenies. Twenty-seven of the isolates tested showed this pattern of inheritance and were tested further in an attempt to obtain additional evidence that would support the assumption that a deletion was involved.

The putative *bm4-Mu* mutants occurred in the tests of three of these isolates, *Bf1-Mu-044-4*, *Bf1-Mu-046-6* and *Bf1-Mu-546-5*. Twenty kernels were planted from the ears of the plants that had reduced transmission of the *Bf1-Mu* homolog through the pollen in the reciprocal crosses with homozygous *Bf1-R* stocks. Two genotypes are expected in the progeny plants from these female outcrosses: *Bf1-Mu/Bf1-R* and *bf1+/Bf1-R*. If plants of the former genotype were pollinated by homozygous *bm4-R* plants, and if the *Bf1-Mu* event was a deletion of sufficient size to include the distal *bm4* locus, bm plants would be expected to segregate in the progeny of this cross. The test involving the *Bf1-Mu-044-4* isolate resulted in seven out of nine progenies that segregated for bm plants. The expected genotypes in these segregating progenies are *Bf1-Mu/bf1+ bm4-R* and *Bf1-R bm4+/bf1+ bm4-R*. The former genotype would result in bm plants with Bf anthers, if *Bf1-Mu-044-4* is a deletion that involves both the *bf1* and *bm4* loci. The latter genotype would result in green plants. A total of 18 bm plants were found in these seven progenies. There are other possible explanations for the results from the reciprocal crosses and the *bm4* test other than a deletion that involves both the *bf1* and *bm4* loci. There are several combinations of two or more simultaneous events induced by the *Mutator* system that could account for these observations. For example, the *Bf1* mutant phenotype could be caused by the insertion of a *Mu* element at this locus and the *bm4* phenotype could be due to a *Mutator*-induced deletion of this locus. Another possibility is that the *Bf1* phenotype is the result of a deletion of this locus and the *bm4* phenotype is the result of an insertion mutation. Perhaps both the *Bf1* and *bm4* phenotypes were the result of the insertion of two different *Mu* elements and a *Mutator*-induced deletion, which occurred in the proximity of these loci, but did not include either of them. Because multiple *Mutator*-induced alterations in one egg involving a short chromosomal region are highly unlikely, the simple explanation of a deletion involving both loci is the most reasonable, until proven otherwise.

The test of *Bf1-Mu-046-6* resulted in one family with one bm plant out of five outcross progenies tested. Although nine outcross progenies of *Bf1-Mu-546-5* were grown, none segregated for bm plants.

The bm plants from the tests of the first two isolates were pollinated by standard plants, resulting in progeny plants of the following genotypes: *Bf1-Mu/bf1+ bm4+* and *bf1+ bm4-R/bf1+ bm4+*. Plants with Bf anthers, the former genotype, were recip-

rocally crossed to homozygous *Bf1-R* plants to determine if the same results were obtained as when the isolate was first tested in reciprocal crosses with homozygous *Bf1-R* plants.

In five out of six reciprocal outcross tests of the *Bf1-Mu-044-4* isolate, the results were close to the original reciprocal outcross tests (average values: male outcross progenies 2.04% Bf seedlings and female outcross progenies 37.66% Bf seedlings). The progeny of one of the bm plants of this isolate, however, did not give results that duplicated those of the original reciprocal outcross test. None of the plants gave results (Table 1) that approach those observed in the original or second reciprocal outcross tests of this isolate. Also there was no consistent pattern of inheritance seen for the six plants tested. They vary with respect to the percentage of Bf seedlings in both the male and female outcross progenies. In the progenies of all but one plant (#2) there are more Bf seedlings in the male crosses than the female crosses. This is not a result expected if a deletion were present.

Table 1. Results of seedling tests of reciprocal crosses of the individual plants from the outcross progeny of the first putative *bm4-Mu* mutant (derived from the *Bf1-Mu-044-4* isolate).

Plant no.	Female crosses +	Bf	Total	% Bf	Male crosses +	Bf	Total	% Bf
2	43	4	47	8.51	67	1	68	1.47
3	24	15	39	38.46	19	12	31	38.71
4	18	19	37	51.35	1	53	54	98.15
5	44	10	54	18.52	40	10	50	20.00
6	37	6	43	13.95	36	15	51	29.41
7	37	10	47	21.28	23	31	54	57.41
Total	203	64	267	23.97	186	122	308	39.61
Total less #4	185	45	230	19.57	185	69	254	27.17

These results suggest that the bm plant crossed with standard had a different origin than the rest of the bm plants of this isolate. If the *Bf1-Mu/Bf1-R* plant pollinated by the homozygous *bm4-R* plant had an active *Mutator* system, which is very likely, there is the possibility that it could have produced an egg carrying a *Mutator*-induced *bm4-Mu* mutant in the homolog with the *Bf1-R* allele. When this egg was fertilized by a sperm with the *bm4-R* allele, a bm plant with the genotype *Bf1-R bm4-Mu/bf1+ bm4-R* would result. A bm plant that had this origin, when pollinated by standard pollen, would have progeny plants of the following two genotypes: *Bf1-R bm4-Mu/bf1+ bm4+* and *bf1+ bm4-R/bf1+ bm4+*. Plants of the former genotype would have Bf anthers, and when crossed reciprocally to *Bf1-R Bf1-R* plants would not be expected to give frequencies of Bf seedlings observed in the original tests of the *Bf1-Mu-044-4* isolate because they do not carry the putative deletion. Such is the situation observed in Table 1. The erratic transmission, however, observed in this table would not be expected if a simple insertion mutant was responsible for the *bm4-Mu* allele. (See below for a discussion of this and similar patterns of transmission exhibited by the other two putative *bm4-Mu* mutants.)

The isolate *Bf1-Mu-046-6* probably does not carry a deletion that includes the *bm4* locus, because only one bm plant was found in the *bm4* test. Further, when plants from the outcross of this isolate with standard were tested in reciprocal crosses with homozygous *Bf1-R* plants (Table 2) the original transmission pattern of Bf seedlings was not observed (i.e., 46.10% Bf seedlings in the female outcross progeny and 27.04% Bf seedlings in the male outcross progeny). If the *Bf1-Mu-046-6* is not a deletion,

Table 2. Results of seedling tests of reciprocal crosses of the individual plants from the outcross progeny of the second putative *bm4-Mu* mutant (derived from the *Bf1-Mu-046-6* isolate).

Plant no.	Female crosses +	Bf	Total	% Bf	Male crosses +	Bf	Total	% Bf
1	47	8	55	14.55	----------			
2	14	8	22	36.36	26	18	44	40.91
4	51	0	51	0.00	53	0	53	0.00
5	31	11	42	26.19	22	17	39	43.59
6	18	7	25	28.00	48	19	67	28.36
8	25	28	53	52.83	29	22	51	43.14
9	27	17	44	38.64	25	30	55	54.55
10	18	5	23	21.74	26	15	41	36.59
Total	231	84	315	26.67	229	121	350	34.57
Total less #4	180	84	264	31.18	176	121	297	40.74

which includes the *bm4* locus, how is the occurrence of this one bm plant explained? It could have occurred in the same manner as the atypical bm plant in the test of the *Bf1-Mu-044-4* isolate. The reciprocal crosses of *Bf1-R bm4-Mu-046-6/bf1+ bm4+* plants to homozygous *Bf1-R* plants show an erratic transmission pattern similar to that of the *bm4-Mu* mutant from the tests of the *Bf1-Mu-044-4* isolate.

The third putative *bm4-Mu* mutant resulted from a different crossing procedure than the former two. A plant of the putative genotype *Bf1-Mu-546-5/bf1+* [from the cross of the original isolate (*Bf1-Mu-546-5/Bf1-R*) by a plant from a standard line] was pollinated by a plant heterozygous for the A-B translocation TB-9Lc, which involves most of the long arm of chromosome nine. The same plant, which was pollinated by TB-9Lc, was outcrossed as a male to a homozygous *Bf1-R* plant. This cross was made to determine if the plant pollinated by the TB-9Lc stock carried the putative deletion, which the results of the original reciprocal cross of this isolate to homozygous *Bf1-R* plants suggested might be present. In the original test, the male outcross progenies had 27.93% Bf seedlings. In the outcross test of the plant pollinated by TB-9Lc, 30.45% of the seedlings were of the Bf phenotype. On the surface these two percentages appear to be reasonably close. However, the former percentage was statistically different from a 1:1 ratio at the one percent level (n = 111), while the latter was not significantly different from a 1:1 ratio at the five percent level (n = 13). Thus, there was a distinct possibility that the plant pollinated by TB-9Lc was not heterozygous for *Bf1-Mu-546-5*, but was instead heterozygous for the *Bf1-R* allele. Because of the small size of the outcross progeny in this test (n = 13) and because the chi square value was close to that expected for significance at the five percent level, the progeny of the cross with TB-9Lc was tested further to determine if this plant was heterozygous for *Bf1-Mu-546-5*. Two Bf seedlings occurred in the progeny of this cross, which were transplanted to the field. Both of these plants had the phenotype expected for hypoploid TB-9Lc plants (i.e., short plants with narrow leaves, rudimentary tassels that only occasionally extrude anthers that shed no pollen, and small ears, which in most plants produce kernels when pollinated). Unexpectedly, these two plants had the brown midrib phenotype. Because there is no other bm mutant known on the long arm of chromosome 9, these plants probably are hemizygous for a *Mutator*-induced mutant at the *bm4* locus. Only one of these plants produced an ear and it was pollinated by a standard plant. If the original plant pollinated by TB-9Lc was heterozygous for the *Bf1-Mu-546-5* allele, all progeny plants of this cross were expected to be of the genotype *Bf1-Mu-546-5/bf1+*, and should

have shown a reduced frequency of Bf seedlings in progenies from the male outcrosses to homozygous *Bf1-R* plants. The results (Table 3) do not duplicate the *Bf1-R* test results of the original isolate. Thus, the hypoploid plant probably does not carry the *Bf1-Mu-546-5* allele. This would mean that the plant pollinated by TB-9Lc was heterozygous for the *Bf1-R* allele and the hypoploid Bf seedlings were hemizygous for this allele. The most logical explanation for the origin of the bm phenotype is that it was the result of a *Mutator*-induced *bm4* mutant on the homolog that carried *Bf1-R* in the original *Bf1-Mu-546-5/Bf1-R* isolate that was pollinated by standard. The homolog with *Bf1-R* and the closely linked putative *bm4-Mu* mutant allele had an erratic transmission pattern (Table 3) similar to that of the previous two *bm4-Mu* mutants. Note: the latter mutant has not been confirmed as being a mutant at the *bm4* locus. It, however, must be on the long arm of chromosome nine and as yet no other mutant with the bm phenotype has been described on this arm. This fact along with its erratic transmission pattern, which is similar to those observed for the other two *bm4-Mu* mutants, strongly suggests that it is a *bm4-Mu* mutant.

Table 3. Results of seedling tests of reciprocal crosses of the individual plants from the outcross progeny of the third putative *bm4-Mu* mutant (derived from the *Bf1-Mu-546-5* isolate).

	Female crosses				Male crosses			
Plant no.	+	Bf	Total	% Bf	+	Bf	Total	% Bf
1	20	42	62	67.74	21	21	42	50.00
2	16	40	56	71.43	18	14	32	43.75
3	18	6	24	25.00	31	31	62	50.00
4	10	17	27	62.96	23	23	46	50.00
5	23	13	36	36.11	----------			
6	17	18	35	51.43	----------			
7	12	8	20	40.00	21	21	42	50.00
8	20	6	26	23.08	17	34	51	66.67
9	13	12	25	48.00	20	23	43	53.49
10	17	7	24	29.17	28	20	48	41.67
1a	18	8	26	30.77	16	19	35	54.29
2a	19	12	31	38.71	18	18	36	50.00
3a	16	8	24	33.33	17	24	41	58.54
4a	16	10	26	38.46	28	27	55	49.09
5a	25	9	34	26.47	----------			
6a	16	7	23	30.43	23	23	46	50.00
7a	25	16	41	39.02	18	24	42	57.14
8a	23	6	29	20.69	21	21	42	50.00
9a	9	1	10	10.00	29	8	37	21.62
10a	15	11	26	42.31	27	18	45	40.00
Total	348	257	605	42.48	376	369	745	49.53

Chi square tests for heterogeneity of the female and male outcross progenies in Tables 1, 2, and 3 were all significant at the one percent level. Why was this erratic transmission pattern observed for all three of these mutants? It would suggest that these *Mutator*-induced mutants at the *bm4* locus must have involved more than simple insertion mutations. Probably they were the result of more complex changes that happened to involve this locus and resulted in the mutant bm phenotype at the same time.

The following are a few unanswered questions about the results reported above: Is it just coincidence that three *bm4* mutants derived from different *Bf1-Mu* isolates happen to have erratic transmission patterns? Could it be that there is something involved in the induction of the *Bf1-Mu* isolates that is responsible for this unusual behavior of a *bm4* mutant, when a mutation occurs at this locus in these stocks? Would *bm4* mutants that were induced directly by the *Mutator* system (i.e., were not derived from a *Bf1-Mu* stock) show the erratic transmission patterns observed for the mutants in this report? What mechanism is responsible for the transmission pattern of these mutants?

It should be pointed out that the results reported here are based on the transmission, not of the mutant *bm4-Mu* allele, but on the transmission of the closely linked *Bf1-R* allele. All plants tested had the putative genotype of *Bf1-R bm4-Mu/bf1+ bm4+* and, thus, the transmission of the *bm4-Mu* allele would be expected to closely approximate that of the *Bf1-R* allele. There remains the possibility, however, that some kind of recombination event is taking place that eliminates the *bm4* mutant allele from the gametes that function and at the same time is responsible for the erratic transmission of the *Bf1-R* allele. This possibility could be tested by crossing sibling plants from those used for generating the data reported in Tables 1, 2, and 3 with plants homozygous for both *Bf1-R bm4-R* and simultaneously scoring the progenies for both the Bf and bm phenotypes. Another test could be made by self-pollinating Bf plants from the progenies of the reciprocal crosses of the putative *Bf1-R bm4-Mu/bf1+ bm4+* plants. Most of the progenies from these selfs should segregate for bm plants, if no crossing over between the *bf1* and *bm4* loci had occurred.

I will gladly supply seeds to anyone who is interested in analyzing these mutants further.

The *P* locus in teosinte

--Zhang, P and Peterson, T

The *P* gene controls phlobaphene pigment synthesis in maize floral organs, most notably kernel pericarp and cob. To understand the molecular evolution of this regulatory gene, we are investigating the *P* gene in the maize relative teosinte. Using materials supplied by John Doebley, we have found apparent visible *P* gene expression in teosinte as a faint brown color in the tassel glume margin. It was previously reported by Ed Coe that the brown color of maize tassel glume margins was correlated with the *P*–specified red cob trait. Further evidence for a *P* gene in teosinte has been obtained by Southern hybridization, PCR, and sequencing. The Myb–homologous DNA binding domains of the maize and teosinte *P* genes are highly conserved. Our long–term interest is in how the tissue–specific expression of the *P* gene was affected by the marked changes in floral organ morphology which occurred in the development of maize from teosinte.

Trans–factors affecting *P–wr* expression: *Ufo* and *sm*

--Chopra, S and Peterson, T

The maize *P–wr* gene specifies white (colorless) pericarps and red cob glumes, and we have previously analyzed the structure and expression of *P–wr* (MNL 69:9, 1995). We have recently begun the analysis of other factors which affect *P–wr* expression, including *Ufo* (Unstable factor for orange; D. Styles) *Ufo* is a dominant factor which intensifies *P–wr* pigmentation in husks and cob glumes, and also expands the tissue–specific distribution of *P–wr* pigmentation to the kernel pericarp and vegetative parts of the plant. Northern blot analysis shows that, compared to *P–wr* and *P–rr* plants, *P–wr Ufo* plants have much higher levels of *C2*, *CHI1*, and *A1* transcripts in young silks and husks. Because the *Ufo* seeds provided by Dr. Styles also carried *sm* (salmon silks), further testing is required to determine whether the transcriptional effect is in fact due to *Ufo* or *sm*.

The *P–wr* gene contains a unique 3' end encoding a putative zinc finger domain

--Chopra, S and Peterson, T

While looking for the reason for the unique cob–glume expression pattern of *P–wr*, we found that the transcribed and trans-

lated 3' end of the *P–wr* cDNA is comprised of a 210 bp insertion relative to *P–rr* (although without any notable features of a transposable element insertion). Southern blotting shows that this sequence is found only in *P–wr* genotypes. The unique *P–wr* sequence encodes a cysteine–rich carboxy–terminal domain similar to the zinc finger or metal binding domains of the type $CX_1CX_7CX_2C$ (C = Cysteine, X= any amino acid. Subscript shows number of residues). This motif also contains phenylalanine and leucine residues which are commonly found in zinc finger domains. To our knowledge *P–wr* is the first example of a gene encoding a protein with both a Myb DNA binding domain and a single zinc–finger domain.

AMES, IOWA
Iowa State University
JOHNSTON, IOWA
Pioneer Hi-Bred

Analysis of the *P–rr* promoter in transgenic maize

--Li, X; Sidorenko, L; Tagliani, L; Chopra, S; Bowen, B and Peterson, T

The maize *P–rr* gene encodes a *myb*–like transcription activator which activates the *C2*, *CHI1*, and *A1* genes to produce a red phlobaphene pigment in floral tissues, such as mature cob glumes, pericarps, and husks. To characterize the tissue–specific activity of the *P–rr* promoter, we produced transgenic maize plants carrying different segments of the *P–rr* promoter fused to the GUS reporter gene. Plasmid construct P1.0b::GUS, which contains the *P–rr* region from –1252 to +352 relative to the transcription start, produced 96 stable callus events and 714 transgenic plants. The majority of these plants expressed GUS specifically in pericarps, husks, and silks; GUS activity was not detectable in endosperm, embryo, and pedicel, or vegetative tissues of mature plants. Interestingly, GUS was expressed specifically in transgenic anther wall. To our knowledge there is no previous report of *P–rr* expression in these cells. With the exception of the anther wall expression, the majority of transgenic plants demonstrated floral–specific GUS expression pattern similar to the pattern of *P–rr*. In conclusion, the 1.5 kb fragment contains the elements required for floral–specific expression of the *P* gene.

We also generated 12 stable callus lines and 76 plants for construct Pb::GUS (–233 to +326), and 15 stable callus lines and 94 transgenic plants for construct P1.2b::GUS (5' 1.2– kb *Sal*I fragment fused to the basal plasmid Pb::GUS). Interestingly, 77% and 54% of transgenic T0 stable transgenic maize transformed with the P1.0b::GUS or P1.2b::GUS, respectively, expressed GUS in their floral tissues. In contrast, only 18% of transgenic Pb::GUS plants expressed GUS in floral tissues. In conclusion, the P1.0 and P1.2 fragments not only enhanced Pb strength in driving expression of the reporter gene in transiently assayed suspension cells and pericarps (X. Li et al., MNL 69:9, 1995), but also boosted tissue–specific Pb activity in stable transgenic maize plants. The pattern of tissue specific expression in plants transformed with P1.2b::GUS was more variable compared to those transformed with P1.0b::GUS. Occasionally, only parts of glumes, husks, and silks of P1.2b::GUS showed GUS blue staining, unlike the uniform GUS expression in transgenic plants containing the P1.0b::GUS constructs. Perhaps, the irregular expression of P1.2::GUS may be due to the presence of the 5' 1.2 kb *Sal*I fragment which is a site of epigenetic modification in the *P–pr* allele as demonstrated by Das and Messing (Genetics 136:1121–1141, 1994) and Lund et al. (Plant J. 7:797–807, 1995).

The Pb, P1.0b, and P1.2b constructs above all contain the maize *Adh1* intron in front of the GUS gene to boost expression. Three constructs which were similar, but without the *Adh1* intron, produced only a few GUS positive plants. These constructs without the *Adh1* intron also had very low activity in transient assays. These results suggest that transient assays should be used as a preliminary test of promoter activity before generating stable transgenic maize.

BALTIMORE, MARYLAND
Carnegie Institution of Washington

***Spm* element: Significance of multiple TnpA binding sites**

--Raina, R and Fedoroff, N

The maize *Suppressor-mutator (Spm)* transposable element encodes two proteins, TnpA and TnpD, which are necessary and sufficient for transposition (Masson et al., Plant Cell 3:37, 1991). TnpA affects the epigenetic state of the *Spm* element by activating the methylated inactive *Spm* promoter (Schlappi et al., Cell 77:427, 1994). TnpA is a DNA-binding protein (Gierl et al., EMBO J. 7:4045, 1988) and there are multiple copies of its 12-bp binding site located at the element's 5' and 3' ends. However, the role of TnpA and TnpD in the transposition of *Spm* is not understood. We have previously reported that TnpA binds to the ends of the element in a concentration-dependent manner (Raina and Fedoroff, MNL 69:13, 1995). We hypothesize that once TnpA is bound to its binding sites, higher order protein-protein interactions bring the ends of the element together. Here we analyze the effect of the presence of multiple TnpA binding sites on binding of TnpA and interaction of DNA-TnpA complexes.

To assess whether the presence of multiple binding sites at the ends of the *Spm* element is important for the formation of higher order complexes, we studied the binding of TnpA to various deletion derivatives of the 5'-end of the element. The derivatives have 1, 2, 3, 6 and 9 binding sites. Over-expression and purification of TnpA in *E. coli* have been described previously (Raina and Fedoroff, MNL 69:13, 1995). Target DNAs with 1 to 9 binding sites (except for one with 2 binding sites) were generated by exonuclease III deletions of the 5'-end of the element (Raina et al., Proc. Natl. Acad. Sci. USA 90:6355, 1993). DNA fragments with 2 binding sites were generated by cloning an oligonucleotide corresponding to TnpA binding sites 2 and 3 at the 5'-end of the element in the *Eco*RV site of bluescript KS+. The fragment was released by digestion with enzymes *Bam*HI and *Pvu*I.

The effect of multiple binding sites on binding of TnpA to DNA was studied by a band-mobility shift assay. The results are shown in Figure 1. The same amount of labeled DNA and protein has been used in all the experiments. The DNA was labeled at both the ends in all cases except for the fragment with 2 binding sites, in which only one end was labeled. The results of this experiment show that the binding of TnpA increases similarly with the protein concentration for all fragments tested. As the protein:DNA ratio increases, more and more sites are occupied (Figures 1 and 2), giving bands of larger size. We have not ob

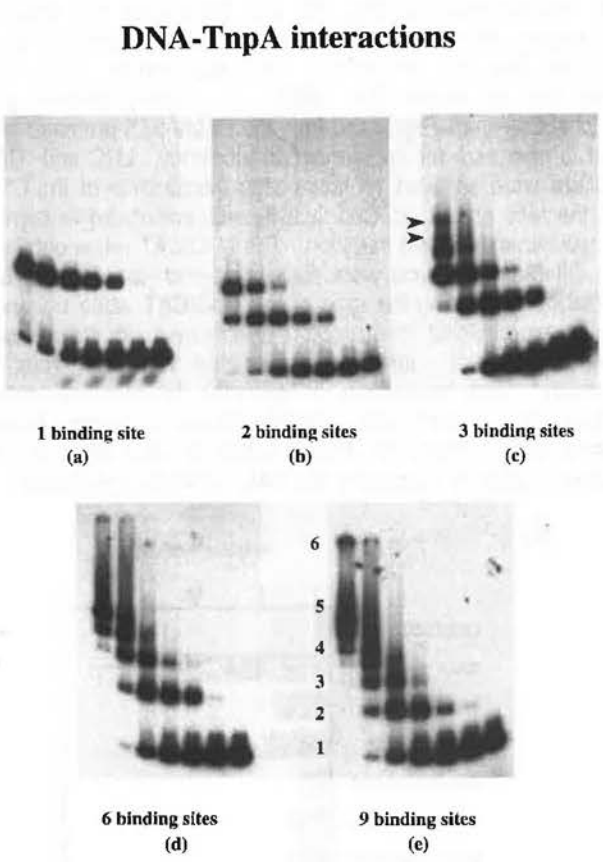


Figure 1. Band shift assay using deletion derivatives of 5'-end of the element and TnpA.

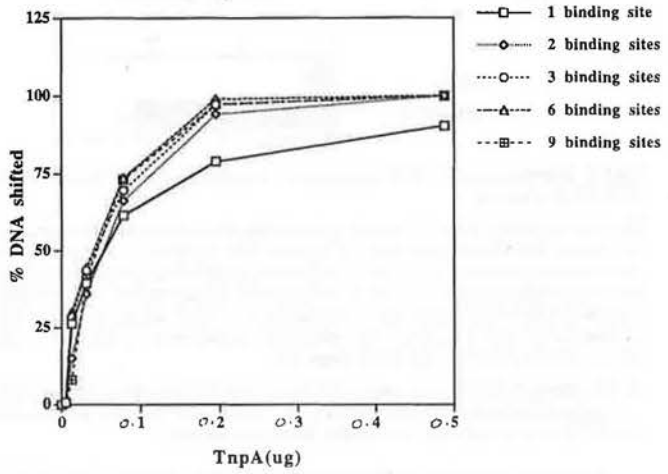


Figure 2. Graphical representation of data in Figure 1.

served stronger binding of TnpA to a tail-to-tail dimeric binding site than a monomeric binding site, as reported previously (Figure 1a, b; Trentmann et al., Mol. Gen. Genet. 238: 210, 1993). Fragments containing 1 and 2 binding sites give one and two slower-migrating complexes, respectively (Figure 1a, and b). These complexes correspond to one or two sites occupied by TnpA. However when a DNA fragment with 3 binding sites is used in these experiments, we observe more than the expected 3 bands (Figure 1c). When DNA with more binding sites is used in these experiments, we find that a higher fraction of the shifted DNA is

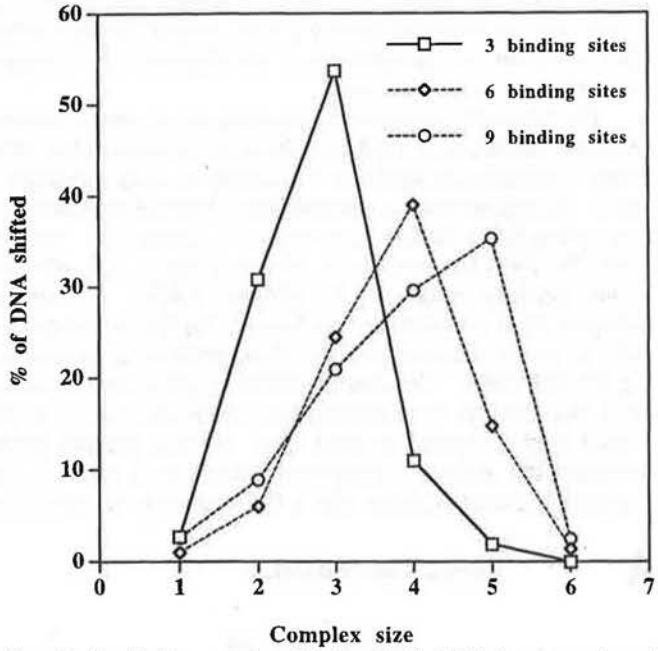


Figure 3. Graphical representation of fraction of shifted DNA in each complex. A representative complex size is shown in Figure 1e.

in large complexes and this fraction increases with increasing numbers of binding sites per DNA molecule (Figure 3). The large complexes probably arise by intermolecular protein-protein interaction between the TnpA molecules already bound to DNA.

Because we see no evidence of dimerization of TnpA with a fragment containing a single binding site, we propose that the dimerization domain of TnpA is involved in the formation of intermolecular TnpA-DNA complexes. This hypothesis is supported by the observation that fraction of shifted DNA in higher order complexes increases with increasing numbers of TnpA binding sites/molecule (Figure 3). We therefore propose that the dimerization domain of TnpA is involved in protein-protein interactions between TnpA molecules already bound to DNA and that it functions to bring the ends of the element together during transposition.

A highly sensitive plant hybrid protein assay system based on the *Spm* promoter and TnpA protein for detection and analysis of transcription activation domains

--Schläppi, M and Fedoroff, N

TnpA is a multifunctional DNA binding protein encoded by the maize *Suppressor-mutator* (*Spm*) transposable element. TnpA is required for transposition and is both a repressor of the unmethylated *Spm* promoter and an activator of the methylated promoter. While analyzing the protein using a yeast GAL4-based hybrid system in transiently transformed tobacco cells, we found that TnpA represses the >10-fold transcriptional activation observed when the GAL4 DNA binding domain is used alone. By contrast, a 33- to 45-fold activation of the *Spm* promoter was observed when the VP16 activation domain was tethered to TnpA. TnpA binding sites, but no TATA box, were required for transcription activation. Among the TnpA deletion derivatives tested, those retaining the coding sequences for the DNA-binding and protein-dimerization domains gave the highest level of transcription activation when fused with the VP16 activation domain. As

shown below, the TnpA gene and TnpA binding sites in the short *Spm* promoter therefore provide a novel, highly sensitive single-hybrid system for identifying and studying plant transcription activation domains in plant cells.

The full-length TnpA coding sequence and 5'- and 3'-terminal deletion derivatives of TnpA were fused to the yeast GAL4 DNA-binding domain and tested for their ability to affect transcription of a LUC reporter gene expressed from a minimal plant promoter containing GAL4 binding sites (Figure 1; Ginigeret al., Cell 40: 767-774, 1985; Trentmann et al., Mol. Gen. Genet. 238: 201-208, 1993; Schläppi et al., Cell 77: 427-437, 1994). The Herpes Simplex VP16 activation domain fused to the GAL4 DNA-binding domain served as a positive control (Triezenberg et al., Genes Dev. 2: 718-729, 1988). The effect of the fusion genes was compared with the baseline transcriptional activation observed with the GAL4 binding domain in plant cells. Effector plasmid DNAs carrying the various translational fusions were coated onto tungsten particles together with a GAL4 binding site-containing LUC reporter plasmid (Fig. 1B) and introduced into tobacco suspension cells by microprojectile bombardment (Russell et al., In Vitro Cell Dev. Biol. 28: 97-105, 1992; Raina et al., Proc. Natl. Acad. Sci. 90: 6355-6359, 1993). A plasmid containing a bacterial CAT gene expressed from the CaMV 35S promoter was used to normalize for transformation efficiency. LUC and CAT activities were assayed 18 hours after introduction of the DNA and the ratio of LUC to CAT activity was calculated to correct for between-experiment variation. The LUC/CAT ratios obtained with different constructs were then compared with the relevant control by calculating the ratio of the LUC/CAT value obtained with an experimental construct to that obtained with the relevant control construct and expressing the ratio as "relative activation." Thus, for example, in Figure 2A, the reference control value is the LUC/CAT ratio obtained with an antisense effector plasmid, while in Figure 2B, it is the LUC/CAT value obtained with an effector plasmid expressing the GAL4 DNA-binding domain.

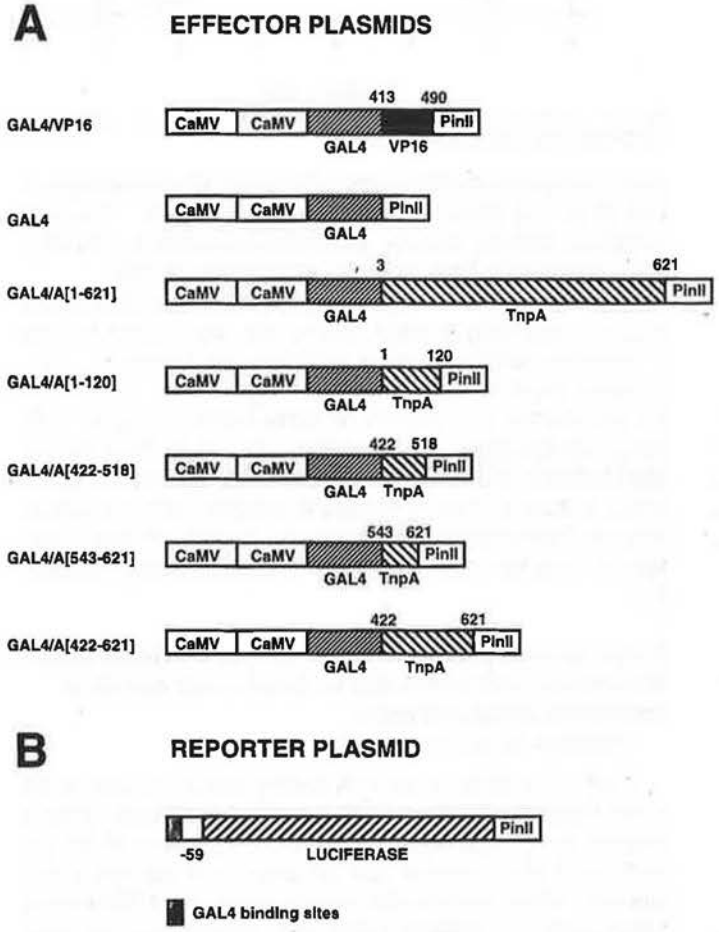


Figure 1. Schematic representation of GAL4 fusion genes and the luciferase reporter gene.

(A) Effector plasmids are those that encode a trans-acting activator or repressor of the luciferase reporter gene. Each construct contains the yeast GAL4 DNA binding domain either alone or translationally fused to the following: VP16, the strong activation domain of the Herpes Simplex virus VP16 (amino acids [a.a.] 413 to 490); A[3-621], full-length TnpA (a.a. 3 to 621); A[1-120], N-terminus of TnpA (a.a. 1-120); A[422-518], the protein dimerization domain of TnpA (a.a. 422 to 518); A[543-621], C-terminus of TnpA (a.a. 543 to 621); A[422-621], the dimerization domain and C-terminus of TnpA (a.a. 422 to 621). PinII, *potato proteinase inhibitor II* terminator; CaMV, Cauliflower Mosaic Virus 35S promoter.

(B) The reporter plasmid contains 5 GAL4 DNA binding sites upstream from a truncated CaMV promoter (bp -59 to +2) and the firefly luciferase gene.

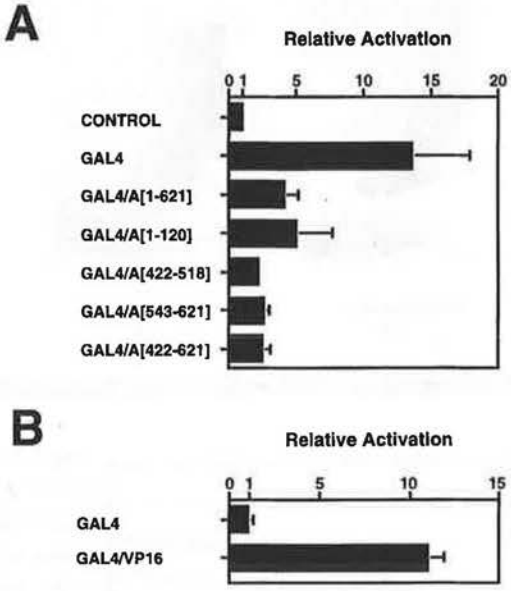


Figure 2. Expression of a GAL4-LUC reporter gene in the presence of GAL4-TnpA and GAL4-VP16 effector plasmids.

(A) Relative activation of the LUC reporter gene in tobacco suspension cells by expression of the chimeric GAL4/TnpA genes shown in Figure 1. The activity of the test plasmid was measured and normalized to an internal CAT control as described in Experimental Procedures. Relative Activation represents the ratio of normalized LUC activity obtained in the presence of a GAL4- or a GAL4/TnpA effector plasmid to that observed with an effector plasmid carrying an antisnese GAL4/VP16 construct. The LUC reporter plasmid contains GAL4 DNA binding sites and a minimal CaMV 35 S promoter (Figure 1B).

(B) Activation of the LUC reporter gene by the chimeric GAL4/VP16 construct shown in Figure 1. Relative Activation is the ratio of normalized LUC activity observed in the presence of the GAL4/VP16 fusion to that observed with GAL4 binding domain alone.

A plasmid containing the coding sequence for the GAL4 DNA-binding domain activates the LUC reporter gene 14-fold (Fig. 2A; relative activation: 14.3 $\pm$ 4.4) in tobacco cells. All of the chimeric genes containing TnpA coding sequences fused to a sequence encoding the GAL4 DNA-binding domain showed lower levels of LUC expression than that detected with the GAL4 DNA-binding domain sequence alone (Fig. 2A). While these observations are consistent with our previous report that TnpA represses its own promoter (Schläppi et al., Cell 77: 427-437, 1994), the fact that even small segments of the coding sequence are inhibitory suggests that their addition to the GAL4 binding domain simply serves to interfere with its ability to interact with other proteins.

When the strong VP16 activation domain is fused to the GAL4 DNA-binding domain, expression of the reporter gene is stimulated only an additional 10-fold over the background value observed with the GAL4 DNA-binding domain alone (Fig. 2B; relative activation: 10.9 ± 0.9). Thus the GAL4-based system is relatively insensitive in plant cells because of the high basal activation observed with the GAL4 DNA-binding domain alone.

As previously reported, TnpA represses its own promoter (Cook and Fedoroff, MNL 66: 11-12, 1992; Schläppi et al., Cell 77: 427-437, 1994). The *Spm* promoter is short (0.2 kb) and contains 9 12-bp TnpA binding sites (Gierl et al., EMBO J. 7: 4045-4053, 1988; Raina et al., Proc. Natl. Acad. Sci. 90: 6355-6359, 1993). To determine whether TnpA can be converted from a repressor into an activator by addition of a strong activation domain, the coding sequence of the VP16 activation domain was fused to different deletion derivatives of the TnpA coding sequence (Figure 3A). TnpA and TnpA/VP16 fusion gene plasmids were co-bombarded into tobacco suspension cells with reporter plasmids in which the LUC gene was expressed from the *Spm* promoter (Fig. 3B). In contrast to the GAL4 DNA binding domain, which itself stimulates LUC expression substantially (Fig. 2), TnpA constructs lacking VP16 have no detectable background activity . Instead, expression of TnpA constructs containing the

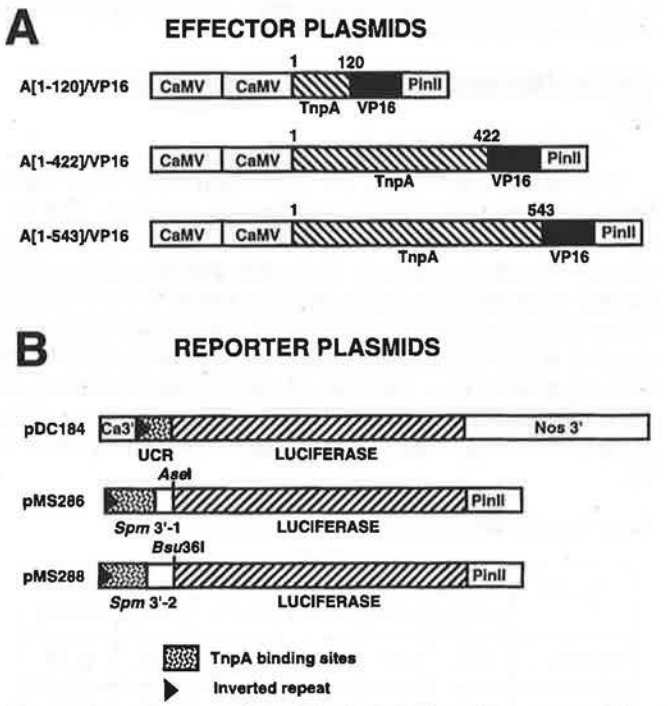


Figure 3. Schematic representation of chimeric TnpA-VP16 and *Spm* promoter-luciferase reporter genes.

(A) Effector plasmids contain translational fusions of the following TnpA domains to the Herpes Simplex VP16 activation domain (a.a. 413 to 490): A[1-120], N-terminus of TnpA (a.a. 1 to 120); A[1-422], N-terminus and DNA-binding domain of TnpA (a.a. 1 to 422); A[1-543], N-terminus, DNA-binding and protein dimerization domains of TnpA (a.a. 1 to 543). PinII, *potato proteinase inhibitor II* terminator; CaMV, Cauliflower Mosaic Virus 35S promoter.

(B) The firefly LUC gene in the reporter plasmids is expressed from either the UCR promoter sequence of the *Spm* element, which contains 9 TnpA binding sites, (Raina et al., Proc. Natl. Acad. Sci. 90: 6355-6359, 1993), or 1 of 2 different fragments of the *Spm* 3'-end in the antisense orientation , each containing 15 TnpA binding sites (Masson et al., Genetics 177: 117-137, 1987; Gierl et al., EMBO J. 7: 4045-4053, 1988). Nos 3', *nopaline synthase* terminator. Ca3', CaMV 35S terminator; PinII, *potato proteinase inhibitor II* terminator.

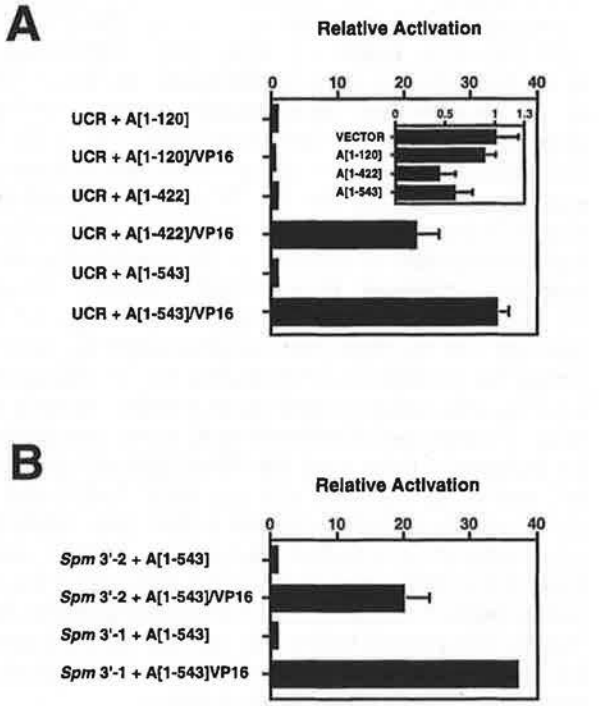


Figure 4. Activation of the *Spm* Promoter by TnpA/VP16 fusion proteins in tobacco cells.

(A) Relative activation of UCR-LUC reporter gene expression (Fig. 3B) by the chimeric TnpA/VP16 fusion proteins shown in Figure 3A. Controls were plasmids carrying the corresponding TnpA gene or gene fragments lacking the VP16 activation domain. LUC activity was measured and normalized as described in Experimental Procedures. Relative Activation is the ratio of normalized LUC activity observed in the presence of the effector plasmid expressing the TnpA/VP16 to that observed with an effector plasmid expressing only the corresponding TnpA gene or gene fragment. The inset shows the corresponding relative activation values for the TnpA gene fragments relative to the bluescript pKS(+) vector control.

(B) Relative activation of 1 µg *Spm* 3'-LUC reporter plasmid cobombarded into tobacco suspension cells with 1 µg effector plasmid containing chimeric TnpA/VP16. Fold Activation is expressed as the ratio of TnpA/VP16-effected relative promoter activity to background activity effected by TnpA alone. The *Spm* 3'-end contains 15 TnpA binding sites. The constructs are shown in Figure 3.

DNA-binding and dimerization domains represses the weak *Spm* promoter, as previously reported (Figure 4A, insert; Schläppi et al., Cell 77: 427-437, 1994).

Expression of plasmids carrying certain TnpA-VP16 fusions activates transcription of the LUC gene from the *Spm* promoter (Figures 3 and 4). A fusion of the VP16 activation domain to the first 120 amino acids of TnpA does not activate expression of the LUC gene (Figure 4A), while VP16 fusions containing the TnpA DNA binding domain do. A VP16-TnpA fusion protein which contains the TnpA binding domain, but lacks the protein dimerization domain, stimulates promoter activity 21-fold over that observed with TnpA alone (Figure 4A, A[1-422]/VP16). The VP16 fusion gene containing both the DNA-binding and the protein dimerization domains of TnpA is the strongest activator (Figure 4A, A[1-543]/VP16). Relative to A[1-543] alone, the A[1-543]/VP16 fusion activates the *Spm* promoter more than 30-fold (relative activation: 34.0 ± 1.79). The range of promoter activation varied between 33- and 45-fold in different experiments. Thus the addition of an activation domain to TnpA converts it to a strong activator of the *Spm* promoter.

Two observations suggest that the TnpA binding sites are the most important determinant of the *Spm* promoter's response to the VP16-TnpA fusions. First, the element's 3'-end, whose se-

quence organization resembles that of the 5'-end and contains 15 TnpA binding sites (Fig. 3B; Masson et al., Genetics 177: 117-137, 1987; Gierl et al., EMBO J. 7: 4045-4053, 1988) can substitute for the *Spm* promoter in the present assay. As shown in Figure 4B, the A[1-543]/VP16 fusion activates expression of the LUC gene from two different *Spm* 3'-end fragments by 20- to 40-fold. Second, the *Spm* promoter is a TATA-less promoter (Raina et al., Proc. Natl. Acad. Sci. 90: 6355-6359, 1993) and addition of a TATA box does not further enhance the ability of a VP16-TnpA fusion protein to activate the LUC gene from the *Spm* promoter (data not shown). Because TnpA is normally a repressor of the unmethylated promoter, the baseline or background activity observed with the *Spm* promoter-driven reporter gene is extremely low, providing a highly sensitive plant-specific system for detecting and analyzing transcription activation domains of proteins. In the present experiments, LUC activity was 33-45 times the background value using the VP16/TnpA/*Spm* promoter hybrid system, as compared with only about 10-fold over background with the VP16/GAL4 system in plant cells. While the absolute value of the activation was lower for the *Spm* promoter-based hybrid protein system, the higher sensitivity of the system permits detection and analysis of much weaker activation domains than the GAL4-based system. In addition, this plant-based hybrid system may permit detection of transcription activation domains which require plant-specific co-factors.

BEIJING, CHINA
Academia Sinica

RAPD analysis of mtDNAs from multiplasmic cms lines

--Wang, Z; Wang, B and Zeng, M

The mitochondrial DNAs of three maize multiplasmic cms (cytoplasmic male sterility) lines: Mo17-cms-19A (T group), Mo17-cms-shang26 (S group), Mo17-cms-C (C group), and their maintainer line Mo17, and a new inbred, Tai-A cms line (unknown group) and its maintainer line C103 were analyzed with 210 random decamer nucleotide primers. The experimental results were as follows:

1) A genetic relationship dendrogram was made and the genetic distance was calculated by cluster analysis with the amplification products clearly amplified from 40 Operon primers. It was found that the relative genetic gap between Tai-A and the other five lines is as long as 24.9, however, its affinity between Mo17-cms-19A and Mo17-cms-C, and the genetic distance, is only 6 between them.

2) A RAPD-fingerprinting map of the six lines was made with five primers: OPAC-02, OPAN-05, OPG-19, OPT-09 and OPT-12, which would provide a rapid and convenient molecular tool to detect the six lines. In the map, RAPD-PCR products: OPAC-02(680), OPAC-02(1053), OPAN-05(680), OPAN-05(370), OPT-12(1230), OPT-09(800) in company with OPG-19(290) can be used as molecular markers to separate and identify Mo17-cms-shang26, Mo17-cms-C, Mo17-cms-19A, Tai-A, Mo17 and C103, respectively.

The mitochondrial DNAs of six lines were digested by restriction endonuclease *Pst*I. From the digestion pattern, it was found that Tai-A apparently differed from the other lines. According to the results of restriction endonuclease pattern and RAPD analysis, we think that Tai-A may be a new kind of cms line differing from T, C, S types and the origin of Mo17-cms-19A, Mo17-cms-shang26 and Mo17-cms-C.

In addition, primer OPZ-05 and primer OPT-09 can amplify special polymorphic products in four cms lines and two maintainer lines respectively. The special RAPD PCR products of OPT-09(800) in C103 and Mo17 were cloned into PUC19 and Southern hybridization results showed that the cloned fragments were either single-copy or low-copy number (Fig. 1).

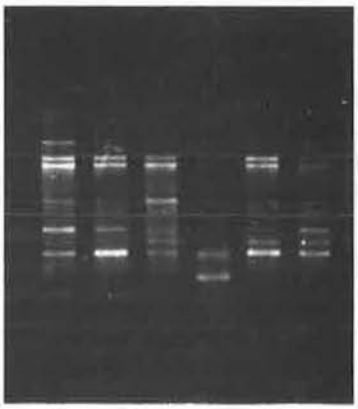


Figure 1. Amplified polymorphic products for primer OPH-07. 1) Mo17-cms-C; 2) Mo17-cms-19A; 3) Mo17-cms-shang26; 4) TaiA; 5) C103; 6) Mo17.

Analysis of biochemical constitution of new germplasm in sweet corn

--Liu, Y; Zeng, M and Ye, S

The new germplasms of the sweet corn which were transferred and bred were used as experimental materials. The biochemical constitution, the heterotic rate and genetic control were studied. The results showed: 1) the new germplasms have high nutritive value and taste quality and were similar to the progenitor type in each biochemical constitution; 2) the heterotic rates were negative on most quality characters, but it is evidently different from the growth vigour character; 3) the external characters and the content of sugar were controlled by a pair of recessive genes in the normal sweet, brittle sweet and supersweet corn (Tables 1-3).

Table 1. Biochemical composition for new germplasm in sweet corn.

Hybrid	Protein g/100g	Lipid g/100g	Soluble carbohydrate·re g/100g	Soluble g/100g	Amylose g/100g	Vc mg/100g
KT105(G)	2.34	4.78	14.38	2.50	44.36	21.50
KT111(G)	2.63	9.03	15.34	2.51	24.30	5.25
KS101(G)	2.04	5.75	17.99	2.12	44.08	15.67
8701(G)	2.05	4.60	13.44	2.32	49.01	13.67
KS101(E)	3.80	4.78	14.49	6.00	0	22.60
8701(E)	3.15	2.41	12.10	8.14	0	23.47
YT83(E)	4.53	4.39	10.21	8.12	0	28.01
YT33(E)	3.97	3.49	14.05	5.94	2.1	35.34

Notes: G — fresh grain E — young ear

Table 2. Amino acid composition for new germplasm in sweet corn (mg/100g dry weight).

Hybrid	ASP	THR	SER	GLU	GLY	ALA	CYS	VAL	ILE	LEU	TYR	PHE	LYS	HIS	ARG	PRO	NH3
KT105(G)	0.87	0.41	0.48	2.96	0.44	0.97	0.13	0.66	0.45	1.33	0.28	0.81	0.29	0.29	0.25	0.91	0.42
KT111(G)	0.77	0.35	0.43	2.38	0.43	1.01	0.13	0.59	0.39	1.07	0.26	0.68	0.27	0.28	0.48	0.92	0.42
KS101(G)	0.61	0.33	0.41	1.56	0.43	0.91	0.17	0.58	0.40	1.14	0.25	0.65	0.29	0.28	0.21	0.92	0.44
8701(G)	0.68	0.29	0.37	2.18	0.37	0.71	0.12	0.51	0.34	0.97	0.17	0.61	0.25	0.23	0.24	0.81	0.38
KS101(E)	1.35	0.62	0.71	3.33	0.80	1.16	1.13	0.92	0.66	1.21	0.33	0.90	0.52	0.33	0.50	0.72	0.44
8701(E)	1.31	0.59	0.64	3.39	0.74	1.02	0.16	0.88	0.61	1.11	0.21	0.94	0.29	0.21	0.27	0.67	0.57
YT83(E)	1.50	0.53	0.59	2.26	0.73	1.06	0.14	0.84	0.57	1.02	0.27	0.76	0.45	0.30	0.39	0.53	0.77
YT33(E)	2.01	0.72	0.82	3.15	0.94	1.28	0.15	1.06	0.77	1.38	0.34	1.08	0.54	0.39	0.61	0.84	0.50

Table 3. Mineral elements for new germplasm in sweet corn (mg/100g dry weight).

Hybrid	K	Fe	Al	P	Zn	Cu	Mn	Ba	Sr	Ti	B	Ca	Na	Mg
KT105(G)	1015.0	3.43	1.02	425.10	3.87	0.37	1.33	0.075	0.266	0.170	0.627	23.57	7.43	126.01
KT111(G)	957.9	2.86	1.21	437.70	3.72	0.49	1.21	0.095	0.200	0.186	0.529	22.41	7.43	149.75
KS101(G)	798.3	2.99	1.03	368.20	3.67	0.92	1.00	0.067	0.139	0.176	0.469	16.55	6.93	128.53
8701(G)	922.0	3.10	0.80	323.70	2.89	0.31	0.96	0.050	0.127	0.147	0.342	13.80	6.74	169.87
KS101(E)	2586.3	4.66	2.24	766.20	8.49	0.14	4.26	0.263	2.371	0.241	1.020	237.30	9.81	244.55
8701(E)	2234.0	4.09	1.76	558.90	7.12	0.76	3.68	0.243	2.304	0.211	0.700	210.10	8.61	226.76
YT83(E)	2746.4	8.65	3.49	878.50	7.83	1.09	4.46	0.155	2.776	0.404	1.398	216.00	10.1	275.63
YT33(E)	3450.4	5.78	2.40	709.00	7.01	1.14	4.55	0.148	2.117	0.298	0.574	154.00	10.1	265.26

Hybrid	Ce	Be	La	Y	Nb	Li	Sc	Cr	Mo	Pb	Th	Co	V	Ni
KT105(G)	0.0326	0.00029	0.00364	0.00075	0.0142	0.0500	0.0068	0.0516	0.0105	0.0159	0.000108	0.00301	0.00432	0.00701
KT111(G)	0.0328	0.00040	0.00364	0.00084	0.0131	0.0651	0.0085	0.0462	0.0144	0.0203	0.000848	0.0033	0.00451	0.00704
KS101(G)	0.0384	0.00031	0.00404	0.00092	0.0152	0.0591	0.0124	0.0436	0.0083	0.0196	0.00201	0.0102	0.00443	0.00711
8701(G)	0.0217	0.00020	0.00299	0.00057	0.00653	0.0304	0.0096	0.0473	0.0103	0.0967	0.000123	0.00154	0.00298	0.00348
KS101(E)	0.0583	0.00067	0.00755	0.00174	0.0277	0.1266	0.2362	0.0463	0.0112	0.0385	0.0177	0.0064	0.00760	0.0141
8701(E)	0.0447	0.000402	0.00619	0.00151	0.02176	0.08421	0.01349	0.0491	0.0095	0.0318	0.00227	0.0048	0.00627	0.0116
YT83(E)	0.0636	0.00054	0.0011	0.00202	0.03112	0.1303	0.02509	0.0516	0.0106	0.0419	0.00343	0.0076	0.00855	0.0163
YT33(E)	0.0675	0.000654	0.0009	0.00194	0.0312	0.118	0.02770	0.0538	0.0150	0.0137	0.00657	0.0075	0.00836	0.01695

Transformation: ovary injection

--Ding, Q; Xie, Y; Dai, J; Mi, J; Li, T; Qiao, L; Tian, Y and Mang, K

About twelve hours after artificial pollination, plasmid (containing the *Bt* gene) was injected into young ovaries. These injected ovaries were kept growing until seeds matured, then harvested and sowed in soil. The chromosomal DNA was isolated from leaves of plantlets and tested with dot blotting, PCR and Southern blotting analysis. A total of 5 out of 363 plantlets demonstrated positive tests in Southern blotting analysis. One of the five was comprehensively identified with a *Bt* gene fragment probe (*Eco*RI digested): the undigested sample of its chromosomal DNA showed a hybridization signal at a size of about 30kb, *Eco*RI digested sample showed an expected 1.2kb band, and *Acc*I(which has a cut site in the region of probe) digested sample showed one 10kb signal band and another weak band at about 0.8kb size while the *Bgl*II digested sample showed a 9kb signal band and light smear (Ding Qunxing et al., Science in China (Series

B) 37(5):563-572). This transgenic plant was normally fertile and its offspring were tested with Southern blotting analysis also. Interestingly, the *Bgl*II digested samples of the offspring's chromosomal DNA showed a different hybridization pattern: one had four bands siting from 30kb to 8kb with almost the same intensity while another had two close bands near 23kb. It seems that the integrating position on chromosome or the copy number of the *Bt* gene might change. Recently, the R4 and R5 generations have been obtained and genetic analysis results will be reported soon. Meanwhile the mechanism of injection transformation has been studied also. Carbon powder and tungsten particles (1nm, with plasmid DNA precipitated onto the particles) were used as tracks respectively in light microscope and electron microscope. The results proved that carbon powder and tungsten particles could enter the embryo sac and spread following its development. This transformation technique is genotype independent, evading tissue culture and regeneration. It's considered that several factors are important: the first is the injection time, which must be after sperms enter the sac and before the fertilized egg divides, which also depends on the varieties, length of silks and temperature etc.; the second is avoiding heavy injury on the ovaries, for this we have designed a micro-glass-tubed (diam. 2-5μm) injector; the third is keeping the injected ovaries vital enough to mature; the fourth, is that a special solution for plasmid DNA (100μg/ml final) was used: 20mmol/L $MgCl_2$, 1.5mmol/L HBO_3, 10mmol/L glycine, 5mmol/L spermidine, 5% PEG6000(w/v).

BERKELEY, CALIFORNIA
University of California

Macrohairless (*mhl1*), a new recessive mutation

--Lane, B and Freeling, M

A new phenotype was observed segregating in a population of plants which also segregated the dominant mutant *Rld1-O/+; +/+*. Subsequent generations revealed that the trait segregated as a single recessive genetic factor. The resulting phenotype of the homozygote is a failure to elaborate the normal complement of macrohairs on the adaxial surface of the leaf blade. When homozygous, the mutation also results in the failure to elaborate the abnormally expressed macrohairs on the abaxial surface of the leaf blade in *Rld1-O/+* heterozygotes. No evidence of instability has been observed. A B-A translocation stock mapping population has been generated and will be screened next season. Further characterizations of the extent and nature of the phenotype are in progress.

Linkage of semi-dominant *Rolled1* mutant alleles

--Lane, B and Freeling, M

In order to test for linkage between several dominant mutants, all of which have in common the expression of the various Rolled phenes, the following experiment was undertaken. Because previous attempts to generate homozygotes were not successful, known heterozygotes for each of several of the alleles were crossed to each other, generating families which segregated one of the two possible critical genotypes: either *Rld1-O/Rld1** or *Rld1-O/+*, *Rld2*/+*. Each phenotypically Rolled plant in the resulting population was outcrossed to a *+/+* tester. The resulting progeny were grown out and families not segregating 1:1 for the Rolled phenotype were analyzed. In addition to confirming the previously reported close linkage between *Rld1-O* (previously referred to as *Rld-1990*) and *Rld1-1441* (S. Chao and M.G. Neuffer, MNL67:33), they revealed a very close linkage between two other mutations exhibiting the Rolled phenotype (Table 1). These will be referred to as *Rld1-1608* and *Rld1-MF*. Contamination cannot be ruled out, therefore the map distances expressed may in fact be smaller.

Mutant pair	No. outcross progeny observed	No. exhibiting Rld phenotype	No. not exhibiting Rld phenotype	Map distance
Rld1-O, Rld1-MF	416	413	3	0.7
Rld1-O, Rld1-1441	438	437	1	0.2
Rld1-1441, Rld1-MF	90	89	1	1.1
Rld1-1608, Rld1-MF	115	115	0	

Another mutation, *Rld1-PB*, showed no recombination with the linked polymorphism identified by the RFLP marker *csu54* in 91 individuals genotyped, also indicating a very close linkage to *Rld1-O*. Based on this information we conclude that the five dominant *Rolled* mutants studied are likely to be alleles of *rld1*.

humpback1, a new recessive leaf mutant, maps to chromosome 1S

--Schneeberger, R; Scanlon, M and Freeling, M

humpback1 (*hmp1*) was identified in an EMS pollen mutagenesis M2 screen in our 1993 San Jose nursery (see Harper et al., MNL 69:22, 1995). The phenotype is inherited as a recessive trait and is characterized by proliferation of sheath just beneath the auricle resulting in a bulged sheath. The phenotype is extremely localized to the distal-most part of the sheath just preceding the auricle and ligule and is more apparent on leaves above the ear node. The auricle and ligule are not affected. The sheath phenotype is often more pronounced on either side of the midrib but usually extends from margin to margin. Husk leaves also show tissue proliferation, however the phenotype is localized to the base of the husk leaves and not at the tip, the location of the blade sheath boundary in husks. Phenotypic expression and penetrance are better in a W23 background and poor in both B73 and Mo17 after two generations of introgression. *hmp1* was included in our 1994 B-A translocation mapping block and screened for phenotypes in our 1995 nursery. Two independent families from crosses of heterozygous *hmp1* by TB-1Sb hyperploid heterozygotes (TB-1Sb/*vp5*) showed *hmp1* phenotype. *hmp1* phenotype was not observed in any other TB crosses. We are currently mapping with RFLP and visible markers to further define the location of *hmp1* on chromosome 1S.

The *semaphore1* mutation maps to 9S

--Scanlon, M and Freeling, M

The *semaphore1* (*sem1*) mutant (previously described as mutant designation *dek*-Mu1364*) is a recessive, small seeded, small embryo mutant with many pleiotropic effects on plant phenotype (Scanlon et al., Genetics 136:281, 1994). These phenotypes include brachytic stature, leaves that droop, and ectopic ligule and acropetal ligule displacement in the midrib region. The mutant was included in B-A translocation mapping projects in the summer 1993 and again in 1995. In crosses of plants heterozygous for the *sem1* mutation by marked hyperploid males of the genotype TB-9Sd/*c2, wx1, sh1*, the progeny included kernels with small endosperm and large embryos, and plump kernels with small mutant embryos. The discordant kernel classes were planted and the small seeds with large embryos yielded nonmutant healthy plants whereas the large seeded small embryo kernels produced small,

brachytic plants with the *sem1* phenotype. The mutation was therefore placed on chromosome arm 9S, distal to *wx1*. Because there are no previously described mutants on 9S with the above mentioned phenotypes, we have designated this new gene *semaphore1*.

The leaf blade reduction mutant *nl*-1517* maps to 3S

--Scanlon, M and Freeling, M

In a 1993 screen of M2 progeny of EMS mutagenized material (see Harper et al., MNL 69:22) a new narrow leaf (*nl*) mutant allele, laboratory designation *nl*-1517*, was identified with a reduced blade phenotype. The blade reduction phenotype shows variable expression. Younger leaves are more affected than older leaves, and leaf blades are shorter and more narrow than in nonmutant siblings. Frequently the blade is entirely absent, although the ligule, auricle and sheath are not affected. Usually, plants with severe leaf phenotypes form no tassels, or develop only rudimentary male flowers. No adverse effects on ear development have been observed. The mutant was included in a B-A translocation mapping project in 1994. The mutant phenotype segregated in the F1 progeny of several crosses between *nl*-1517* heterozygotes and males which were marked, hyperploid heterozygotes of the genotype TB-3Sb/*cl1*. Therefore, the new mutant *nl*-1517* is placed on chromosome arm 3S, distal to *cl1*.

***Vestigial glume* (*Vg1-R*) plants exhibit cell death in the ligule**

--Jesaitis, L and Freeling, M

The dominant mutant *Vg1-R* was first noted for greatly diminished glumes in both the tassel and ear (J. Hered. 30:143-145, 1939). Later it was found that *Vg1-R* also severely reduces the ligule (Laughnan, MNL30:67, 1956; Galinat, personal communication). Here we report on our studies of *Vg1-R* ligule development. We inspected developing ligules both macroscopically and microscopically in *Vg1-R* heterozygotes after three generations of introgression into Mo17. The first two leaves of the *Vg1-R* seedling produce long, wild type-appearing ligules. Before leaf three emerges from enveloping older leaves, the ligule of leaf 2 degenerates gradually until just the base remains. This process can be observed over a period of 24 hours. The ligule of leaf 1 remains unaffected. In longitudinal sections, degenerating ligules contain distal cells with collapsed walls, indicating that cell death plays a role in *Vg1-R* induced ligule loss.

Leaf 3 and all subsequent leaves also exhibit reduced ligules. Unlike leaf 2, however, the ligules of these later leaves are already diminished at the time of leaf emergence from enveloping lower leaves. Based on histological examination, ligules of later leaves appear to initiate normally from the adaxial leaf surface. At this point, we are in the process of investigating whether diminished growth and/or cell death is involved in ligule reduction in these later leaves. The fact that ligules of leaf 2 and subsequent leaves become simultaneously subject to reduction suggests that *Vg1-R* triggers a switch leading to diminished ligules throughout the plant.

Experiments are currently underway to determine the effect of wild type gene dosage on *Vg1-R* phenes, to determine whether *Vg1-R* is cell autonomous, and to transposon-tag *Vg1-R*.

Generation of heritable unstable chromosome 7S stocks from TB-7Sc

--Tyers, R and Freeling, M

Unstable chromosomes may be used to uncover recessive embryonic lethal mutations in sectors of the plant. This allows analysis of post-embryonic effects of these mutations in the sporophyte. Such chromosomes have been produced from TB translocations, as has been previously reported by Wayne Carlson (Theor Appl Genet 43:147, 1973) and Achille Ghidoni (Theor Appl Genet 43:151, 1973). Their putative ring chromosomes appeared in the progeny of crosses where the male carried a supernumerary B-A chromosome (A A x A A B-A).

We used a recessive allele of *viviparous9* (*vp9*) as a marker for instability of TB-7Sc. Sectors hemizygous for *vp9* are white in a green background. We derived two stocks that heritably uncover *vp9* in variably sized sectors. Each unstable B-7 chromosome appeared in the progeny of a TB-7Sc hyperploid crossed by a wild type tester (7 7B B7 B7 x 7 7).

One of these putative ring chromosome stocks has been subjected to preliminary molecular and cytological analysis. Tissue was collected from two plants showing large leaf to leaf sectors and DNA was prepared from both within the sector and from surrounding green tissue. Southern analysis using *rs1* sequence as a probe showed loss of one copy of this gene, which lies on chromosome 7S, in the white sectors. Examination of meiocytes revealed pachytene configurations consistent with ring chromosomes. However the expected anaphase I double bridges that would indicate the presence of ring chromosomes have not yet been observed.

CANBERRA, AUSTRALIA
CSIRO Plant Industry

Linkage of *Gdcp1* with the *Rp1* locus

-- Ayliffe, M and Pryor, T

Glycine decarboxylase is a nuclear encoded mitochondrial enzyme involved in the metabolism of 2 carbon glycine into 3 carbon serine.

Overall reaction:

2 Glycine + NAD+ ----> Serine + CO_2 + NH_3

The enzyme complex is formed from four subunits (Oliver, Ann. Rev. Plant Phys. Mol. Biol. 45:323-337, 1994) and the 100kD P subunit has been shown to function as the amino acid decarboxylase part of the complex.

The fungus *Cochliobolus victoriae* is the causal agent of a blight in oats due to the production of a host-specific toxin, victorin. The victorin binding protein in oats has been identified as the 100kD P subunit of glycine decarboxylase (Wolpert et al., Plant Cell 6:1145-1155, 1994). Sensitivity to victorin and consequent susceptibility to fungal isolates that produce the toxin is specified by a single dominant gene *Vb* in the host. The *Vb* gene is thought to be coincident with a gene *Pc-2* which specifies resistance to the oats crown rust, *Puccinia coronata*. It is therefore of interest to determine whether or not the gene (*Gdcp*) coding for the P subunit of glycine decarboxylase maps at any of the 5-6 loci known to specify resistance against rust infection in maize.

A comparison of the amino acid sequence of the GDC-P subunit from oats, pea and *Flaveria* made it possible to design primers which amplified, from a maize cDNA library, a 400bp PCR prod-

uct that showed high homology to the GDC-P coding region. The PCR product was cloned and the cloned insert has been used as a probe in RFLP analysis to map loci, which specify the P subunit of glycine decarboxylase. Three lines of evidence suggest that one of the loci observed maps to the short arm of chromosome 10 at or near the *Rp1* complex specifying resistance against the maize rust *P. sorghi*.

i. Mapping in the Recombinant Inbred Family-1 (CM37 x T232) (Burr et al., TIG, 7:55-60,1991) revealed three *Gdcp* loci, called *pic7A*, *7B* and *7C* , that segregated in genomic DNAs digested with *Eco*RI or *Bgl*II. Two loci, *pic7A* and *7B*, are linked (about 25%) and show loose linkage to chromosome 6. The *pic7C* locus mapped near *npi285* (R=0.07) and *bnl3.04* (R=0.18).

ii. Crosses involving the 10S terminal deletion -*def(bnl3.04-Rp5-Rp1-M)*- show that the *pic7C* band is covered within this deletion. The deletion does not cover the marker *npi422*, which is located several map units proximal to *Rp1*. These data then place this *Gdcp* gene on 10S in a distal segment that also contains the *Rp1* locus.

iii. The *Gdcp1* locus maps close to *Rp1-D13* in a backcross family: A plant heterozygous for *Rp1-D13/rp* was backcrossed to the susceptible parent (*rp/rp*) and the resultant progeny segregated 15 resistant to 23 susceptible. No recombinant progeny were recovered when these progeny were scored for the RFLP markers *bnl3.04* and *npi285* that flank the *Rp1* locus. One of the 23 susceptible seedlings was recombinant for the *Gdcp* marker. While this individual cannot at present be distinguished from a potential contaminant the data suggest that the *Gdcp* locus is distal to the *bnl3.04* locus. A proximal location is ruled out by the deficiency data. These data require confirmation.

A gene (*Gdcp1*) coding for the P subunit of glycine decarboxylase maps near the *Rp1*-complex. The *Gdcp1* gene is very different from the known structure of plant genes specifying resistance against fungi, bacteria and viruses (Staskawicz et al., Science 268:661-667, 1995). Consequently it is unknown if this map location has some functional significance in terms of rust resistance or whether the linkage of a *Gdcp* locus to a rust resistance gene is fortuitous, reflecting synteny between the maize and the oat genomes.

'Trisomic' 10S maize lines

--Pryor, T and Brock, D

We have previously reported (MNL 67:25-26) the recovery of a chromosome fragment (mini-1) that rescues lethal oil yellow genotypes. This mini-1 is thought to be a partial isochromosome that covers the proximal part of 10S at least as far as the *oil yellow* locus (*Oy*). This conclusion is based on three observations: (i) *oil yellow* somatic variegation correlated with lagging and loss of the mini-1 at mitotic and meiotic anaphase; (ii) gene dosage experiments indicating that the mini-1 chromosome has two doses of the wild type allele *Oy+*; (iii) the recovery of plants with derivative mini chromosomes such as those with two small or 1/2 minis (telocentrics) and those with a large mini. Two independent recoveries of the large mini, called Lg-1 and Lg-2, have been made and both appear to be heteromorphic with one arm about the same size as the original mini-1 while the other approximates the size of the short arm of chromosome 10. Our interpretation is that we have recovered a crossover between the mini-1 and the regular 10S. This gives rise to a chromosome in which the large arm comprises most or all of 10S and the small arm is the 10S proximal region up to *Oy+*, which was present in the original mini-1. Unlike mini-1, the Lg-1 chromosome frequently forms trivalent associations with chromosome 10 at meiosis confirming the presence of 10S. However, the full extent of this 10S will be determined genetically and by the ability of this chromosome to rescue a homozygous lethal terminal deletion (*def(bnl3.04-Rp5-Rp1-M)*.

The Lg-1 chromosome has been recovered in both the olive (*oy/oy*) and the lethal yellow (*Oy/Oy*) backgrounds. These stocks can be maintained by selecting green seedlings segregating among selfed progeny. The Lg-1 chromosome shows about 25% pollen transmission and 12% via the egg. These stocks will provide a useful source of trisomic 10S material for genetic study.

CHESTNUT HILL, MASSACHUSETTS
Boston College

Genic instability of a maize inbred line derived from anther culture

--Ting, YC and Nguyen, DQ

Last summer plants of a maize inbred line derived from repeated selfings of a microspore plant of KH-13 were grown in the field. During the last few years, genic stability of this inbred was rated as high. However, in the middle of last June, a month after the emergence of seedlings, some of them appeared yellow-green in leaf color, followed by slow growth of the plants. Two months later, it was apparent that plants of this inbred line could be classified into two distinct groups. In other words, they demonstrated segregation. As the plants were counted, it was clear that among a total of 72 plants, 11 of them were dwarf and yellow green. On the other hand, the sib plants of this inbred line grew to normal height, and the color of plants was dark green. When the plants attained tasselling stage, it was observed that the dwarf, yellow green plants were completely male sterile. No ear shoots were developed either. Hence, it was impossible to make any progeny tests. Nevertheless, this observation does constitute a further evidence that anther culture derived plants may not be genically stable. In contrast, in the same field, plants of five other maize inbred lines were also grown. One of them was a descendant of an anther culture developed microspore-plant. In a total of approximately 500 plants, no segregation of any characteristics was found.

Tassel plant of maize

--Ting, YC and Nguyen, DQ

It is known that morphogenesis of inflorescences of flowering plants is under genic control. Whenever a controlling gene(s) is turned on by induction factors, low temperature, ionizing radiation etc., the developmental pathway is normally as follows: the vegetative meristem gives rise to inflorescence meristem. In turn, the inflorescence meristem is transformed into floral meristem. Then, the floral meristem develops into floral parts. This is also true for maize. However, if an intrinsic developmental factor involved in the regulation of floral initiation is inactivated, maize floral development can be arrested. The following is an example of this altered development.

In the last summer, among a row of semi-perennial maize, one plant was particularly vigorous and bore more tillers than the others. However, it was slow in development. When the tassel of this plant emerged, it appeared strong and pendant, and its antheses were totally aborted. In consequence of this, many plantlets,

starting from the proximal portion, grew out from the tassel of the main stalk (culm). By a single count, 78 of them were scored. Under close examination of these plantlets, it appeared that they originated from paired spikelets (Figure 1). Subsequently, this plant was tentatively designated tassel plant, or Tpl for short. In addition, some variations, such as in plant color and growth pattern among the plantlets, were observed, indicating segregation occurring during meiosis. This suggests that the plantlets might differentiate from the microspores. Nonetheless, this can not be ascertained until their chromosome number is determined.

Figure 1. Plantlets of a tassel plant. Size reduced by about 50 percent.

When the plantlets had reached about two weeks old, two-dozen of them were removed from the tassel and planted in pots in the greenhouse. About 50 percent of these transplanted plantlets continued to grow into large normal plants while the others reverted into pistillate flowers. Cross-fertilizations were attempted between these flowers and the sib tetraploid, but no seed sets were obtained. On the other hand, those plantlets left on the main tassel also continued to grow. Later about 10 percent of them also reverted to pistillate flowers with two or more silks.

Cross-fertilizations were also attempted, but no viable seeds were found. The rest of the plantlets continued to grow to four to five-leaf stage. Then, they withered and died.

One of the above plant's tillers grown from the basal node also had a larger than average tassel. In addition to having more than 50 plantlets developed, it had a few antheses. Then they were followed by dehiscence. Consequently, its pollen was applied to silks of one half of its ear, and those of the other half were outcrossed to a sib (4n). At harvest, 73 well-developed kernels were obtained. Presumably one half of them developed from selfings, and the other, from crossings. There are now more than 10 plants descended from both selfings and crossings, growing in the greenhouse. These plants are normal in phenotypic appearance and are growing well. A planned genetic as well as tissue culture investigation is under way with these plants.

COLOGNE, GERMANY
Max Planck Institut für Züchtungsforschung

Probes for small transfer cell-specific proteins

--Willmott, RL; Hueros, G; Varotto, S and Thompson, RD

A cDNA clone was isolated from a cDNA bank constructed from 10-days after pollination (DAP) endosperm mRNA and has been characterised in detail (Hueros et al., Plant Cell 7:747-757, 1995). This was the first reported gene to be exclusively expressed in basal region of the endosperm. This area is highly specialised to facilitate uptake of solutes during grain development. Due to the location of the expression of the gene it was referred to as *BET1* (for basal endosperm transfer layer). Subsequently a *bet1* (glycinebetaine 1) locus was found to exist in MaizeDB (#40554), therefore to minimize confusion we suggest the transfer cell-specific genes be referred to as *betl*.

So far two transfer cell-specific cDNAs have been isolated (*betl1* and *betl2*, ID #105963 and 105964 in the MaizeDB respectively). *betl1* belongs to a small multigene family of which four different members have been characterised, and two copies of *betl2* are present in the maize genome. Both genes are strongly expressed between 9 to 20 DAP, *betl2* being more highly expressed then *betl1*. The proteins encoded by *betl1* and *betl2* share some common features: the deduced amino acid sequences comprise small proteins with calculated Mr of 7 kD. The sequences start with a hydrophobic region characteristic of a signal peptide and the encoded proteins are cysteine rich. The *betl1* polypeptide contains one copy of the extensin motif, SPPPP and is found in cell wall fractions. The function of *betl2* remains to be eludicated, however the protein has two interesting features, a potential glycosylation site and the possibility of numerous disulphide bond formations. Neither *betl1* nor *betl2* share obvious similarities with sequences in current databases.

Genomic clones corresponding to the *betl1* cDNA have been isolated and characterised. Interestingly two clones were derived from a distinct but closely related locus, provisionally termed *betl3*. The *betl3* coding sequence displays 90% similarity to *betl1*. From the predicted amino acid sequence it is evident that the proteins contain no extensin motif. Preliminary evidence indicates that *betl3* expression may not be limited to the transfer cell layer, which may point to a different role for this protein.

COLUMBIA, MISSOURI
University of Missouri

Pl-Rhoades* is more susceptible to DNase I cleavage than *Pl-Blotched

--Hoekenga, OA and Cone, KC

Pl-Rhoades (*Pl-Rh*) and *Pl-Blotched* (*Pl-Bh*) are alleles with strikingly different phenotypes. *Pl-Rh* leads to uniform pigmen-

tation in the plant and is silent in the kernel. *Pl-Bh* leads to variegated pigmentation in both the plant and the kernel. *Pl-Rh* and *Pl-Bh* have essentially identical DNA sequences, but *Pl-Bh* DNA is hypermethylated relative to *Pl-Rh*. The degree of methylation correlates with the phenotype (more methylated, less pigment) and with mRNA levels (more methylated, less mRNA) (Cocciolone and Cone, Genetics 135:575, 1992). In other systems, transcriptionally inactive genes are frequently methylated and located in tightly packed or condensed chromatin (Eden and Cedar, Curr Op Genet Dev 4:255, 1994). If this trend holds for the *Pl* gene, then the chromatin structure of *Pl-Rh* should be more "open" than that of *Pl-Bh*.

To address this prediction, we compared the chromatin structure of the two *Pl* alleles using a nuclease protection assay (Spiker, Murray and Thompson, PNAS USA 80:815, 1983). In this type of assay, "open" chromatin should be more accessible to nuclease digestion than tightly condensed chromatin. Nuclei from *Pl-Rh* and *Pl-Bh* husks were incubated with the nuclease DNase I. The DNA was purified, digested with restriction enzymes, and analyzed on Southern blots. The results indicated that both genes are susceptible to DNase I cleavage at the same sites within the coding region in 5' flanking sequences. However, *Pl-Rh* is more susceptible to DNase I digestion than *Pl-Bh*. These observations are consistent with our expectations. *Pl-Rh* and *Pl-Bh* were predicted to share the same DNase I sensitive sites, as an active *Pl-Bh* should be indistinguishable from *Pl-Rh*. Furthermore, the enhanced susceptibility of *Pl-Rh* correlates with its higher transcriptional activity and lower level of DNA methylation. Future experiments will be aimed at investigating chromatin structure of the two alleles in the kernel as a step in trying to explain the ectopic expression of *Pl-Bh* in the kernel.

An allele of sh2

--Neuffer, MG

An allele of *sh2*, *sh2-N2340*, had been produced by Dr. Gyula Ficsor, using EMS treatment of mature kernels of a purple kernel ACR line. It expresses as a partially collapsed kernel that resembles denting or a less extreme expression of *sh1*. It is dominant to the reference *sh2* allele and has about the same viability. Stocks are available at the Co-op.

COLUMBIA, MISSOURI
USDA-ARS and University of Missouri
ATHENS, GEORGIA
USDA-ARS
TIFTON, GEORGIA
USDA-ARS

Lost locus resurfaces? The possible involvement of *brown pericarp1* in determining silk maysin concentration

--Byrne, PF; McMullen, MD; Snook, ME; Musket, T; Widstrom, NW; Wiseman, BR and Coe, EH

Concentration of maysin, a C-glycosyl flavone, in maize silks is an important resistance factor against the corn earworm, *Helicoverpa zea* (Boddie). Because maysin synthesis occurs as a branch of the flavonoid metabolic pathway, our research has sought to identify and estimate the contributions of loci from that pathway that affect maysin levels.

In a study of the population (GT114 x GT119)F2, silk maysin concentrations of 285 plants were measured with reversed-phase HPLC. RFLP analysis was conducted on the same plants, using probes encoding flavonoid pathway enzymes or linked marker loci, a total of 39 loci distributed on all chromosomes except chromosome 8. Single-factor analysis of variance was used to detect significant associations between maysin concentration and genotypic classes at individual RFLP loci, based on a comparison-wise error rate of 0.05. Epistasis was evaluated by testing the significance of all possible pairwise combinations of loci (excluding closely linked loci) in two-way analyses of variance.

Last year (MNL 69:53-54) we reported the results of our analysis to date: major effects on maysin concentration were associated with the *p1* region of chromosome 1 (accounting for 58% of the total phenotypic variance) and the *c1 - bz1* region of chromosome 9 (accounting for 6.7% of the variance). We were uncertain which locus in the latter region affected maysin levels, but felt that *c1* was a likely candidate because of its partial homology with *p1*, its similar role as a pathway regulator, and testcross results indicating different *c1* alleles in GT114 and GT119.

To better estimate the position of the responsible locus on chromosome 9, we probed for additional loci on either side of the *c1 - bz1* region, namely *umc109*, *umc105a*, *wx1*, and *csu147*. Analysis of variance showed a peak in percent variance explained (10.8%) at *umc105a*, midway between *bz1* and *wx1*. This position is close to the reported location of *brown pericarp1* (*bp1*) (Meyers, Ohio J. Sci. 5:295-300, 1927; Emerson et al., Cornell Univ. Agric. Exp. Stn. Memoir 180, 1935). The homozygous recessive condition at that locus together with a functional *p1* factor for pericarp color was reported to result in the production of brown pigmentation in the pericarp in place of red phlobaphenes. Though *bp1* was identified and mapped over 60 years ago and included on linkage maps for many years, stocks containing the mutation have apparently been lost, and the locus was removed from working maps in 1983. We believe that the locus detected in our study by *umc105a* may be *bp1* for the following reasons:

(1) The agreement in chromosome location, approximately midway in the interval between *bz1* and *wx1*.

(2) Identical interactions with the *p1* locus. In our study, *umc105a* affected maysin concentration only when it was homozygous recessive and a functional *p1* allele was present, i.e., only when the pathway was activated by *p1*. These are the same conditions required for observation of the brown pericarp phenotype.

(3) Parallels with *a1*-controlled brown pericarp. Recessive *a1* plus dominant *p1* produce brown pericarp and is reported to also enhance accumulation of C-glycosyl flavones, the class which includes maysin, in pericarp and silks (Styles and Ceska, Can. J. Genet. Cytol. 19:289-302, 1977; Styles & Ceska, Maydica 34:227-237, 1989). A block at the *a1* step in the pathway leading to phlobaphenes and 3-deoxyanthocyanins (Fig. 1) presumably leads to a build-up of flavanones and other intermediates, some of which are then shunted into the flavone branch of the pathway. Because of the similarities of effects, the site of action of *bp1*, like that of *a1*, seems likely to be in the pathway leading from flavanone to 3-deoxyanthocyanins and phlobaphenes.

To determine whether GT119, the source of the *umc105a* allele conditioning higher maysin values, carries a recessive allele at *bp1*, we plan to cross the line to a red pericarp stock. F2 progeny that segregate for brown pericarp would support, but not prove, a recessive *bp1* allele in GT119. To conduct additional experiments we continue searching for an existing *bp1* stock; we would appreciate

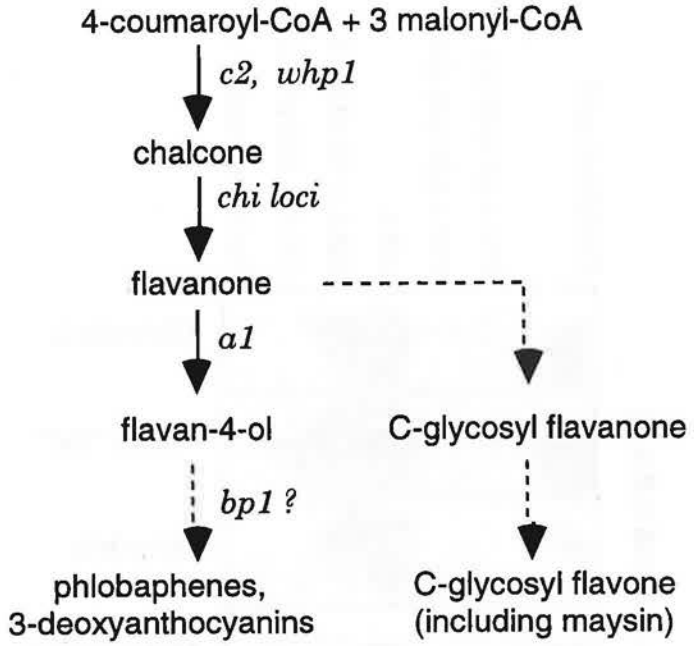


Figure 1. Part of the *p1*-controlled portion of the flavonoid pathway in maize. Loci are shown in italics. Dashed lines indicate steps that are less well characterized or that require more than one enzyme.

hearing from MNL Cooperators having such a stock or additional information about *bp1*.

CORVALLIS, OREGON
Oregon State University

Effects of somatic embryogenesis and genetic background on the phenotype of the shootless mutant *dks8*

--Hardeman, K and Rivin, CJ

In the W22 background, the mutation *dks8* results in small seeds that contain no observable shoot component and yet produce a functional root meristem, and a normal appearing cotyledon. Although the *dks8* mutant kernels are capable of germinating a primary root, the root is devoid of any root hairs. To determine if the *dks8* mutation was due to a lack of function in the seed or the embryo itself we asked if somatic embryos also had a shootless phenotype. To undertake this experiment, we introduced the *dks8* allele into the maize line H99 because it forms embryonic callus at high frequencies.

Interestingly, we found that the phenotype of the *dks8* kernels in H99 was significantly altered from the previously defined *dks8* phenotype. When the H99 *dks8* kernels were germinated on a hormone-free growth medium, they germinated into seedlings having pale leaves and seminal roots which, like the primary root, lacked root hairs. The seedlings died after expanding 5-6 leaves. We are further characterizing the phenotype of the H99 *dks8* seedlings and attempting to determine the basis for the change in phenotype in the H99 background.

To determine if the *dks8* mutation was autonomous to the embryo, we derived embryogenic callus from wildtype and mutant embryos, induced them to form somatic embryos, and determined their phenotypes. The results, shown in Table 1, show that the phenotypes of the somatic embryos reflect the phenotype of the callus source: Somatic embryos derived from wildtype callus formed green shoots and roots with root hairs, while the *dks8* somatic embryos were either shootless or made a pale sickly shoot and in either case the roots lacked root hairs. This result suggests that the defect in *dks8* mutant development is embryo-autonomous.

Table 1. Summary of tissue culture experiment.

Mutant embryos:	
Total embryos used:	144
Total forming callus:	94
Total forming organs:	42
root and shoot:	15
root only:	27
Note: all roots lacked root hairs and all shoots were pale and slow growing.	
Wildtype embryos:	
Total embryos used:	279
Total forming callus:	232
Total forming organs:	102
root and shoot:	100
root only:	2
Note: roots made root hairs and shoots were green and grew well.	

GA signalling in the developing embryo: evidence for a GA / ABA balance governing vivipary and maturation

--White, CN; Proebsting, WR and Rivin, CJ

The hormone abscisic acid (ABA) plays a central role in suppressing precocious germination in developing maize seeds and in modulating the expression of maturation phase genes. Kernels that are blocked in ABA synthesis do not mature to dormant, desiccation-tolerant seeds, but instead germinate on the ear midway through kernel development. This precocious germination has been widely considered to be a default developmental program, but it is also possible that ABA is required to counteract a hormonal germination signal. Because gibberellins (GAs) and ABA act antagonistically in many aspects of plant development, we hypothesized that ABA antagonizes a positive GA signal that induces precocious germination, and perhaps also suppresses maturation phase gene expression. This model makes three testable predictions: 1) Active GAs should be present in pre-maturation phase embryos, 2) reduced GA levels should suppress precocious germination in ABA-deficient kernels, and 3) inhibition of GA synthesis may induce the expression of maturation phase mRNAs in the absence of exogenous ABA. In a series of experiments, we obtained data in support of each of these predictions.

Using gas chromatography-mass spectroscopy, we measured GA and ABA levels in developing wildtype maize kernels over the course of development. Seven different GAs were identified in developing seeds, two of which are known to have biological activity, GA_1 and GA_3. As shown in Figure 1, these GAs are present in pre-maturation stage embryos, reaching maximum levels during a developmental window just prior to the peak in ABA accumulation.

To gauge the developmental role of embryo GA, we conducted experiments to manipulate the relative GA and ABA levels over the course of kernel development. Seeds deficient in ABA were created by spraying developing wildtype ears with fluridone, or by using *vp5* (*viviparous*) segregating ears. Reductions in GA levels were achieved through the use of the GA biosynthesis inhibitors paclobutrazol and ancymidol or by genetic blocks with either *dwarf1* or *dwarf5*. We found that vivipary of ABA-deficient kernels was highly suppressed in the dwarf background and in ears that were treated with GA biosynthesis inhibitors prior to stage 2. The resulting seeds are both dormant and desiccation-tolerant.

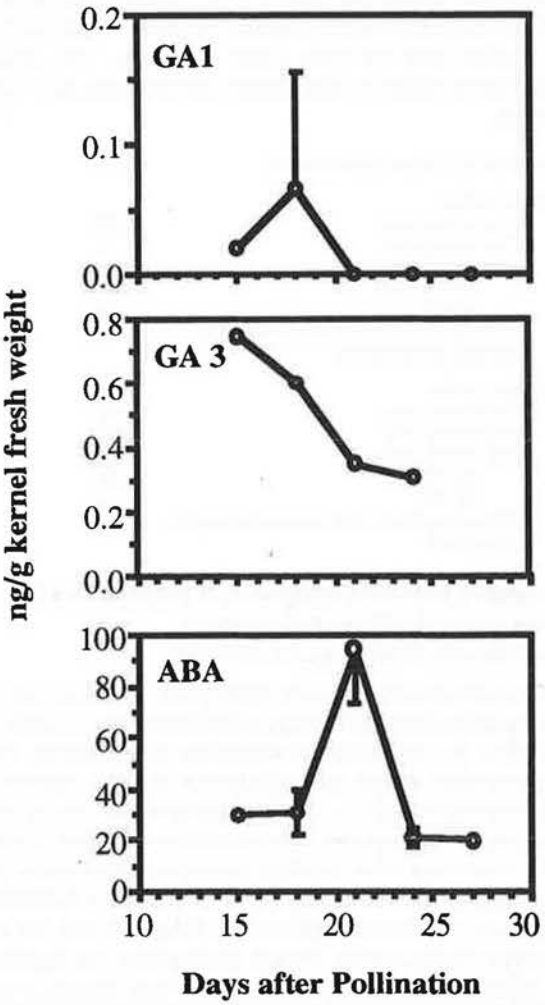


Figure 1. Temporal accumulation of GAs in developing kernels.

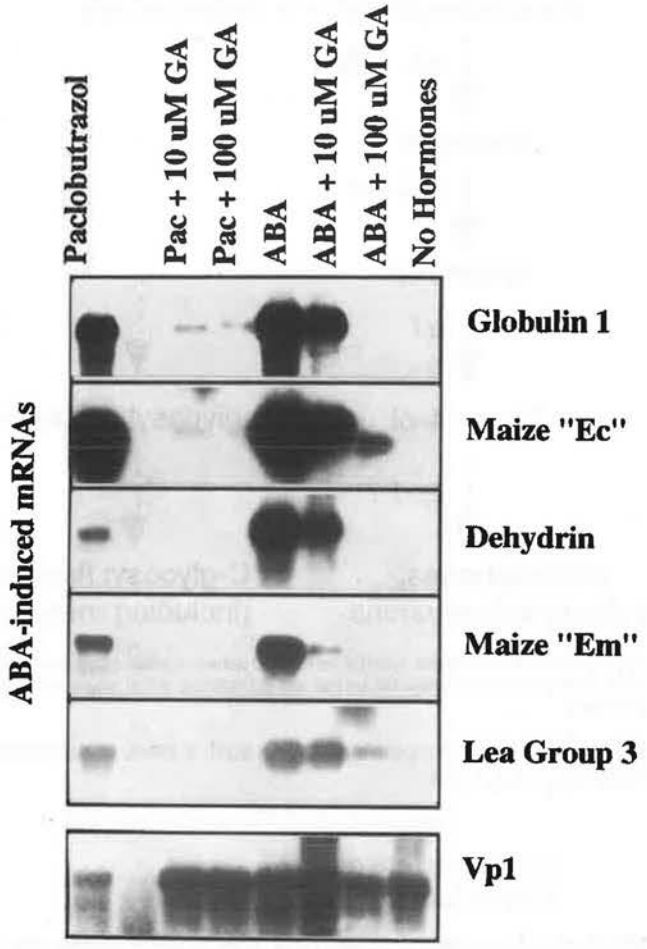


Figure 2. GA biosynthesis inhibition mimics ABA effects on cultured embryos.

In contrast, a GA deficit was found not to suppress vivipary in *vp1* mutant kernels, which have normal ABA levels, but exhibit no seed-specific ABA responses.

When GA biosynthesis inhibitors were applied to cultured embryos, they mimicked the effects of ABA, by suppressing germination and inducing the accumulation of maturation-phase mRNAs. Figure 2 shows the accumulation of maturation mRNAs in pre-maturation embryos cultured for three days in media supplemented with paclobutrazol ± GA or ABA± GA. The ABA-inducible mRNAs in the northern blots are undetectable in pre-maturation phase embryos and are precociously expressed in culture upon treatment with exogenous ABA. As shown, paclobutrazol treatment also induced these mRNAs, while the addition of exogenous GA reduced their steady state levels. The ABA-inducible messages also require the *Vp1* gene product, but *Vp1* mRNA levels were not affected by these culture treatments (bottom panel).

From these results, we speculate that GA present in the early developing embryo stimulates a developmental program leading to vivipary in the absence of sufficient levels of ABA . When GA levels are reduced, an ABA/GA ratio is established that is appropriate for the suppression of germination and the induction of maturation-phase gene expression in ABA-deficient kernels. The failure to suppress vivipary via reduction of GA levels in *vp1* kernels suggests that the *Vp1* product functions downstream of the sites of GA and ABA action in programming seed development.

CORVALLIS, OREGON
Oregon State University
ALBANY, CALIFORNIA
Plant Gene Expression Center

The maize shootless mutation *dks8* does not map to known *Knotted*-like genes or shootless dek loci

--Hardeman, K; Chuck, G; Hake, S and Rivin, CJ

The shootless mutation *dks8* (defective kernel shootless *Mu8*) leads to small seeds that contain an embryo with a functional root meristem and normal appearing cotyledon, but no observable shoot components. Previously, *dks8* was found to cosegregate with a *Mu8*-hybridizing fragment in 70 individuals (Sollinger and Rivin, MNL 67: 34-35, 1993). As we have only one allele of *dks8*, we were interested in determining its map position to allow us to determine if any previously isolated defective kernel mutation mapped to a similar location. In addition, we were interested in whether any of the *Knotted*-like genes in maize mapped to the *dks8* location, as a shootless mutation in *Arabidopsis* has been shown to be mutated in an *Arabidopsis Kn1*-like gene (J. Medford

and K. Barton, pers. comm).

The *Mu8*-hybridizing fragment that is tightly linked to *dks8* was cloned and the flanking region was assigned the map location 2S-36 using the recombinant inbred (RI) family Tx303 x CO159. Therefore, the *dks8* mutation resides on chromosome arm 2S. Two defective kernel mutations have previously been mapped to chromosome arm 2S, *et2* and *dek3*. Allelism tests revealed that *dks8* is not allelic to *et2*. Allelism tests with *dek3* are in progress. No known *Knotted*-like genes map to this area of 2S.

The *Mu8* flanking sequence appears to represent a gene with two copies in the genome, as it was found to hybridize less strongly to an additional fragment. This other locus was also mapped using the RI family Tx303 x Co159 and it maps to position 10L-116.

DEFIANCE OHIO
Defiance College

Epigenetic programming of paramutant *R* allele expression with light and temperature conditions applied at a specific stage of seedling development

--Mikula, BC and Kappen, T

R. A. Brink reported in 1956 that paramutation at the *r* locus contradicted a basic assumption of Mendelian genetics: alleles emerge from heterozygotes unchanged. The regularity of the phenomenon of paramutation has made it possible to challenge another assumption of Mendelian genetics: that environmental conditions have no heritable effect on gene expression. Under paramutagenic conditions all *R* alleles from a heterozygote with *R-st* are heritably changed. A weakly paramutagenic *R-st* allele reduces *R* pigment expression to an intermediate level of variegation. Since all *R* alleles are changed under paramutagenic conditions, the regularity of paramutation presented threshold conditions which made it possible to show that environmental conditions can cause heritable changes in the expression of a particular allele. Compared with the inflexibility of standard Mendelian genes, there was, with paramutation at the *r* locus, a high probability of being able to assay the environmental influence on paramutant *R* allele expression in a single generation in an inbred line and thus avoid segregating modifier arguments. We reported in MNL 67, 68 and Genetics 140:1379-87 conditions and times during early development when different levels of paramutation could be programmed. In MNL 66 we reported testcrosses from early pollen samples of plants, which as seedlings received specific light and temperature conditions, showed higher levels of paramutation (more weakly variegated) than those pollen samples made seven days later from the same plant.

The differences in paramutation between early and late pollinations suggested that a gradient of paramutation could be found if pollen was sampled from a single plant over the duration of anthesis, usually seven to eight days. Figure 1 shows frequency histograms for pigment scores of kernels from testcrosses of a single plant made each of the eight days that pollen was shed. 50 kernels from each of the eight testcross ears were scored for the level of *R* pigment variegation by matching each kernel against a set of 20 standard kernels. The frequencies of kernels that score as weakly pigmented (highly paramutated) appear on the left half of each histogram; more fully pigmented kernels are positioned in the score categories to the right half of each histogram. The

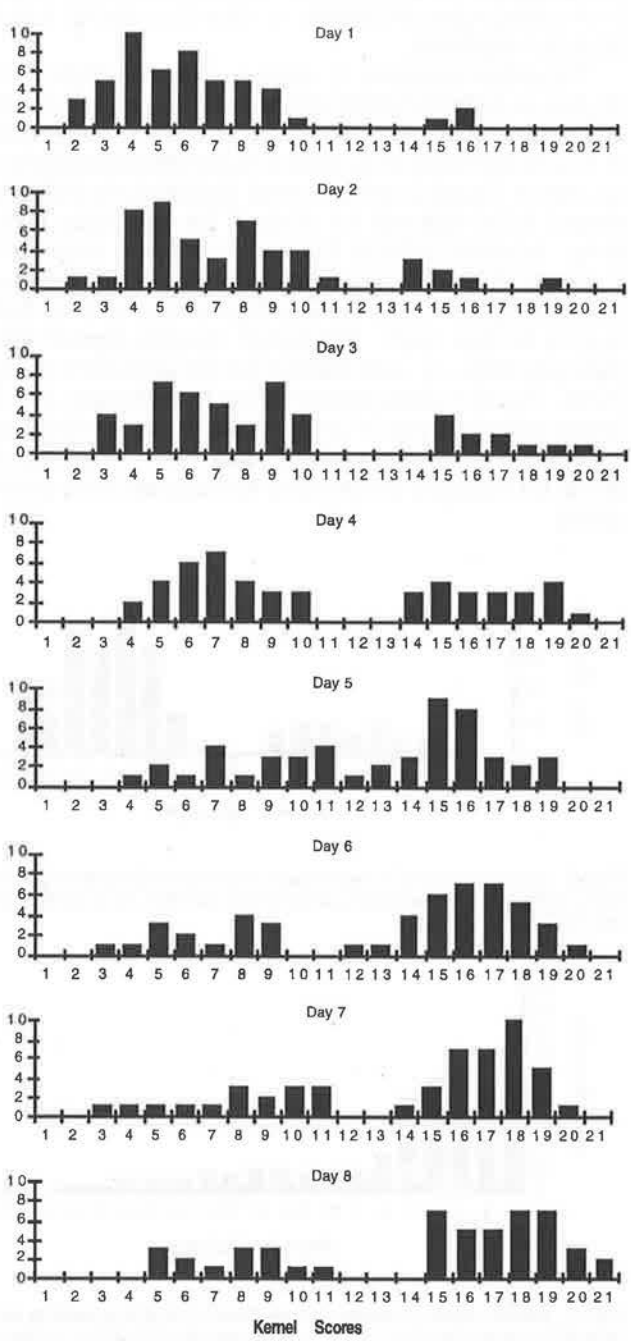


Figure 1. Testcross kernel scores from a single plant showing the frequency of weakly pigmented and strongly pigmented kernels in testcrosses made each day over the eight days that pollen was shed. 50 pigmented kernels from each testcross ear were scored against a set of 21 standard kernels ranging from colorless to fully pigmented, 1 to 21 respectively. With each day that pollen was tested, frequency histogram profiles are gradually skewed to the right as anthesis progresses down the tassel.

seedling was raised in 22 C continuous light (LL) conditions for 15 days then shifted to 12 hr light-dark cycles (LD) for six days before removal to field conditions for testcrossing at maturity.

The pollen collections from the first three days that pollen was shed show most kernels scored in the lower half of the scoring range (fewer pigmented cells, most paramutation). The last three histograms show most kernel pigment scores in the upper half of the scoring range (least paramutation). When all eight histograms

are compared, sequentially, the transition from frequencies of least to most pigmented kernels is visible as a gradient over the eight days of anthesis.

The pollen collections of Figure 1 represent epigenetic responses to controlled environmental conditions applied at a specific stage of development. More extreme changes in paramutation of *R* allele expression in response to environmental conditions can be seen in Figures 2 and 3. Kernel pigment-score profiles are skewed to the right and left halves of the histograms, respectively. All plants tested in Figures 2 and 3 were started in LL conditions at 22 C. Figure 2 represents testcross scores of kernels from eight plants that as seedlings received 12 hr LD cycles at 22 C for days 16-21. The darkest testcross pigment scores (least paramutation) were found in the last pollinations of single plants. Figure 3 shows pigment scores for testcrosses from the lowest tassel branches of seven plants that as seedlings were subjected to LL conditions at 32 C, days 15-21. These pigment scores are skewed to the left half of the histogram (more paramutation).

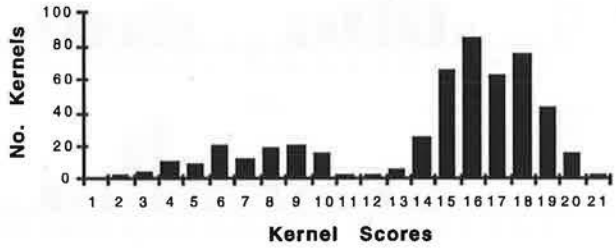


Figure 2. Testcross scores of 50 kernels from each of eight plants which as seedlings received four LD cycles at 22 C followed by two LL cycles at 32 C, days 16-21. Up to day 16, seedlings were held in 22 C LL conditions.

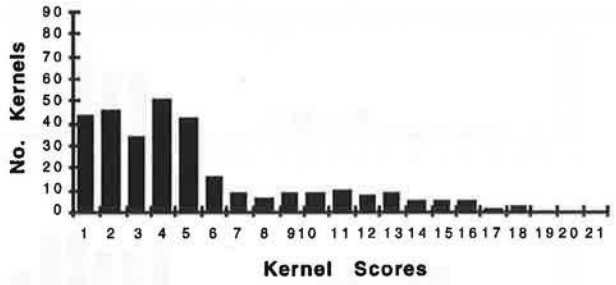


Figure 3. Testcross scores of 50 kernels from each of seven plants which as seedlings received seven 32 C LL cycles, days 15-21. Up to day 15, seedlings were held in 22 C LL conditions.

Figure 1 shows that different levels of epigenetic programming of *R* allele expression can be directed selectively at the earliest gametes from the upper part of the tassel or at the last gametes shed from the lower branches of the tassel. Figures 2 and 3 show that under different controlled conditions more or less paramutation can be programmed into the gametes from the upper or lower part of the inflorescence. The differences in gamete expression, under paramutagenic conditions, are the product of environmental conditions administered to meristematic tissue at a specific stage of development, the period during which the plant is susceptible to floral induction. Specific environmental conditions applied at the time of change-over from vegetative to floral stages of development identifies a threshold that makes it possible to regard the differences in the level of paramutant *R* allele expression as a useful reporter system for the more significant epigenetic event, that of floral induction. Significant differences in the number of nodes, tassel branches and time to anthesis (MNL 66) correlate with the differences reported as paramutation scores in the aleurone layer of the seed. Is it possible the *r* locus, responsible for a transcriptional activator, may play a more significant role in development than just the control of kernel pigment?

Since paramutation has been reported to be associated with methylation, the above information suggests a stage during development when methylation at the *r* locus can be initiated. The induction of change from vegetative to floral development is methylation associated in a species of *Arabidopsis* (Burn et al., Proc. Nat. Acad. Sci. 90:287-291). Light and temperature signals that time plant development in transgenic petunias are found to be highly correlated with methylation changes (P. Meyer et al., Mol. Gen. Genet. 243:390-399). Cause and effect relationships have been difficult to resolve in methylation studies. The epigenetic programming of the *r* locus as well as transgenes in petunia suggest that control of light and temperature conditions during early development will be essential if methylation is to be resolved as cause or effect when associated with gene programming.

DURHAM, NORTH CAROLINA
Duke University

Promising germplasm for rootworm resistance in maize

--Eubanks, M

In 1972, Branson and Guss (Entomol. Soc. Amer. Proc. North Central Branch 27:91-95) reported resistance to corn rootworm, *Diabrotica virgifera* LeConte, in eastern gamagrass, *Tripsacum dactyloides* L., a wild relative of maize. In 1993 (MNL 67:39-41) and 1994 (MNL 68:30-41), I reported evidence from petri dish and pot bioassays for rootworm resistance in maize that was crossed with a hybrid between diploid perennial teosinte, *Zea diploperennis* Iltis (Doebley and R. Guzmán) and *T. dactyloides*.

Additional pot bioassays have been conducted to address the question of whether rootworm resistance is expressed in accordance with Mendelian segregation in the *Z. diploperennis-T. dactyloides* hybrid referred to as Tripsacorn. In the first of these, 13 Tripsacorn S1 plants, grown in 4 inch pots, were infested with 50 Western corn rootworm larvae each, 30 days after germination. Within a few days after infestation, two plants died and two more exhibited severe lodging. Two weeks after infestation, plants were removed from pots and roots were washed for examination. Roots ranged from severely eaten to traces of larval feeding and extensive root growth. Four of the plants were identified as susceptible and nine plants considered resistant/tolerant. A chi square value of 0.25 is obtained from these numbers based on expected ratios of 3:1. Such deviation would be expected 50% of the time due to chance alone. The segregation ratio approaching 3 resistant to 1 susceptible suggests Mendelian segregation for a dominant gene for resistance.

Another bioassay was conducted with a total of 20 Tripsacorn S1 plants: 16 treatment and 4 control plants. Seed was germinated on moist filter paper in petri dishes and seedlings were transferred into 4-inch pots. Infestation of 50 newly hatched Western corn rootworm larvae was at 6 weeks after planting. Plant height was measured weekly throughout the trial. Seventeen

days after infestation, the plants were removed from pots and roots gently washed for examination under a microscope. Four plants had no feeding scars, 8 had minor feeding damage, and 4 had extensive feeding. Results signal homozygous dominant plants are more resistant than heterozygous plants, and homozygous recessive plants do not carry resistance.

An interesting phenomenon was observed in this bioassay. The record of plant height revealed a noticeable spike in plant growth at time of infestation when compared with control plants. Infestation appears to stimulate a growth hormone response concurrent with a defence response by infested plants carrying the resistance gene.

Another pot bioassay conducted under the same conditions as the previous one tested S1 plants of Sun Star, a new hybrid between *Z. diploperennis* and a diploid *T. dactyloides* (all previous hybrid plants tested were derived by crossing *Z. diploperennis* with a tetraploid *Tripsacum*). Out of 16 Sun Star plants, 4 were albino and died. The remaining 12 showed no feeding damage, indicating Sun Star is another promising source for rootworm resistance.

Bioassays testing *Z. diploperennis-T. dactyloides* hybrids, referred to as Tripsacorn and Sun Star, indicate there is a gene for resistance to corn rootworm that is inherited in accordance with Mendelian segregation. These plants provide a genetic bridge for moving rootworm resistance from *Tripsacum* into maize.

FREIBURG, GERMANY
Universitat Freiburg

Juvenile-adult phase transition of vegetative traits is not affected in the root deficient mutant *rtcs*

--Hochholdinger, F; Hetz, W and Feix, G

Vegetative development of maize can be divided into a juvenile and an adult phase. Each phase is characterized by specific traits that appear in two distinct forms during development (Lawson and Poethig, TIG 11:263-268, 1995). Juvenile traits always appear in basal parts of the maize plant, since the polar growth of the apical shoot meristem separates the juvenile and adult phase spatially as well as temporally. The transition between the phases is however gradual. The most obvious phase specific markers are presence or absence of epicuticular waxes and epidermal macrohairs on the leaf blade. Beside some further leaf and shoot related traits, the presence of "adventitious roots" (crown roots) is a distinct juvenile trait (Moose and Sisco, Plant Cell 6:1343-1355, 1994).

The mechanism of the juvenile adult transition is unknown, however it is assumed that the root stock exerts an influence on the transition. This allusion was now tested with help of the root deficient mutant *rtcs* recently isolated by us (Hetz et al., MNL 66:45, 1992).

rtcs is characterized by a drastically reduced root system, lacking also the "adventitious" roots considered as a juvenile vegetative trait. Instead of the complex root system of a wild type plant, consisting of a primary root, lateral seminal-, crown- and brace roots, the mutant *rtcs* displays only a primary root, which is nevertheless sufficient to produce a fertile plant. The *rtcs* plants were now used for a study of occurrence and timing of the juvenile-adult phase transition by examining in comparison to wild type siblings the phase specific markers of the leaf epicuticular wax formation (examined by toluidin blue staining) and the formation of macrohairs. Surprisingly we could not detect any significant difference between *rtcs* and wild type plants in the expression of these traits (Table 1). Also the total number of leaves in wild type and *rtcs* showed no significant difference.

Table 1. Epicuticular wax and hairs in wildtype and *rtcs* plants.

Trait	wild type (14)	*rtcs* (11)
Total number of leaves	13.9±0.6	12.5±0.8
First leaf with hairs	5.6±1.2	6.1±0.8
First leaf partially lacking wax	7.1±1.0	7.3±1.1

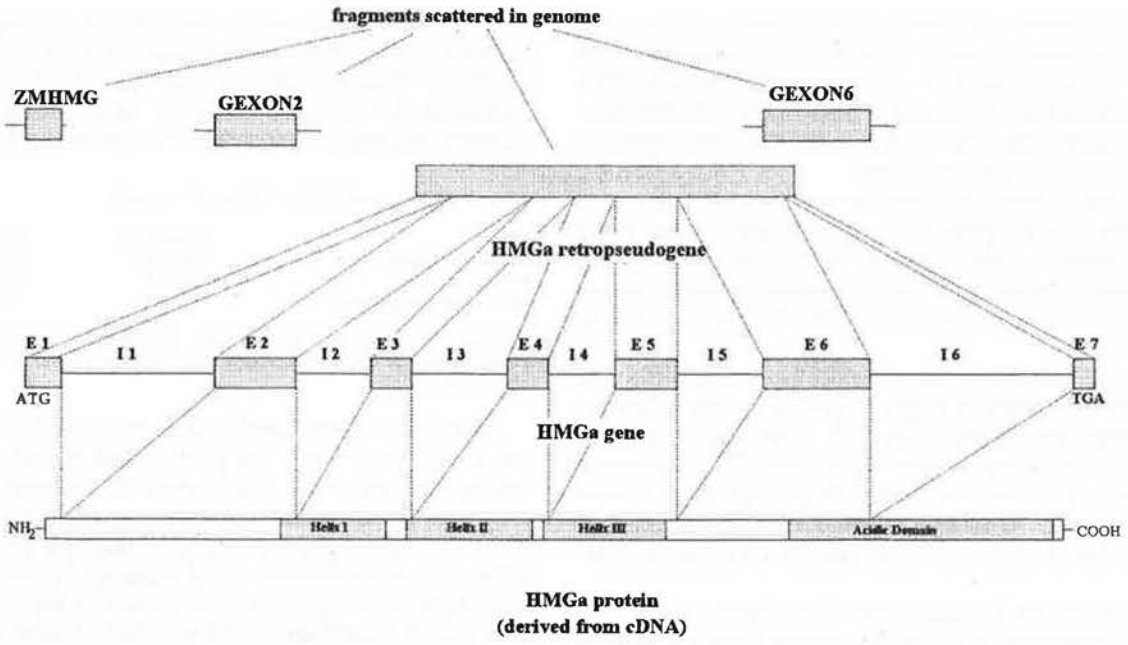
Each value is the average ± two standard errors. The averages for *rtcs* mutants are paired with the averages for their wild type siblings. The number of plants of each type is given in parantheses.

At the time of the juvenile-adult phase transition (between leaf 5 and 7 in our case) the wild type had formed primary-, lateral seminal- and crown roots whereas *rtcs* displayed only the primary root. So far we have not made a quantitative determination of the total size of the root system of wild type and *rtcs* plants at the time of the juvenile - adult transition by determining the root length and weight of all roots present at this time. The results of such experiments might give more detailed insights into the question, to what extent factors produced by the root system in general or more specifically by particular roots promote the juvenile phase or inhibit adult development. In this case phase change might be sensitive to the size of the root system as discussed in Lawson and Poethig (1995).

Genomic organization of the maize HMGa gene

--Krech, AB; Grasser, KD and Feix, G

High mobility group (HMG) proteins are abundant non-histone proteins of the eukaryotic chromatin with assumed functions in chromatin structure and its regulated expression. In maize, four different HMG proteins (a, b, c and d) have been identified. In the case of the HMG-box containing HMGa protein, studies have so far been performed with a cloned cDNA (Grasser and Feix, Nucl. Acids Res. 19:2573-2577, 1991) and with isolated and recombinant proteins (Grasser et al., Plant J. 6:351-358, 1994). Our current work on the genomic organization of HMG coding sequences (working with Southern analysis and cloned genomic fragments) revealed that several HMG protein coding sequences (complete and fragments) are scattered in the genome. In addition to the gene (consisting in the coding region of seven exons) three separate single exon containing fragments and a complete retropseudogene have been identified. This finding reminds us of the results obtained with the human HMG system (Stros and Dixon, Biochim. Biophys. Acta 1172:231-235, 1993). Our current picture of the HMGa gene system is summarized in the scheme on the following page.



Structure of the HMGa gene and genomic fragments

The HMGa gene and the fragments GEXON2 and GEXON6 were obtained by screening genomic libraries prepared from maize line A619. The structure of ZMHMG was taken from the literature (Yanagisawa and Izui, Plant Mol. Biol. 23:915, 1993). The retropseudogene was obtained by PCR amplifications from DNAs of different maize lines including A619. The cDNA was previously isolated from a cDNA library (Grasser and Feix, 1991). The -helices I, II and III are part of the HMG-box DNA binding domain.

GAINESVILLE, FLORIDA
University of Florida

The maize inbred line Va20 carries a new restoring gene for S-type cytoplasmic male sterility (CMS)

--Kamps, T and Chase, C

CMS is the maternally inherited inability to shed viable pollen, and a CMS plant is male sterile unless it carries the appropriate gene that restores fertility. These restorer genes are generally referred to as restorers of fertility (*Rf*). In maize, three major groups of male sterile inducing cytoplasms occur and these groups are, in part, defined by their nuclear restorer genes. Our investigations have focused on fertility restoration of the S-type cytoplasm.

CMS-S maize plants are characteristicaly restored to fertility by the gametophytically expressed nuclear gene, *Rf3*. Additional CMS-S *Rf* genes were uncovered among unexpected male fertile progeny by Laughnan and Gabay (Maize Breeding and Genetics, pp. 427-447, 1978). These new restorers are distinct from *Rf3* by map positions and, with the exception of *RfIV*, by their deleterious pleiotropic effects. Laughnan and Gabay localized the position of *Rf3* to the long arm of chromosome 2 (2L). We have since identified a more precise location of the *Rf3* gene from the inbred Ky21(S) (*Rf3-Ky21*) to be in the interval between *whp* and *bnl17.14* (MNL 66:45, 1992).

Linkage analyses for fertility restoration by the inbred lines CE1(Vg) and Va20(CA) were also performed. An analysis of 45 testcross progeny revealed the estimated map position of CE1 restorer (*Rf3-CE1*) to be 8.9 cM distal to *whp* and 8.9 cM proximal to *bnl17.14*. This is similar to the results reported for the *Rf3-Ky21* gene. Conversely, analysis of Va20(CA) testcross progeny showed no linkage of fertility restoration with either the *whp* or the *bnl17.14* marker. Neither was linkage detected with other 2L RFLPs including *npi291*, *npi297*, *npi122*, *npi456* and *npi298*, indicating that the Va20(CA) restorer was not allelic to either *Rf3-CE1* or *Rf3-Ky21*.

The population from the three-way-cross W182BN(CA) X [Va20(CA) X Ky21(S) was generated to conduct a direct linkage analysis between the Va20(CA) restorer and *Rf3-Ky21*. All but one of 76 progeny examined were semi-fertile, i.e. shed pollen was composed of approximately 50% normal, starch-filled grains and 50% aborted, empty grains as expected for gametophytic restorer genes. Southern analysis with the *Rf3-Ky21* linked markers, *whp* and *bnl17.14*, showed a segregation ratio of 2 Ky21 : 1 Va20 alleles. This segregation pattern is indicative of two major unlinked gametophytically expressed restorer genes and is consistent with our earlier data.

Additional studies compared fertility restoration in F1 and BC1 populations generated by crossing the Va20(CA), Ky21(S) and CE1(Vg) with four different male sterile inbreds. Male fertility was assessed by examining pollen shed from individual progeny. Va20 progeny were more variable in male fertility than either CE1(Vg) or Ky21(S) and exhibited the most frequent occurrence of unexpected male steriles. Some Va20 F1 hybrid combinations produced male steriles whereas all hybrid combinations using either Ky21(S) or CE1(Vg) parents were semi-fertile. Furthermore, we have observed that populations generated by recurrent crossing of Va20 restored progeny to the male sterile inbred W182BN(CA) tend to show an increase in male sterility. These sterility data combined with the linkage analysis suggest that the Va20 CMS-S restorer system is unique and is likely more complicated than the classic CMS-S restorer, *Rf3*.

The Va20 inbred does not exhibit any of the deleterious effects characteristic of the 9 "new" CMS-S restorers reported by Laughnan and Gabay. The possibility that the Va20 restorer and *RfIV* are different genes has yet to be examined. This can initially be achieved by conducting a direct linkage experiment, like that described above, between these two restorers.

HAIFA, ISRAEL
Newe Ya'ar Research Center
URBANA, ILLINOIS
University of Illinois

Mapping of RAPD markers linked to chromosomal regions affecting sugar accumulation in *sugary enhancer* sweet corn

--Katzir, N; Tadmor, Y; Juvik, J and Bar- Zur, A

The objective of our study was to map genes affecting characteristics associated with the *se* gene. RAPD analysis of NILs was used to identify putative informative primers. Two pairs of NILs (IL678a and IL451b), which differ for the *se* mutation, and IL677a, the original *su1 se1* line, were compared. Three hundred and forty arbitrary, ten-mer primers were used to amplify the different genotypes. Of the 340 primers, only one, OPN20, generated an amplification product (675 bp long) which was present in all three *su1 se1* genotypes, but not in their *su1 Se* isolines. Two primers, UBC281 and UBC425, generated products (900 and 700 bp, respectively) that were polymorphic between one pair of NILs (IL678a), but not between the other pair of NIL (IL451b). These two products were also produced by IL677a.

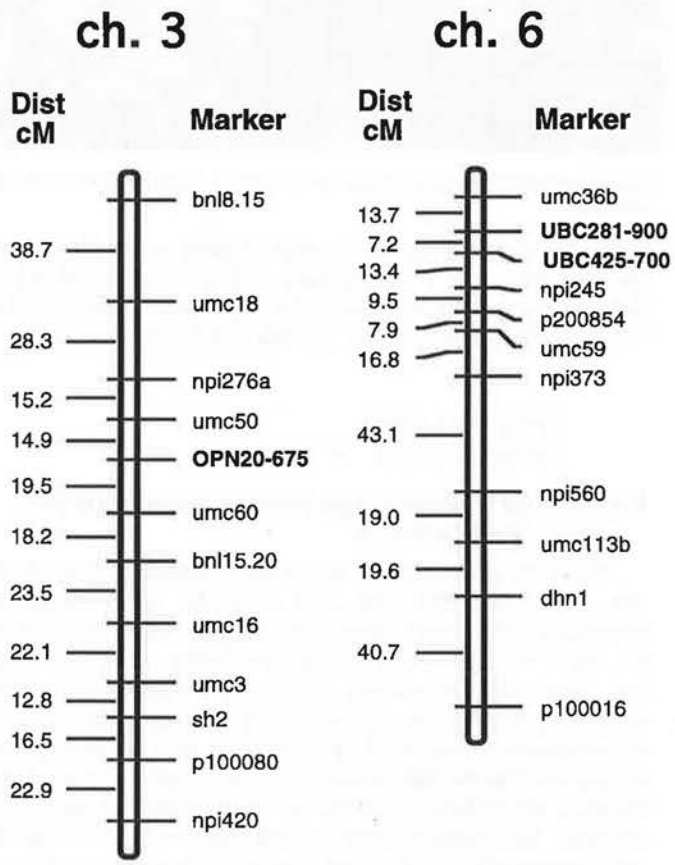


Figure 1. Chromosomal location of *OPN20-675*, *UBC281-900* and *UBC425-700* (the second number is the size of the amplification product in bp).

The three RAPD bands, described above, were mapped to chromosomes 3 and 6 adjacent to *umc50* and *umc59* respectively (Fig. 1) using the W6786 *su1 Se* x IL731a *su1 se* F2:3 population (Tadmor et al., Theor. Appl. Genet. 91:489-494, 1995). These regions were reported there as being associated with kernel sugar content. In that study the *se1* locus was mapped to the long arm of chromosome 2 adjacent to *umc36*. Interestingly, all three RAPD markers were mapped to two chromosomal areas affecting sugar and taste (Azanza et al., Genome, in press), yet none was mapped to the *se1* location on chromosome two. RFLP analysis of the same two pairs of NILs with *umc36* did not detect polymorphism.

Elevated sugar content was one of the criteria in the development of the NILs and is a major characteristic by which *se* is selected in breeding programs. Our data indicate that more than one locus effects elevated sugar content in *su1* kernels. This demonstrates the complication in the phenotypic selection for *su1 se* genotype and the advantage of Marker Assisted Selection for the *se* phenotype.

HAMBURG, GERMANY
University of Hamburg

Chalcone synthase antisense expression in transgenic maize leads to white pollen phenotype

--Muller, E; Ulrich, S and Wienand, U

Constructs containing the maize chalcone synthase cDNA (*C2*) in the antisense orientation were transformed into the maize line H99 via particle bombardment of 13 DAP embryos. Transgenic plants derived from independent transformation events were analyzed for their phenotype and chalcone synthase expression. The most noticeable phenotypic alteration was the complete loss of colored tissue in the transgenic plants, especially in the stem and anther tissues. The pollen of the primary transgenics was different in color from the wild type pollen and had the white color typical for the white pollen mutation (*c2, whp*). Analysis of the pollen indicates that no or only little amounts of flavonoids were produced. The outcrossed population could be easily screened using the colorless (green) phenotype of the seedlings as a selectable marker to identify progeny containing the antisense gene. These plants are currently under further investigation.

IBARAKI, JAPAN
Institute of Radiation Breeding

Induction of bicellular pollen and dihaploidization of tetraploid maize

--Kato, A

Recently, antimicrotubule agents have been used in chromosome doubling in maize anther culture. These chemicals were originally developed as herbicides. Compared with colchicine, they are very cheap and effective. Trifluralin is one of them and I examined the effect of trifluralin on in vivo maize microsporogenesis and succeeded in the induction of restituted bicellular pollen.

I sprayed 0.05-0.2% of a Trefanocide (44.5% trifluralin emulsion) solution (with the addition of 0.1% of spreading agent Alsoap) on the tassels of a diploid inbred line Oh43 at 8-10 days

before flowering. At that time microspores in the anthers were at the monocellular to bicellular stages. Microscopic observation revealed the presence of restituted bicellular pollen grains (Fig. 1) mixed in the normal tricellular pollen grains in the 0.2% treatment. The sperm cells in the bicellular pollen grains were diploid since they presumably originated from the nondisjunction of the chromosomes at the second pollen mitosis.

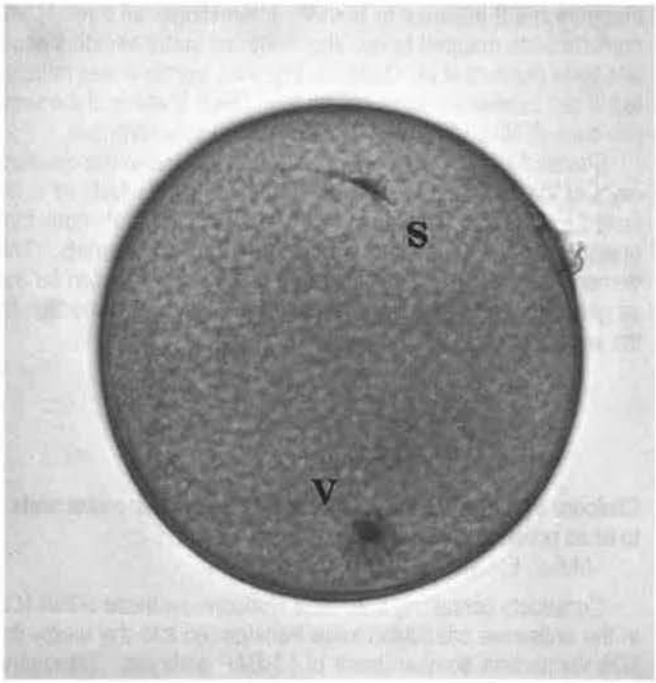


Figure 1. Restituted bicellular pollen grain induced by trifluralin treatment (S - sperm cell, V - vegetative nucleus).

The ears pollinated with the treated pollen exhibited an increased number of shriveled kernels which resembled a 2n x 4n cross in maize (Fig. 2). In the 0.2% treatment, 46% of the kernels were shriveled (Table 1). Thirty-seven percent of the shriveled kernels had a small embryo. I carefully planted the shriveled kernels in moist vermiculite but none of them germinated.

Table 1. Kernel development on the ears pollinated by trifluralin-treated pollen.

Trefanocide concentration (%)	No. of ears pollinated	No. of plump kernels	No. of shriveled kernels
0.0	3	977 (99.4)	6 (0.6)
0.05	2	710 (98.6)	10 (1.4)
0.1	2	519 (86.2)	83 (13.8)
0.2	7	694 (54.0)	590 (46.0)

The restituted bicellular pollen has only one sperm cell. If the sperm cell fertilizes only polar nuclei and if the egg cell is not fertilized, the ovule may develop into a haploid kernel. I determined whether the bicellular pollen produced by diploid plants induced dihaploids on tetraploid maize ears. I pollinated the ears of a tetraploid maize line Q28-1 with trifluralin-treated Oh43 pollen (0.3% Trefanocide solution). I obtained 117 plump kernels from the seven ears. Ploidy levels of the 85 seedlings among them were determined: 65 seedlings were tetraploid, 12 were triploid and eight were diploid. The tetraploid cases may have originated from the union of a diploid sperm cell and diploid egg cell and the triploid cases from the union of a haploid sperm cell and diploid egg cell. In both cases polar nuclei must have been fertilized by a

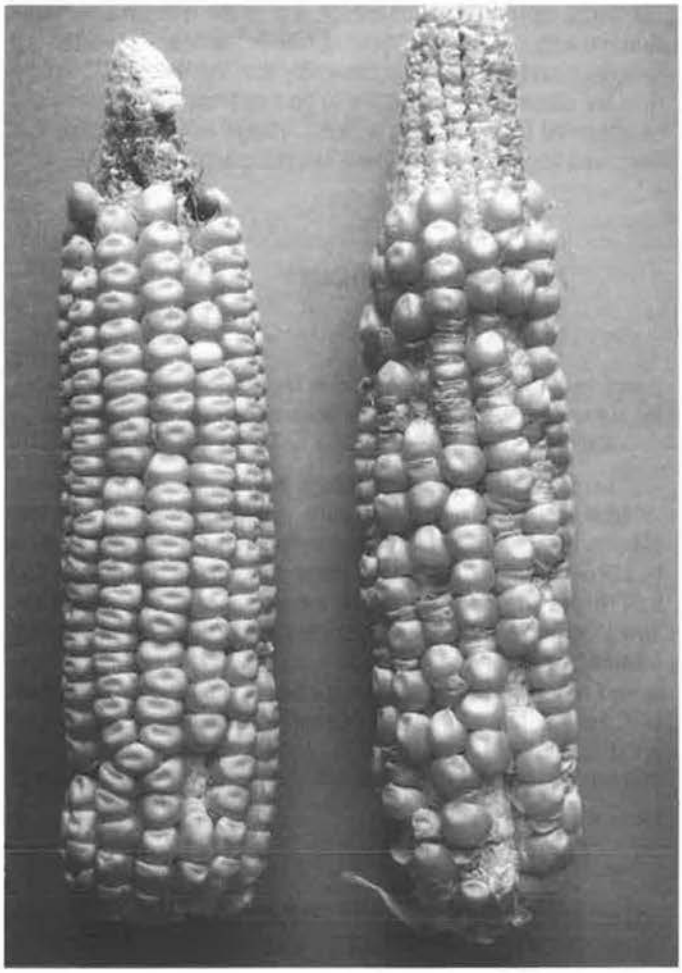


Figure 2. Control ear (left) and ear pollinated with trifluralin (0.2% Trefanocide solution)-treated pollen (right).

diploid sperm cell, because the union of polar nuclei (2n+2n) of tetraploid maize and a haploid sperm cell (n) should result in the development of shriveled kernels. The eight diploid cases were attributed to dihaploidization and the rate was 9.4%.

IOWA CITY, IOWA
University of Iowa

Analysis of the chromosome-type breakage-fusion-bridge cycle
--Zheng, Y and Carlson, W

The study of dicentrics in maize was initiated by McClintock (Mo. Agric. Exp. Stn. Res. Bull. 290:1-48, 1938; Genetics, 26:234-282, 1941; Cold Spring Harbor Symp. Quant. Biol. 9:72-81, 1941; 14:13-37, 1951; PNAS 28:458-463, 1942; Carnegie Inst. Wash. Ybk. 42:148-150, 1943). She studied both chromatid- and chromosome-type dicentrics. The chromosome-type dicentrics were constructed by introducing two broken chromosomes, one from the male and one from the female, into the zygote. Fusion of the broken ends of the two chromosomes produced the dicentric. McClintock's studies showed that chromosome-type dicentrics are unstable during early plant development because they undergo the chromosome-type breakage-fusion-bridge cycle. Eventually, the dicentrics are converted to monocentrics and the

cycle ceases. McClintock did not identify the time during development of dicentric stabilization.

The type of chromosome that McClintock used to produce dicentrics is referred to as duplication 9 (Dp-9). It contains a complete chromosome 9 plus a duplication of nearly all of the short arm, attached inversely to the end of the normal short arm. The duplicated region of Dp9 was combined with the B-9 chromosome of TB-9Sb through crossing over (Carlson, Corn and Corn Improvement, pp. 259-341, 1988). It should be noted that McClintock produced several duplication 9 chromosomes. The one used here is referred to as Type-I in Figure 9 of McClintock (Genetics, 26:234-282, 1941). At the first division of meiosis, the B-9-Dp9 chromosome frequently engages in foldback pairing and internal crossing over, with production of a chromatid-type dicentric B-9. This dicentric forms a single bridge at anaphase II. Following breakage of the bridge and DNA replication, the broken ends fuse and form a chromatid dicentric again. This initiates McClintock's chromatid-type breakage-fusion-bridge cycle. The cycle continues during the first pollen mitosis. However, at the second pollen mitosis, nondisjunction interrupts the cycle. Mitotic nondisjunction of the B-9 produces one sperm with the dicentric and another without it. In this process, the chromatid-type dicentric B-9 is converted into a chromosome-type dicentric. Consequently, a B-9-Dp-9 chromosome can produce chromosome type dicentrics when transferred through the male parent. This makes production of the dicentrics simpler than with McClintock's method.

In order to construct chromosome dicentrics with B-9-Dp9, kernels with a dominant *C Wx* phenotype were selected from crosses of 9-B(*wx1*) 9-B(*Wx1*) B-9-Dp9(*C1 C1*) X 9(*wx1*) 9-B(*Wx1*) B-9(*c1*) B-9(*c1*). Plants grown from the seeds were classified for pollen type. Plants with all *Wx* pollen and 50% pollen sterility were selected. These should be 9-B(*Wx1*) 9-B(*Wx1*) B-9-Dp9. The selected plants were crossed as male parents to a tester: 9(*bz1 yg2*) 9(*bz1 yg2*) X 9-B(*Wx1*) 9-B(*Wx1*) B-9-Dp9(*Bz1 Yg2 Yg2 Bz1*). Fertilization of the egg by sperm containing a B-9 dicentric and of the polar cells by sperm lacking the B-9 gives the desired type. The endosperm has a recessive brown (*bz*) phenotype. The embryo has a B-9 dicentric and should give a variegated yellow and green (*Yg/yg*) phenotype.

A total of 747 brown seeds were planted in a search for chromosome dicentrics. The plant phenotypes were classified as: 194 green (26.0%), 66 yellow (8.8%), 54 dead or did not germinate (7.2%), 433 variegated green and yellow (58.0%). The variegated plants were studied in detail. Among 433 variegated plants, the primary root tips of 410 were checked for double bridges in mitotic anaphase. They were found in 364 plants. The percentage of variegated plants with double bridges was 88.8%. Next, 148 plants with double bridges were examined at weekly intervals for up to 10 weeks. A single root tip was examined each time to check double bridge configurations in 25 anaphase cells per plant. The data are summarized in Table 1. The percentage of variegated plants with double bridges in the roots declined gradually during plant development, indicating that the dicentric chromosomes were stabilized over the 10 week period in most plants. Only a few plants (6.5%) showed double bridges at week 10. From the curve in Figure 1, it appears that there is no specific time for elimination of the dicentric condition.

The findings do not distinguish between a) gradual elimination of dicentrics at different times in different sectors of a plant, or b) elimination of dicentrics at a specific time in development for each plant, with the time varying between plants. It should also be noted that the method of dicentric B-9 stabilization has not yet been completely documented. McClintock found, with a dicentric 9, that conversion to monocentrics occurred. With the B-9 dicentric, conversion to monocentrics is found, but lagging and loss of the dicentric in anaphase may also occur. Both events "stabilize" the dicentric by eliminating double bridges.

Table 1. Percentage of variegated plants with double bridges over time. The number of variegated plants checked each week varied since the root tips of some unhealthy plants were not available each week and some plants died.

Week #	1	2	3	4	5	6	7	8	9	10
Number of plants examined	148	132	119	126	140	143	146	107	103	77
Number of plants with double bridges	134	105	74	64	46	41	27	10	8	5
% of plants with double bridges	90.5	79.5	62.2	50.8	32.9	28.7	18.5	9.3	7.8	6.5

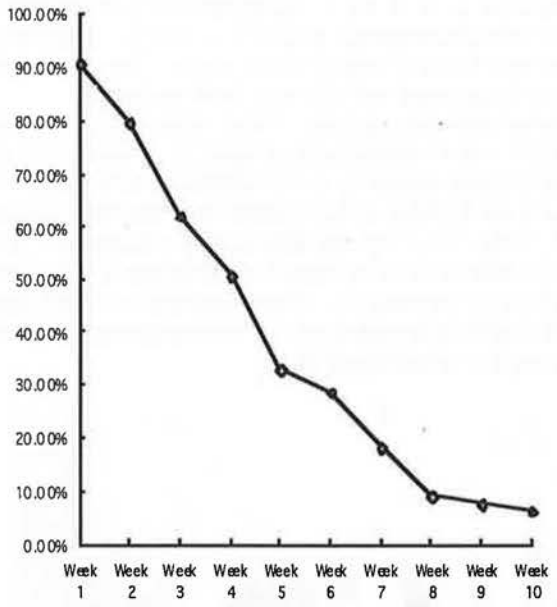


Figure 1. Percentage of variegated plants with double bridges during plant development. The data are listed in Table 1.

Mini-chromosomes

--Zheng, Y

A crossover between the B-9 chromosome from TB-9Sb and the duplication 9 chromosome from McClintock (Genetics, 26:234-282, 1941) has been used to establish a chromosome breakage-fusion-bridge cycle, as described in an accompanying article. Briefly, a B-9-Dp9 chromosome is capable of self-pairing and crossing-over to produce a chromatid breakage-fusion-bridge cycle. Subsequently, nondisjunction at the second pollen mitosis converts the chromatid cycle to a chromosome cycle. Crossing 9-B 9-B B-9-Dp9 plants as male parents to a *bz1 bz1 yg2 yg2* tester produces some progeny with the *bz* endosperm phenotype. Among these kernels, many have a B-9 chromosome dicentric in the embryo. Since the dicentric undergoes a chromosome-type breakage-fusion-bridge cycle, the phenotype of the correct plants is variegation for green and yellow stripes.

In order to study the fate of B-9 dicentric chromosomes during development, tassel samples (sporocytes) were collected from 41 variegated plants and examined in meiosis. Most of the plants

had been checked previously for double bridges in primary root tip cells and 34 showed double bridge configurations. Therefore, at least 34 of the plants initially contained a B-9 dicentric.

When the chromosomes were checked at pachytene, a lot of diversity was found in chromosome structure between plants and even within the same plant. Breakage occurred at various positions between the two centromeres, producing both long and short chromosomes, as well as sizes in between. "Mini-chromosomes" were identified in 13 of the 41 variegated plants at pachytene. The term "mini-chromosomes" is used for a collection of very small chromosomes that are heterogeneous in size. They all probably arose from bridge breakage at or near the B centromere.

In metaphase-I cells , the mini-chromosomes orient on the plate along with the other chromosomes (Figure 1). In anaphase-I, the mini-chromosomes usually lag and do not migrate early to one pole, unlike complete B chromosomes (Carlson and Roseman, Genetics, 131:211, 1992). They often split after lagging in anaphase I. They can also be observed in metaphase-II and anaphase-II cells. These are preliminary observations, without quantitation at this point. The main finding is that extremely small chromosomes frequently arise among the variegated plants.

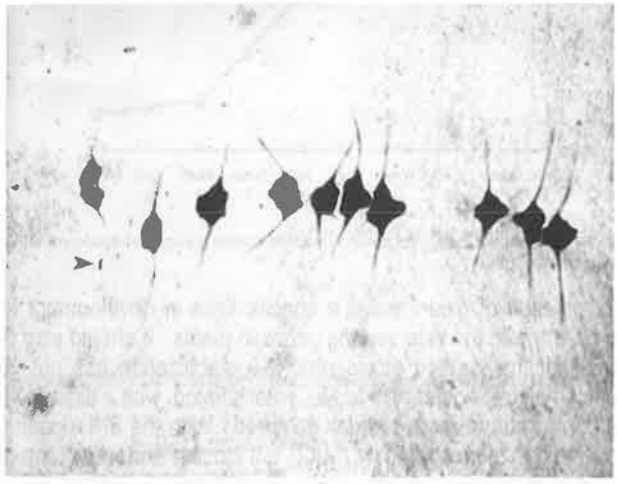


Figure 1. A mini-chromosome in a metaphase-I cell.

Construction of 9S telocentrics

--Zheng, Y and Carlson, W

Carlson and Curtis (Can. J. Genet. Cytol. 28:1034-1040, 1986) produced unusual constructs, referred to as proximal duplications, for chromosomes 3 and 9. In the chromosome 9 construct, the normal 9 bivalent is replaced with 9-B chromosomes from TB-9Sb and TB-9La. The homozygous stock contains 9-BSb 9-BSb 9-BLa 9-BLa. No B-9's are present.

Plants homozygous for proximal duplication 9 were crossed as female to one of the progenitor lines, TB-9Sb. The purpose of the cross was to produce hemizygous 9-BSb 9-BSb 9-BLa plants. The 9-BLa chromosome should be frequently unpaired in these plants and more susceptible to misdivision in meiosis than other chromosomes. Selection of the hemizygous plants depended on using a *C1-I* marked TB-9Sb. The cross was: 9-BSb 9-BSb 9-BLa(*C1*) 9-BLa(*C1*) X 9-BSb 9-BSb B-9(*C1-I*) B-9(*C1-I*). Among the progeny, white seeds with colored scutellum were selected. The plants should contain 9-BSb 9-BSb 9-BLa. This constitution was confirmed by 1) classifying pollen and finding 50% pollen sterility, and 2) doing testcrosses to *C1 C1* plants and finding no color inhibition.

The selected plants were crossed as male to a *c1 c1* tester and two different *bz1 bz1* testers. From these crosses, a number of variegated seeds were obtained. Previous evidence suggested that variegation is a marker for misdivision (Carlson, Annu. Rev. Genet. 12:5-23, 1978). Among 26 variegated seeds checked from crosses of *bz1 bz1* x 9-BSb 9-BSb 9-BLa(*Bz1*) and *c1 c1* x 9-BSb 9-BSb 9-BLa(*C1*), four contained a telocentric 9S. As a control, twenty eight non-variegated seeds were also checked. No 9S telocentrics were found. The results suggested that the use of variegation as a selective phenotype for telocentrics is effective.

The telocentrics found above were not maintained. However, another group of variegated seeds was planted in the field. The second group was propagated in crosses as female to *c1 c1* or *bz1 bz1* testers. Progeny with dominant *C* or *Bz* phenotypes were selected and classified in root tips for chromosome type. Twelve telocentrics of 9S and five isochromosomes of 9S were recovered. The rate of telocentrics found in these variegated seeds was 12/164 = 7.32%. In the prior screen of seedlings the rate was 4/26 = 15.38%.

The method for isolating telocentrics presented here is effective for several reasons, but the main advantage is the ability to form the telocentric in pollen parent crosses. This allows for the selection of variegated kernels, which are probably less common in egg parent crosses. It also means that a single plant, with an appropriate constitution for misdivision, can be used in many crosses. Future work includes making the telocentric stocks homozygous (9-BSb 9-BSb telo-9S telo-9S). In addition, more proximal duplication stocks are being constructed. The limiting feature of this technique is the availability of appropriate endosperm markers on different chromosome arms for classification of variegation.

High frequency centromeric misdivision

--Carlson, W

Studies with the B-9 chromosome of the translocation, TB-9Sb, led to the isolation of an apparent isochromosome (Carlson, Chromosoma 30:356, 1970). Subsequently, it was found that the chromosome was, in fact, a pseudoisochromosome (Carlson, Genetics 97:379, 1981). The two arms differ in terms of the presence or absence of centric heterochromatin, as depicted below. (B chromosome regions are solid black).

Pseudoisochromosome

The pseudoisochromosome is stable during plant development but is unstable when transmitted through the pollen parent. It frequently produces variegated kernels in testcrosses using *bz1* or *c1* as a marker. When kernels with variegated endosperm phenotypes were germinated, telocentrics were frequently found in the plants. Therefore, variegation is associated with misdivision of the chromosome (Annu. Rev. Gen. 12:5, 1978). The reason for variegation may be the absence of a telomere at the terminal centromere, due to a lack of "healing" in the endosperm. Two types of telocentrics were recovered, corresponding to the two arms of the pseudoisochromosome.

Type 1 telo

Type 2 telo

The type 1 and type 2 telocentrics are stable both in plant development and in pollen parent crosses. They seldom produce variegated kernels in testcrosses and misdivide infrequently. Nevertheless, it was possible to produce the type 1 isochromosome by misdivision of the type 1 telocentric (Genetics 97:379, 1981). The type 1 isochromosome is stable during development, but produces large numbers of variegated kernels in pollen parent crosses, just as with the pseudoisochromosome.

Recently, an explanation was found for the difference between the two isochromosomes and the type 1 telocentric, in terms of stability. This past summer, a number of crosses were made in which the type 1 telocentric was univalent in meiosis. The crosses were of the type: *bz1 bz1* X 9-B 9-B type 1 telo (*Bz1*). In the progeny, variegation for purple and bronze phenotypes (*Bz bz*) was frequent, suggesting high levels of misdivision. The rate of *Bz bz* kernels for three ears was 48 variegated kernels per 597 total, or 8.0%. The variegated classification was restricted to kernels in which at least 1/6 of the endosperm phenotype was recessive. In addition, a number of recessive *bz* kernels were found in these crosses. With a normal (standard) B-9 the presence of *bz* kernels is expected, since nondisjunction at the second pollen mitosis frequently "uncovers" the recessive. However, the type 1 telocentric is incapable of nondisjunction, due to the absence of centric heterochromatin. Therefore, the *bz* kernels must have another source. A cytological study was made of the *bz* kernels found on the same three ears mentioned above. The plants derived from *bz* kernels were classified as follows:

20 chromosomes = 12
21 chromosomes with an isochromosome = 13
21 chromosomes with a telocentric = 1
22 chromosomes with two telocentrics = 0

No cases of true nondisjunction, with 22 chromosomes, were found. Instead, many of the kernel types appear to be cases of misdivision. One explanation is that misdivision in meiosis transmitted a damaged telocentric to the second pollen mitosis. This telocentric replicated or divided improperly to form an isochromosome. The 13 *bz* kernels with an isochromosome in the plant can be explained by migration of the isochromosome to one pole, giving 0-iso disjunction. The 12 *bz* kernels with only 20 chromosomes could have resulted from lagging of the isochromosome at anaphase and 0-0 disjunction. (Note: the 20 chromosome class is not a case of self-contamination, since a marker in the pollen parent was present in the seeds). The single case of a plant with one telocentric is less easy to explain. However, it is not the result of simple nondisjunction.

The findings are preliminary, but they appear to invalidate prior speculations on the cause of isochromosome instability. They show that the type 1 telocentric can be just as unstable as the original (pseudo-) isochromosome or the type 1 isochromosome. The required condition is a lack of pairing with another chromosome in meiosis. In retrospect, it appears that the original isochromosome and all its derivatives suffer from the same defect: they are unstable when univalent in meiosis. The isochromosomes are unstable in all their crosses, even when a pairing partner is present, because they tend to self pair. The telocentric is unstable only in those crosses in which a pairing partner has been excluded. The finding of a specific defect in centromere behavior for one set of chromosomes may help explain the functioning of one part of the maize centromere. In addition, the fact that the type 1 telocentric is now known to be unstable when univalent provides a simple system for studying the process of misdivision. It is much simpler to follow, cytologically, misdivision of a chromosome with two chromatid arms (telocentric) than one with four arms (isochromosome).

IRKUTSK,RUSSIA
Institute of Plant Physiology and Biochemistry

Protein synthesis in mitochondria under different redox conditions

--Konstantinov, YM; Subota, IV and Arziev, AS

It is known that gene expression can be efficiently regulated at the level of translation along with transcriptional and posttranscriptional levels. However specific molecular mechanisms of such regulation, especially regarding translation in mitochondria, are poorly known.

As previously shown, redox conditions can provide a profound effect on the template activity of the mitochondrial genome regarding RNA and DNA syntheses in organello (Konstantinov et al., Biochem. Mol. Biol. 36:319-326, 1995). Moreover, the activation of transcription in mitochondria under oxidising conditions and its inhibition under reducing conditions can indicate possible redox regulation of genetic processes in mitochondria. With consideration for the existence of multi-level regulation of gene expression, a question arises at what levels such regulation can exist during functioning of mitochondrial genes.

The aim of the present work was to examine the mitochondrial protein synthesis in organello under changes of redox conditions by the addition of potassium ferricyanide as an oxidising agent and sodium dithionite as a reducing agent.

The mitochondria were isolated from 3-day-old etiolated seedlings of hybrid VIR 46MV by a standard method of differential centrifugation. Protein was determined by the Lowry method, protein synthesis was measured in mitochondria according to the method of Bhat et al. (Biochemistry 21:2452-2460, 1982) with the use of [14C]-leucine (specific radioactivity was 1760 GBq/mol). Protein synthesis reactions in seedling mitochondria were highly sensitive to chloramphenicol (50 ug/ml). In order to study the effect of oxidation phosphorylation uncoupler on in organello protein synthesis carbonyl cyanide chlorophenylhydrazone (CCCP) at a final concentration of 1 μM was used.

The effect of redox conditions on the kinetics of protein synthesis in maize seedling mitochondria is shown in Table 1.

Table 1. Kinetics of protein synthesis in isolated maize mitochondria in the absence and the presence of potassium ferricyanide or sodium dithionite.

	Incorporation of [14C]-leucine, counts/min/mg protein			
Conditions	5 min	10 min	15 min	20 min
Control	554	1432	2833	4986
Ferricyanide (5 mM)	1098	2221	3931	6039
Dithionite (5mM)	180	132	310	1190

The activity of protein synthesis is seen to increase in the presence of potassium ferricyanide used as an oxidising agent, while this process is strongly inhibited when mitochondria were

supplemented by sodium dithionite as a reducing agent. Thus, redox conditions used affected pronouncedly the activity of the protein synthesizing system in isolated plant mitochondria.

In addition, the effect of redox conditions on protein synthesis has been examined in the presence of carbonyl cyanide chlorophenylhydrazone (CCCP), an uncoupler of oxidative phosphorylation. It is seen in Table 2 that the effect of potassium ferricyanide on the protein synthesis is negligible in the presence of CCCP, while the treatment with simultaneous addition of sodium dithionite and CCCP resulted in more profound inhibition of translation. Since the addition of CCCP alone caused a significant decrease in the activity of mitochondrial protein synthesis, apparently due to development of an energy deficient state in mitochondria, the changes in the redox conditions' influence in the presence of the uncoupler is related, in our opinion, mainly to disturbances in energy supply of this process.

Table 2. The effect of potassium ferricyanide and sodium dithionite on protein synthesis in maize mitochondria in the presence of CCCP.

Conditions	Incorporation of [14C]-leucine, counts/min/mg protein
Control	7380
CCCP	4005
Ferricyanide	11863
Ferricyanide + CCCP	8044
Dithionite	2804
Dithionite + CCCP	1411

The effect of potassium ferricyanide on the translation activity has been examined in the presence of such an inhibitor of template RNA synthesis as ethidium bromide in order to elucidate whether changes at the transcriptional level are the main reason for changes in mitochondrial protein synthesis in the presence of redox agents (Table 3). It is expected from data given in Table 3 that redox conditions can affect the expression of mitochondrial proteins directly at the level of translation.

Table 3. The effect of potassium ferricyanide on protein synthesis in maize mitochondria in the presence of ethidium bromide.

Conditions	Activity of protein synthesis in mitochondria (% of control)
Control	100
Ferricyanide	167
Ethidium bromide	28
Ferricyanide + ethidium bromide	54

As a whole, we assume that translation along with other genetic processes in maize mitochondria can be subjected to redox control.

JOHNSTON, IOWA
Pioneer Hi-Bred

Mapping *ms*-LI89*

--Albertsen, MC; Fox, TW and Trimnell, MR

I was fortunate to have met and visited in 1987 with the well known maize geneticist and plant breeder, Prof. C. H. Li (now deceased), from the Peoples Republic of China. He was another of those individuals who had an incredible wealth of knowledge about maize. Our conversation eventually came around to the subject of maize male sterility. I mentioned to him that I was interested in receiving as many male-sterile mutations as I could so as to better understand the process of pollen development in maize. A year or so later he sent me a few seeds of a new male-sterile mutant he had found. He attached the following note, originally written in his handwriting.

> "This new male sterile gene was first found in 1978 and proved to be nonallelic to *ms2*, *ms10*, and *ms1*. By using a T4-9(5657) stock which has breakpoints at 4L.33 and 9S.35 and the *su1* in the linkage test, I obtained 5-6% crossover between su--T and 8-13% between T--ms(L) from different sets of the tested material. From the su-seeds I provided herewith, you will get mostly male steriles as non-crossovers, and from Su-kernel(s) mostly heterozygote translocations, t/T, which are to be readily identified from pollen examination. The identification of ms t/T genotype (any crossovers) can be made by the seed set only (semi-steriles)..."

I do not know the origin of the material, other than that it was from a 1987 source. Of the *Su* kernels that we planted, we obtained eight male fertiles and four male steriles. From the *su* kernels, we obtained one male fertile and 10 male steriles. The mutant segregated as a single recessive allele on chromosome 4. We knew that there were no recessive male sterile mutants currently described on chromosome 4 and that this was likely a new genetic male sterile. To verify and to further develop bulk segregant analysis, we crossed this mutant (our designation *ms*-LI89*) with A632 and selfed the progeny. Equal amounts of DNA from 20 male-fertile plants and DNA from 20 male-sterile plants from the self were pooled according to fertility classification. Each pool was digested with *Bam*HI, *Eco*RV, and *Hin*dIII, run on a gel, and southern blotted. Initially, two RFLP markers on each arm of chromosome 4 were used to screen the southern blots. Both probes from 4L, *bnl7.65* and *php20608*, gave polymorphisms with at least one enzyme. Two additional probes from 4L, *umc15* and *umc19*, also gave polymorphisms. To confirm and narrow down the map location, blots were made using DNA from the individuals that comprised each bulk. The data indicated that the allele responsible for male sterility is between RFLP markers *umc158* and *umc15* on chromosome 4L.

Based on Prof Li's genetic tests and our molecular work, we normally would propose a new *ms*-designation for this mutant. There are, however, two dominant male-sterile mutations on chromosome 4, *Ms41* and *Ms44*. They originally were distinguished from each other by virtue of the ability of *Ms41* to shed a small amount of pollen in certain environments, and this pollen being used to conduct an allelism test with *Ms44* (Albertsen and Neuffer, MNL 64:52, 1990). The suggested location of *ms*-LI89* by our molecular analysis placed it provocatively close to *Ms44*. Although there is no instance to date of a dominant male-sterile mutant and a recessive male-sterile mutant being allelic, we did not want to make a definite call until we conducted further linkage tests. Suggestions as to how to proceed are welcomed.

***Ms*-gene designations**

--Albertsen, MC

I would like to volunteer to help coordinate the designation of new male-sterile mutations. There are several gaps in designating the existing known male-sterile mutations as shown by the following current listing: *ms1*, *ms2*, *ms3*, *ms4* (original stock lost), *ms5*, *ms6* (original stock lost), *ms7*, *ms8*, *ms9*, *ms10*, *ms11*, *ms12*, *ms13*, *ms14*, *ms15* (original stock lost), *ms16* (original stock lost), *ms17*, *ms18* (original stock lost), *ms19* (original stock lost), *ms20*, *Ms21* (original stock lost), *ms22*, *ms23*, *ms24*, *ms25*, *ms26*, *ms27*

(proposed use by P. Bedinger), *ms28*, *ms29* through *ms40* (not used), *Ms41*, *Ms42*, *ms43*, *Ms44*, and *ms45-m1::Ac*. I propose to "fill-in" the gaps so as to reduce the confusion concerning the number of male-sterile mutations officially described in maize, and to reduce the possibility of the same mutant designation referring to more than one mutant. Unfortunately, this already has happened for *ms4*, which originally was used by Beadle in 1931 and subsequently re-used as a designation for a mutagen-induced male-sterile mutation that bears no relationship to Beadle's original *ms4*. Additionally, *ms6* often is referred to as being allelic to polymitotic (*po*). Beadle's 1932 description of *ms6* bears no resemblance to *po*, and as such, strongly suggests that the original stock of *ms6* has been lost.

I also would like to suggest that in the future, before anyone uses a new numbered designation for a particular male-sterile mutation, they at least identify the chromosome arm on which the allele is located. This will greatly facilitate the daunting task of making all the necessary allelism crosses that must subsequently be made by other researchers who also may have unmapped male steriles waiting to be officially designated. If the appropriate chromosome arm is known, the number of required crosses is reduced considerably. Unfortunately, for example, we will be unable to give new designations to any of the male steriles that Dr. Earl Patterson described last year until new allelism crosses are made. This suggestion, of course, would not preclude anyone from using their own *ms*-xxxx* designations for new male steriles that they are in the process of describing.

Description of a corn genome project at Pioneer Hi-Bred

--Helentjaris, T and Fincher, R

With continued improvements in molecular genetic technologies, it has now become feasible to undertake projects with the aim of isolating and identifying most, if not all, of the expressed genes within an organism, as is currently underway in the Human Genome Project. In one strategy, often referred to as the "EST approach" and pioneered by Craig Venter and associates (Adams et al., Nature Supp. 377:3-174, 1995), large numbers of cDNA clones are prepared, sequenced (usually by a single-pass from the presumed 5' end of the mRNA), and then categorized based upon their identification by sequence similarity to known gene sequences from within GenBank and other databases. With the high rate of evolutionary conservation at the amino acid level, it has proven practical to identify up to 35% of these clones by sequence similarity to another gene with a previously studied function, often crossing species and even phyla boundaries to detect these functional relationships. In fact one of the greatest impacts of these types of projects may be the ability to "access" the results of biological studies in any other species by finding a "homolog" in your own species of choice through sequence similarity detected at the amino acid level with other better studied entries in the public databases. Given the abilities to produce large and representative cDNA libraries, to efficiently sequence hundreds of thousands of such clones, and to identify many clones by similarity analyses, such projects are capable of isolating and identifying tens of thousands of cloned genes with putative functions. Initial studies in corn on a relatively small scale (Keith et al., Plant Physiol. 101:329-332, 1993; Shen et al., Plant Mol. Biol. 26:1085-1101, 1994) have already amply demonstrated the utility of this approach by providing plant researchers with maize homologs for many important genes.

Consequently, given the power of this general approach to significantly increase our general knowledge of genes and their functions, Pioneer Hi-Bred has decided to undertake a large-scale corn EST program in conjunction with Human Genome Sciences (HGS). Pioneer researchers will endeavor to produce gene-enriched libraries which will be submitted to HGS for single-pass sequencing from the presumed 5' terminus of the original mRNA. We plan to explore the use of standard, high complexity cDNA libraries prepared from a variety of tissues and treatments, normalized libraries, subtracted libraries, and other innovative approaches, all in an effort to identify as many genes as possible. By comparison with other sequences already in the public databases, we then hope to identify many of these genes to some putative functions. In line with this general goal, we are also exploring additional research strategies to establish both the genetic map locations and expression patterns of these clones, as well as to deploy our technology for mutational analyses of many of these genes (Meeley and Briggs, MNL 69:67&82, 1995).

Pioneer is currently developing plans which will provide opportunities for collaborative research in this area with researchers in the public sector. The EST information will provide for many new investigations in a variety of areas of plant biology. Once the details are finalized on the organization of these potential collaborations, they will be communicated to the maize research community. Pioneer welcomes this continued opportunity to work with the maize research community with the goals of both meeting Pioneer's product development objectives and advancing the state of knowledge of maize genetics.

KIRKSVILLE, MISSOURI
Northeast Missouri State University

Microsatellite repeat variation within the *y1* gene of maize and teosinte

—Phelps, TL and Buckner, B

In a previous study we demonstrated that allele–specific length polymorphisms exist in a $(CCA)_n$ microsatellite that is present 11–bp upstream of the transcriptional initiation site within the maize *y1* allele cloned from the hybrid line Q60 (Phelps and Buckner, MNL 69:84–85, 1995). We have extended this study to include additional maize alleles and one or two accessions of six teosinte species, subspecies or varieties. Sequence analyses demonstrate that the $(CCA)_n$ microsatellite varies in repeat number from 3 to 11 (Figure 1 and Table 1). In addition, the $(CCA)_n$ repeat is flanked by the imperfect pentanucleotide repeat (PyCATC; Py = C or T). Three different organizations of the pentanucleotide repeat were observed (designated types 1, 2 and 3 in Table 1). Type 1 contains both the (CCATC) and (TCATC) sequence duplicated as well as a trinucleotide CTG repeated 33 bp 5' of the $(CCA)_n$ repeat. Types 2 and 3 contain three copies of the pentanucleotide repeat but differ by a single base in the first repeat. We have further subdivided these categories based on the number of $(CCA)_n$ repeats found. The only sequence variability found within the $(CCA)_n$ repeat was a C to T transition in the second and fifth $(CCA)_n$ repeats of type 3a and 3c, respectively. In total, 12 different sequence polymorphisms were observed in this study (Figure 1 and Table 1). Therefore, the $(CCA)_n$ microsatellite, as well as the sequence directly adjacent to

Table 1. Sequence organization of the microsatellite-containing region of the *y1* gene of maize and teosinte.

Type	Organization of pentanucleotide repeat flanking $(CCA)_n$ microsatellite repeat in *Y1*	$(CCA)_n$	Genetic Material and Sequence Identity[a]
1	CCATC TCATC TCATC $(CCA)_n$.....CCATC	11	Q60 = H99
2a	CCATC TCATC --------- $(CCA)_n$.....CCATC	10	M14 = *y1-8549* = y1-wmut
2b	CCATC TCATC --------- $(CCA)_n$.....CCATC	8	B73 = standard *y1*
2c	CCATC TCATC --------- $(CCA)_n$.....CCATC	6	*Z. mexicana* (PI 384060) ≠ (PI 566681)
3a	-------- TCATC TCATC $(CCA)_n$.....CTATC	11	*Z. huehuetenangensis* (PI 441934) ≠ (Ames 21880)
3b	-------- TCATC TCATC $(CCA)_n$.....CTATC	7	*Z. parviglumis* (PI 331786)
3c	-------- TCATC TCATC $(CCA)_n$.....CTATC	6	*y1-lemon yellow* = Black Mexican Sweet = Strawberry popcorn = Knobless Wilber's Flint ≠ *Z. perennis* (Ames 21875)
3d	-------- TCATC TCATC $(CCA)_n$.....CTATC	3	*Z. diploperennis* (PI 462368) = (Ames 2317) = *Z. perennis* (Ames 21881)
3e	-------- TCATC TCATC $(CCA)_n$.....CTATC	5	*Z. luxurians* (Ames 21876) = (Ames 311282)

[a] =, The sequences presented in Figure 1 are identical; ≠, sequences are not identical.

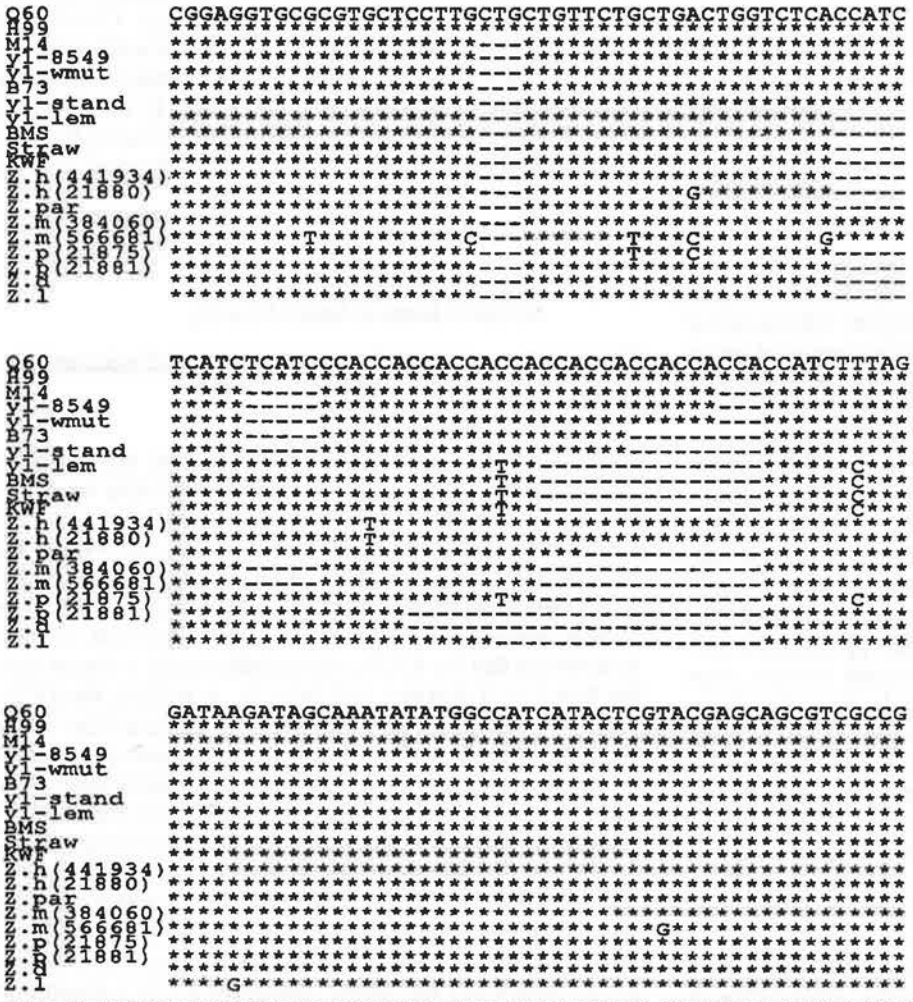


Figure 1. Sequence of the microsatellite–containing region of the *y1* gene of maize and teosinte. Abbreviations are as follows: *Q60,* an allele present in the maize stock designated Q60, which is a hybrid of inbred lines Q66 and Q67; *H99*, *M14* and *B73*, alleles pre sent in inbred lines H99, M14 and B73 respectively; *y1–8549* and *y1–wmut*, alleles described by Robertson and Anderson (J. Hered 52:53–60, 1961); *y1–stand*, standard recessive allele of *y1*, *y1–lem*, *y1–lemon yellow* provided by GF Sprague; *BMS*, Black Mexican Sweet; *Straw*, Strawberry popcorn; *KWF*, Knobless Wilbur's Flint; *Z.h (441934)*, *Z. mays* var. *huehuetenangensis* (PI 441934); *Z.h (21880)*, *Z. mays* var. *huehuetenangensis* (Ames 21880); *Z. par*, *Z. mays* ssp. *parviglumis*; *Z.m (384060)*, *Z. mays* ssp. *mexicana* (PI 384060); *Z.m (566681)*, *Z. mays* ssp. *mexicana* (PI 566681); *Z.p (21875)*, *Z. perennis* (Ames 21875); *Z.p (21881)*, *Z. perennis* (Ames 21881); *Z.d*, *Z. diploperennis*; *Z.l*, *Z. luxurians*. An asterisk indicates the same base as that found in the Q60 allele. A hyphen indicates the base found in the Q60 allele was not present.

it, exhibit a high degree of variability.

Each of the annual teosinte types analyzed in this study can be distinguished based on the sequence of the microsatellite–containing region of *y1* (Figure 1 and Table 1). In addition, sequence polymorphisms that flank the microsatellite region of *y1* allow the two accessions of *Z. mays* ssp. *mexicana* and *Z. mays* var. *huehuetenangensis* to be distinguished (Figure 1 and Table 1). The perennial teosintes *Z. diploperennis* and *Z. perennis* (Ames 21881) were found to exhibit the type 3d organization of the pentanucleotide repeat with 3 (CCA) repeats, which was the least number of repeats observed. However, another accession of *Z. perennis* (i.e., Ames 21875) exhibited type 3c organization of the pentanucleotide repeat containing 6 (CCA) repeats. Therefore, the $(CCA)_n$ repeat number is variable within this *Zea* species. Interestingly, the sequence flanking this region in *Z. perennis* Ames 21875 could be distinguished from that of the *Z. may* ssp. *mays* type 3c sequences by polymorphisms that flank the microsatellite (Figure 1 and Table 1). Further analysis of teosinte will be necessary to determine if the degree of variability in this region of the *y1* gene is sufficient to make it a good marker for studying genetic variability within and among populations of teosinte.

KISHINEV, MOLDOVA
Institute of Genetics

Existence of pollen grains with a pair of morphologically different sperm nuclei as a possible cause of the haploid- inducing capacity in ZMS line

--Bylich, VG and Chalyk, ST

Maternal haploids in maize can be obtained when haploid-inducer lines are used as pollen parent. It is quite logical to assume that pollen contains a factor or factors determining the haploid-inducing capacity.

Enaleeva et al. (XI Intern Symp, Leningrad: 29-30, 1990) studied the events which occur in embryo sacs after pollination with pollen of the haploid-inducer line PEMS-2. This line induces nearly 8% of maternal haploids when it is used as a male parent. The development of either the embryo or central cell was established in some embryo sacs. Some embryo sacs have been discovered where development of the embryo lags behind that of the endosperm. These events are explained by failure in double fertilization. Single fertilization of an egg or of a central cell occurs. The authors supposed that the developing triploid endosperm can stimulate the unfertilized egg to divide and to develop into a haploid embryo.

In our work the pollen of the ZMS haploid-inducer line has been studied. This line induces up to 3 and more percent of maternal haploids. Pollen from MK01 line has been used as the control. Study of the pollen grains has been carried out using an automatic system which includes a light scanning microscope and a computer complex. Fresh mature pollen has been fixed in a mixture of ethanol and acetic acid. Staining has been done after hydrolysis in HCl. A sample containing 3165 pollen grains was analyzed.

It has been established that the pollen grains of the ZMS line can be divided into five types. This division has been carried out according to morphological traits of sperm nuclei. The types are as follows.

1. The pollen grains with two normal well developed sperm nuclei (NN) belong to the first type. The percentage of such pollen grains is 93.50%.

2. The pollen grains with sperm nuclei, still incompletely structured (GG), are included in the second type. Such sperm nuclei differ from the normal ones in their larger size and round shape. Perhaps, they have not undergone complete development and are not ready for fertilization. The percentage of such pollen grains is 0.09%.

3. The third type of pollen grains is characterized by the presence of two sperm nuclei smaller than normal, with configuration nonspecific for maize and increased chromatin density (gg). The presence of such sperm nuclei might result from pollen grain senescence or effects of unfavourable enviroments. Their percentage is 0.09%.

4. The fourth type of pollen grains differs from the above mentioned ones in the presence of two morphologically different sperm nuclei (NG). One sperm nucleus is quite normal for its morphological traits. The other one differs in its larger size and an uncertain round shape that corresponds to the sperm nuclei of the second type of pollen grains. 176 pollen grains belonging to the fourth type have been found, for a percentage of 5.56%.

5. The fifth type embraces the pollen grains which, like ones of the fourth type, have two sperm nuclei differing from each other. One sperm nucleus is quite normal and the other one is significantly smaller in its size and possesses increased chromatin density (Ng). The second sperm nucleus corresponds to those observed in pollen grains belonging to the third type. 24 pollen grains have been discovered and studied belonging to the fifth type, for a percentage of 0.76%.

The fourth and fifth types of pollen grains are of certain interest. We have not observed pollen grains with two different sperm nuclei in the MK01 control line. It may be assumed that the presence of a single normal sperm and a single sperm incapable of fertilization causes induction of maternal haploids. It is still difficult to judge if the pollen grains belonging to both types, NG and Ng, can serve as the haploid-inducing factor or the pollen grains of only one type possess the ability to induce haploids. In any case the total percentage of the pollen grains included in the fourth and fifth types is 6.32% of the pollen from the ZMS line. It exceeded approximately two-fold the maximal percentage of the maternal haploids which the ZMS is capable of inducing. Bearing in mind that Enaleeva et al. (1990) have observed single development either of the embryo or of the endosperm it may be assumed that a normal sperm nucleus of the fourth and fifth types (NG and Ng) can fertilize an egg, or a central cell. This can explain why the frequency of the maternal haploids induced is approximately two-fold less than that of the pollen grains with a single normal sperm nucleus.

We assume that the presence of two morphologically different sperm nuclei may result from their different speed of development. The presence in a pollen grain of one normally developed sperm nucleus and a second sperm nucleus which is either insufficiently well developed or has lost its ability for fertilization because of senescence may be the main cause for induction of maternal haploids in ZMS line.

MADISON, WISCONSIN
University of Wisconsin

Heterochrony and inbreeding

--Abedon, BG and Tracy, WF

We have observed alteration in the timing of the juvenile and/or adult-vegetative phases as a result of recurrent selection for agronomic traits in a number of maize populations (Abedon and Tracy, p. 70 in Abstr. 37th Annu. Maize Genet. Conf., 1995). Correlated responses to selection may be caused by a number of factors including pleiotropy, inbreeding, linkage, and genetic drift. Our objective was to determine the effects of inbreeding on several morphological traits that are used as markers of the timing of juvenile and adult-vegetative phases in order to better interpret results from our recurrent selection studies.

Populations with different levels of inbreeding were generated by selfing 20 plants from the *sugary1* population Minn11P c3, which had previously undergone three cycles of recurrent selection for pseudostarchiness. For this experiment, seed from individual plants was mixed in a balanced bulk for each generation of inbreeding to form populations S1, S2, S3, S4, and S5. These five populations plus the original population (S0) were grown in 1995 in randomized complete blocks over two planting dates (15 May and 13 June) with four replications per planting date. Three-row plots were overplanted and thinned to 15 plants per row. Data were collected on ten plants from the middle row of each plot. The following developmental traits were evaluated: first leaf with adult wax, last leaf with juvenile wax, last node with adventitious roots, tiller number, first leaf with pubescence, and ear leaf and total leaf number. First leaf with adult wax was evaluated only in the early planting date. Several traits were also examined that are known to exhibit inbreeding depression, including: leaf length, leaf width, days to 50% anthesis and silking, ear height, and plant height. Data were analyzed by analysis of variance and LSD ($p<0.05$) was used for means comparisons.

Inbreeding depression was evident for all traits known to respond to inbreeding. Leaf length, leaf width, ear height, and plant height decreased significantly, and flowering time was significantly later, between the S0 and S5 populations (Table 1). Of the traits associated with phase change, only tiller number and total leaf number decreased significantly between the S0 and S5 populations (Table 2). Ear leaf number and most developmental traits associated with the timing of vegetative phases (first leaf with adult wax, last leaf with juvenile wax, first leaf with pubescence, and last node with adventitious roots) were unaffected by inbreeding with no significant differences between most populations, particularly S0 and S5 (Table 2).

Table 1. Agronomic trait means at six levels of inbreeding (S0-S5), pooled over blocks and planting dates.

Inbreeding generation	Agronomic trait					
	Leaf length (cm)	Leaf width (cm)	Ear height (cm)	Plant height (cm)	Days to 50% anthesis	Days to 50% silking
S0	84.6	9.5	91.5	187.7	72.1	74.0
S1	76.6	7.8	76.4	164.3	72.5	74.6
S2	75.9	7.7	77.8	163.8	74.0	76.4
S3	73.8	7.4	79.8	157.7	75.0	77.4
S4	71.9	7.4	76.6	154.1	75.6	77.8
S5	71.9	7.6	72.2	154.5	76.3	78.5
LSD($p<0.05$)	2.4	1.2	7.4	9.6	0.6	0.7

Table 2. Developmental trait means at six levels of inbreeding (S0-S5), pooled over blocks and planting dates.

Inbreeding generation	Developmental trait						
	First adult wax	Last juvenile wax	First leaf with hairs	Tiller #	Last node with adv. roots	Leaves below ear	Total leaf #
S0	6.9	10.0	5.8	1.8	6.8	12.1	18.0
S1	7.1	9.7	5.7	1.5	7.0	11.5	17.1
S2	7.0	10.0	5.9	1.5	6.9	11.8	17.1
S3	7.4	9.9	6.0	1.6	7.2	11.8	17.0
S4	6.9	9.1	5.8	1.0	6.8	11.5	17.0
S5	7.2	9.7	6.0	1.1	7.0	11.8	17.4
LSD ($p<0.05$)	0.4	0.6	0.3	0.4	0.3	0.5	0.5

These results indicate that most morphological markers of the juvenile (last leaf with juvenile wax, last node with adventitious roots) and adult (first leaf with adult wax, first leaf with pubescence) vegetative phases are not affected by inbreeding depression, suggesting that these traits are governed primarily by additive gene action. Tiller number, which has been used as a marker of the juvenile-vegetative phase in studies of heterochronic mutants, was significantly affected by inbreeding depression, suggesting that dominant gene action governs this trait. Tiller number may not be a useful heterochronic marker in wild type populations of maize. In a diallel of six maize populations, Revilla et al. (p. 84 in Abstr. 87th ASA Meeting, 1995) found a significant ($p<0.05$) correlation among last leaf with juvenile wax, first leaf with adult wax, and last node with adventitious roots (last leaf with pubescence was not evaluated in that study), but no correlation between any of these traits and tiller number. Together, these results suggest that the timing of vegetative phase change in Minn11P c3 is governed primarily by additive gene action, although a dominance component may exist. This agrees with Revilla et al. who found significant ($p<0.05$) general combining ability for these same traits while specific combining ability was not significant.

MADISON, WISCONSIN
University of Wisconsin
COLUMBIA, MISSOURI
USDA-ARS

Alteration in the timing of vegetative phase change associated with nine cycles of divergent selection for rind penetrometer resistance in Missouri Stiff Stalk Synthetic

--Abedon, BG; Darrah, LL and Tracy, WF

Vegetative development in maize can be divided into juvenile (basal) and adult (distal) phases, each with distinct morphology and physiology (Poethig, Science 250:923-930). Juvenile leaves lack trichomes and are covered with an epicuticular waxy bloom, giving the leaves a grayish appearance. At juvenile nodes, adventitious roots are produced and axillary buds develop into tillers. Adult leaves have three types of trichomes (macrohairs, bicellular, and prickle) and are covered with glossy wax, which gives them a green appearance. Adult nodes do not produce adventitious roots. Axillary buds from adult nodes either develop into ears or are suppressed. The existence of heterochronic mutants (*Corngrass1*, (*Cg1*), *glossy15* (*gl15*), *Teopod1*, *Teopod2*), which alter the timing of vegetative phases, suggests that heterochrony has a strong genetic basis in maize. Studies involving these mutants

Table 1. Developmental trait means in MoSSS divergently selected for rind penetrometer resistance.

	Developmental trait									
Cycle	First adult wax	Last juv. wax	Leaf hair	Tiller #	Adv. roots	Ear leaf #	Leaf #	Ear ht. (cm)	Plant ht. (cm)	50% silk (d)
C9high	6.4	7.9	5.3	0.1	7.3	12.3	18.8	126.6	195.7	75.0
C4high	6.5	8.0	5.2	0.1	6.8	13.2	19.3	109.5	210.8	76.0
C0	7.1	9.3	6.5	0.4	6.8	14.8	20.4	188.1	254.5	77.3
C4low	6.7	8.7	6.6	0.6	6.9	14.6	23.4	135.4	221.4	77.3
C9low	7.1	11.3	7.1	0.8	7.0	15.1	20.4	132.0	201.2	76.0
LSD (p£.05)	0.2	3.2	0.4	0.3	0.6	0.4	4.7	51.6	16.2	1.5

indicate that the juvenile and adult-vegetative phases are regulated independently of each other (and of reproductive initiation) but overlap in a transition zone that normally occurs between leaves five and eight in most US field corn backgrounds.

Variation in the timing of developmental phases (heterochrony) has adaptive value and evolutionary importance in a number of plant species (Lord and Hill, p. 47-70 in Development as an Evolutionary Process, Alan R. Liss, New York, 1987). Until recently, there was little evidence of an adaptive value for heterochrony in maize. Abedon and Tracy (J. Hered., in press) found that adult resistance to common rust (*Puccinia sorghi* Schw.) and European corn borer (*Ostrinia nubilalis* Hubn.) is delayed in *Cg1*, which has an extended juvenile-vegetative phase. Passas and Poethig (p. 83 in Abstr. 37th Annu. Maize Genet. Conf.) found that an accelerated transition to an adult epidermis in leaves of *gl15* mutants resulted in increased resistance to European corn borer relative to wild type sibs. These results suggest that heterochrony may have adaptive value in normal populations of maize and be a source of variability for agronomic performance.

Stalk lodging can cause substantial yield losses in maize production fields. Efforts to develop stalk lodging resistant germplasm at the University of Missouri have focused on recurrent selection for rind penetrometer resistance (RPR) in Missouri Stiff Stalk Synthetic (MoSSS). RPR is measured at the middle of the internode below the ear node. Two populations, divergently selected for high and low RPR, have been developed. Previous studies indicate that selection for high and low RPR has resulted in increased and reduced stalk lodging resistance, respectively. Our objectives were to investigate heterochrony and other developmental changes associated with nine cycles of divergent selection for RPR in MoSSS.

In 1995, five cycles (C9high, C4high, C0, C4low, C9low) were grown in randomized complete blocks with three replications at the West Madison Agricultural Experiment Station, Madison, WI. Two row plots were overplanted and thinned to 15 plants per row. Data were collected on 20 plants per plot. The duration of the juvenile-vegetative phase was determined based on the last leaf with juvenile wax, last node with adventitious roots, and tiller number. Ear leaf and total leaf number were also determined because some heterochronic mutants that affect the duration of the juvenile-vegetative phase also affect leaf number. The timing of adult-vegetative phase initiation was determined based on the first leaf with adult wax and first leaf with pubescence. The timing of reproductive phase initiation was estimated based on total leaf number and days to 50% anthesis. Ear height, plant height, and days to 50% silk emergence were also recorded. Data were analyzed by analysis of variance (data not shown) and LSD ($p<0.05$) was used for means comparisons.

Significant differences among cycles were observed for many traits (Table 1). Last leaf with juvenile wax showed an increasing trend while tiller number increased significantly between C9high and C9low, indicating that selection for high RPR truncated the juvenile phase while selection for low RPR elongated the juvenile phase. First leaf with adult wax increased significantly between C9high and C0 but did not change between C0 and C9low. First leaf with pubescence increased significantly from C9high to C9low. These results indicate the selection for high RPR resulted in a faster initiation of the adult-vegetative phase, while selection for low RPR delayed the onset of pubescence without affecting the first leaf with adult wax (suggesting that these traits are regulated independently).

Variation in the timing of vegetative phases was not associated with changes in the timing of reproductive initiation since total leaf number was not significantly different for any cycle (although a trend toward lower total leaf number was observed between C0 and C9high). Ear leaf number decreased from C0 to C9high, indicating that selection for high RPR resulted in a shift of ear placement downward on the plant. Ear leaf number was unchanged between C0 and C9low. Flowering time became earlier in both directions of selection. This may have been an artifact of the recurrent selection program since recombination was stopped in each cycle before the latest plants had flowered. These results indicate that no relationship exists between the timing of vegetative and reproductive phases in these populations. Ear and plant height decreased significantly in both directions of selection while no significant difference was observed for last node with adventitious roots.

The heterochronic effects due to selection that were observed in this study suggest that a faster transition to the adult-vegetative phase is associated with increased RPR in MoSSS. Physiological differences between vegetative phases may contribute to variation in stalk strength. We plan to replicate this experiment in 1996 in order to confirm these results. Further investigations are also being initiated in order to determine the relationship between heterochrony and agronomic traits in other populations.

MEXICO CITY, MEXICO
CIMMYT

Dual ancestry of *Zea*: Sequence evidence at the *adh1*, *adh2*, *sh1* and *o2* loci

--Bird, RMcK

When last year (MNL 69:100-101) I suggested that comparisons of gene sequences should allow one to test models of evolution and domestication, I had forgotten a paper I read a decade ago, and I had yet to read several more recent papers, all revealing unusual variance within species of *Zea*. Werr et al. (EMBO J. 4:1373-1380, 1985) noted such great difference between two maize alleles of the *sh1* locus that they estimated that the two alleles reflected millions of years of separate evolution. They found 16 silent (synonymous 3rd codon) base differences (3.0%) among 540 silent positions in 2100 bp of exon DNA that they could compare in genomic and cDNA sequences from two maize lines. They also found 10 base differences (3.7%) in 270 bp of 3'-untranslated DNA. Using the evolutionary rate of 5.37 base substitutions per 1000 silent positions per million years determined by Miyata et al. (J. Mol. Evol. 19:28-35, 1982) for several animal genes, these indicate that the two alleles separated 3.0 million years ago (Mya) (evolutionary distance = (26/810) / (5.37 / (1000 x 1 My)); age of separation = 1/2 x distance).

Gaut and Clegg (PNAS 88:2060-2064, 1991) estimated that the *adh1-1S* and *adh1-1F* alleles of maize separated ≈2.6 Mya calibrated on the separation of rice from other grasses at 50 Mya, separation of *Pennisetum* from *Sorghum* and *Zea* at 25 Mya, and a mean coding region substitution rate of 3.63×10^{-9} per site per year. Their estimation of the *Pennisetum-Zea* substitution rate at silent exon sites was 7.90×10^{-9} per site per year over the 25 million years. Later they reported (PNAS 90:5095-5099, 1993) on 8 alleles from *Z. mays, Z. diploperennis* and *Z. luxurians*, finding 81 polymorphic nucleotide sites in 1483 silent positions and at these sites up to 46 nucleotide differences (between the *adh1-Pollo* allele and the *adh1+1S, adh1+Coroico* and *Zea luxurians* alleles). This can be used to estimate a maximum separation for these alleles of 2.0 Mya, based on the 7.90×10^{-9} /site/year silent site substitution rate (=(46/1483) / (7.90 / (1000 x 1 My)) x 1/2).

Based on the same rate, Goloubinoff et al. (PNAS 90:1997-2001, 1993) concluded that polymorphism in a 315 ±15 bp segment of the *adh2* locus indicates that "the gene pool of maize must be at least several million years old" (p. 2000). They included a wide range of materials in their study--a tripsacum, several teosintes and modern and archaeological maize. A further analysis of their data (below) provides yet another conclusion about the evolution of *Zea*. And, most recently, Hartings et al. (MNL 69:18-19) calculated two ages of separation for alleles at the *o2* locus: 1.06 and 1.86 Mya, based on Kimura's neutral nucleotide substitution rate of 5×10^{-9} per site per year.

These estimates, of course, are subject to redefinition of the times when rice separated from other grasses, when *Pennisetum* separated from *Sorghum* and *Zea*, and adjustment of the synonymous substitution and other silent rates. Also, given that these great differences within the maize and the several teosinte gene pools are due to introgression between two very different ancestors (below), these are *minimal* estimates in large part because recombination within the loci will have created many alleles with reduced differences over time. I have found no reports of divergence between species of *Zea* on the level of thousands of years.

This variation may be explained by the Intersectional Introgression Model of maize origin (Bird, MNL 69:100-101, 1995), that the two sections of *Zea* separated for several million years and, within the last 5000 years, were involved in a hybridization and mutual introgression between a domesticated pure maize and a wild teosinte. This is more parsimonious (straightforward, simple) than proposing that there were multiple domestications of very different *Zea* species, which have since combined into one species, or that there are extremely high base substitution rates in maize *and* teosinte, or that several species of *Zea* are separately maintaining shared ancestral polymorphism.

I would like to demonstrate further evidence that two long-separated ancestors were involved. Figure 1 is the result of taking the partial sequences of alleles of the *adh2* locus presented in Figure 3 of Goloubinoff et al., deleting all portions with no or one shift, placing only the differences in a table, sorting the table to place similar sequences together and dissimilar ones far apart, and marking with either light or dark background those "shifts" which belong to one of two very different "linked sets". Thus, for nucleotides 56-103, the g-0000-g-t-gct-t-c linked set (Set T), from alleles *9A* and *9B* of *mexicana* teosinte, *12B* of *Z. luxurians*, *4* of Tabloncillo, and *1A* and *1B* of Northern Flint, is shaded darkly, while the a-agct-a-c-000-c-g set (Set B), from alleles *7A* of the Cabuza (Chile) archaeological kernels and *BF* of a Corn Belt inbred, is shaded lightly. For this zone of the locus, the other alleles are mostly recombinations of the two opposite linked sets. There is very little possibility that such linked sets are due to fairly recent independent mutational events. Rather they are most likely the result of the accumulation of shifts over millions of years in two separate taxa, followed by a relatively recent mutual introgression and recombination of the two sequences. On the other hand, the shift to "t" at nucleotide 75 in allele *8A* and to "c" at nucleotide 79 in alleles *7B* and *8B* could be independent events. Possibly the identical sequences of alleles *11B* of *Z. diploperennis* and *6* of the charred Junín (Peru) cobs and kernels represent a third pattern and ancestor. Here the 56-103 set is g-agct-a-c-gct-t-g, and nucleotides 30, 52 and 125 are often "g" in these and alleles *12A* of *Z. luxurians* and *5* of Kculli. However, this pattern can be explained as a subset derived from the introgression of two ancestors plus early independent change. What the two ancestors supplying sets T and B might be is not revealed here where a relatively small sample has been studied.

There also seems to be some linkage of the T and B sets to numbers of repeats in the GA microsatellite region (nucleotides 10-35 upstream of the transcription start site): (GA)12-13 in alleles *9A*, *12B* and *1A*, (GA)4 in alleles *7A* and *10A*, and even (GA)8 in alleles *6* and *11B*. At least in this microsatellite zone the polymorphism seems conservative.

Another, perhaps as interesting, feature is the remarkably high yet parallel polymorphism in all the species studied. Seven shifts separate the two alleles of the *Z. luxurians* sample, ten separate the *parviglumis* alleles, and 11 separate two of the alleles from the archaeological Cabuza kernels. But the variation runs in parallel such that an allele from *mexicana* teosinte is identical to one from *Z. luxurians*, and one from *Z. diploperennis* is identical to that from the 440 year-old Junín cobs and kernels! As Goloubinoff et al. say (p. 2001), "a phylogenetic analysis [of these

position:		-10-35	-9	30	32	51	52	56	75-78	79	81	92-94	100	103	125	127	158	185	213
				> exon 1 <												> exon 2			-- >
STATE: top		(ga)13	g	c	g	t	c	g	0000	g	t	gct	t	c	c	ct	g*	g*	g
bottom		(ga)4	t	"	"	c	"	a	agct	a	c	000	c	g	"	"	a	a	a
other		(ga)5-9	c	g	a		g		t	c					g	00			
	allele																		
Z mex mexicana	9A	13	g	c	g	t	c	g	0000	g	t	gct	t	c	c	ct	g	g	g
Z luxurians	12B	13	g	c	g	t	c	g	0000	g	t	gct	t	c	c	ct	g	g	g
Northern Flint	1A	12	g	c	g	t	c	g	0000	g	t	gct	t	c	c	ct	g	g	a
Z mex parviglum	10B	5	g	c	g	c	c	g	0000	a	t	gct	t	c	c	ct	g	g	g
Z mex mexicana	9B	9	t	c	g	c	c	g	0000	g	t	gct	t	c	c	ct	g	g	g
Cabuza(a)	7C	5	g	c	g	t	c	g	0000	g	t	gct	t	g	**g**	ct	g	a	g
Z diploperennis	11A	6	g	c	**a**	c	c	g	0000	g	t	gct	t	g	**g**	ct	g	g	g
Northern Flint	1B	4	t	c	g	c	c	g	0000	g	t	gct	t	c	c	ct	g	g	a
Tabloncillo	4	4	t	c	g	c	c	g	0000	g	t	gct	t	c	c	ct	g	a	a
Confite Morocho	3	4	t	c	g	c	c	a	0000	g	t	gct	t	c	c	ct	g	a	a
Cabuza(a)	7B	4	t	c	g	c	c	g	agct	**c**	c	gct	t	c	c	ct	g	g	a
Los Gavilanes(a)	8A	6-7°	g	c	g	c	c	g	**t**	a	c	000	c	g	c	**00**	g	g	g
Trip pilosum	TP	7†	**c**	c	**a**	c	c	g	0000	a	c	000	t	g	c	**00**	g	g	g
Z luxurians	12A	6	g	c	**a**	c	c	g	agct	a	c	gct	t	g	**g**	ct	g	g	g
Kculli	5	7	g	c	g	c	**g**	g	agct	a	c	gct	t	g	**g**	ct	g	g	g
Junín(a)	6	8	g	**g**	g	c	**g**	g	agct	a	c	gct	t	g	**g**	ct	g	g	g
Z diploperennis	11B	8	g	**g**	g	c	**g**	g	agct	a	c	gct	t	g	**g**	ct	g	g	g
Los Gavilanes(a)	8B	5-7°	g	c	g	**c**	c	a	agct	**c**	c	000	c	g	c	ct	a	a	a
Corn Belt inbred	BF	7†	g	c	g	c	c	a	agct	a	c	000	c	g	c	ct	a	a	a
Z mex parviglum	10A	4	t	c	g	**c**	c	a	agct	g	c	000	c	g	c	ct	a	a	a
Cabuza(a)	7A	4	t	c	g	**c**	c	a	agct	a	c	000	c	g	c	ct	a	a	a

* a silent nucleotide shift.
(a) indented: archaeological.
° see Goloubinoff et al. Fig 2.
† in Tripsacum and BF also a GA>AA change.

Figure 1. Non-unique nucleotide shifts noted in 13 modern and ancient *Zea* and *Tripsacum* materials by Goloubinoff, Pääbo and Wilson (1993).

data] yields no evidence in support of the notion that modern races of maize emerged from a single common ancestor, such as a specific line of *Z. mays parviglumis* or *Z. mays mexicana.*" However, the II Model does explain the evidence, though perhaps needing to be expanded to include *all* the *Zea* species as products of the introgression of the last four millennia.

The definition of experimental reference sets for *Zea*
--Bird, RMcK

Part of a new project at CIMMYT, in which we are characterizing maize genebank accessions through DNA fingerprinting, will be the selection of several sets of materials to be made available for a wide range of studies as references or points of comparison. We feel there is need for such sets--much research has been based on materials chosen without regard for comparability to other studies or repeatability using the same stocks. How could one compare or even repeat studies if one study were of isozyme differences between maize and teosinte, the "teosinte" being a few landrace samples of *Z. diploperennis* and *Z. mexicana* from a U.S. genebank and the maize being from ears in a private collection, and the other study were of RFLPs, the teosinte being an accession of *Z. luxurians* from CIMMYT and the maize being a set of Peruvian lines supplied by a geneticist? Yet many studies are based upon such arrays of materials.

Previously I defined two reference sets -- 12 maize accessions in one, the other with seven teosinte accessions (Maize for Biological Research, W. F. Sheridan, ed., pp 341-350, 1982). Entries

were listed in order of "utility". The criteria for selection were distinctiveness using current information, lack of evidence of inter-racial introgression, availability in a public genebank, and, to some degree, adaptation to U.S. conditions. Researchers at Pioneer Hi-Bred International have studied 30 inbred lines in many ways (Smith et al., Maydica, 36:213-226, 1991 and three earlier papers). These form a reference set for Pioneer use, but several public lines, Mo17, B73 and A632, have been included, so these three can be compared using morphological, agronomic, isozyme and RFLP data, a small reference set.

The criteria above are those being used here except we will pay less attention to U.S. adaptation and will look for use of the entry in prior comparative studies. One set will sample the overall variation of the genus *Zea* increasing the 7-teosinte set to ca. 12 members. The second set may include the 12 maize races in the 1982 set, though checked for appropriateness of the member accessions and availability at CIMMYT. Another set might be inbreds such as the U.S. public lines listed above plus some CIMMYT, European, African and/or Asian inbred lines. Here an added criterion is the sampling of known and suspected heterotic groups.

Phyllotaxy of maize

--Bird, RMcK

In yet another way maize is different from the usual plant -- the phyllotaxy of the alicoles of its ears does not follow the Fibonacci series. The leaves of most higher plants fall into 2, 3, 5, 8, 13, 21, etc. ranks along the stem where there is one leaf per node or 4, 6, 8, + ranks for opposite or whorled phyllotaxies. Maize ears, however, have ranks (stachys) of every number from 3 to 16 or more, switching, as rank numbers increase, between whorled, even-numbers of ranks and spiral, odd-numbers of ranks with single alicoles per node.

By clearing the glumes from sweet-corn cobs after dinner, marking the spikelet pairs and trying different spiral patterns, I found one rule governed all: alicoles two ranks apart are linked in a spiral or a whorl. Thus, on a cob with seven ranks (14 kernel rows), one follows the rule in a spiral going twice around the cob passing through seven contiguous nodes to reach the next alicole in the same rank, a "2/7" phyllotaxy. On a cob with eight ranks, one finds alicoles two ranks apart are linked in a whorl of four, and the next whorl of four is offset by one rank. I have never seen a 3/8 phyllotaxy in maize.

Of course, this is not the full story. While cobs with even numbers of ranks have ranks which parallel the axis, those with odd numbers have slightly spiraled ranks meaning that a phyllotaxy such as 2/7 really needs to be defined by a number like 21/77. But that's another study, as is the morphogenetic basis of this phenomenon.

MEXICO D.F., MEXICO
ORSTOM and CIMMYT

Studies on the genetic control of apomixis in *Tripsacum*

--Grimanelli, D; Leblanc, O; Perotti, E; González-de-León, D and Savidan, Y

Apomixis in higher plants refers to several mechanisms of asexual reproduction through seeds. In all cases, apomictic processes bypass both meiosis and egg cell fertilization, producing offspring which are exact genetic replicas of the mother plant. In *Tripsacum* (x=18), the closest apomictic relative of corn, all polyploids reproduce through the diplosporous type of apomixis (Leblanc et al., Am. J. Bot. 82:57, 1995). Diplospory results from meiotic failure in megasporocytes that directly develop into mature unreduced female gametophytes through three or more mitoses. Typically, it is a facultative phenomenon, and an apomictic plant usually produces both asexual (apomeiotic) and sexual (meiotic) embryos. Apomixis in *Tripsacum*, as in other apomictic species studied, has been thought to be controlled by one dominant allele.

As part of an effort to transfer apomixis to maize from *Tripsacum*, we recently reported the identification of RFLP markers linked with diplospory in a maize-*Tripsacum* F1 population (Leblanc et al., TAG 90:1198, 1995). We used the markers to analyze various generations of maize-*Tripsacum* hybrids and backcross derivatives and define a model for the genetic control and inheritance of diplosporous reproduction. Here we report some results and propose a transposon-tagging-based strategy for further studies of apomixis in *Tripsacum*.

As expected, maize and *Tripsacum* genomes are significantly colinear. This is obviously of great interest for mapping *Tripsacum*: we can switch from anonymous mapping to comparative mapping, and screening for a specific zone in the *Tripsacum* genome can be based efficiently on maize mapping information.

An important feature of apomixis is its relation to polyploidy: except for rare exceptions, apomicts are polyploids, while sexuality in the same species, if known, is usually found at lower ploidy levels. Two hypotheses have been proposed regarding the mechanism thought to prevent apomixis in diploid genotypes. The first one (Nogler, Bot. Helv. 92:13, 1982) assumes that the allele or alleles responsible for the apomictic development are not transmitted through haploid gametes. Therefore, apomixis would not be recovered in diploid plants. The second one proposes a dosage effect in which diploid plants do not express apomixis, although the corresponding alleles may be transmitted (Mogie, Biol. J. Lin. Soc. 35:127, 1988; Noirot, J. Evol. Biol. 6:95, 1993). Our results (Grimanelli et al., manuscript in preparation, summarized in Fig. 1) suggest that the gene(s) controlling apomixis in *Tripsacum* are linked with a segregation-distorter-type allele promoting the elimination of the "apomixis allele(s)" when transmitted through haploid gametes. This would explain why apomixis is not recovered in diploid plants, and has strong implications for transferring apomixis to diploid crops.

Furthermore, a significant difference appeared when we looked at the segregation of four RFLP loci surrounding the gene of interest in both the apomictic tetraploid and the sexual diploid *Tripsacum*. It seems that recombination is restricted at the tetraploid (apomictic) level as opposed to both the diploid (sexual) in *Tripsacum* and maize, as represented in their RFLP maps.

Because the specific chromosome segment shows a restricted level of recombination, the classical model of monogenic inheritance for apomixis probably needs more careful analysis: whatever the number of genes involved, they surely behave as a single locus in segregating populations. This observation is consistent with the existence of a segregation distorter linked with the "apomixis allele(s)". Meiotic drive systems can usually be associated with chromosomal structural modifications, such as inversions, that locally restrict recombination, further creating linkage disequilibrium between the distorter allele, the target loci, and eventually

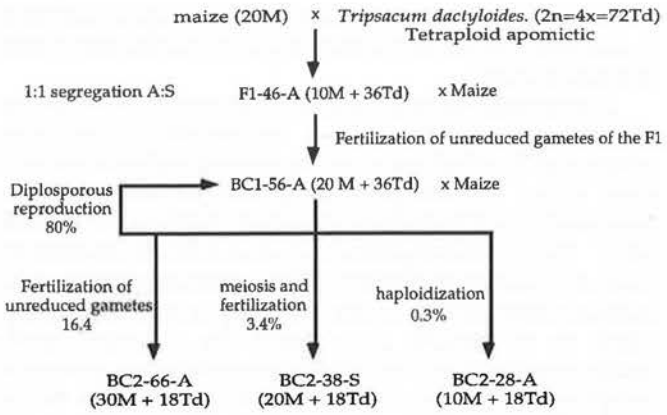


Figure 1. Chromosome numbers, constitution and modes of reproduction in maize-*Tripsacum* hybrids and some backcross derivatives (A: apomictic, S: sexual, M: maize, Td: *Tripsacum dactyloides* x=18). Under the hypothesis of Mendelian inheritance of apomixis, the character is expected to segregate 1:1 in the BC2-38 plants. Of ca. 6000 progenies we produced from the facultative apomictic BC1 plants, 218 BC2-38 plants originated from the sexual development of embryos, but none was apomictic. By contrast, rare dihaploid plants were produced through parthenogenetic development of such reduced gametes, and were found to be apomicts. Segregation of the diagnostic bands for mode of reproduction is consistent with the expression of the trait. The segregation indicates a strong selection against the apomictic allele(s). The analysis of further generations (data not shown) suggests that the distortion is best explained by the presence of a segregation distorter allele, linked with apomixis.

modifier alleles (for a review of segregation distorters, Lyttle, Ann. Rev. Gen. 25:511, 1991).

Several on-going programs are aiming at the isolation of the genetic system responsible for apomixis, and its transfer to crops. The usual hypothesis is that a single allele could account for the whole developmental process of apomictic reproduction. Our results do not claim the existence of several genes, but at least suggest the possibility of a cluster of linked loci. To determine the number of genes controlling apomixis, as well as potentially to isolate the corresponding alleles, we started a transposon tagging experiment. Apomictic maize-*Tripsacum* dihaploids (10 chromosomes of maize + 18 chromosomes of *Tripsacum*) were crossed to *Mutator* lines, kindly provided by Mike Freeling. Because apomixis is essentially a facultative phenomenon, most of the progenies are clones of the mother plants, but about 10% result from fertilization of unreduced gametes. Those plants consequently have 20 chromosomes of maize plus 18 of *Tripsacum*, and are both apomictic and *Mu* active. We are presently checking the level of *Mu* transposition.

This transposon tagging experiment has three major objectives. First, we expect to obtain evidence for the existence of regulatory activities: while the plants remain perfectly apomictic, the level of expression of the trait (level of facultativeness) may vary, due to disruptions of some regulatory genes. Second, from a qualitative point of view, we may disrupt apomictic development totally or partially, and therefore get information concerning the number of genes involved. A major target in that case is the segregation distorter allele, since it represents a strong limitation for the transfer of apomixis to maize. Finally, we should be able to analyse the behavior of *Mu* when transmitted through ameiotic gametes.

MILAN, ITALY
DIFCA* and Dept. of Genetics and Microbiology**
University of Milan

The dappled mutants affect endosperm development

--Castiglioni**, PF; Allegra**, D; Hoxha*, M; Todesco **, G; Dolfini**, S and Gavazzi*, G

While screening for mutants affecting aleurone pigmentation we isolated several independent mutants exhibiting a mutable aleurone pattern. The mutants are referred to as *Dap* (*d*efective aleurone *p*igmentation) and their origin, segregation values and kernel weight are given in Table 1. Two additional isolates, *Dap*-9* and *Dap*-10*, have not yet been analyzed.

Table 1. *Dappled* mutants description.

Mutant symbol	Origin	Mutant segregation Dap%	S.E.	n	Mutant weight (%WT)
Dap-1*	EMS	43.1	1.0	5053	58.4
Dap-2*	EMS	40.9	2.3	922	55.8
Dap-3*	EMS	43.9	1.2	1779	63.0
Dap-4*	UV	36.3	6.1	1008	75.2
Dap-5*	XRAYS	38.7	1.9	1143	70.7
Dap-6*	EMS	47.8	2.1	2174	40.8

The phenotype of *Dap* seeds consists of purple tissue of variable size and shape on a yellow background, as previously described by Stinard and Robertson (MNL 61:7-9, 1987). In addition, opaque white sectors are frequently observed on the yellow background. *Dap*-6* can be easily distinguished from the other isolates, since it conditions dark purple sectors on a weak red background as if pelargonidin rather than cyanidin is accumulating. All six *Dap* mutants are associated with a significant reduction in seed size, leading sometimes to extremely defective seeds.

The segregation values reported in Table 1 are observed when *Dap/+* females are crossed to purple aleurone males. In fact, a common feature shared by all *Dap* isolates is the observation that crosses in which *Dap* plants are used as females segregate for colored and dappled seeds, while crosses in which *Dap* plants are used as males give only colored seeds. These segregations disclose a significant shortage of the mutant over the expected one-half and a dominant expression of the mutant over the wild-type allele.

Although dappled is not expressed in male outcrosses, it is male transmissibile in the case of *Dap*-3*, *Dap*-4* and *Dap*-6*, but not of *Dap*-1*, *Dap*-2* and *Dap*-5* isolates. Its recovery, however, is erratic and lower than the expected one-half (compare results obtained in 1994 and 1995 in Table 2). So, when *Dap/+* plants enter the cross as males, in three cases *Dap* gametes contributing to the endosperm formation are apparently selected against; on the contrary, in the other three isolates male transmission leads to gene silencing in the endosperm, since the

Table 2. Male transmission of *Dap* as determined in the progeny ears from outcrosses of heterozygous dappled males to purple aleurone females. Results obtained in summer 1994 and 1995 are presented separately.

Mutant symbol	Male *Dap* Transmission (%) in : 1994	n(1)	1995	n(1)
Dap-1*	none	53	none	61
Dap-2*	none	31	ND(2)	
Dap-3*	44.4	54	18.2	66
Dap-4*	34.2	38	14.7	34
Dap-5*	none	49	none	70
Dap-6*	16.6	78	none	58

(1) no. ears examined
(2) ND : Not Determined

mutant is recovered and expressed again in the next generation, if transmitted through the female.

The reduced frequency of *Dap* seeds recovered in both male and female outcrosses and the lack of recovery of homozygous *Dap* seeds in the selfed progeny of *Dap/+* heterozygous plants could be the result of a gametophytic selection against *Dap* alleles operating more drastically in the male versus female gametophytic generation. If selection is mediated by chromosome breaks, pollen sterility should be observed and indeed the field analysis of plants heterozygous for *Dap*-1*, *Dap*-2*, *Dap*-3* and *Dap*-6* confirms the expectation (estimated pollen sterility of 30% or more).

To inquire about *Dap* mutants and their transmission, it would be useful to establish their chromosomal location. We first attempted to obtain this information with *Dap*-1* and *Dap*-2*, because we had some indication of their linkage with *sh1*, a marker of the short arm of chromosome 9. The recombination values of the three point testcross of heterozygous *Dap Bz Sh / + bz sh* females to homozygous *+ bz sh* males are 17.7 ± 1.7 for *Dap-bz* and 2.9 ± .7 for *bz-sh* (n = 490). To establish if *Dap* is proximal or distal to the *sh-bz* segment a three point testcross was done with *bz* and *wx* (*bz-wx* distance 25 cM). The results place *Dap* proximal to *bz*, leaving still undefined the orientation of *Dap* in regard to *wx*. Assuming *Dap* is distal to *wx* the recombination values of the *bz wx + / Bz Wx Dap* testcross are 18.0 ± 1.6 for *bz-wx* and 2.1 ± .6 for *wx-Dap* respectively (n= 606). *Dap*-2* also appears to be located on the short arm of chromosome 9 (*Dap*-2-sh* recombination value : 18.3 ± 1.2; n = 1000), suggesting a possible allelism between the two mutants.

To test the allelism of *Dap* mutants, one can cross different *Dap* isolates inter se, select dappled seeds in the F1 and outcross F1 females to purple aleurone stock. One-third of the ears so obtained should be homozygous *Dap* in the case of allelism or segregate *Dap* vs. colored seed in a 3:1 ratio in the case of non allelism and independent assortment; if the two *Dap* are linked, one-third of the progeny ears should segregate a majority of *Dap* seeds (75% or more, depending on the linkage intensity).

Out of seven outcrosses of *Dap*-1/Dap*-3* F1 females, five segregate *Dap* and colored seeds with a *Dap* shortage (37%), while two ears show an excess of *Dap* seeds (66.9%), a result expected in case of non-allelism. Progeny ears of *Dap*-1/Dap*-4* female outcrosses segregate *Dap* and colored seeds with a shortage of *Dap*. This unexpected result could indicate allelism, if we assume that *Dap*-1/Dap*-4* seeds are not viable. For a cytological characterization of the mutant, different approaches were followed. Histological sections were obtained from seeds of different *Dap* mutants, at 25 days after pollination and after an exposure to light for 48 hours. The presence of a continuous aleurone layer was observed in all mutants, demonstrating that the lack of anthocyanin accumulation in colorless sectors is not the consequence of the absence of aleurone cells in the depigmented areas. The same conclusion was reached by scanning electron microscopic analysis on the *Dap*-1* mutant.

In order to correlate cellular morphology with presence or absence of pigments, fixation and histological procedures were performed preserving anthocyanins in the aleurone cells. Colorless aleurone cells show an abnormal morphology, if compared to pigmented cells. In general, colorless cells appear irregular in morphology, smaller and flatter than normal ones and occasionally binucleate. More than one layer of aleurone cells may be present and sub-aleuronic cells are irregular and disconnected. The defect is confined to cells of the endosperm, since histological sections of mature seed embryos do not reveal any difference between normal and mutant seeds.

To investigate the lack of pigment in aleurone cells, in situ hybridization experiments were set up, with the aim to check for the presence of *A1* mRNA in colored and colorless regions of the aleurone. *A1* is a structural gene coding for dihydroquercetin reductase, an enzyme of the pathway which leads to anthocyanin accumulation. The experiments show a correlation in all *Dap* mutants between the presence of *A1* mRNA and the presence of anthocyanins in colored aleurone cells. On the other hand, in cells devoid of pigments, the *A1* transcript seems absent (Fig. 1). These results would demonstrate that the anthocyanin biosynthetic pathway in mutant cells is blocked and could help in further studies on this mutation.

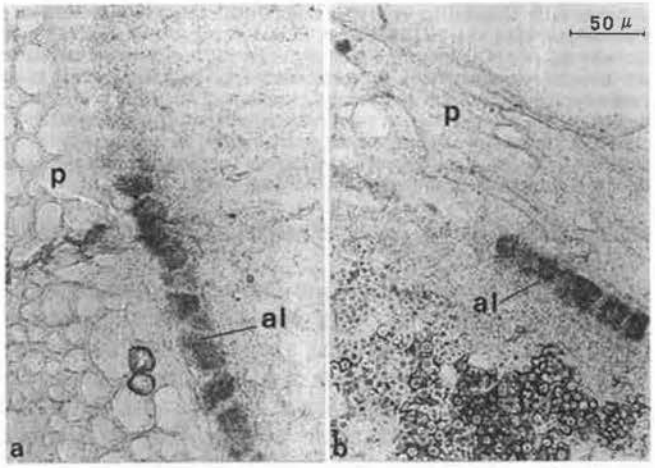


Figure 1. a and b. Presence of *A1* transcripts exclusively in colored aleurone cells of *Dap*-2* seeds (25 DAP) visualized by in situ hybridization; al aleurone, p pericarp.

MILAN, ITALY
Istituto Biosintesi Vegetali-CNR

Transformation of maize endosperm cells by electroporation

--Locatelli, F; Castelli, S; Genga, A; Viotti, A and Manzocchi, LA

In vitro endosperm cell cultures represent a valid system to investigate cereal seed maturation, in that they maintain some physiological features of the native tissue (Felker and Goodwin, Physiol. Plant. 88:1235-1239, 1988). In this laboratory, long term endosperm cell cultures have been established from A69Y wildtype and opaque-2 maize. Cultured cells synthesize (though at low levels) zeins with the typical pattern of the native endosperms (Manzocchi, Bianchi and Viotti, Plant Cell Rep. 7:639-643. 1989; Manzocchi, Plant Cell Rep. 9:555-558, 1991). Cells have been used to isolate protoplasts, which have been transformed by polyethylene glycol in experiments of transient expression and stable integration (Giovinazzo, Manzocchi, Bianchi, Coraggio and Viotti, Plant Mol. Biol. 19:257-263, 1992; Faranda, Genga, Viotti and Manzocchi, Plant Cell, Tissue Organ Cult. 37:39-46, 1994).

We present preliminary data here on the transactivation of a 21Kd zein promoter by the transcriptional activator OPAQUE2, through transformation by direct delivery of DNA to endosperm cells by electroporation, according to the method of D'Halluin et al.

(K. D'Halluin, Bonne, Bossut, De Beukeleer and Leemans, Plant Cell 4:1495-1505, 1992).

The DNA constructs used in the experiment were: p472-GUS, containing the *uidA* (beta-glucuronidase) gene under the control of the 800bp promoter of a 21 kd zein gene, fused to a zein enhancer-like element; and p501, containing the 1550 bp coding region of maize *Opaque2* gene, under a CaMV 35S promoter (Quattrocchio, personal communication). Aliquots of approximately 200 mg of A69Y endosperm cultured cells were electroporated, in the conditions described by D'Halluin et al., in the presence of 20 ug DNA of each construct. After electroporation, they were plated on standard agar growth medium (Manzocchi, 1991). The expression of the GUS reporter gene was detected on cell extracts at different times after electroporation, with the spectrofluorimetric method (Jefferson, Kavanagh and Bevan, EMBO J. 6:391-397, 1987).

Data reported in Table 1 show that, in the presence of the sequence coding for the transcriptional activator O2, the expression of GUS under the control of a zein 21 Kd promoter is 6 fold enhanced. Enhancement can be detected both at short times after cell transformation, and several months later. These data are in agreement with a possible stable integration of the constructs in the DNA of a number of cells; this would confirm, in a stably transformed homologous cell system, the transactivation of a zein promoter by the transcriptional activator O2, which had been observed by Ueda et al. (Plant Cell 4:701-709, 1992) in experiments of transient expression. In this experiment no selectable marker was employed, but experiments of co-transformation with NPTII and *bar* constructs are in progress, in the aim to select stable transformants.

Table 1. GUS expression (pmoles MU/min/mg protein) in cultured A69Y maize endosperm cells transformed through electroporation.

		DNA	
Weeks after electroporation	---	p472	p472+p501
2	0.6	7.9	33.2
16	0.44	1.06	6.48

We can conclude that the method of intact cell electroporation can be successfully employed to transform maize endosperm cell cultures; with a suitable selection system allowing the isolation of transformed cell lines, and their molecular characterization, it will provide a useful tool in the study of gene regulation in maize endosperm.

Does the combined action of methylation and a maternally imprinted factor repress endosperm expression of paternal specific alleles of the zein multigene family?

--Castelli, S; Ciceri, P; Genga, A; Lazzari, B and Viotti, A

We are interested in elucidating the molecular mechanisms underlying the specific expression of those zein genes that undergo parental imprinting in maize endosperm. Previous data on zein gene modification and transcription (Bianchi and Viotti, Plant Mol. Biol. 11:203-214, 1988; Lund et al., Plant J. 8:571-581, 1995) suggested that endosperm-specific expression of some zein alleles occurs via parental imprinting. This could be mediated by the differential methylation of the maternal and paternal zein gene sequences, the hypomethylation state of the maternal copies correlating with their expression (imprinted state).

It is reported and generally accepted that mutations at the *Opaque2* regulatory locus severely reduce the synthesis and the accumulation of the heavy chain zeins (H1 and H2 bands in SDS-PAGE). In analyzing many maize lines carrying different mutations at the *O2* locus (Bernard et al., Plant Mol. Biol. 24:949-959, 1994) we confirmed the previous observation only for some of them. We noticed, however, that several lines showed the presence of the H1 band or only a moderate reduction of both H1 and H2 bands. Two dimensional analysis, carried out first by charge and then by size fractionation, evidenced that those *o2* lines showing the presence of the H1 band in fact expressed three to four polypeptides with different charge.

These particular patterns allowed us to further and more accurately investigate the imprinting phenomenon by proper crosses between H1-plus (H1p) lines and H1-null (H1n) lines. A preliminary analysis using the H1p line, NYR*o2-It*, in reciprocal crosses with three different H1n lines (Rossman*o2-R*, W64A*o2-T* or Mo17*o2-R*) indicates among the six possible crosses the absence of the H1 band only in the Rossman*o2-R* /NYR*o2-It* cross. This suggests the presence of a maternally imprinted factor (MIF) that specifically represses the expression of those zein genes contributing to the H1 band. This was confirmed by the analysis of the reciprocal crosses between three other H1p lines (W22*o2-It*, 3316*o2-It*, Bianchi*o2-It*) and two of the three H1n lines used in the previous experiments (Rossman*o2-R* and W64A*o2-T*). Within the twelve resulting crosses only the ones that have as maternal contribution -to the endosperm complements- the Rossman*o2-R* genotype show the absence of the H1 polypeptides.

We should remark that the link between a specific modification state of certain zein alleles and a MIF is not an exclusiveness of the crosses between Rossman*o2-R* and the H1p-lines. In fact, the imprinting phenomenon has been observed also for the other size class zein polypeptides in reciprocal crosses involving other lines, with maintenance of the specific uniparental behaviour.

At present, the working hypothesis not only favours the occurrence of the trans-acting factor(s) MIF (line specific?) but also predicts the possibility that the zein modified genes mediate the action of the MIF by remaining in the default methylation state when they participate in the crosses as paternal contribution to the endosperm complements (Lund et al., Plant J. 8:571-581, 1995).

MOSCOW, RUSSIA
Institute of Plant Physiology

Cross-tolerance to drought, salt and low temperature of maize plants regenerated from PEG-resistant cell lines

--Dolgykh, YI; Larina, SN and Shamina, ZB

Drought-tolerant plants have been regenerated from PEG-resistant callus lines of hybrids Chi31xCateto S.G. and Chi31xTuxpeno Norteno (MNL 69:105-106,1995). Their responses under salt and low temperature stresses were compared with the responses of the initial plants used for callus production.

Fifty kernels from each regenerant family were placed under moisture at 10 and 26 C. The relative rate of emergence of seedlings at 10 C was determined. The frequency of germination in all regenerant families exceeded the control value (Table 1). Seedlings after selection on PEG were also more tolerant to frost (-3 C for 2.5 h) than initial plants.

To determine the salt-tolerance, kernels of nine regenerated plants were germinated on 2% NaCl solution and then the

Table 1. Emergence of the seedlings at 10 C.

Family number	Germination, %
Control	22.0
R 90	66.7
R 91	34.8
R 96	56.5
R 98	40.0
R 121	84.0

seedlings were grown in soil with increasing concentrations of NaCl (0.5 to 1.2%). When the content of salt reached 1% all initial plants and plants of one regenerant family were lost. In other families 7.1 to 77.8% of plants stayed alive and could grow on 1.2% NaCl (Table 2). Part of the families were homogeneous: all seedlings demonstrated a similar level of viability and growth activity (fam. 90,91,98,121). In other families segregation took place: average viability was low but surviving plants grew on salty soil very well (fam.68).

Table 2. Viability and growth rate of seedlings on 1.2% NaCl.

Family number	Viability,%	Fresh weight	Dry weight(g/plant)
Control	0.0	-	-
R 90	20.0	10.8	1.65
R 91(1)	38.9	11.9	1.60
R 91(2)	33.3	4.0	0.51
R 96	0.0	-	-
R 98	77.8	13.3	1.63
R 119	76.5	11.2	1.60
R 121	11.8	5.1	0.49
Control	0.0	-	-
R 68	9.1	22.2	2.42
R 83	7.1	10.5	1.20

These results show that the resistance of in vitro cultivated cells to osmoticum can be realised in the regenerated plants as tolerance to several environmental stresses.

Tissue-specific isoperoxidases in differentiating and dedifferentiating maize cells

--Zabrodina, MV; Serdobinskii, LA; Dolgykh, YI and Khavkin, EE

Regenerated plants and their sexual progeny were obtained from immature embryo-derived callus cultures of A188 inbred, and the isoperoxidase spectra were studied in their etiolated and green leaves as described elsewhere (Khavkin and Zabrodina, Russ. J. Plant Physiol., 41:754, 1994). In somaclones, in contrast to the initial plants, the leaves manifested a peroxidase band coinciding, by its mobility, with the root-specific isozyme Px12. This band was barely discernible in the young leaves of the regenerated plantlets grown in agar and became heavily stained in the green leaves of the 11 to 20-day-old plants grown in sand or soil (Fig. 1A and B).

The anodal isoperoxidase spectra in the calli obtained from different tissues were quite similar and differed considerably from the isozyme patterns of the respective explant tissues: a new band appeared in the position of the Px12 isozyme, and Px9 band staining was enhanced. The primary calli from the scutellum and the apical meristem were two exceptions from this pattern: we did not observe the Px12 band in these calli, however, the corresponding band finally appeared in the scutellum callus after several subcultures. In the roots regenerated from the calli of different origin, Px9 and Px12 staining increased to the level of the primary roots of the initial A188 seedlings (Fig. 1C).

We presume that cell dedifferentiation in vitro may somehow disrupt the tissue-specific control over peroxidase expression, and the newly established pattern of peroxidase manifestation is

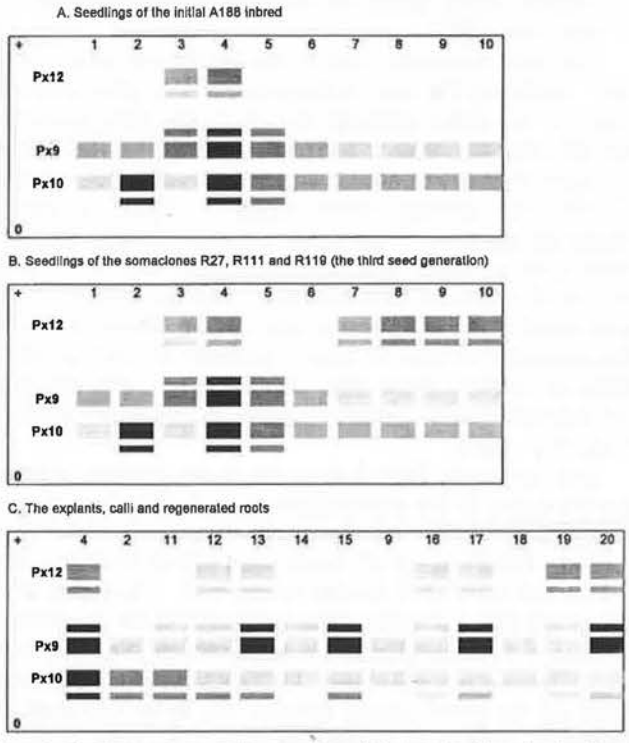


Figure 1. The fast-moving anodal isoperoxidases in intact and cultivated maize tissues. Seedling tissues (the numbers in brackets stand for the seedling age, days) : 1, endosperm (3); 2, scutellum (3); 3, embryo axis (3); 4, primary root (7), 5, mesocotyl (7); 6, coleoptile (7); 7, etiolated leaf (7); 8-10, green leaf (11, 14 and 20). Cultivated in vitro tissues: 11, primary scutel lum-derived callus; 12, scutellum-derived callus after prolonged subculturing; 13, roots regenerated from scutellum-derived callus; 14, apical meristem-derived callus; 15; roots regenerated from meristem-derived callus; 16, leaf-derived callus; 17, roots regenerated from leaf-derived callus; 18, developing tassel; 19, tassel-derived callus; 20, roots regenerated from tassel-derived callus.

further maintained as a meiotically heritable state. The age-dependent quantitative changes in Px12 staining suggest that both in the calli and intact plants, this isoperoxidase could be related to vascular differentiation.

MOSCOW, RUSSIA
Institute of Agricultural Biotechnology
COLUMBIA, MISSOURI
USDA-ARS

The clusters of development genes as seen against the UMC 1995 map

--Khavkin, E and Coe, EH

Previously (MNL 68:61, 1994; MNL 69:106, 1995; Russ. J. Plant Physiol. 42: 408 & 558, 1995) we have hypothesized that corn developmental genes associate into functionally meaningful clusters, 10 to 30 cM long, comprising the loci for environmental and hormonal sensors (e.g., *phy1*, *abp1*, *d8* and *vp1*), the growth machinery genes (e.g., for the enzymes of hormone synthesis) and the master genes presiding over the spatial and temporal transitions in cell growth and development (e.g., homeobox genes). The initially delineated clusters accounted for most of the naked eye polymorphisms related to growth and development, including *les* and *nec* loci presumably associated with programmed cell death. The clusters that manifested the most comprehensive pattern of developmental genes usually included *knox* and/or other homeobox

Chromosome 1 (115 QTLs)

Bin	Genes	cDNAs	QTL number
0			
1	*ct2, ms9*	**knox1**	
2	*lls1* *rab30,* les2, vp5 *rth3*		
3	ms17, ts2, *les5* *nec2, ms28*	**tmz1-1** phyB1	
4	*as1, rs2, ms14* *les20*	*obf1*	
5			
6	*br2*	**MCR, zmm6, MC**	
7	br1, vg1	**MCR**	
8	ad1, an1, *id1*		
9	*ptd1* *ts3,* tb1	**zag1, zap1**	
10	mpl1, d8, **kn1**	*phyA1,* **knox3, MCR, zag6b** tbp1, **MCR, knox8**	
11	*vp8, rd1, ij2, py2* *tls1,* ts6	**zmm4**	

Chromosome 2 (61 QTLs)

Bin	Genes	cDNAs	QTL number
0			
1			
2	al1/ y3, lg1, *les1* gl2, *tr1* d5, *nec4*		
3			
4	*gl11, les18,* sk1 les1, *wrp1* *les15, ts1, ba2*		
5			
6	*les10, les19*	**tmz1-2** **MCR**	
7			
8	les4		
9	*d10*		
10	**gn1**	**knox4, MCR**	

Chromosome 3 (122 QTLs)

Bin	NEPs	cDNAs	QTL number
0			
1			
2	cr1 *ns1,* cg1, cg2 d1	**zag4a**	
3	*ra2* tp3, *gl19*		
4	rt1 **lg3,** rg1	obf6	
5	ts4 *pm1* *rd3,* vp1, te1	**zag2,** abp1, **zag2a** **zag1, zap1**	
6	lxm1, lg1 lg2, ba1 *yd2, ms23*	**MCR**	
7	na1 *ms3, rea1*	obf3A	
8			
9	ga7		
10			

Chromosome 4 (47 QTLs)

Bin	NEPs	cDNAs	QTL number
0			
1	*ph1,* asr1, ri1		
2	*ga1,* sos1		
3	ts5, la1		
4	cp2? st1		
5	orp1 tga1	orp1, **zag4c, tmz1 3, MCR, zag3**	
6			
7	tu1, *nec5, ns2*		
8	ms41, ms44		
9	mgs2	**knox7**	
10		cdc2A	
11			

Chromosome 5 (89 QTLs, including 35 QTLs in bin 5.04))

0		
1		**MCR**
2	*ms42*, *ms13*, d9	phyA2
3	*na2* am1, nl2	**tmz1-4** **knox10**, tbp2
4	gl17, *nec6*, *nec3* vp2, ps1, *td1* *bv1*, *ms5*, *wi4*	**knox6** **MCR**
5	ga2, *nec7*	**MCR**
6	hsf1	**zag5**
7	*eg1*	
8		
9		

Chromosome 6 (56 QTLs)

Bin	Genes	cDNAs	QTL numbers
0			
1	po1, *rgd1* *les13*, *wi1* sl1, *ms1*	**tmz1-5** cdc48, **tmz1-6**	
2			
3			
4	pl1? *dep1?*	pl1? **zag1**	
5	**dhn1**		
6	*pt1*, *tan1?*	**zag1**	
7	**py1**	**hox2/ zmhox2**	
8			

Chromosome 7 (36 QTLs)

Bin	Genes	cDNAs	QTL number
0			
1	**rs1 / kn2**, *hs1*		
2	vp9, *les9*, ra1 rs4, ms7	**MCR** *orp?*	
3	tp1, *va1* tp1i, ij1, sl1	**MCR** **zmm7**	
4			
5	*ptd2*		
6	bd1 pn1		

Chromosome 8 (66 QTLs)

Bin	Genes	cDNAs	QTL number
0			
1			
2	*ct1*		
3	*bif1*	**zmm2, tmz1-7** **MCR, MCR**	
4	*ctl1*, *sdw1*	**MCR** **hox1/ zmhox1a**	
5	*nec1*, *lg4* *des17*, *ms43*	**knox11, knox5**	
6			
7			
8	*ms8*	obf3B?	
9			

Chromosome 9 (85 QTLs, including 28 QTLs in bin 9.03)

Bin	Genes	cDNAs	QTL number
0			
1	yg2	**MCR** **MCR**	
2	rlc1, ga8 *lo2*, *baf1*	**zmm3**	
3	*mgs3*, d3, *ms2* gl15, *trn1* *les8*	**knox2** obf2	
4			
5		phyB2	
6			
7	bf1	**zmm8** **MCR**	
8	rld1	cdc2C	

Chromosome 10 (29 QTLs)

Bin	Genes	cDNAs	QTL numbers
0		**MCR** **tmz1-9, MCR**	
1			
2	cr4 *les6*, *les16*, *mac1*		
3	y9, orp2	orp2, **zmm1**	
4	mgs1, *bf2* nl1, *ms11*, ll1 ms10, tp2	**MCR**	
5			
6			
7			

Figure 1. Genes and QTLs for growth and development. Tentatively located genes and sequences are italicized; homeobox genes and sequences are in bold. MCR are MADS-box containing RFLPs. Coinciding MADS-box sequences mapped in different laboratories could represent one and the same locus.

sequences. The majority of over 400 major QTLs for plant architecture, growth and development in vivo and in vitro, the grain yield as the integer of growth, and ABA accumulation and effects, mapped within these clusters.

Figure 1 presents the profiles of the developmental genes, cDNA sequences and QTLs refitted to the new UMC 1995 map. Several new genes, e.g. for gametophyte development, and new homeobox sequences were added using the data from the 1995 Gene List, 1995 UMC and BNL maps and the papers by Kerstetter et al. (Plant Cell 6:1877, 1994), Fischer et al. (Nucl. Acids Res. 23:1901, 1995) and Mena et al. (Plant J. 8: 845, 1995). The QTL database was supplemented from several additional sources (CIMMYT, 1994 QTL data in MaizeDB; Abler et al., Crop Sci. 31:267, 1991; Schön et al., Heredity 70:648, 1993; Doebley et al., J. Hered. 85:191, 1994; Ragot et al., Crop Sci. 35:1306, 1995; Ajmone-Marsan et al., Theor. Appl. Genet. 90:415, 1995; Austin and Lee, MNL 69:7, 1995; Beaumont et al., Genome 38:968, 1995; Berke and Rocheford, Crop Sci., 35:1542, 1995).

Taking into consideration the mapping accuracy, the clusters of developmental genes generally coincide with the location of homeobox sequences and with the QTLs for growth, development and grain yield, especially in chromosomes 1, 3, 5, 8 and 9. The most prominent and challenging exceptions are the bins 2.02 and 4.07, where only a few QTLs correspond to several important developmental genes, and homeoboxes are missing, while in the bins 6.04 and 7.05/06, the largest QTL peaks and/or several homeobox genes are inadequately matched by naked eye polymorphisms; in contrast, in the bins 2.10 and 10.00 homeobox genes are not substantiated with the classical developmental genes and QTLs.

When accepted as a working model, the cluster hypothesis poses several questions which at present can be answered only tentatively, by referring the reader to other relevant evidence. (1) *What are the putative functional and physiological advantages of gene association into clusters*? We presume that the clusters are the units of genes expressed in concert to contribute for plant growth, development and apparently some of the plant responses to stress. The close association of the functionally related genes in the clusters would contribute to compartmentation of signal molecules and help cooperatively recruit the transcription factors, e.g. MADS-box proteins, into multicomponent regulatory modules of high specificity (Krumlauf and Gould, Trends Genet. 8:297, 1992; Jacob, C. R. Acad. Sci. 316:331, 1993; Shore and Sharrocks, Eur. J. Biochem. 229:1, 1995) and thus would facilitate fine tuning of growth and development. (2) *Why are several physiologically different traits of plant development mapped by one and the same molecular probe?* We may envision QTLs as projections onto the phenotype of the key structural loci providing for the *various* essential elements of growth and development (*dwarf* and *viviparous* genes are good examples) or of the master switches of development, like *knox* and *MADS-box* genes, and thus such loci are pleiotropic by definition. (3) *Why is one and the same developmental trait mapped to several widely distant loci?* Two answers are possible. First, the loci defined as *different genes* can manifest one and the same *physiological trait* (e.g., stunted growth). Second, drawing an analogy from metabolic regulation, we may believe that the position of a bottleneck locus in one and the same developmental pathway may change in different genotype x environment interactions, and thus different key genes are manifested in various segregating populations employed for QTL mapping. (4) *Why so many clusters?* One partial answer to the evident redundancy of developmental clusters is the hypothesis of paleopolyploid corn origin; in addition, later duplication events could contribute to the redundancy: it is remarkable that most clusters border the centromeres where duplicated regions are most often found (Helentjaris, MNL 69:67, 1995). (5) *What is the adaptive significance of developmental gene associations?* A suggestion to support the advantage of clusters comes from the evidence of selective pressure maintaining the polygenic complexes that comprise relatively few pleiotropic genes (e.g., for plant height and flowering control) as the integral units through the evolution of *Poaceae* (Lin et al., Genetics 141:391, 1995; Paterson et al., Science 269:1714, 1995); the superiority of clusters may reside in the complementary gene interaction within a conserved chromosome segment resulting in numerous manifestations of heterosis (Bingham et al., Crop Sci. 34:823, 1994). (6) *How do different genes for physiologically similar functions* (e.g., plant height) *and the whole clusters as functional units interact when redundant and located on different chromosomes?* The recent topic of homology-dependent gene silencing may hopefully provide some explanation in the near future.

MUNCHEN, GERMANY
Ludwig-Maximilians-Universitat

Towards an in vitro recombination system mediated by the maize *Activator* (*Ac*) element transposase

--Rudenko, GN and Kunze, R

Transposition of *Ac* is mediated in vivo by the element-encoded transposase, a protein of 807 AA with a molecular weight of 112 kD. *Ac* is structurally similar to some other eukaryotic transposable elements. These elements generate 8 bp duplications at their genomic integration sites and the sequences of their terminal inverted repeats are similar. The polypeptide sequences of the TPases of these elements are highly homologous along their ca. 600 C-terminal residues. This suggests a common mechanism of transposition. It is believed that *Ac* transposition occurs in a non-replicative manner via a "cut-and-paste" mechanism similar to that of the P element from *Drosophila* and bacterial transposons Tn7 and Tn10. Genetic data indicate an association of *Ac* transposition with DNA replication. However, no in vitro transposition products or reaction intermediates involving eukaryotic transposases have been described until now.

To study the activities of the *Ac* TPase on the enzymatic level, two interrelated aspects are being approached. One concerns the identification of *Ac* TPase enzymatic activities and the biochemistry of specific TPase-mediated DNA rearrangements. Localization, mapping and further dissection of the specific *Ac* TPase catalytic domain(s) responsible for the recombination reactions is the second scope.

To begin with dissection of the components required for a cell-free transposition system, we have primarily concentrated our attention on the wild type *Ac* TPase (1-807 AA) and its N-terminally truncated derivative (103-807 AA). Both proteins are functional in vivo and recognize in vitro specifically the 11 bp terminal inverted repeats of the element and multiple AAACGG or similar sequence motifs present in its subterminal regions. These proteins as well as a number of mutant derivatives were overexpressed in *E.coli* cells and purified either using Ni-chelate affinity chromatography and gel filtration on Superdex 200 column and/or

by preparative SDS-polyacrylamide electrophoresis. Final preparations are free of contaminating proteins as judged by Western blot analysis and visual inspection of protein gels. Purified proteins have been tested for DNA-binding activity using gel-retardation assays.

It is important to note that all recombinases studied to date have a DNA-topoisomerase activity. Association of a topoisomerase-like activity with *Ac* TPase might be a key to our understanding of the *Ac* TPase functionality. Therefore purified TPase preparations have been tested for relaxation activity in standard assays using either a negatively supercoiled substrate DNA construct containing a complete *Ds* element (a non-autonomous *Ac* derivative) or φX 174 DNA as a control. We have been able to detect such an activity for the wild-type transposase and a number of its derivatives. The relaxation activity of the TPase is ATP-independent. It is not stimulated by additions of mono-, divalent (except Mg) cations and spermidine. Preliminarily the protein can be classified as a type I DNA-topoisomerase.

The topoisomer pattern generated by the TPase on transposon- containing DNA is however qualitatively different from the one obtained for φX 174 DNA. Under conditions when φX 174 DNA is fully relaxed, transposon-containing DNA always remains underrelaxed. The protection of some supercoils from the topoisomerase activity indicates a different mode of interaction between TPase and a substrate DNA depending on the presence or absence of a transposable element in its context.

To study TPase-DNA interactions in more detail we have used glass-fiber filters to selectively bind DNA-protein complexes out of reaction mixtures. This allows separation from free DNA which is not retained on the filter. In the absence of divalent cations strong binding of the TPase could be detected not only to the *Ds*-containing plasmid DNA but also to single- and double-stranded φX 174 DNAs. Selectivity of TPase binding towards *Ds* containing DNA can however be induced by addition of divalent cations (Mg or Ca). Under these conditions TPase does not bind to either of the φX 174 DNAs. The nucleoprotein complex formed between TPase and DNA is also quite unusual since it can be dissociated only by a treatment with protein denaturants. Comparative studies made on linear or circular DNA substrates lead us to a preliminary conclusion about the existence of a topological lock between TPase and DNA in the form of protein clamp around DNA.

Experiments are under way to determine in which way the structural features of TPase-DNA complexes and a topoisomerase activity displayed by the TPase could be involved in transpositional recombination.

Identification of an interaction domain of the *Ac* transposase protein

--Essers, L and Kunze, R

Activator encodes a transposase protein (TPase) which is crucially involved in the transposition reaction. TPase binds to repetitive subterminal sequence motifs and the terminal inverted repeats of *Ac* (Kunze and Starlinger, EMBO J. 8:3177-3185, 1989; Becker and Kunze, MNL 69:38, 1995). By immunochemical in situ staining it was found that the TPase forms large aggregates in the cell nuclei, and genetic experiments suggest that it acts as an oligomer (Heinlein et al., Plant J. 5:705-714; Kunze et al., PNAS 90:7094-7098, 1993). We assume that the TPase is the key and possibly sole protein component of a transposition complex (the "transpososome"), where it brings the ends of the transposable element and the new insertion site in close contact. In this model of the transpososome direct TPase interactions have a fundamental function. To localize the TPase protein/protein-interaction domain(s) we made use of the yeast two-hybrid-system. Initial experiments have demonstrated that the wild type TPase and a functional, amino-terminally truncated TPase(103-807) derivative, respectively, interact in the yeast cells (Essers and Kunze, MNL 69:41, 1995).

By progressive deletions from the amino- and carboxy-terminus of the TPase reading frame we have identified an approximately 100 amino acid domain close to the the carboxy-terminus (residues 664-754) which is required for a specific interaction with the TPase (103-807). A TPase derivative lacking 100 amino acids from the C-terminus [TPase (103-709)] does not interact with the full length TPase and the TPase (103-807), respectively. Thus, the TPase (664-754) domain is the only interaction domain detectable with the yeast two-hybrid-system.

The putative interaction domain contains a region (amino acids 685-750) which is highly conserved in transposase proteins of transposable elements originating from plant and insect species (Essers and Kunze, MNL 69:39-41, 1995). We have noticed earlier that an insertion of two amino acids within this conserved region at residue 709 results in complete inactivation of the protein in vivo, whereas similar insertions at the (non-conserved) residues 754 and 771 do not affect the transpositional activity (Kunze et al., PNAS 90:7094-7098, 1993). This correlates well with the results from the two-hybrid-system. The insertion at residue 709 abolishes protein/protein-interaction in yeast, whereas the 754 and 771 mutants still interact.

According to our experience it is important to verify the data obtained from the genetic two-hybrid-system by biochemical techniques. We have expressed the putative interaction domain (amino acids 674-777) with a N-terminal histidine-tag in *E. coli* and tested the fusion protein by chemical crosslinking experiments for protein-protein interaction. Preliminary results indicate that the fusion protein can be crosslinked with EGS [etyhlene glycol-bis(succinic acid N-hydroxysuccinimide ester)] at standard concentrations, whereas no crosslinking of the control protein lysozyme was observed.

As the self-interacting TPase protein fragment consists of approximately 100 amino acids, it is likely that it contains only one interaction domain. It probably mediates a symmetric interaction ("head-to-head") between two TPase monomers. The TPase binds to the subterminal regions of *Ac* and *Ds* elements at multiple, five or six bp target sites which are frequently arranged as direct repeats. Thus, it seems unlikely that the proposed "head-to-head" contacts are involved in stabilization of neighbouring TPase molecules on one end of the transposon. However, such contacts could mediate the conjunction between the two transposable element ends in a transpososome. The tight connection between both *Ac* ends may be a prerequisite for the initiation of the excision reaction.

The carboxy-terminus of the *Ac* transposase can activate gene expression in *S. cerevisiae*

--Essers, L and Kunze, R

In the course of our two-hybrid studies to localize the *Ac* transposase interaction domain (see above) we detected a transcription activation function in yeast of the C-terminal 24

residues. A fusion of this transposase segment to the C-terminus of the GAL4 DNA-binding domain results in a weak, but significant transcriptional activation of the lacZ gene in the absence of the GAL4 activation domain. This activity is lost if approximately 100 amino acids are removed from the C-terminus of the TPase derivatives. Interestingly, this activation activity is only detectable if more than 300 amino acids are deleted from the N-terminus of the transposase. We therefore assume that in longer hybrid transposase proteins either the fused GAL4 DNA-binding domain or the N-terminal transposase moiety itself masks the activation function by steric hindrance. However, the C-terminus of the *Ac* TPase has a very hydrophilic character and thus is probably located on the surface of the protein. As the transposase protein binds closely upstream of the *Ac* promoter, it is tempting to speculate that it could have a positive autoregulatory activity. However, it remains to be determined if transcriptional activation by the *Ac* transposase is also occurring in plants or if it is rather a coincidental phenomenon in yeast.

Methylation of transposase binding sites at the 5'-end of *Ac* differs in the active and inactive states of the element

--Wang, L and Kunze, R

Activator (*Ac*) transposes following replication from only one of the two daughter chromatids. It has been suggested that DNA methylation in conjunction with methylation-sensitive transposase (TPase) binding to DNA may control the association of *Ac* transposition and replication. This mechanism requires that the TPase binding sites within *Ac* are methylated prior to replication. By restriction analysis of genomic maize DNA with methylation sensitive enzymes it has been shown that the three *Hpa*II sites and the *Pvu*II site at the 3'-end of *Ac* in the *wx-m9::Ac* allele are methylated, whereas no methylation could be detected at the 5'-end. In contrast, during the inactive state of *Ac* in the *wx-m9::Ds-cy* allele the 5'-end of the element is also hypermethylated (Chomet et al., EMBO J. 6:295-302, 1987; Schwartz and Dennis, Mol. Gen. Genet. 205:476-482, 1986). The TPase binding sites are not accessible by any restriction enzymes, however. We have therefore determined the methylation state of these sites at both *Ac* ends by genomic sequencing. We used the positive display protocol which is based on the conversion of unmethylated cytosine residues to uracil by bisulfite treatment. This procedure allows the methylation state of individual molecules to be determined (Frommer et al., PNAS 89:1827-1831, 1992). We have meanwhile completed the analysis of the active *Ac* in the *wx-m9::Ac* allele, and the analysis of the inactive *Ac* in the *wx-m9::Ds-cy* allele is in progress.

The active *Ac* elements in *wx-m9::Ac* endosperm exhibit intriguing methylation patterns at their ends and fall into two distinct groups. Half of the elements are unmethylated throughout the 256 residues at the 5'-end (the promoter end). The other half is partially methylated between *Ac* residues 27 and 92. In contrast, at the 3'-end all *Ac* molecules are heavily methylated between residues 4372 and 4554, including the CpG sequences within the TPase binding sites (AAACGG). The more internally located *Ac* sequences and the flanking *Waxy* DNA are unmethylated. In addition, methylation of non-symmetrical cytosines (C's in other than CpG or CpNpG sequences) in the hypermethylated regions of *Ac* is common. The observed methylation pattern suggests that the *Ac* element is a "methylation island" which contains certain regions whose methylation (and demethylation?) is governed by signals within the *Ac* sequence. These signals seem to act specifically on *Ac* as the hypermethylation of the *Ac* 3'-end remains restricted to *Ac* and is not extending into the flanking CpG-rich *Waxy* DNA.

Preliminary results indicate that the methylation pattern of the inactive *Ac* in the *wx-m9::Ds-cy* allele partially differs from the active *Ac*. The 3'-ends of both elements are hypermethylated to a similar degree. In contrast to the active *Ac* , however, the inactive element is also hypermethylated throughout the 5'-end except the terminal inverted repeat. Obviously, 5'-end methylation of the inactive element is not restricted to the *Hpa*II restriction sites that are predominantly located in the 5'-untranslated region (Schwartz and Dennis, Mol. Gen. Genet. 205:476-482, 1986), but includes the TPase binding sites.

The inactive *Ac* behaves like a non-autonomous *Ds* element, i.e. it is mobilized if TPase is provided in trans. Thus, methylation of TPase binding sites at both ends of the element does not inhibit transposition, although TPase does not bind to fully methylated target sites (Kunze and Starlinger, EMBO J. 8:3177-3185, 1989). However, after replication the TPase binding sites will transiently be hemimethylated and can be bound in this state by TPase. Our data are compatible with the hypothesis that DNA methylation in conjunction with methylation-dependent DNA binding of TPase is responsible for replication-dependent transposition and the strand selectivity of transposition.

OTTAWA, CANADA
Agriculture and Agri-Food Canada

Release of inbreds with high *Gibberella* ear rot resistance

--Reid, LM and Hamilton, RI

The first inbreds (CO387, CO388, and CO389) from the Plant Research Centre's ear rot breeding program have been released. Their development began as a result of observations in the Ontario Soil and Crop Improvement Association (OSCIA) half acre plots of eastern Ontario, Canada, in the fall of 1986 during a *Gibberella* ear rot (pink mold, *Fusarium graminearum*) epidemic. Four hybrids were significantly less infected, one of which was the single cross hybrid CO272 X CO265. The source for this resistance has now been shown to be CO272, an inbred which appears to possess a single dominant gene for resistance to infection through the silk (Reid et al., J. Hered. 85:118-121, 1994). A component of this resistance may be a buildup of the wax layer on CO272 silk (Bergvinson and Reid, MNL 69:114, 1995). CO272 was developed from (BS10 x CO109) $CO109^2$ beginning in 1975. BS10 was formerly known as BSTE (Iowa two ear synthetic). CO109 was developed by Dr. F. Dimmock from the cultivar Early Butler in the 1950's. CO265 was developed by Dr. L.S. Donovan from the 1970's commercial hybrid Pioneer 3990 (75 RM).

In the development of the new lines, CO272 was used as the donor parent followed by inbreeding, inoculation and resistance screening for several generations. Artificial inoculations were conducted by injecting 2 ml of a 5×10^5 spores/ml macroconidial suspension of *F. graminearum* into the silk channel 6 days after pollination. At harvest, only those ears with no visible symptoms of infection on the kernels were selected and advanced to the next generation. In test crosses with susceptible checks, outstanding resistance to artificial infection via the silk has been evident.

CO387 was developed from the CO272 X CO266 hybrid. CO387 has reddish-brown dent-flint kernels and a similar silking

date as CM105. CO388 and CO389 were developed from the backcross population of (CO272 X B73) CO272. CO388 has orange dent kernels and CO389 has yellow-orange flint kernels. Both are similar in silking date to A632. All three inbreds will be released under a research agreement to the corn seed industry.

PIRACICABA, BRAZIL
Universidade de Sao Paulo

Qualitative and quantitative analysis of storage proteins in single and double mutants

--Ricardo A. Azevedo

The *Ask1* mutant (dominant mutation), which leads to an overproduction of threonine due to an altered aspartate kinase that is less sensitive to lysine inhibition, was transferred to near isogenic conversions to the inbred line Cat100-1 in normal and *o2* versions. Endosperms of the single mutants *Ask1 Ask1*, *o2 o2*, double mutant *Ask1 Ask1 o2 o2*, and the wild type were used for protein extraction. Storage proteins were extracted in albumins + globulins, zeins, and glutelins fractions.

The effect of the *o2* mutation in reducing the synthesis of the zein fraction from 57.6% to 27% was observed, whereas albumins + globulins increased from 9.5% to 22.6% and glutelins from 32.9% to 50.7%. With the introduction of the *Ask1* mutation this effect was intensified since the double mutant *Ask1 Ask1 o2 o2* showed a further reduction in the zein fraction from 27% to 20.9% and increases in albumins + globulins from 22.6% to 25.3% and glutelins from 50.7% to 53.8%.

The storage protein fractions were also applied to PAGE-SDS and the pattern of bands analysed. Zein in the *o2* mutant presented 3 bands and although the introduction of the *Ask1* mutation had caused an alteration in the concentration of zein compared to the *o2* mutation, this alteration did not alter the distribution of the bands. The same result was also observed for the other protein fractions indicating that the effect of the *Ask1* mutation on the *o2* mutant is not related to a specific polypeptide. These results were confirmed by testing protein fractions by conventional isoelectric focusing in amphoteric buffers.

PISCATAWAY, NEW JERSEY
Rutgers University

Are *P*-locus epiallele methylation status and phenotype set during inflorescence or embryo development by maternal influence?

--Bradeen, J; Timmermans, M and Messing, J

P-pr is an epiallele of the full red *P-rr* allele characterized by variable patterned pericarp and red cob (Das and Messing, Genetics 136:1121). Also characteristic of *P-pr* is somatic instability as evidenced by frequent cob sectors. Methylation status of the *P-pr* epiallele in leaf DNA correlates inversely with kernel pigmentation levels and the *P-pr* pericarp ranges from virtually fully pigmented (similar to *P-rr*) to virtually unpigmented (Das and Messing, Genetics 136:1121; personal observations). In the current study, we examine causes of variability of *P-pr* phenotype and determine when the methylation status of the epiallele is set. Two approaches were used: comparison of within and between plant *P-pr* methylation levels for plants originating from "sector" and "nonsector" portions of sectored cobs ("sector study") and correlations between *P-pr* phenotypes of sibling plants and their original cob position ("ear map study").

In the sector study, ten BC1 cobs ((*P-pr* x 4Co63:*P-ww*) x 4Co63:*P-ww*) with distinct large sectors were selected and ten seeds were planted from each sector and nonsector portion of each cob. Three inch leaf tip samples (or whole leaves for small leaves) were collected from every true leaf of every plant. *P-pr* phenotypes were determined at harvest for all *P-pr*/*P-ww* heterozygotes and support previous observations that somatic sectors yield penetrant phenotypic modification. *Sal*I digestions of DNA extractions from each leaf of phenotypically selected plants were hybridized with clone p15 (Das and Messing, Genetics 136:1121), allowing determination of methylation status. Methylation status correlated inversely with pigmentation, as expected. Importantly, methylation status was consistent for each leaf of every plant; by the time the first leaf was harvested, methylation status and consequently *P-pr* phenotype had been determined. This suggests seedling environmental factors are likely not important in determining methylation status or *P-pr* phenotype within that plant. Furthermore, these results suggest *P-pr* methylation status and phenotype are determined prior to or at germination, most likely in either the gametes or embryo.

In the ear map study, ten BC1 cobs were selected with differing but uniform pigmentation levels. Ear maps were prepared and seed order was randomized prior to planting. Following harvest, cobs were superimposed upon corresponding enlarged ear maps, allowing visual analysis of cob position effects on *P-pr* phenotype. Although original ear map cobs were uniform (i.e. lacking apparent sectors), progeny cob pigmentation was confined to particular ear map regions, with similarly colored cobs arising from seed from a common region. These results are consistent with the possibility that *P-pr* phenotype is determined during female inflorescence development, with kernels that give rise to similarly colored cobs arising from a common progenitor cell. (Note that determination of *P-pr* methylation status during embryo development is not precluded by these observations. However, determination during embryo development requires methylation status to be set for each individual embryo, and mechanisms explaining the observed clustering of similarly colored cobs must be more complex.) These results further suggest maternal somatic instability is an important factor in generating variability in progeny cob pigmentation and probably methylation levels (work in progress). The mechanism giving rise to somatic instability that has no apparent phenotype in the individual but affects the phenotype of its progeny (as observed in the ear map study) may be the same as or different from that which gives rise to visible sectors in the affected individual (as observed in the sector study). Ear map experiments designed to determine environmental effects on phenotype suggest these effects are likely minimal. However, environmental effects on future generations have not yet been determined (work in progress).

Positional cloning of *dzr1*: Physical analysis of the 22-kDa α-zein cluster region

--Llaca, V and Messing, J

Zeins, the storage proteins in maize, constitute 50-60% of the total protein in mature seeds. They are expressed in the endosperm, under strict developmental control. They are classified into four major groups: 1) α-zeins are 19-kDa and 22-kDa proteins encoded by many genes grouped in separate clusters, where

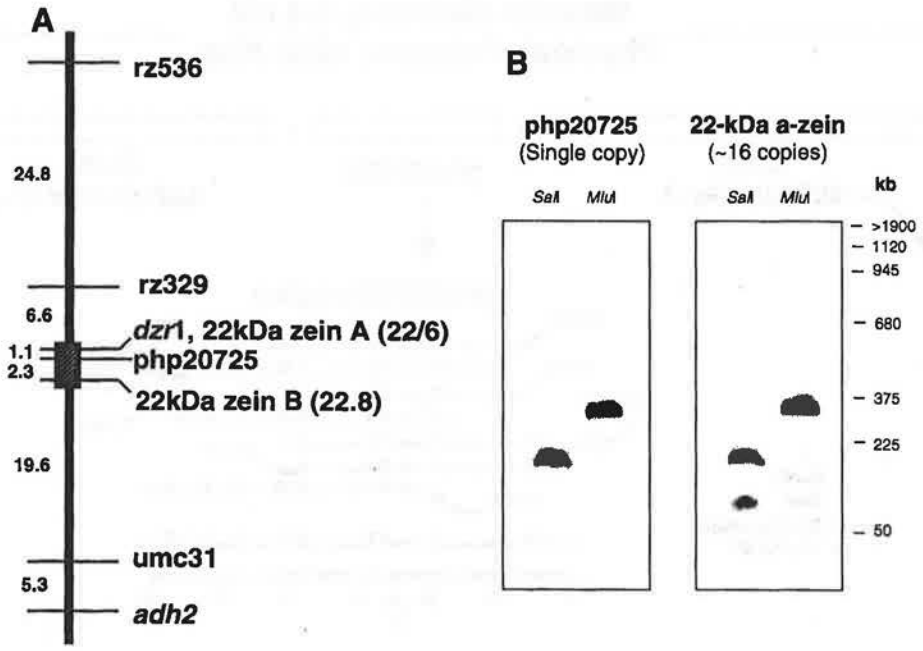


Figure 1. Maximum size of the 22-kDa α-zein cluster. A) Genetic map of the cluster (chromosome 4S) as previously described (Chaudhuri and Messing, Mol. Gen. Genet. 246:707, 1995). B) Southern blot of gel shown in A), and hybridized to a 500 bp 22-kDa α-zein specific probe.

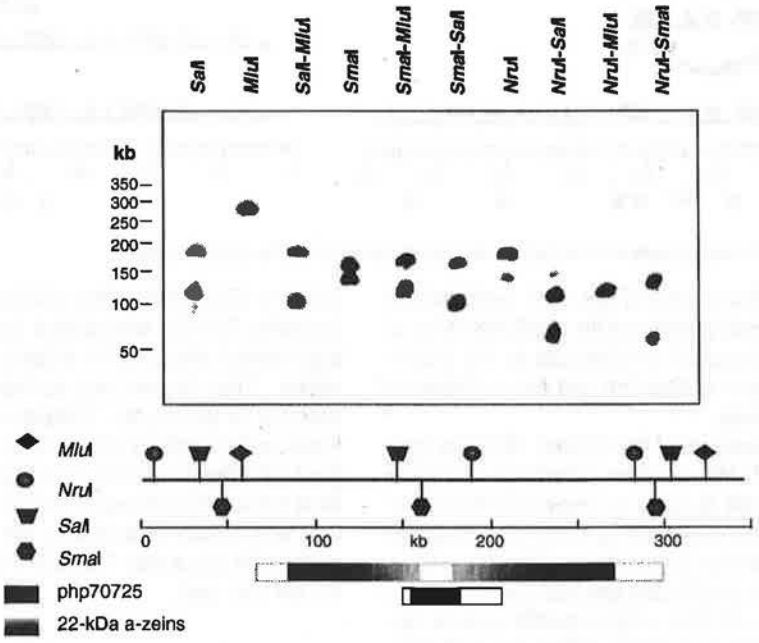


Figure 2. A) Long-range restriction map of the 22-kDa α-zein cluster for 4 restriction endonucleases. B) Southern blot of gel shown in A), and hybridized to a 500 bp 22-kDa α-zein probe. Single- and double-digestions are indicated on top of each lane.

pseudogenes are also present. Conversely, the other three groups, 2) β-zeins (15 kDa), 3) γ-zeins (16 kDa and 27 kDa), and 4) δ-zeins (10 kDa and 18 kDa) are encoded by unique or a few genes (Heidecker et al., Genomics 10:719, 1991). The suboptimal nutritional value of maize for both humans and livestock is due to a large extent to the abundant expression of δ-zeins, which are deficient in lysine, tryptophan and methionine. The maize inbred line BSSS53 has a 30% higher level of methionine than standard lines (Phillips et al., Crop Sci 21:601, 1981). This increase is due to overexpression and accumulation of the 10-kDa -zein, which has an unusual high (23%) content of methionine. The overexpression of the high-methionine zein is postranscriptionally regulated in trans by the product of the *dzr1* (delta-zein regulator 1) gene. This gene shows allele-specific parental imprinting (Chaudhuri and Messing, Proc. Natl. Acad. Sci. U.S.A. 91:4867, 1994). *dzr1* is tightly linked to a cluster embodying most of the genes and pseudogenes for the 22-kDa -zeins. This cluster spans 3.4 cM on chromosome 4 (Chaudhuri and Messing, Mol. Gen. Genet. 246:707, 1995).

As part of our initial approach to isolate and characterize *dzr1*, we are constructing the complete physical map of the region where the 22-kDa -zein cluster and the *dzr1* gene are located.

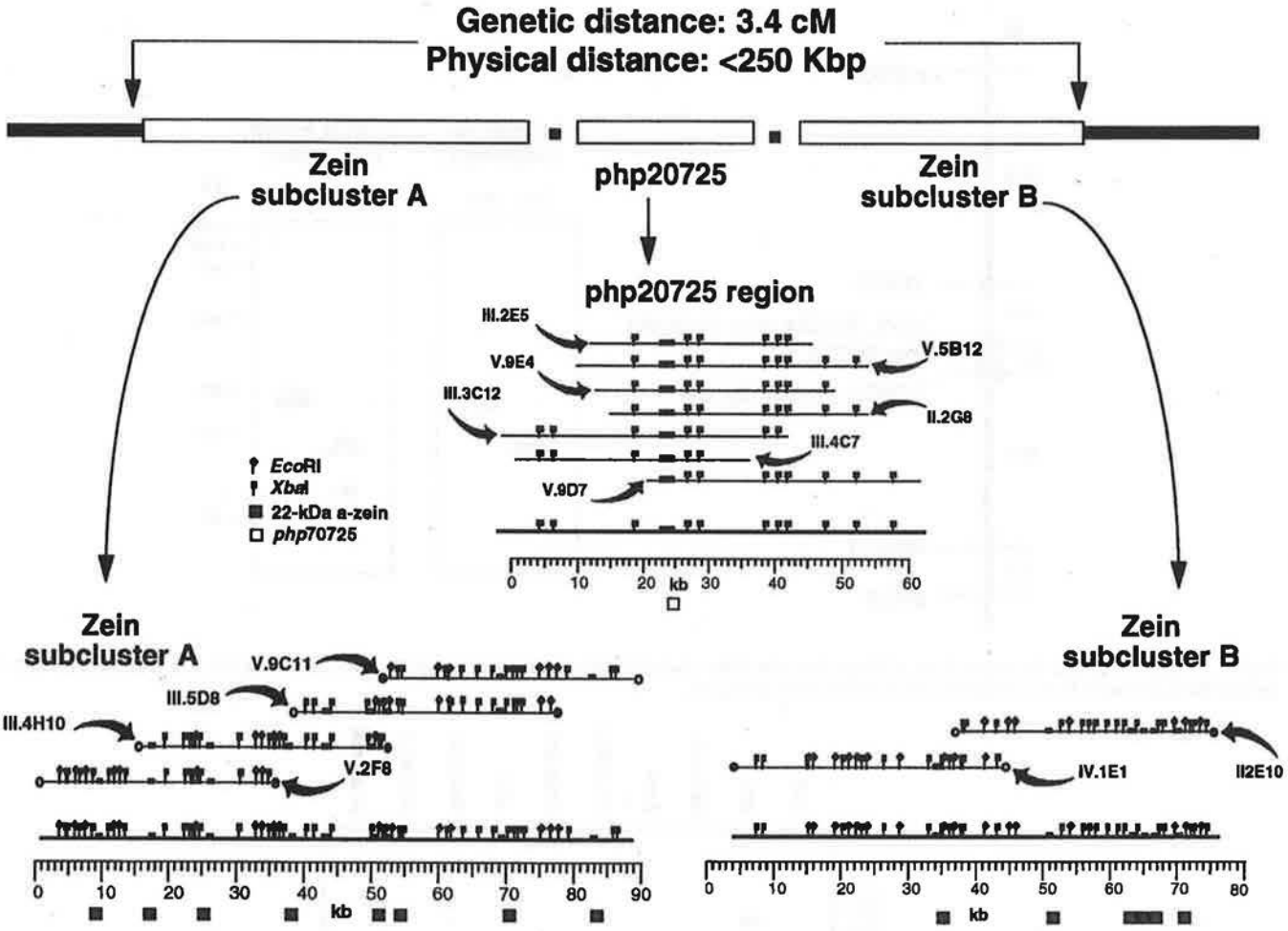


Figure 3. Partial cosmid overlaps for the two zein subclusters and the *php20725* intermediate region in the 22-kDa α-zein cluster region.

This map should facilitate the cloning of the *dzr1* gene, which would provide novel approaches to increase the nutritional value of maize. This study is also expected to contribute to the understanding of imprinting in maize endosperm and the evolution of clustered gene families in cereals.

Long-range restriction analysis of the cluster. We have optimized high-molecular-weight DNA isolation techniques and used pulsed field gel electrophoresis to make a long-range restriction map of the chromosomal region where the 22-kDa α-zein cluster is located. We wanted to determine the maximum size of the locus and the relationship between genetic and physical distance in the region. As Figure 1 shows, 22-kDa α-zein-specific probes hybridize to a single *Mlu*I fragment of 350kb, and to two *Sal*I fragments, of 200kb and 100kb. Further restriction mapping (Figure 2) indicates that the cluster has a maximum size of 225-250kb and is divided into two subclusters of genes. The two clusters are 3.4 cM apart. One restriction fragment length polymorphism (RFLP) marker, *php20725*, maps between the subclusters, at 1.1 from one subcluster and *dzr1*, and 2.3 cM from the other. By Southern hybridization analysis we have estimated that there are 15-17 22-kDa α-zein related sequences (i.e., genes and pseudogenes) for the inbred line BSSS53.

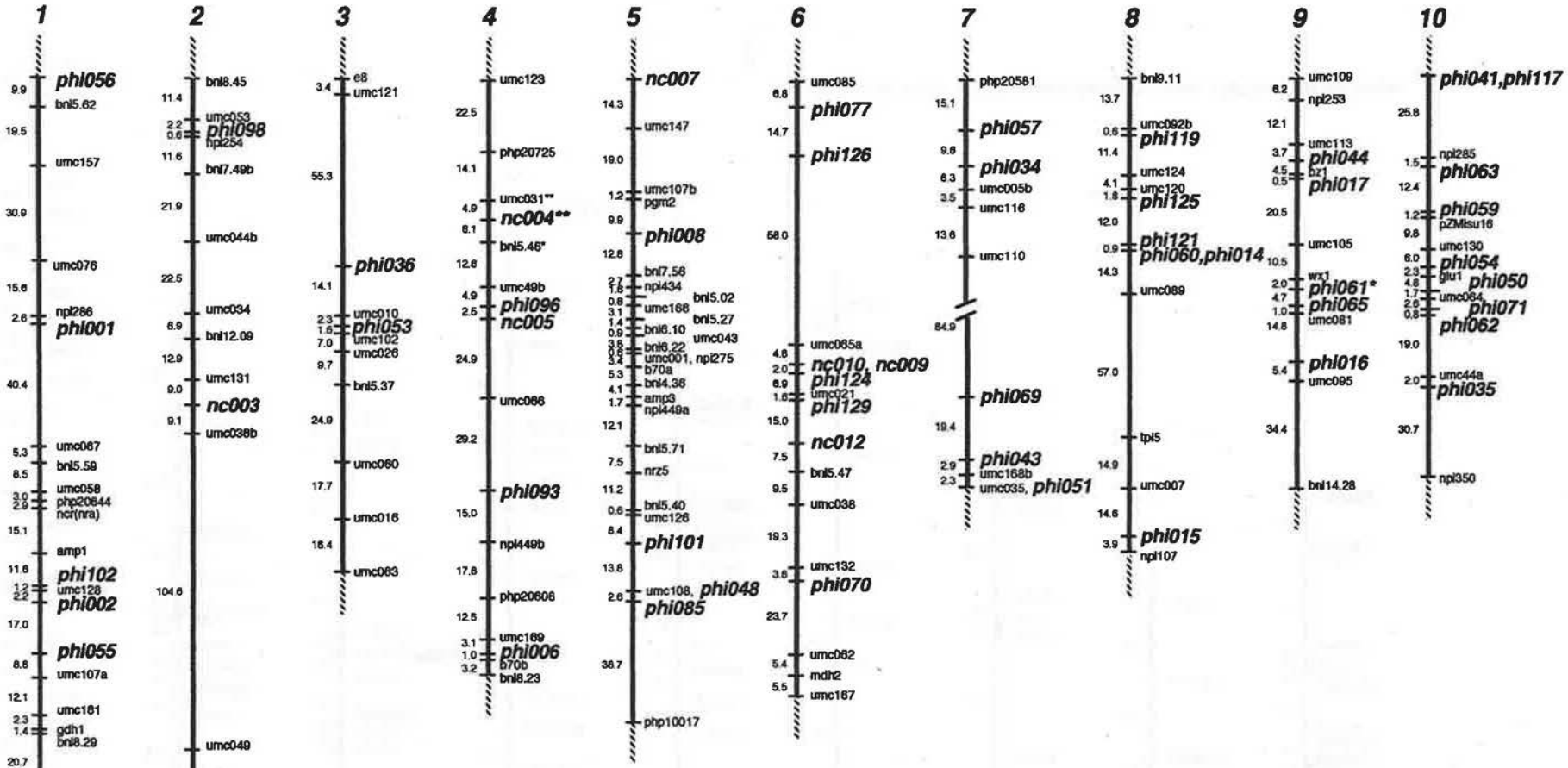
Cosmid analysis. To provide a more detailed restriction map, we have constructed an overlapping, representative cosmid library (>8 genome equivalents) for BSSS53. The library has been amplified in 1700 independent sublibraries. We are isolating cosmids harboring 22-kDa zein-related sequences and the RFLP single copy marker *php20725* in order to create an overlap of the whole region. Thus far, we have isolated 15 independent recombinant cosmids for the region. Thirteen cosmids have been ordered into three partial overlaps which cover a total of 200kb and include at least 14 different 22-kDa zein-related sequences (Figure 3). We have subcloned and sequenced 22 zein sequences to identify overlaps and identify in particular the gene 22/6 through its specific amino acid sequence. The 22/6 α-zein gene is located at less than 0.1 cM from *dzr1*.

RALEIGH, NORTH CAROLINA
USDA-ARS
JOHNSTON, IOWA
Pioneer Hi-Bred International, Inc.
AMES,IOWA
Iowa State University

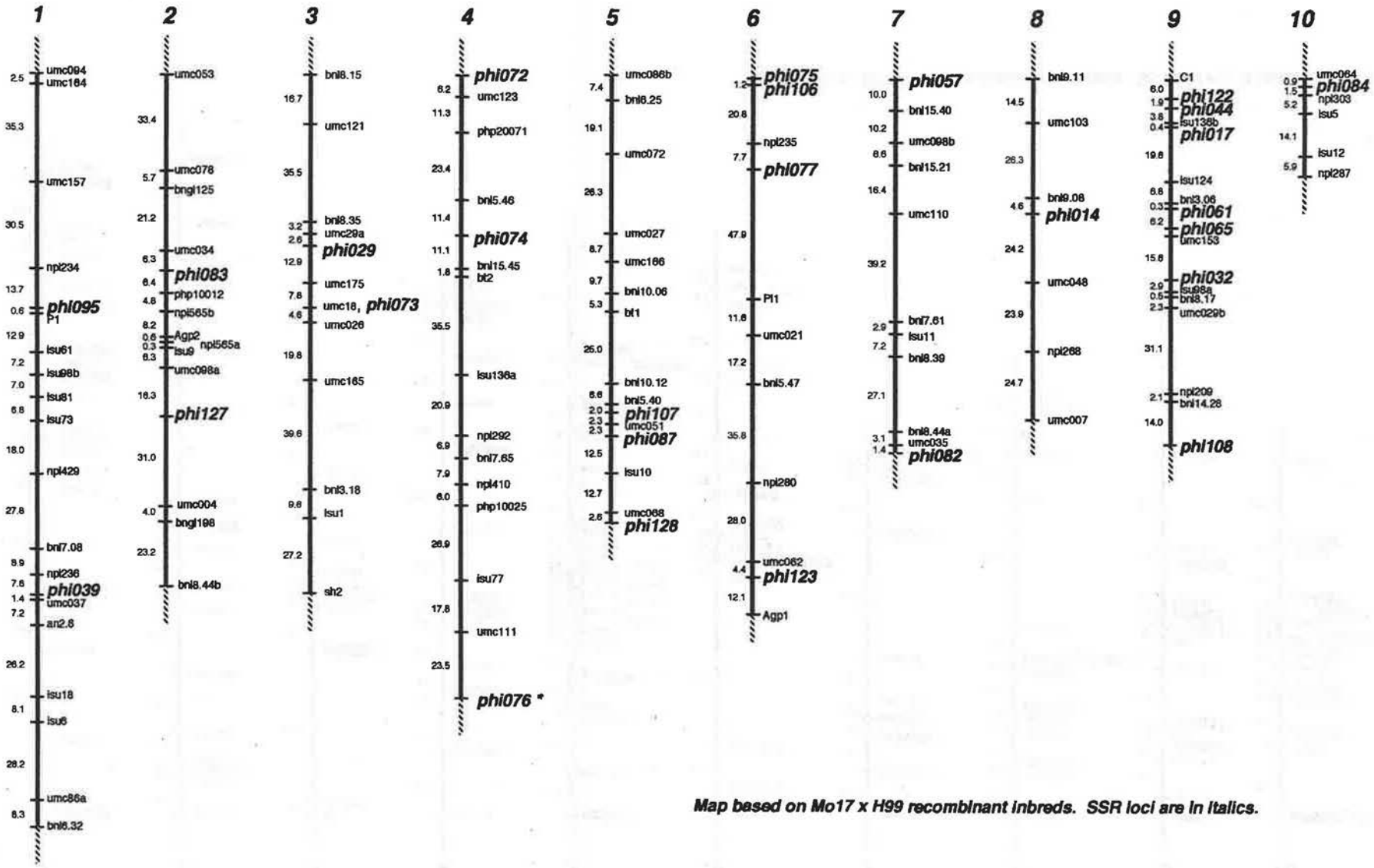
Mapping Simple Sequence Repeats in maize

--Senior, ML; Chin, E; Austin, D; Lee, M and Smith, S

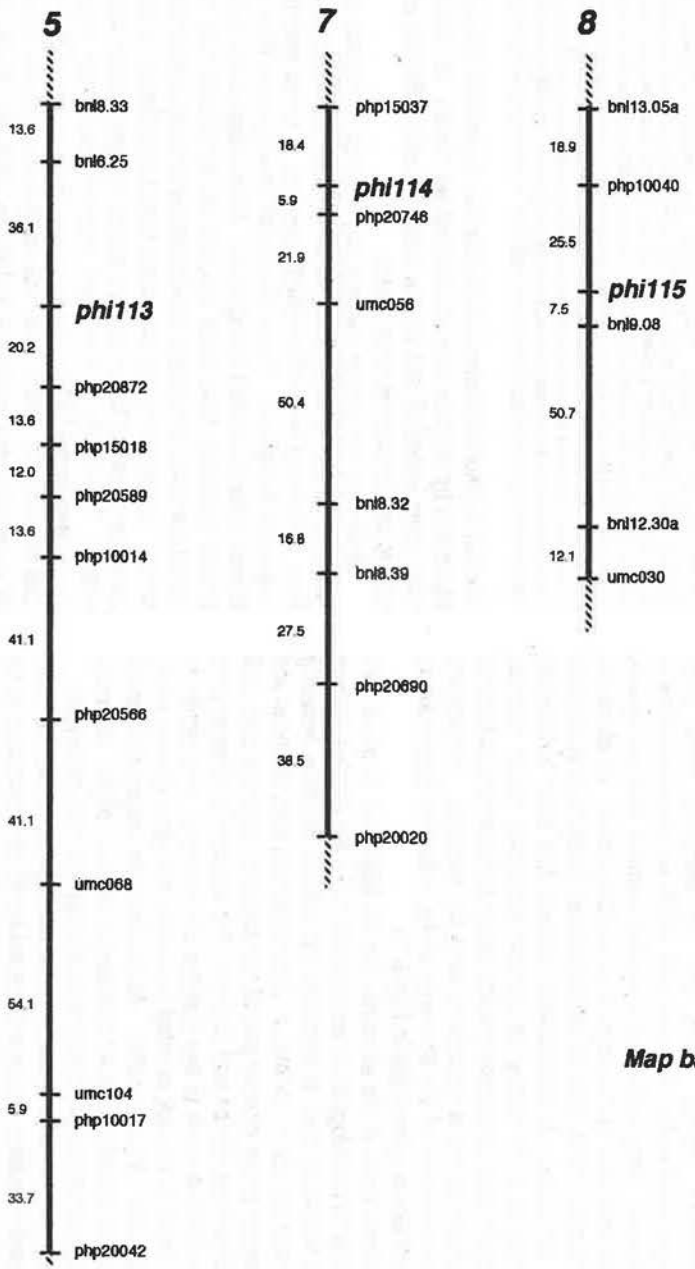
To date, 127 Simple Sequence Repeats (SSRs) have been identified in maize. Sixty of the SSRs were identified through searches of the Genbank and EMBL databases. These were



Map based on B73 x Mo17 recombinant inbreds. SSR loci are in italics.



Map based on Mo17 x H99 recombinant inbreds. SSR loci are in italics.



Map based on B73 x G35 recombinant inbreds. SSR loci are in italics.

mapped to 42 distinct loci throughout the genome. Primer sequences for these SSRs are available through MaizeDB. An additional 59 SSRs have also been identified through various sequencing efforts in progress at Pioneer Hi-Bred International. Forty-two of these have mapped to 31 loci in maize. Primer sequences for the latter group will be made publicly available in the near future. The microsatellites were mapped using DNA of 192 recombinant inbreds of the cross B73 x Mo17, 185 recombinant inbreds of the cross Mo17 x H99 or 34 recombinant inbreds of the cross B73 x G35. The B73 x Mo17 population was used as the primary mapping population. Primer pairs that were not polymor-phic in B73 x Mo17 were mapped using the Mo17 x H99 population. A few primer pairs did not show polymorphism among B73, Mo17 or H99, but were still considered to be useful markers based on the results of inbred screening and were mapped using the B73 x G35 population. Linkage analyses were performed using MAPMAKER/EXP 3.0 (Lander et al., Genomics 1:174-181, 1987; Lincoln et al., Whitehead Inst. Tech. Rep., 3rd ed., 1992). The maps are shown on the accompanying pages. SSR loci are shown in bold and italics.

REHOVOT, ISRAEL
Weizmann Institute of Science

Evolution of *Ac/Ds* transposable elements

--Rubin, E and Levy, AA

Ac/Ds transposable elements constitute a family which comprises several members (Banks et al. C. S. H. Symp. Quant. Biol. 50:307-311, 1985). Only two *Ac* elements have been characterized so far, *Ac1* and *Ac9*, which are almost identical in sequence. They both have imperfect terminal inverted repeats (TIRs) and differ in the range of sequencing errors. *Ds* elements, on the other hand, form an heterogeneous group, both in structure and sequence. A transposable element has been traditionally defined as a *Ds* based on genetic properties rather than on molecular data: any element which cannot mobilize itself, but can be mobilized by *Ac* is considered as a *Ds* element. Subsequent characterization of *Ds* elements at the molecular level done in several labs is summarized in Figure 1A.

Three kinds of *Ds* elements can be identified: 1- those with virtually no homology to *Ac* except in the TIRs, like the *Ds1* element (also known as *rUq*) ; 2- elements with internal deletions, including *Ds9* and the *Ds* in *Wx-m5* ; 3- *Ds*'s containing both deletions and insertions in the internal part of the element, including *Ds2*, and the *Ds*'s from *Wx-b4* and *Sh2-m1*. The double *Ds* element from *Sh-m5933* is made of two identical *Ds* elements, very similar to that found in *Wx-m5*, inserted one within the other (Doring et al., Nature 307: 127-130, 1984). All *Ds* elements, except *Ds1*, share extensive similarity with *Ac*, indicating a common origin. However, the mechanism by which they were derived from *Ac* is not known.

In order to better understand the underlying mechanism of *Ds* element formation, we have screened for de novo formation of *Ds* elements in transgenic tobacco, which offers a *Ds*-free environment. We have used PCR with the primers shown in Fig. 1B and genomic DNA template from plants transformed with *Ac* or with a *Ds* element which differs from *Ac* only by a 4bp insertion (constructs pAGS4411 and pAGS4081 given by H. Dooner). Internal deletions (Fig. 1B) were obtained only with *Ac*-containing template but not with *Ds* or with a stable *Ac*. This suggests that

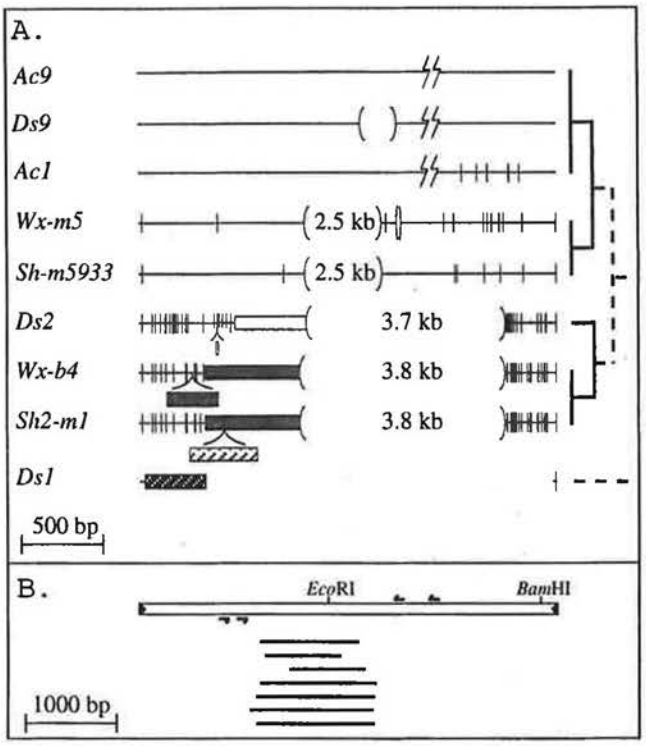


Figure 1. (A) Classification of known *Ds* elements. *Ds* elements for which sequence data are available (with the exception of *Ds9*, for which only a high-resolution restriction map is available) were compared to *Ac*. Deletions, compared to *Ac*, are shown in parentheses. Small polymorphisms are indicated as vertical lines. Blocks of insertions are shown as boxes. Boxes with the same filling are related. The phylogenetic tree, describing relatedness but not distances among *Ds* elements, is shown on the right, rooted on the unknown progenitor of the *Ac/Ds* family. It is based on a minimal evolution tree derived from the sequences of the subterminal regions at the left and right ends of the element, which are shared by all elements. In *Sh-m5933*, two elements, identical to the one shown here are inserted one within the other. (B) Nested PCR was used to detect de novo *Ds* elements formed in transgenic tobacco plants. Primer position is indicated by small arrows above (forward primers) and below (reverse primers) a schematic representation of *Ac*. The position and size of each deletion relative to *Ac* was determined by sequencing, and is shown as a bold line. Primer length is not drawn to scale.

internal deletion formation is transposition dependent and probably occurs by abortion of an *Ac*-induced gap repair. No insertions have been identified, but we are currently using different primer sets to test for such de novo events.

While only two almost identical *Ac* elements are known, an increasing number of sequences related to *Ac*-encoded transposase, from maize and from other distant species, is being reported in sequence databases. These sequences usually come from other known distantly related transposons. Other sequences, with unknown functions, have been reported as *Ac*-related. No "host" genes with a known function have been found so far, with homology to *Ac*. This suggests that *Ac* comes from a superfamily of ancient transposons rather than it being a recent host gene which became mobile. The family of *Ac*-related elements had been originally designated as the hAT family, for *hobo*, *Tam3* and *Ac* (Calvi et al., Cell 66: 465-471, 1991), other elements were added to this family as summarized by Essers and Kunze (MNL 69: 39-40, 1995). Here we report on further extension of *Ac*-related sequences with the addition of two transposons, *Hermit* and *Hector* (Fig. 2), and four sequences of unknown function. Two of these sequences, from *C. elegans*, share only one block of homology with all the other sequences. This block (see sequence in "conserved region III" by Essers and Kunze MNL 69:39-40, 1995) might be "the hAT-box" common to all members of the hAT superfamily. Two other se-

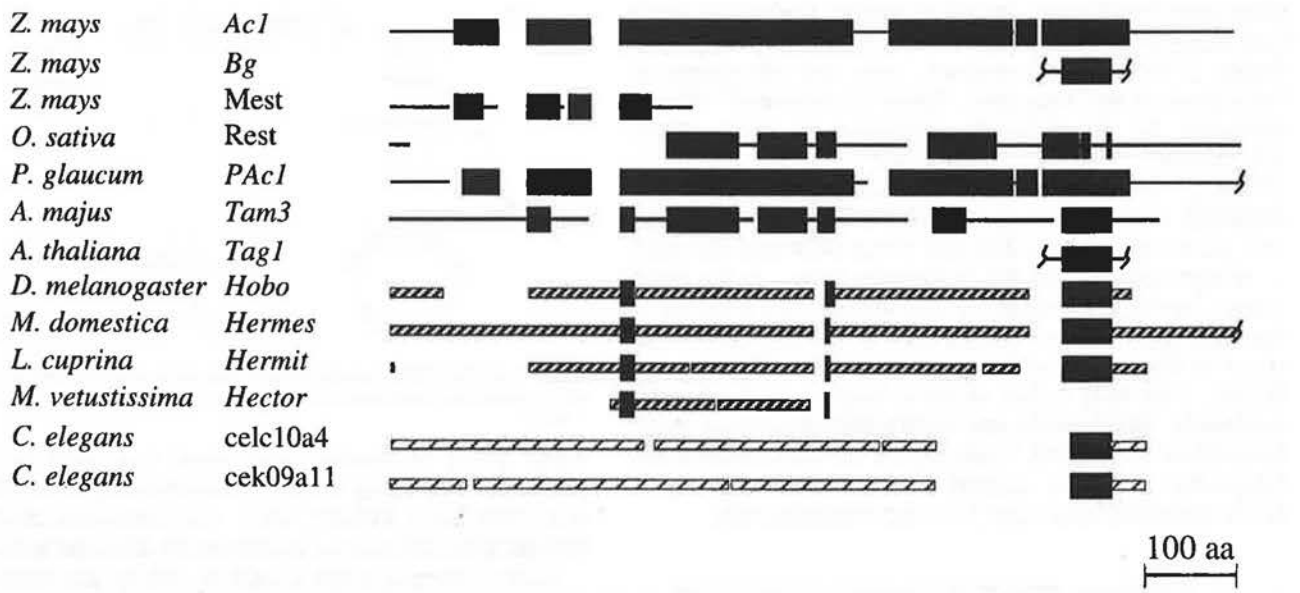


Figure 2. The hAT superfamily. Sequence databases were screened for similarity to *Ac*, *Hobo* or *Tam3* using iterative DBase searching. Alignments were performed using the Macaw package, using both the GIBBS and diagonal parsing algorithms. Sequences whose gene symbol is in italics are thought to be transpositionally active. For some sequences, obtained through genome projects of different species, no function was assigned (Mest, Rest, celc10a4 and cek09al1). For Rest alignment was done with preliminary sequencing data obtained in our lab. Boxes with similar filling are homologous. Horizontal lines indicate unique sequences.

quences, namely the maize and rice ESTs, have been recognized as entries in the plant sequences database and were further sequenced in our lab. The definition of conserved blocks in the hAT superfamily might be helpful to better understand transposase functions and to further extend the superfamily to other species.

Transcriptional regulation of *Ac* by its own transposase

-- Fridlender, M and Levy, AA

Mobility of the maize *Ac-Ds* transposable element family depends on the production of *Ac*-encoded transposase (TPase), a DNA-binding protein which recognizes internal sites near both *Ac* termini. TPase binding sites at the 5' subterminal region were mapped at or near sequences which may be important for transcription activation (Kunze and Starlinger, EMBO J. 8:3177, 1989). The proximity between the TPase binding sites and the transcription start site led us to hypothesize that TPase may regulate its own transcription, as was found for other transposable elements. This hypothesis was tested in tobacco, in transgenic plants and in protoplasts transformed with different fusions of *Ac* promoter and leader sequences to a *ß-glucuronidase* (GUS) reporter gene. The activity of the *Ac* promoter, from nucleotide 1 (at the 5' termini of *Ac*) to 346, and *Ac* promoter and leader (1-960) was determined using plasmids pAcpGUS and pAcplGUS respectively (see Fig. 1). Plasmid pJD330 (35S-GUS) was used both as a positive control for GUS expression and as a control for the TPase effect on the expression of a non-*Ac*-related promoter. In addition a promoter-less GUS gene (plessGUS) was used as a negative control (Fig. 1). A TPase-encoding construct (St-Ac) was made by subcloning the TPase gene under the regulation of a 35S promoter. All plasmids were built both in a bluescript backbone for use in transient assays and in binary vectors in order to obtain tobacco transgenic plants.

DNA from each of the GUS-fusion plasmids, or calf thymus DNA, was transformed into tobacco protoplasts, with and without the TPase producing plasmid pSt-Ac. GUS activity was determined in protoplast extracts, by the fluorimetric assay with

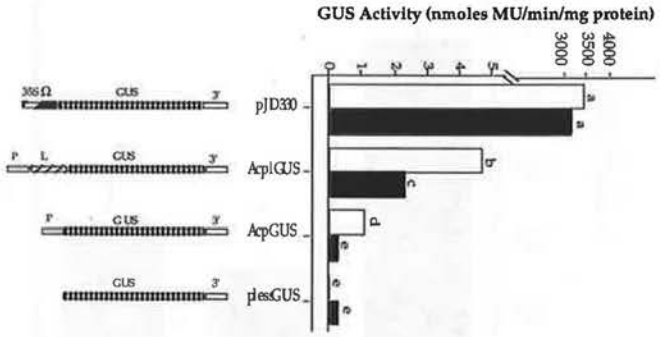


Figure 1. Transposase effect on GUS expression in transient assays. GUS activity is shown following transformation of tobacco protoplasts with constructs pJD330, pAcplGUS, AcpGUS or plessGUS, without (white columns) or with (black columns) transposase produced from clone pSt-Ac. Treatments with different letters (a to e) are different (P<0.05) as determined by a multiple ranking test (SAS, 1990).

MUG substrate. The average GUS activity of six replicates per treatment is shown in Figure 1. In treatments without the TPase-producing plasmid we found that the *Ac* promoter-leader is ~800 fold weaker than the 35SΩ promoter, as deduced from GUS activity obtained with pAcplGUS and pJD330 respectively. When GUS-carrying plasmids were co-transformed with the TPase-producing plasmid, pSt-Ac, we observed a significant reduction in GUS activity, of two fold with pAcplGUS, and four fold with pAcpGUS (Fig. 1). On the other hand, the activity of the 35S promoter in pJD330 was not affected by the TPase (Fig. 1). Therefore, we show that TPase can repress specifically *Ac* promoter expression, independently of position effects.

In order to determine the effect of TPase on *Ac* promoter activity in transgenic plants, crosses were done between T1 plants carrying the TPase producing clone (pSt-Ac) and T1 transformants carrying the GUS gene in which transcription was driven by *Ac* promoter and leader (pAcplGUS). The genotype of the progenies from three independent hemizygote T1 pAcplGUS plants X T1 pSt-Tpase was determined by Southern blots and GUS activity was measured for each of the 15-20 F1 sibling

plants grown in each cross. In such an analysis, sibling plants which have identical genetic origin and background and identical genetic dosage of the pAcplGUS construct, differ only with regards to the presence of the TPase gene. Kanamycin resistant F1 siblings segregate for the following genotypes in equal ratios: (pAcplGUS/_ , _/_) : (pAcplGUS/_, TPase/_) : (_/_, TPase/_). The effect of TPase on the element promoter was expressed as the percentage of GUS activity of double hemizygote plants carrying both GUS and TPase constructs compared to siblings carrying only the GUS-fusion gene. In the three crosses, we found a reduction in GUS activity in the presence of the TPase gene, from two fold in cross 1 to 6.5 fold in cross 28 as shown in Figure 2. Plants expressing only the TPase (_/_ , TPase/_) had GUS activity similar to background levels (data not shown). Similar results were found independently by J. Jones (personal communication). Taken together our and Jones's results suggest that the TPase-mediated repression observed occurs at the transcriptional level rather than post transcriptionally.

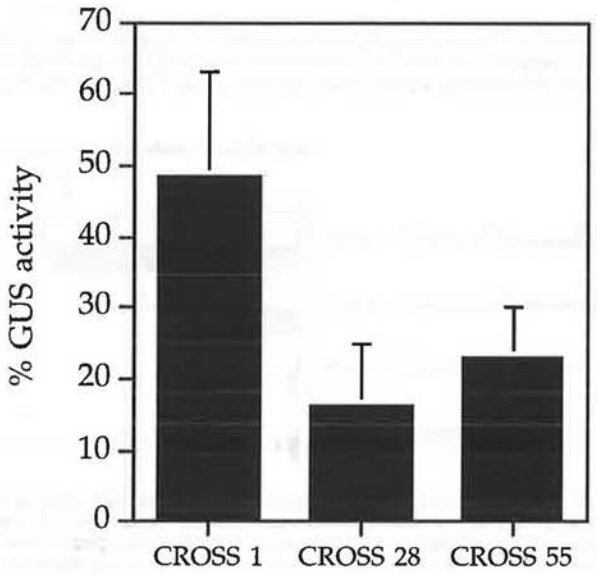


Figure 2. Transposase effect on *Ac* promoter--sibling comparisons. The transposase effect on GUS expression was studied in young leaves of F1 plants, in three crosses between pAcplGUS and TPase-producing pSt-Ac parents (cross 1, 28, 55). GUS activity of double hemizygote plants carrying both GUS and TPase constructs (as determined by Southern blots) is expressed as a percentage of the GUS activity in siblings hemizygous for the pAcplGUS construct only. The average GUS activity of the pAcplGUS siblings (the 100% value), was 9, 488, and 248 nanomole MU/mg protein/min, for cross 1, 28 and 55 respectively. Standard errors of the means are represented by bars on top of each column.

Ac joined ends are detected upon element excision

--Gorbunova, V and Levy, AA

The transposable element *Ac* has been the subject of intensive studies and is thought to transpose via a cut-and-paste mechanism. Nevertheless, little is known on how it excises and what are the intermediates of transposition. In order to test the possibility that extrachromosomal circles are formed upon *Ac* excision, we have used PCR with primers shown in Figure 1, to search for joined ends. The presence of joined ends is indicative of either circle formation or of presence of two adjacent elements in direct orientation (Fig. 1). Nested PCR was performed with primers 2 and 3 in the first round and with primers 1 and 4 in the second round. The templates consisted of genomic DNA from transgenic to-

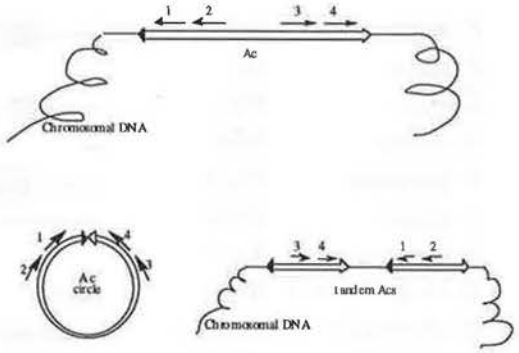


Figure 1 (A) Set of PCR primers (arrows) designed to amplify joined *Ac* ends. (B) Molecules that could serve as templates for amplification with the primers 1, 2, 3, and 4.

bacco plants transformed with constructs pAGS4411 and pAGS4081, which carry *Ac* and *Ds* elements respectively (Dooner et al., Plant Cell 3: 473-482, 1991). DNA from a line carrying the *bz2::Ds2* allele and an active *Ac* element was also used as template.

In all *Ac*-carrying plants, a band of ~520 bp was observed on EtBr-stained gels. This band has the size expected for precise joining of the terminal inverted repeats (TIRs). It was found only in lines carrying an actively transposing *Ac* or *Ds* element, but not in the absence of transposition, suggesting that its formation is transposition dependent. The 520 bp band was cloned and individual clones sequenced (Table 1). The amplified sequences

Table 1. Sequence at the junction of joined *Ac* ends

		Conceptual head-to-head joining of *Ac* ends			
	-----	*CATCCTACTTTCATCCCTG*		*TAGGGATGAAAACGGTC*	-----
		A[a]			
		Sequences of the PCR clones			
1	-----	CATCCTACTTTCATCCCTG	G	TAGGGATGAAAACGGTC	-----
2	-----	CATCCTACTTTCATCCCTG	C	TAGGGATGAAAACGGTC	-----
3	-----	CATCCTACTTTCATCCCTG	AC	TAGGGATGAAAACGGTC	-----
4[a]	-----	CATCCTACTTTCATCCCTG	GC	TAGGGATGAAAACGGTC	-----
5	-----	CATCCTACTTTCATCCCTG	GC	TAGGGATGAAAACGGTC	-----
6	-----	CATCCTACTTTCATCCCTG	CT	TAGGGATGAAAACGGTC	-----
7	-----	CATCCTACTTTCATCCCTG	CC	TAGGGATGAAAACGGTC	-----
8	-----	CATCCTACTTTCATCCCTG	AA	TAGGGATGAAAACGGTC	-----
9	-----	CATCCTACTTTCATCCCTG	TTG	TAGGGATGAAAACGGTC	-----
10	-----	CATCCTACTTTCATCCCTG	CTAA	TAGGGATGAAAACGGTC	-----
11	-----	CATCCTACTTTCATCCCTG	7 bp[b]	TAGGGATGAAAACGGTC	-----
12	-----	CATCCTACTTTCATCCCTG	21 bp	TAGGGATGAAAACGGTC	-----
13	-----	CATCCTACTTTCATCCCTG	21 bp	TAGGGATGAAAACGGTC	-----
14	-----	CATCCTACTTTCATCCCTG	27 bp	TAGGGATGAAAACGGTC	-----
15	-----	CATCCTACTTTCATCCCTG	64 bp	TAGGGATGAAAACGGTC	-----
16	-----	CATCCTACTTTCATCCCTG	GC	deletion of 33bp	-----
17	-----	CATCCTACTTTCATC	TAC	TAGGGATGAAAACGGTC	-----
18	-----	CATCCTACTTTCATC	T	ATGAAAACGGTC	-----
19	-----	CATCCTACTTTCATCCCT		GGGATGAAAACGGTC	-----
20	-----	CATCCTACTTTC		GATGAAAACGGTC	-----
21	-----	C		ATGAAAACGGTC	-----
22	-----	deletion of 41 bp		AACGGTC	-----
23	-----	CATCCTACTTTCATCCC		TAGGGATGAAAACGGTC	-----
24	-----	CATCCTACTTTCATCCCTG		GGGATGAAAACGGTC	-----
25	-----	CATCCTACTTTCATCCCTG		deletion of 29 bp	-----
26	-----	CATCCTACTTTCATCCCTG		AACGGTC	-----

a) The *bz2::Ds2* allele of maize, which generated the sequence #4, contains an insertion of *Ds* element with perfect TIRs.
b) Clones 11 - 15 contain insertions of the indicated size, sequences are not shown.

corresponded to *Ac* joined ends with short insertions or deletions in between the TIRs. Note that no molecules were found with perfect joined ends. Short deletions in both TIRs were found in 9 out of 26 sequenced joined ends. These stuctures are probably unable to reintegrate in the genome. Moreover, they cannot correspond to tandem jumps as at least one end should remain intact. Therefore we conclude that these deleted joined ends were amplified from circular molecules which are abortive transposition products formed upon element excision. Another type of molecules, which had one end intact and a deletion in the other end,

were found in 5 out of 26 sequences. These molecules could be interpreted either as transposition of *Ac* in itself near its termini, or as an *Ac* circle. In the latter case, such a circle would probably be unable to reinsert. Sequences with intact TIRs are of two types: those with insertions resembling the flanking donor site, and those with insertions unrelated to the donor. The latter are probably not caused by tandem jumps but rather by circularization of the ends. The former could in principle be caused by tandem jumps, or alternatively, flanking sequences might be carried by the circularized element as a result of the excision process. We are in the process of determining the origin of the joined ends and of the footprints between the ends. Moreover we are testing whether circular *Ds* molecules with intact termini can reintegrate into the genome via the transposition pathway.

Ac-induced homologous recombination in transgenic tobacco

--Shalev, G and Levy, AA

Ac has been shown to induce intrachromosomal recombination between direct repeats flanking *Ac* insertion in the maize *P* locus (Athma and Peterson, Genetics 128:163-173). We have further investigated *Ac*-induced homologous recombination (HR) in transgenic tobacco plants transformed with the constructs described in Figure 1. Our recombination assay is based on reactivation of

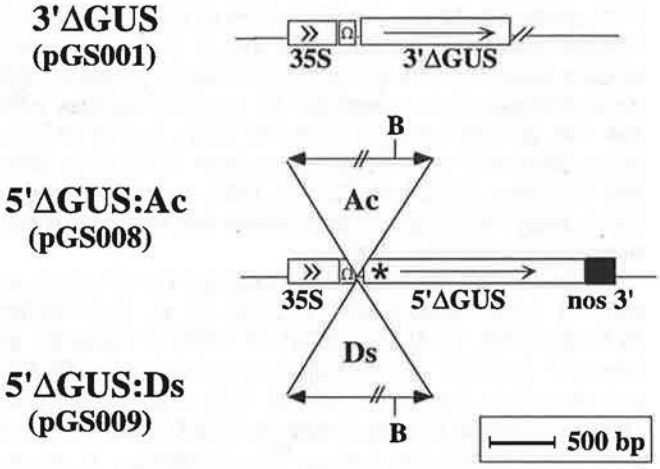


Figure 1. Constructs used to monitor homologous recombination in various tobacco tissues. *GUS* transcription is driven by the 35S cauliflower mosaic virus promoter fused to the Ω leader from tobacco mosaic virus. pGS001 and pGS008 or pGS009 were the recombination partners. pGS001 has a 500 bp deletion in the 3' end of the *GUS* gene, pGS008 and pGS009 have a 12 bp deletion in the 5' of the gene (•) which abolishes *GUS* activity. B= *Bam*HI.

the ß-*Glucuronidase* (GUS) gene following ectopic HR between two defective GUS genes. In this assay, one HR partner carries the pGS001 construct (3' deleted GUS gene). The second HR partner carries either the pGS008 construct (5' GUS deletion and *Ac* between the 35S promoter and the deletion), or pGS009 (5' GUS deletion and *Ds* between the 35S promoter and the deletion). T1 plants transformed with pGS001 were crossed with T1 plants transformed with pGS008 or pGS009. Blue sectors, following X-Gluc in-situ staining of F1 seedlings, were detected only in crosses with pGS008, i.e. in the presence of *Ac* but not *Ds*. These events are interpreted as *Ac*-induced somatic recombination between ectopic sequences. Data summarized in Table 1 suggest that *Ac* enhances ectopic recombination by at least two orders of magnitude. We are in the process of physically characterizing these putative recombination events.

Table 1. Frequency and localization of blue sectors in seedlings.

Seedling population	No. of stained seedlings [a]	No. of blue sectors detected in various seedling organs [b]				
		R	H	C	1st	Total
F_1 (5'ΔGUS:*Ac* X 3'ΔGUS)	1266	46	53	50	24	173
F_1 (5'ΔGUS:*Ds* X 3'ΔGUS)	2400	0	0	0	0	0
3'ΔGUS	3300	0	0	0	0	0
5'ΔGUS: *Ac*	1500	0	0	0	0	0
wild type tobacco	500	0	0	0	0	0

a - Kanamycin resistant seedlings were histochemically stained for GUS activity. Wild type seedlings were not germinated on Kanamycin. One third of the kan^R seedlings are double heterozygote for the 5'ΔGUS:Ac and 3'ΔGUS constructs or 5'ΔGUS:Ds and 3'ΔGUS. 3/4 are kan^R in the selfed 3'ΔGUS T_2 or selfed 5'ΔGUS:Ac seedlings. b - Blue sectors were detected in the root (R), hypocotyl (H), cotyledon (C) and first true leaves (1st).

ST. LOUIS, MISSOURI
Monsanto Co.
URBANA, ILLINOIS
University of Illinois

Wrinkled auricle (rough sheath?)

--Duncan, DR and Widholm, J

In 1988, a large plant regeneration effort was conducted to examine the type of somaclonal variation that might arise in the H99 genotype. R0 plants from approximately 9 month old cultures (initiated in the summer of 1987) were planted on the South Farm of the University of Illinois in Urbana. These plants were self pollinated and the R1 progeny were planted again on the South Farm in the summer of 1989. Five of eight progeny of a single R0 plant produced a heritable phenotype which we have called wrinkled auricle. Plants expressing the phenotype show varying degrees of folds or waves (wrinkles) of excess tissue in the region of the auricle. A normal H99 leaf has a distinct white to translucent auricle that does not extend completely around the stem. In the wrinkled auricle phenotype the auricle and leaf are wrapped around the stem. Consequently, as the girth of the stem increases the wrinkles often tear leaving tattered tissue with browning edges at the base of each leaf. The phenotype is first noticed at the V4 or V5 leaf stage and does not appear to be expressed in any manner in more juvenile tissue. In extreme cases, the plants "buggy whip" as they mature and are highly contorted but fertile. The leaf blade, per se, does not show any signs of abnormality.

We have attempted over the past several years to do genetic analysis of the trait, with little success. We know the trait is heritable but its expression is extremely sensitive to environmental conditions. H99 grows well in a greenhouse and the trait is expressed well in that environment. Space limitations have forced us, however, to attempt to work with this trait under field conditions. Under the hot and rather dry conditions of Jerseyville, Illinois we have seldom seen the trait expressed in field grown plants. Plants from remnant seed from the field plantings, when grown in a greenhouse, do express the trait.

Plants grown in the field during 1993 expressed the trait. The field conditions in 1993 were extremely wet and relatively cloudy with record levels of rainfall (the season was so wet that this field planting ended up somewhere in the Gulf of Mexico as a result of flooding). The 1993 field observation and the fact that the trait is expressed well under greenhouse conditions, suggests that the water status of a plant containing the wrinkled auricle mutation may regulate the expression of the phenotype. We also

cannot rule out a role for heat in regulating the expression of the trait, although the summer greenhouse conditions are as hot or hotter than our field conditions. It is possible that wrinkled auricle is akin to one of the rough sheath genotypes, but we have not pursued this possibility.

Presently, we do not have the facilities or commitable time to continue studying this somaclonal variant. We would be more than happy to supply seed to anyone interested in studying this material further.

ST. PAUL, MINNESOTA

The few days required to induce *Zea diploperennis* to flower in Minnesota

--Carlson, LA

In late April of 1994 65 *Zea diploperennis* plants, P.I. No. 441931, were planted in isolation in St. Paul, Minnesota. Sixty-three were induced to flower by covering them with 30 gallon galvanized trash barrels from 7:00 pm until 7:30 am for a variable number of nights. Again in 1995 volunteer plants from the shattered seeds were exposed to short days for various numbers of days. The volunteer plants from this 250 square meter plot exceeded 100 plants.

No. of plants	No. of long nights to produce silking	No. of days to flower	No. of silking locations
1	3	none	none
1	5	55 days-tassel only	none
1	7	41 days-tassel only	none
7	9	36	5
2	11	25	6
5	13	23	7
10	15	17	4
7	17	17	11

Constant observations plus data would suggest tropical maize, at least *Zea diploperennis,* can be induced to flower by covering with barrels for only 11, 12, or 13 days.

In a separate experiment 23 plants were identified at time of first silkings. Days to shattering of seed from the ear were recorded. Shattering was assumed when the top one or two seeds would disarticulate with a soft bending of the seed from the ear. Experience indicated it only takes one or two days from a ripe color until disarticulation takes place.

No. of plants	Days to disarticulation	No. of seeds collected
2	25	45
4	28	48
7	25	25
10	27	106

The seed of *Zea diploperennis* in Minnesota reached physiological maturity in 27 days during the weather conditions of August 1995.

ST. PAUL, MINNESOTA
University of Minnesota

Plastid localization of a multifunctional acetyl-CoA carboxylase

--Egli, M and Gengenbach, B

Acetyl-CoA carboxylase (ACCase; E.C. 6.4.1.2) catalyzes synthesis of the malonyl-CoA required for subsequent synthesis of fatty acids and secondary metabolites in plants. Its activity is positively correlated with rates of fatty acid synthesis in both leaves and developing oil seeds, and thus it may be important in regulating plant lipid synthesis. Current information indicates that plastidic ACCase activity in dicots is due to a multisubunit ACCase enzyme similar to that in bacteria but which is absent in the *Poaceae* (Konishi and Sasaki, Proc. Natl. Acad. Sci. 91:3598-3601, 1994). In contrast, most ACCase activity in leaves and oil-storing embryos of maize is associated with a high-molecular weight, multifunctional plastid-localized polypeptide (Egli et al., Plant Physiol. 101:499-506, 1993; Somers et al., Plant Physiol. 101:1097-1101, 1993). Complete coding sequences for higher plant MF ACCase polypeptides from wheat (Gornicki et al., Proc. Natl. Acad. Sci. 91:6860-6864, 1994), and several dicots (Anderson et al., Plant Physiol. 109:338, 1995; Roesler et al., Plant Physiol. 105:611-617, 1994; Schulte et al., Plant Physiol. 106:793-794, 1994; Shorrosh et al., Proc. Natl. Acad. Sci. 91:4323-4327, 1994) have been described. Although de novo FA synthesis occurs in plastids, these genes appear to encode cytosolic isoforms or their cellular location is unclear (Schulte et al.).

We recently published the complete coding sequence of a multifunctional maize ACCase that corresponds to one of four distinct types of ACCase genomic clones (Egli et al., Plant Physiol. 108:1299-1300, 1995; Lutz et al., 37th. Ann. Maize Genetics Conf., poster 34, 1995). The N-terminus of the predicted maize ACCase polypeptide is longer than that of predicted cytosolic ACCase isoforms and it appears to have several properties typical of chloroplast transit peptides: (1) no acidic residues within aa# 1-49, (2) high S content within aa# 23-35, and (3) an R-rich region between S- and D-rich regions (aa# 36-49) (Von Heijne and Nishikawa, FEBS Lett. 278:1-3, 1991). In vitro chloroplast import assays were used to demonstrate that this putative transit peptide is indeed functional.

Truncated ACCase cDNAs encoding the first structural domain of biotin carboxylase (Waldrop et al., Biochemistry 33:10249-10256, 1994) plus (BCN1; nt 1-833) or minus the putative cTP (-pBCN1; nt 278-833) were synthesized by RT-PCR and cloned into the *Eco*RV site of PCR-script (Stratagene). Linearized, capped transcripts were translated in vitro in a wheat germ system (Ambion) to produce ^{35}S-polypeptides. In vitro import of ^{35}S polypeptides by mesophyll chloroplasts of 7-d old leaves of maize (A188) and pea ("Little Marvel") was tested as described by Cline et al. (J. Biol. Chem. 260:3691-3696, 1985). Aliquots of the import supernatants from lysed chloroplasts and of the original in vitro-translated proteins were analysed by SDS-PAGE in 8-25% Phast gels (Pharmacia) and ^{35}S-proteins were detected by autoradiography.

Both pea and maize chloroplasts imported ^{35}S-BCN1 polypeptides but neither imported -pBCN1, which begins at ACCase aa#83 (V -> M mutation) and lacks a transit peptide. As estimated by SDS-PAGE, 30-min import converted the original 32-kD BCN1 polypeptide to a doublet of 27.2 and 27.5 kD in maize and produced an additional 30-kD band in pea. Formation of the 27.2-kD polypeptide could result from cleavage after ~aa #47, a likely cleavage site because it lies between S- and D-rich regions, and R residues are located at -2, -7,and -8 (Gavel and Von Heijne, FEBS Lett. 261:455-458, 1990). Time-dependence of BCN1 import was further examined (1-30 min) to determine if any imported polypeptides were a result of incomplete processing or proteolysis. Import was maximal after 15 min, but import time

had no effect on the relative amounts of different-sized import products. The data suggest that, in maize, efficient cleavage of BCN1 occurs at two closely adjacent sites and that partially-processed products are also formed during BCN1 import by pea chloroplasts.

The maize ACCase gene described here (Genbank accession # U19183) encodes a protein that contains a chloroplast transit peptide which functions in both monocots and dicots; this is the first plastidic multifunctional ACCase to be identified in a higher plant.

Characterization of two unique Long Interspersed Nuclear Elements (LINEs), *colonist1* and *colonist2*

--Lutz, S and Gengenbach, B

Maize acetyl-CoA carboxylase (ACCase) is encoded by a small gene family, of which four genes have been characterized: A1, A2, B1, and B2. Type A and B genes are 96% identical, with conserved introns and 3' non coding regions. Differences within the A1-A2 and B1-B2 pairs occur mainly in flanking sequences. The Type B genes are also distinguishable from the Type A genes, and from each other, by the presence of an insertion into an intron 1400 bp from the translational start site of A1. Type A genes do not contain this insertion and the insertion in the B1 and B2 genes varies in size and sequence arrangement.

The insertion in Type B1 is at least 6kb and is flanked by a 3-bp direct repeat. Nucleotide sequence of this insertion shows the presence of two unique domains encoding polypeptides with homology to the reverse transcriptase (RT) domains of LINE-like non-viral retrotransposons, which include three LINEs from plants: *Cin4* from maize (Schwarz-Sommer et al., EMBO J. 6:3873-3880, 1987) , *del2* from lily (Leeton et al., Mol. Gen. Genet. 237:97-104, 1993), and *BNR* from sugar beet (Schmidt et al., Chromosome Research 3:335-345, 1995). Genomic library screening with each of the two RT domains from maize ACCase Type B1 resulted in two different sets of positive clones (none of the positives from either set contain both RT domains together, as in B1), suggesting these RT domains are part of unique LINEs. These unique elements are designated *colonist1* and *colonist2*.

LINEs were first discovered in mammals and have now been found in every eukaryotic species examined. LINEs are believed to move via an RNA intermediate and are characterized by the following features: lengths of 6-7kb, frequent deletions of the 5' end, two open reading frames (one coding for a reverse transcriptase), two cysteine-binding motifs, short direct repeats usually <20bp, and an adenine rich terminus. LINE copy number is variable with mammalian LINEs being highly abundant (10^4 to 10^5 copies per genome) while *Cin4* is moderately abundant (50-100 copies per genome) (Hutchinson, In: Mobile DNA, DH Berg, MM Howe, eds., Amer. Soc. Microbiology, Washington DC, pp 593-617, 1989; Z. Schwarz-Sommer et al., 1987).

Characterization of *colonist1* and *colonist2* suggests that *colonist1* inserted first into this ACCase intron with *colonist2* subsequently inserting into *colonist1*. Sequence from the 3' end of *colonist1* has 73% identity over 480 nucleotides, in reverse orientation, to the largest (1.8kb) intron from *shrunken2* of maize (Hannah et al., Plant Physol. 98:1214-1216, 1992). *Colonist1* is characterized by a RT domain having much greater amino acid identity (40% in 102 amino acid overlap) to Q, a LINE from mosquito (Besansky, Insect Mol. Biol. 3(1):49-56, 1994), than it does to *Cin4* from maize. Neither of the two copies of *colonist1* so far studied contain an adenine rich terminus. *Colonist2* has an RT domain with 44% identity to *Cin4* over 198 amino acids of overlap and contains the consensus CX1-3CX7-8HX4C cysteine motif characteristic of the 3' end of this open reading frame. *Colonist2* appears to have an adenine rich terminus of variable length. Genomic Southerns showed *colonist1* and *colonist2* to be present in the genome at a copy number of 100-500.

LINEs are generally present as a single family within a given species with the exception of *Drosophila melanogaster* which has several families of LINE-like sequence (Di Nocera et al., Genetica 94:173-180, 1994). With the addition of *colonist1* and *colonist2* to the list of characterized LINEs, maize becomes the first plant genome shown to contain more than one family of LINE sequences.

STE-ANNE-DE-BELLEVUE, CANADA
McGill University

Reaction of waxy and non-waxy maize inbreds infected with *Fusarium graminearum*

--Chungu, C and Mather, DE

Fusarium graminearum Schwabe, the asexual state of *Gibberella zeae* (Schw.) Petch causes ear rot of maize in most maize growing areas in the world. The pathogen penetrates ears by growth of the mycelia down the silks to the kernels or through wounds made by insects or birds. The characteristic symptom of the disease is a pink to reddish coloration on the surface of infected kernels and husks.

Warren (Phytopathol.68:1331-1335, 1978) observed that some *opaque-2* maize inbreds were more susceptible to *F. moniliforme* ear rot than their normal-endosperm counterparts. Similar observations were reported by Reid et al. (Can. J. Plant Sci. 72:915-923, 1992) with *F. graminearum*. *Opaque-2* kernels tend to be softer, which may allow pathogens to penetrate the kernels easily.

Waxy maize differs from normal dent maize in that its endosperm starch is 100% amylopectin whereas that of normal maize is composed of 75% amylopectin and 25% amylose. This difference is important to the manufacturers of food and industrial products. According to Coe et al. (Corn and Corn Improvement, p142, 1988), the waxy kernel type displays uniform marble-like opacity and has kernel hardness similar to that of normal kernels. Little is known about the relative resistance of waxy inbreds and their non-waxy counterparts to ear rot caused by *F. graminearum*. The objective of this study was to compare the responses of waxy and non-waxy inbreds to *F. graminearum*.

An experiment was conducted at Ste-Anne-de-Bellevue (Quebec, Canada) in 1993 (the experiment was seeded again in 1994, but failed due to poor germination). Eleven waxy and non-waxy inbreds (seed provided by David Bauté from MaizeX, Ontario and R.I. Hamilton, Plant Research Centre, Ottawa) were planted in a split-plot design with four replications. Inbreds were randomized as main-plot units and two inoculation methods (silk channel injection and a kernel-stab technique) as subplots. Individual ears were inoculated by: (a) injecting 2 ml of the macroconidial suspension in the centre of the silk channel seven days after silk emergence, and (b) by inoculating the ears using a kernel-stab technique, 15 days after silk emergence. In the latter technique, a probe consisting of four nails (1.5 cm) fixed to a cylindrical wooden handle was dipped into inoculum and then used to stab

through the husk to wound three to four kernels in the middle of the ear. Primary ears of the waxy inbreds were bagged before silking to avoid contamination with pollen from their normal counterparts and were later hand-pollinated. Inoculated ears were harvested in mid-October and disease severity assessed by rating the percentage of rotted area using a 7-class kernel rating scale where 1= no symptoms present, 2=1-3%, 3=4-10%, 4=11-25%, 5=26-50%, 6=51-75%, and 7=76-100% of the kernels infected. Disease incidence was calculated as the percentage of ears with severity rating of 2 or greater. Data were analyzed using the general linear models analysis of variance, and mean comparisons were performed using Duncan's multiple range test.

Effects due to inbreds were significant ($P<0.05$) for both disease incidence and severity (Table 1). Differences between the two inoculation methods were significant only for disease severity.

Table 1. Mean values for disease severity and incidence in waxy and non-waxy inbred lines with inoculation techniques at Ste-Anne-de-Bellevue in 1993.

	Silk-Channel		Kernel-stab	
Genotype	Severity	Incidence	Severity	Incidence
A632	5.4ab†	92a	5.6a	96a
A632Htwx	5.5ab	100a	5.4a	96a
A641	5.1ab	100a	5.7a	100a
A641Htwx	4.7ab	100a	5.7a	100a
CM105	6.1a	100a	5.1a	100a
CM105wx	5.8ab	100a	6.1a	100a
LH74*LH146wx	5.8ab	100a	6.2a	100a
LH82	4.5b	100a	5.5a	100a
LH82wx	5.3ab	100a	5.8a	100a
Mo17Ht	6.2a	100a	6.1a	100a
Mo17wx	4.5b	100a	4.9a	100a

†Means followed by the same letter within columns are not significantly different at 0.05 probability level.

Disease incidence values were high for both waxy and non-waxy inbreds. Most inbreds exhibited high disease severity with both inoculation methods. Three inbreds, A641wx, LH82 and Mo17wx had only moderate disease severity after silk-channel injection. However, these inbreds were all susceptible with the kernel-stab method. One inbred, Mo17wx, exhibited lower disease severity than its normal counterpart. It appears that most of the inbreds evaluated in this study do not have sufficient resistance in the silk and kernels to slow or inhibit the spread of ear rot.

To avoid pollen contamination, the ears of the waxy inbreds were bagged prior to silking and the bags remained on the ears four weeks postinoculation. The environmental conditions within the bags could have influenced the spread of ear rot on the waxy inbreds. Enerson and Hunter (Can. J. Plant Sci. 60:1123-1128, 1980) found increased colonization intensity in ears inoculated with a toothpick and bagged for 35 to 63 days. In contrast, Sutton and Baliko (Can. J. Plant Pathol. 3:26-32, 1981) found that bagging after inoculation suppressed the growth of *F. graminearum*. In this study, it was not possible to determine the effect bagging had on disease development.

This study showed that the inbreds differed in their reaction to infection by *F. graminearum* when the silk channel method was used, however, none of the waxy inbreds differed from their non-waxy counterparts. No significant difference was observed among inbreds when inoculum was directly applied to the kernels. We did not find any evidence that the waxy endosperm trait confers ear rot resistance or susceptibility. However, our comparisons of waxy vs. non-waxy lines were confounded by the fact that ears of the waxy lines were bagged to prevent pollen contamination.

SENDAI, JAPAN
Tohoku University
JOETSU, JAPAN
Hokuriku Natl. Agr. Exp. Stn.

Heterochromatic knob-specific repeated sequence is associated with the formation of chromosome bridges in cultured cells and in germinating roots of aged seeds

-- Fluminhan Jr., A; Ohmido, N; Fukui, K; Kameya, T

The behavior of chromosomes in anaphase cells of embryogenic calli (Type II cultures) has been analysed by means of fluorescence in situ hybridization (FISH) with the 180-bp highly repeated DNA sequence found to be a major component of maize heterochromatic knobs (Peacock et al., PNAS 78:4490-4494, 1981; Dennis and Peacock, J. Mol. Evol. 20:341-350, 1984). Configurations showing the delayed segregation of sister-chromatids, considered to be an initial event in the development of bridges (MNL 66:87-88, 1992; Fluminhan and Aguiar-Perecin, in press), were hybridized in situ with the probe pZm4-14 (kindly supplied by Dr. James Birchler, Univ. of Missouri). Plasmid DNA with the insert was used as the template for direct-labelling during PCR amplification. Biotin-labelled probes were hybridized at 37 C for 8 hours, in a 2xSSC / 50% formamide solution, after heating at 70 C for 6 min., according to Fukui et al. (Theor. Appl. Genet. 87:893-899, 1994). After staining with fluorescein-isothiocyanate (FITC)-avidin conjugate, signals were amplified by applying a biotinylated anti-avidin solution, followed by incubation with a fluorescein-avidin solution. Chromosomes were then counterstained with a DAPI solution, and examined by fluorescence microscopy. Images were captured by a cooled CCD camera (Photometrics) mounted on the microscope. Digitized images were photographed by a color image recorder.

FISH with selected anaphase configurations confirmed the involvement of the knob-specific repetitive sequence with the event of delayed segregation of sister-chromatids (Figure 1). This observation seems to correspond to the hypothesis described by Phillips et al. (Proc. 7th Intl. Cong. Plant Tissue Cell Cult., pp. 131-141, 1990), that variation in DNA methylation could be a principal factor in the occurrence of chromosome breakage in tissue cultures. Dennis and Peacock (1984) have reported that the 180-bp repeats could show up to ten CG or C_G regions among the different clones sequenced. Since these sites are recognized to be particularly susceptible to methylation of the cytosine, the detection of methylated bases by in situ procedures, as reported in mammalian cells (Miller et al., Nature 251:636-637, 1974), represents an interesting aspect for future investigation.

Furthermore, we have analysed chromosomal aberrations arising during the first mitosis in root tips germinated from long-term stored seeds of different genotypes. Configurations showing the initial event of delayed segregation of sister chromatids have been analysed by FISH as described above. The results were very similar to those observed in cultured cells (Figure 2). This observation suggests that both systems (culture in vitro and storage of dried seeds) could be under the influence of common or related mechanisms of cellular senescence, which would lead to the occurrence of apparently identical cytological abnormalities at mitosis, as discussed elsewhere (Fluminhan and Kameya, Theor. Appl. Genet., in press).

The behavior of broken chromosomes through successive cell divisions has also been investigated. We have collected evidence

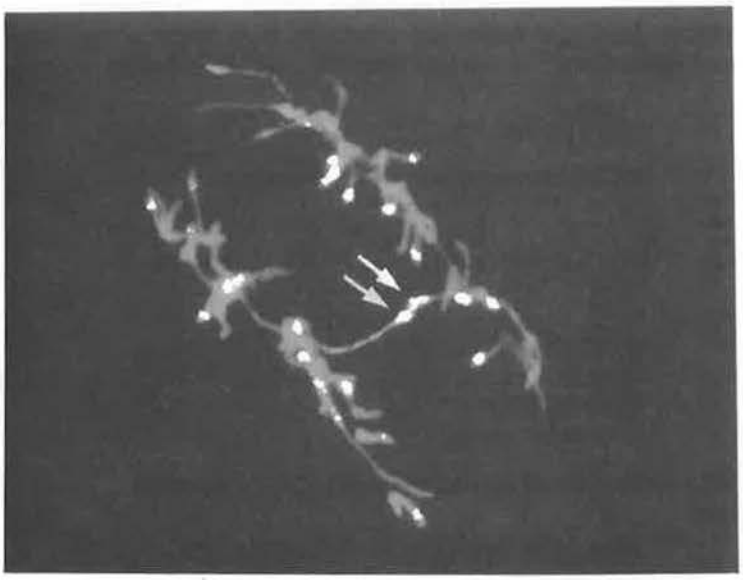


Figure 1. Anaphase cell of an embryogenic callus of S5 progeny obtained from cv. Mexico Amber Kernel after fluorescence in situ hybridization (FISH). The arrows show hybridization sites to the knob-specific repeated sequence on the initial event of delayed segregation of sister chromatids.

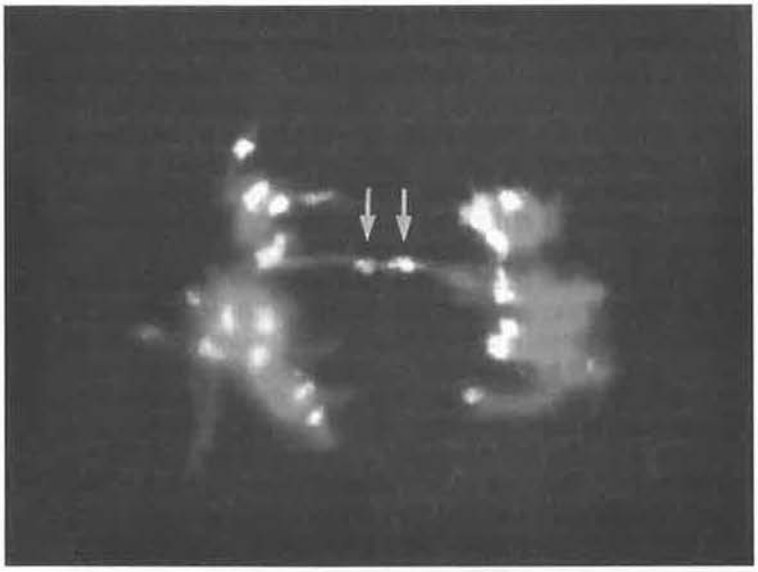


Figure 2. Anaphase cell of germinating roots of aged seeds after FISH. The arrows show hybridization sites on a configuration of delayed segregation of sister chromatids.

indicating the occurrence of breakage-fusion-bridge cycles in both systems. Figure 3 shows a late anaphase observed in our studies with cultured cells, with one single bridge containing two hybridization sites to the knob-specific sequence. This figure could have originated from successive B-F-B cycles, as illustrated in Figure 4. Analysis of such configurations by FISH with the telomeric repetitive sequences (TTTAGGG)n has supported the proposed mechanisms. A complete report on these findings is in preparation.

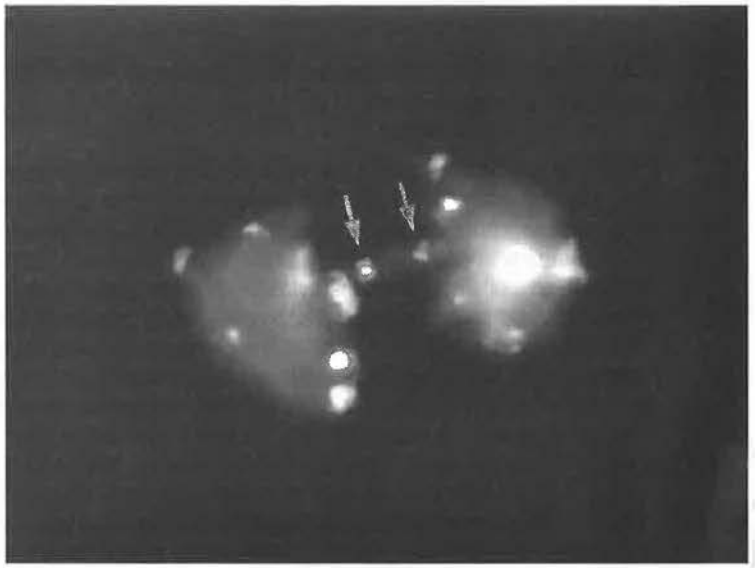


Figure 3. Late anaphase of cultured cells after FISH with the knob-specific repeated sequence. The arrows show hybridization sites on a chromosome bridge possibly originated from successive breakage-fusion-bridge cycles.

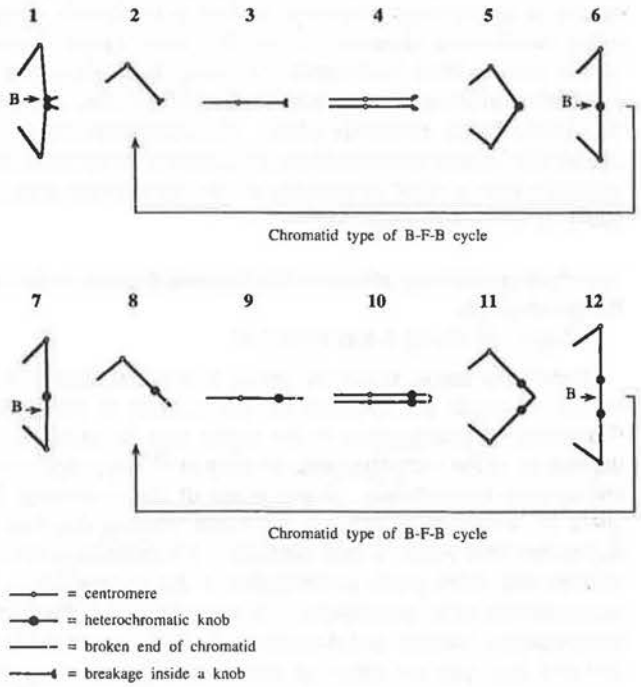


Figure 4. Diagram illustrating the origin of a broken chromosome at mitotic anaphases in cultured cells and in root tips from germinating aged seeds of maize, and its subsequent behavior. 1. Bridge configuration resulting from the initial event of delayed segregation of sister-chromatids (Figures 1 and 2). 2. Primary breakages frequently occur inside the knob. 3. One of the sister cells receives a deficient chromosome with a freshly broken end. 4. Fusion of replicated broken ends during the subsequent mitosis. 5 and 6. A dicentric chromosome is formed that will undergo the chromatid type of breakage-fusion-bridge cycle during each successive nuclear division, conforming to the behavior described by McClintock (PNAS 25:405-416, 1939; Genetics 26:234-282, 1941) with the analysis of gametophyte tissues. 7. Bridge configuration resulting from a previous round of breakage-fusion-bridge. 8. Breakage between the centromere and the knob of the dicentric. 9. The chromosome containing the knob and a freshly broken end is sent to one of the sister cells. 10. Fusion of the replicated broken ends. 11. A dicentric with two knobs is formed (Figure 3). 12. Breakage at different locations gives rise to diverse deficient-duplicated chromosome types. Letter B indicates positions of breakages. A further discussion about these mechanisms is presented in Fluminhan and Aguiar-Perecin (in press) and in Fluminhan and Kameya (Theor. Appl. Genet., in press).

STANFORD, CALIFORNIA
Stanford University

The effect of 5-azacytidine treatment on *Mutator* activity when applied to developing kernels

--Taylor, R and Walbot, V

MuDr is an autonomous element of the *Mutator* family inserted into the *Bronze2* gene (*Bz2*). Methylation has been implicated in the down regulation of *Mutator* activity. To reactivate the inactive *Mutator* element, developing kernels were treated with 5-azacytidine, an inhibitor of DNA methylation. *Mutator* stocks containing *bz2::MuDr* have shown no *Bz2* function when crossed to *bz2* lines for 6 generations. The reporter line generates excision spots when crossed with an active *Mutator* line, but when self-crossed or outcrossed to *bz2* this inactive line yields only about one excision spot per 50 ears. To assess the role of DNA methylation in the inactivity of *MuDr*, 5-azacytidine was applied to young ears and excision of the *Mutator* was observed as anthocyanin spots on mature ears. Using a method previously described (Walbot et al. Maydica 39:19-28, 1994) the husk tissues were carefully peeled back from ears 10-15 days after fertilization and small paper towels soaked in either water or 10 mM 5-azacytidine were applied. The husk tissues were replaced with the aid of an elastic band. Only one application was applied to the ears. The ears were harvested and scored for the presence of excision sectors on the kernels. No excision events were observed in either the water control (6 ears) or the 5-azacytidine treatments (16 ears), suggesting that 5-azacytidine treatment during kernel development does not affect the activity status of inactive *MuDr*. The experiment will be repeated with additional applications of 5-azacytidine because short exposure time or rapid breakdown of the 5-azacytidine may account for the lack of reactivation.

Toxicity of cyanidin and anthocyanidin 3-glucoside accumulation in the gametophyte

--Taylor, R; Chiusi, A and Walbot, V

Functional maize pollen is yellow due to the presence of flavonoids which are required for germination of the pollen. Production of anthocyanin in the pollen can be obtained via expression of the *r-ch:Hopi* gene, an allele of *R*. *R* is a regulator of anthocyanin biosynthesis. A proportion of plants carrying this allele in combination with *Pl* produces varying degrees of expression from yellow to dark red pollen. It is presently unknown whether this anthocyanin accumulation is due to sporophytic or gametophyte gene expression. To test whether anthocyanin intermediates, cyanidin and cyanidin 3-glucoside accumulated by *bz1* and *bz2*, had an effect on pollen viability, we compared segregation ratios of pollen with and without anthocyanin. These anthocyanin intermediates are known to be toxic to maize plants when expressed at high levels. We used plants with genotypes *Bz1/bz1* and *Bz2/bz2* which also contained at least one copy of *r-ch:Hopi* and *Pl*. Reciprocal crosses were made to *bz1* and *bz2* tester and ears were analyzed for their segregation ratio. If the accumulation of these products had no effect on the viability of the pollen we would expect purple to bronze kernels at a ratio of 1:1. The table shows the segregation ratios for the test crosses.

No significant differences in the segregation ratios were observed between the yellow pollen and red pollen crosses. The segregation ratios were 1:1 among test and control crosses. Therefore pollen viability does not seem to be affected by the accumulation of cyanidin and/or cyanidin 3-glucoside. To ascertain whether there is a sporophytic effect, the toxic affects of homozygous *bz1* and *bz2* *r-ch:Hopi* plants are now being examined.

	Bronze1 Number of ears (95%) Segregation ratios (purple:bronze)				Bronze2 Number of cases (95%) Segregation ratios (purple:bronze)		
Color	1:1	>1:1	1:>1	Color	1:1	>1:1	1:>1
Yellow	8	0	0	Yellow	21	1	0
Red	9	1	0	Red	13	1	0
Pink	3	0	0	Pink	5	1	0

STANTON, MN
Northrup King Co.
ODENSE, DENMARK
Odense Universitet

RFLP map position of the casein kinase 2 (CK-2) α subunit in maize

--Hanten, J; Edwards, M; Warner, T; Boldyreff, B and Issinger, O-G

Casein kinase 2 (CK-2) is a ubiquitous and multifunctional serine/threonine specific protein kinase that has been implicated in the control of cell growth and proliferation. CK-2 has been characterized extensively in animals and has been shown to phosphorylate various protein substrates including RNA polymerases, topisomerases, oncoproteins, and certain receptor proteins. In plants, less is known about the substrates of CK-2. The subunit composition of CK-2 in animals is α, α', and β with molecular weights of 42, 38, and 28 kDa, respectively. The holoenzyme is comprised of a tetramer consisting of α, α', and β2. Two CK-2-like enzymes have been isolated in maize, CKIIA and CKIIB, with reported molecular weights of 135 and 39 kDa respectively (Dobrowolska et al., Eur. J. Biochem. 204:299-303, 1992).

To confirm the presence of a CK-2 α gene in maize, a maize cDNA library was screened with oligonucleotide probes specific for conserved regions of the animal CK-2 α. A clone was isolated which exhibited a 75% protein sequence homology to the human CK-2 α (Dobrowolska et al., BBA 1129:139-140, 1991). This clone was expressed in *Escherichia coli* with a reported molecular weight of 39 kDa and designated as recombinant maize CK-2 α (rmCK-2 α) (Boldyreff et al., BBA 1173:32-38, 1993). This work has demonstrated that the rmCK-2 α is functionally similar to the recombinant human CK-2 α (rhCK-2 α) in several respects. First, the rmCK-2 α was shown to be immunologically similar to the rhCK-2 α by western analysis with affinity purified polyclonal and monoclonal anti-human CK-2 α antibodies. Second, the rmCK-2 α self assembles with the rhCK-2 β to form a complex which sediments at the same position as the native mammalian CK-2 holoenzyme. Third, similar phosphorylation profiles are exhibited between rmCK-2 α and rhCK-2 α when different substrates and various polyamines are assayed.

Maize CK-2 α was characterized in a RFLP mapping population to establish its chromosomal map position. It was anticipated that this information would be useful in determining linkage and homology among other maize casein kinase-like genes as they become mapped. An 896bp portion of the maize CK-2 α open reading frame was mapped by RFLP in a F2 population with 200 individuals using 68 polymorphic markers spread over the genome. It was determined with MAPMAKER IBM version 3.0b that maize

CK-2 α was located on the long arm of chromosome 2 (2L) approximately 9.6 centimorgans (cM) distal from *umc36*. In a selfed population with 300 individuals using 108 polymorphic markers, the maize CK-2 α probe mapped again on chromosome 2L, 4.9 cM distal from *umc36*. A secondary polymorphism mapped to the short arm of chromosome 4 (4S), 4.5 cM proximal to *bnl5.46*. It is not clear what degree of homology exists at chromosome 4S, but it is possible that this secondary sequence arose via chromosomal duplication, a well characterized feature of the maize genome (Helentjaris et al., Genetics 118:353-363, 1988). It is also possible that another casein kinase-like enzyme or a distinctly different enzyme within the maize genome share homology with maize CK-2 α.

TSUKUBA, JAPAN
National Institute of Agrobiological Resources

Agrobacterium-mediated gene transformation in maize

--Ishige, T

Generally, genetic transformation in grasses has been achieved by particle bombardment of intact tissues or electroporation of protoplasts. Recently *Agrobacterium tumefaciens* has been used to introduce foreign genes into rice chromosomes, and fertile rice transformants were obtained (Hiei et al., Breeding Science Suppl. 1:52, 1994). We report here the gene transformation of maize using the Ti-plasmid vector of *A. tumefaciens*.

Maize calli were initiated from immature embryos of F2 seed of an A188/B73 cross. Type II calli were selected and their regenerability was evaluated. The chimeric gene RB-NoS-NPTII-35S-HPT-35S-GUS-LB was constructed in PBI 101 binary vector and was transformed into LBA4404 strain of *A. tumefaciens* by electroporation. Maize calli were co-cultured with *A. tumefaciens* for three days in liquid N6 medium containing 2 mg/l of 2,4-D and the calli were transplanted in N6 selection media containing 2 mg/l of 2,4-D, 0.25 mg/l of hygromycin B, 3 mg/l of cefotaxime and 0.3% of gelrite. The GUS activity of selected calli was analyzed by staining the intact tissues. The calli were transferred to N6 regeneration medium lacking hormones and containing 0.25 mg/l of hygromycin B, 3 mg/l of cefotaxime and 0.3% of gelrite. The regenerated shoots were transplanted in soil and the genomic DNA of the leaf was extracted to confirm the integration of the introduced gene by PCR and Southern blot analysis.

All of the callus lines infected with *A. tumefaciens* showed a blue color due to their GUS activity and GUS activity was not expressed in control calli in the absence of *Agrobacterium* infection (Fig. 1). The Southern blot analysis and PCR showed that the introduced gene was integrated in the corn genome (Fig. 2). A gene transfer method of maize using *A. tumefaciens* infection was thus developed.

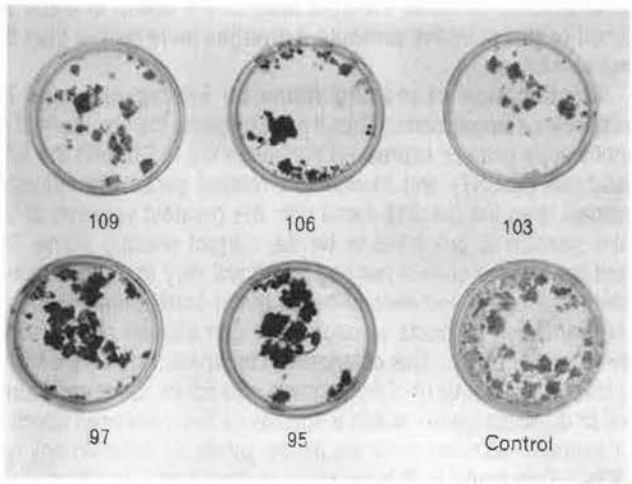


Figure 1. Expression of GUS in maize tissues after co-cultivation with *A. tumefaciens*. The numbers are given to distinguish the calli from other cell lines of the F2 embryo. The GUS activity was determined by staining cells with X-gluc. The activity level varied among callus lines. Control calli without gene transformation did not show any GUS activity.

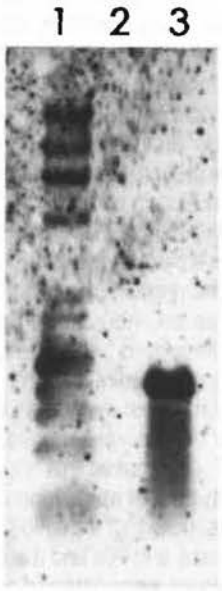


Figure 2. Southern analysis of the transformed maize. Lane 1: λ*Hin*dIII, φχ174*Hae*III size markers. 2: control. 3: transformed maize by *A. tumefaciens*. DNA (10μg) was digested with *Bam*HI, and separated by electrophoresis in a 0.7% agarose gel. The DIG-labeled DNA of the HPT region was used as a probe of hybridiza tion.

TUCSON, ARIZONA
University of Arizona

Identification of anonymous maize coding sequences by evolutionary considerations

--Winkler, RG

In the past year I have worked with two anonymous maize cDNAs; in both cases there was no obvious preferred reading frame. In both cases there was no AUG near either 5' end nor were there stop sites that eliminated any of the reading frames from consideration. Although the sequence of one was extended by RACE, there still was not an AUG near the 5' end. In both cases I have been able to define a reading frame using a simple evolutionary

consideration: Because the third base of the codon is under reduced or little selective pressure it diverges more rapidly than the first two bases.

Identification of reading frame by interspecies and intraspecies comparisons. Thus if one compares the sequence of an anonymous gene or expressed sequence tag (EST) with the EST database (dbEST) and identifies a related gene with sufficient overlap, then the reading frame with the greatest variation at the third position is predicted to be the correct reading frame: the third base of the correct reading frame will vary at a much higher rate than the first and second bases of the correct reading frame. The translated products of each gene can also be compared to give a similar result. This criterion can be applied in multiple ways: 1) from any genomic or cDNA sequence to ESTs, 2) for gene families or duplicate genes within a species or even between species, for example between duplicate maize genes, 3) between any two ESTs. This could in fact be used to systematically identify the reading frames of anonymous ESTs or genomic sequences.

Identification of reading frame by identification of internal duplications within a gene. In addition to gene duplication, a second driving force in evolution is internal duplication to produce repeated peptide units. Thus internal duplications within a gene can also be used to predict correct reading frames by the same third position criteria. This can be approached by matrix analysis of the predicted peptides to determine which frame conserves the peptide repeats. This could also be used to systematically define the reading frames of many anonymous ESTs and similarly could be applied to genomic sequences as a test of the possibility that duplicated sequences are protein coding.

Identification of the limits of the coding sequence by interspecies and intraspecies comparisons. A related criterion can be used to predict the gene product of a genomic or cDNA sequence. Since coding sequences are under much greater selective pressure than the 5' and 3' untranslated sequences, interspecies comparisons can be used to predict coding regions. This has been used in the past for many known genes: the human to mouse comparison is very powerful as are interspecies comparisons in plants. The rapid increase of EST data makes this approach more widely applicable. When I compared an anonymous fully sequenced maize cDNA with dbEst I observed that a peptide of 80 amino acids was conserved between maize and rice and maize and *Arabidopsis* (the rice and *Arabidopsis* genes were obtained and fully sequenced). In addition to establishing the correct reading frame this suggested that the entire protein was 80 amino acids long as there was no conservation beyond this. This was surprising because the first AUG of the maize gene was at bp 300 which is unusually long for a 5' leader sequence. There were no stop sites in the first 300 bp. Although it is possible that exon-sharing could be an explanation for this conservation, it is not likely as this transcript is single copy.

The value of these approaches is that by simple computer comparisons one can rapidly derive testable hypotheses that predict the coding frame and coding region of an anonymous sequence. Once a peptide is identified it is much easier to start deriving hypotheses on its function by further analysis.

Update on the genetic mapping of the *opaque2*-modifier genes

--Moro, GL; Carneiro, N and Larkins, B

o*paque2*-modifiers are genes with the ability to convert the soft chalky endosperm, as found in maize *opaque2* mutants, to a hard, vitreous phenotype. Modified *opaque2* genotypes or Quality Protein Maize (QPM) have increased levels of the essential amino acid lysine and a normal appearing kernel. QPMs have been developed independently at CIMMYT (Mexico) and University of Natal (South Africa). Our lab is working on the biochemical, genetic and molecular characterization of endosperm modification (for details see Lopes et al., MNL 69:125, 1995). Genetic mapping using CIMMYT's QPM identified two loci associated with modification, the first near the telomere of chromosome 7L and the second at the 27-kD γ-zein locus, near the centromere on 7L (Lopes et al., Mol. Gen. Genet. 247:603-613, 1995). We are now extending the mapping effort to QPM lines from South Africa. Two crosses are being analyzed: G10 QPM x W64A*o2* and G6 QPM x W64A*o2*. Our strategy is to perform bulked segregant analysis in the F2 generation in order to identify RFLPs associated with the modified phenotype. So far we found only one modifier closed linked to the γ-zein locus. We could not find any polymorphism near the extreme of 7L. Also, our results suggest that the duplicated γ-zein locus (AB) is not necessary for modification, as previously thought. Among the 27 F2 individuals of the modified bulk in the G10 (AB locus) x W64A*o2* (ReA locus) cross we found one plant heterozygous for the γ-zein locus (ReAAB). Its seeds had all clearly vitreous endosperm with no phenotypic segregation for modification. The zein profile of these seeds was typical of modified *opaque2* endosperm, with high levels of γ-zein and low levels of α-zein. Some F3 plants originated from these seeds had the ReA γ-zein locus and their seeds were also fully modified. We are now performing the biochemical analysis of these seeds to verify their zein profile. Also we continue to cover other areas of the genome looking for other loci involved in the process of modification.

TUCSON, ARIZONA
University of Arizona
WEST LAFAYETTE, INDIANA
Purdue Univeresity

Elongation factor-1α (EF-1α) is a biochemical marker for lysine content in maize endosperm

--Moro, GL; Habben, JE; Carneiro, N; Hamaker, B and Larkins, B

We recently reported a very high correlation ($r = 0.95^{**}$) between the content of lysine and the concentration of the protein synthesis factor EF-1α in the maize endosperm (Habben et al., PNAS 92: 8640-8644, 1995). In order to extend our analysis to a broader sample of the maize germplasm we characterized 93 normal and *opaque2* inbred lines. Amounts of total protein, zeins and non-zeins were measured by microKjeldhal, and lysine content was determined by amino acid analysis. For twenty selected genotypes covering the observed range of lysine content an ELISA was used to estimate the relative concentration of EF-1α and a ninhydrin assay was used to determine the relative levels of free amino acids. Considerable differences in lysine and protein contents were observed among normal and *opaque2* genotypes, with the effect of the mutation being highly dependent on the genetic background. Not surprisingly, the lysine content was significantly correlated with the non-zein fraction ($r = 0.83^{***}$ for all genotypes and $r = 0.80^{***}$ for the selected lines). Most of endosperm lysine

is protein-bound and, essentially, all the lysine-containing proteins are non-zeins. Confirming our previous results, a high correlation ($r = 0.88^{***}$) was observed between EF-1α and lysine contents. It is remarkable that a single protein is at least as predictive of the lysine content as the total non-zein fraction. The nature of this relationship is still unknown. Although EF-1α is a lysine-rich protein its mass accounts for only 3-5% of the total lysine in the endosperm. Therefore, the high correlation must reflect some commonality between EF-1α and other lysine-rich proteins. We are now working on identifying such proteins. Independent of that, this relationship provides an approach to study the mechanisms regulating the synthesis and accumulation of lysine-rich proteins. We are also investigating the levels of heritability for EF-1α content, in order to assess its utility as an index for lysine content in breeding programs. Additionally, we are working on the characterization of the maize EF-1α gene family.

URBANA, ILLINOIS
University of Illinois and Maize Genetics Cooperation Stock Center

Chromosome location of the three Oh51A pseudorestorer genes and their usefulness in studying apparent cases of gene silencing

--Gabay-Laughnan, S

The Laughnan laboratory has been identifying and analyzing spontaneous nuclear restorer genes of *cms-S* for over two decades. Among the many spontaneous nuclear revertants that have been identified is a class we now refer to as "pseudorestorer" (MNL 63:122, 1989; MNL 63:122-123, 1989). When these phenotypically fertile plants are crossed as pollen parents there is no seed set on the ears; the pollen fails to function. Because this class of "restorer" gene produces nonfunctional pollen we gave it the symbol *Rf-nf*. To date, eight independently-occurring spontaneous revertants have been identified as *Rf-nf* genes.

We are using the *wx*-marked reciprocal translocation series to map the *Rf-nf* genes to chromosome (Maize Handbook pp.255-257). Three *Rf-nf* genes arose in the inbred line--cytoplasm combination *cms-RD* Oh 51A and each has now been located to chromosome. The *Rf-nf* gene 81-67-9 is in chromosome 3 according to our crosses with *wx* T3-9c and *wx* T3-9(8447). *Rf-nf* 79-21-27 has been mapped to chromosome 6 by use of *wx* T6-9(4505) and *wx* T6-9(4778). *Rf-nf* 79-23-27 has been placed on chromosome 8 by use of *wx* T8-9d and *wx* T8-9(043-6). We have previously mapped newly arisen *Rf* genes to chromosomes 3 and 8 but this is the first case of an *Rf* gene in chromosome 6.

In the course of studies on the allelic relationships of the *Rf-nf* genes, we found that crossing an *Rf-nf*/*rf* plant by an unrelated inbred line yields F1 plants that produce functional pollen grains. Crosses of these F1 plants as pollen parents often produce progeny segregating male-sterile plants and, in some cases, all male-sterile progeny (MNL 68:105-106, 1994). Since restoration of *cms-S* is gametophytic, all progeny of a cross *cms-S rf*/*rf* x *cms-S Rf*/*rf* are expected to be fertile. Crosses of these same restored F1 plants as female parents give the expected fertile and sterile plants. Therefore, the appearance of sterile plants in the crosses of the F1 plants as male parents cannot be explained by the failure of the *Rf-nf* gene to express in a particular nuclear background. We have been studying the basis for this apparent "gene silencing". Now that we have located the three Oh51A *Rf-nf* genes to chromosome, we are in a position to take a unique approach to the analysis of this phenomenon.

By crossing each Oh51A *Rf-nf* gene with its respective non-restoring (*rf*) *wx*-marked reciprocal translocations we effectively link the *Wx* gene to the *Rf-nf* gene. The heterozygote can be symbolized *Rf-nf* N *Wx*/*rf* T *wx*, where N stands for nontranslocation (or normal) and T for translocation. Since the *wx*-marked translocations are carried in nuclear backgrounds unrelated to Oh51A (e.g. W23, M14 or W23/M14), these F1 plants should exhibit functional pollen. By crossing pollen from these plants onto a *cms-S rf* T *wx*/*rf* T *wx* tester strain we can follow the *Rf-nf* gene by its linkage to *Wx*. This will allow us to determine if the apparent gene silencing is due to unexpected transmission of *rf* (kernels will be *wx*) or to silencing of *Rf-nf* (kernels will be *Wx*).

Is *tb*-8963* really an allele of *tb1*?

--Jackson, JD

The COOP's *tb*-8963* mutant, on chromosome 1, was allele tested with *tb1-ref*, which traces back to Burnham (MNL 33:74, 1959). A positive test was observed. The *tb*-8963* mutant can be traced back to an E. G. Anderson 1957 stock. If anyone has further information concerning the origin of these two mutants or similar stocks please forward to the Stock Center.

Allelism testing of unplaced *golden* stocks in Maize COOP's collection

--Jackson, JD

This report summarizes allele testing of stocks of unplaced *golden* mutations in the Maize COOP's stock collection. Some of these unplaced mutations have been found in other COOP stocks and some have been sent in by cooperators over the years. Crosses were made between homozygotes or known heterozygotes. In most cases plants were scored at the seedling stage as well as at maturity. Proposed new designations have been assigned to these alleles. These stocks have been increased and placed on the 1996 stocklist. During the screening of unplaced *pale-green* mutants, one culture was observed to have more of a golden phenotype and upon testing was determined to be allelic to *g2*. It is expected that with further sorting of unplaced mutations in the COOP's collection additional golden phenotypes will be discovered and allele tested.

previous designation	allelism test with *g1*	allelism test with *g2*	new designation
g4	positive	negative	*g1-g4*
*g**--56-3005-24	positive	negative	*g1*-56-3005-24
*g**--1-7 (x-55-16)	positive	negative	*g1*-1-7 (x-55-16)
*g**--68-609-13	positive	negative	*g1*-68-609-13
*g**--56-3040-14 (*pg**-56-3040-14)	negative	positive	*g2*-56-3040-14
*g**--59-2097	negative	positive	*g2*-59-2097
*g**--94-1478	negative	positive	*g2*-94-1478

***g4* recovered from Maize COOP stocks**

--Jackson, JD

The *golden4* mutant, once thought to be lost, has been recovered from stocks at the Maize COOP Stock Center. This mutant was originally placed to linkage group 1 (Eyster, Bibliographia Genetica 11:187-392, 1934), which was later renamed linkage group 9 or chromosome 9 (Emerson, Beadle, and Fraser, Cornell Univ Agric Exp Stn Memoir 180:1-83, 1935). In 1962 *g4* was

shown to have no significant linkage in a 3-point linkage test with *wx1* and *bm4* on chromosome 9 (Brawn, MNL 36:49, 1962) and was then dropped from the 1983 genelist. It was recently relocated again among "unplaced goldens" in the COOP's stock collection.

The recovered stock traces back to maize genetic stocks grown by the COOP at Cornell in 1937. Notes in the records describe distinctly yellowish seedlings that persist and become more yellow at maturity. Tests by Brawn and others indicated *g4* to be allelic to *g1* on chromosome 10. Crosses were done in the COOP nursery that confirm *g4* is allelic to *g1*, and the COOP *g4* does not seem to be linked to *wx1*. The stock has been increased and placed with other *g1* alleles.

Reverse germ orientation mutants

--Jackson, JD

In the course of studies with the Laughnan *cms-S* restorer genes, a mutation was observed in an *RfVI* strain. This new trait conditions the germ orientation of embryos causing them to face the base of the ear as opposed to the tip. Genetic analysis indicates it is a simply inherited trait and is inherited as a maternal plant character. Similar mutations were reported previously by Brieger (MNL 22:55, 1948) and Joachim (MNL 29:53, 1955; MNL 30:84-85, 1956; Proc. Minn. Acad. Sci. 24:37-43, 1956). Brieger reported an abnormality in which development of the second flower was observed. Joachim concluded that the so-called "reverse germ" in her studies is due to the development of only the lower florets in an earshoot as opposed to the usual condition of only the upper florets functioning. The name "reversed germ" was common in the literature (reviewed in Joachim, Proc. Minn. Acad. Sci. 24:37-43, 1956) and no other name was suggested. Reversed germs are found in the sweet corn variety Country Gentleman in which both the upper and lower florets function causing crowding and uneven rows (Kiesselbach, Am. Jour. Bot. 13:35-39, 1925).

A *reversed germ* mutation was recovered by Sachan and Sarkar (MNL 52:119-120, 1978) in the course of a mutagenesis study. They proposed the three letter symbol *rgo* for the trait and their mutant is now designated *rgo1* (see following article). I have designated my new mutation *rgo*-VI*. A similar trait has been recovered by Frances Burr. It showed up as a sector on a selfed ear carrying *y1-m261::dSpm*. This *rgo* stock was crossed to *rgo*-VI* for allelism and gave a positive result. The relationship of these mutations to *rgo1* is under study.

Recovery of *rgo1*

--Jackson, JD

A mutation disturbing the orientation of the germ in relation to the cob, i.e. the embryo facing the stalk end of the ear as opposed to the tip end, has been recovered. It was originally called *reverse germ orientation (rgo)* by Sachan and Sarkar (MNL 52:119-120, 1978) and is now designated *rgo1*. Seeds were provided by Dr. Sarkar of the Indian Agricultural Research Institute in New Delhi, India. These were germinated and transplanted to the field. Due to the hot, dry summer and poor growing conditions only a few ears that exhibit the trait were recovered. Stocks will be regrown to increase them further.

VIENNA, AUSTRIA
Joint FAO/IAEA Division of Nuclear Techniques in Food and Agriculutre
SEIBERSDORF, AUSTRIA
FAO/IAEA Agriculture and Biotechnology Laboratory

How similar are plant telomeres?

--Weck, E and Grasso, G

The comparison of cereal species through RFLP hybridizations has shown a surprising amount of colinearity among the related genomes. Some molecular tools are more useful for intergenomic comparisons than others. RFLPs are generally more useful, probably due to the preservation of large regions of sequence within genes and structural elements of similar function. RAPDs, and perhaps PCR markers in general, may not be as useful, sampling a much smaller region of the genome which varies enough to alter reaction products under the exacting conditions of PCR.

The PCR comparison of common structural elements, such as telomeres, should be useful for intragenomic comparisons. The use of PCR technology offers laboratories working on under-investigated species the opportunity to examine these relationships with currently available microsatellite-like telomere sequences.

We have used a telomere specific primer (Richards and Ausubel, Cell 53:127-36, 1988) which points toward the centromere and a maize subtelomere derived primer to compare maize and rice with a number of other species that are important in developing countries: baselle (*Basella* spp., African spinach); tef, of great importance in southern Ethiopia; banana, important in tropical countries; and date palm, which is of special agricultural importance in northwest Africa.

The telomere specific primer produced a smear background in all species examined along with a number of distinctive bands for most species (Fig. 1). The maize subtelomere-derived primer produced distinctive band patterns in most species examined. This suggests that primers derived from gross structural features of chromosomes may be generally useful for species comparisons. It will be interesting to examine the sequences of subtelomeres from other plant species. Comments to: weck@ripo1.iaea.or.at

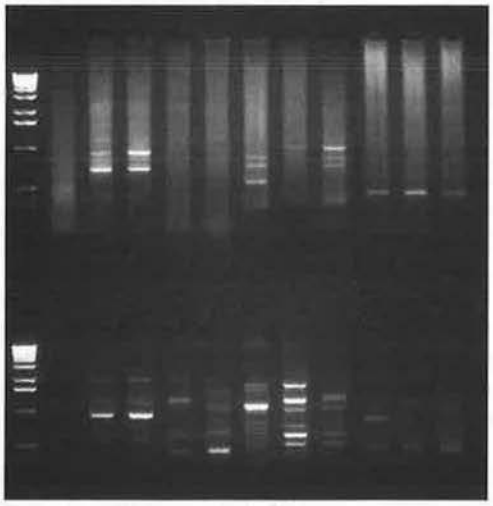


Figure 1. Telomere primer, CCCTAAACCCTAAACCCTAAACCCTA, top, and maize subtelomere primer GAAATTGAGTCTCCCAACCATATC, bottom. L to R, marker (1 kb ladder, GIBCO-BRL), date palm, tef 37, tef KM, baselle (Congo flowering), baselle (Sri Lanka) , rice (IR43), banana (Burro Cemsa), banana (Burro Criollo), maize (Stock center- 909B), maize (325C), and maize (M141); 58 C annealing temperature.

WALTHAM, MASSACHUSETTS
University of Massachusetts

Canopy and yield enhancement per acre with dense populations
--Galinat, WC

Maximum yields per acre are obtained when the maximum amount of solar energy is captured by photosynthesis in the crop plant without significant amounts escaping down to the weeds and ground below. In dense stands of modern maize (30,000 or more plants per acre), there are so many partially overlapping leaves that little energy escapes and if the plant is adapted to cope with survival in high density populations, the yields may be enormous (Fig. 1). Like humans adapted to city life by cultural evolution, the

FIG. 1.

maize plant must become adapted to high density populations by its biological evolution through plant breeding. This has been achieved by an erection of short leaves so that direct rays of sunshine may penetrate down about five leaves to the energy sink level of the ear. In addition, a reduction in tassel size conserves energy for use in kernel development and reduces the sun-shade effect of the tassel on the plant. In the sense of obtaining the maximum canopy per acre in contrast with maximum canopy per plant, the modern field corn hybrids have arrived, and breeding evolution continues in this direction, except for the subsistence farmers and specialty corns, including sweet corn, where all the great genetic diversity has been generated in the past. As the cheap high density maize crowds out the low density maize of the past, we lose the raw material for breeding. There is also a loss of the farmer-breeder culture associated with the indigenous maize. Despite nostalgia, there is no turning back cultural evolution. We are only mortal, but changes in culture and crops continue.

Fig. 1 is a view from a car window on a trip from Des Moines to Ames, Iowa in August 1994. The density was about 30,000 plants per acre, when U.S. corn acreage was 60 million and total yield 10 billion bushels.

Evolutionary diversification in low density isolated gardens
--Galinat, WC

Maize evolved from teosinte and then diversified at low density in isolated gardens with individual plants and ears judged on their merits. At the time of maize introduction, each garden contained only a few isolated species, like being introduced into an island in the Galapagos Archipelago where it was free from competition with its own related kind and open to an adaptation into an ecosystem with the other inhabitants and with its new environment.

Maize frequently found itself in association with beans and squash, with bean vines twisting up the maize stalks and squash vines spreading around to fill empty space related to large rocks and stumps (Fig. 2). The intercropping of maize, beans and

FIG. 2.

squash with relatively few plants of each kind in small gardens is an extension of their natural ecosystem. The consequence in the thousands of isolated gardens located in diverse environments was an explosion of genetic diversity with over 300 distinct races of maize evolving by the time of Columbus.

The direction of the diversification in an individual garden was in the eyes, hands and mind of the farmer-breeder in charge. He considered factors of beauty, utility and tradition, in contrast now with the industrial maize breeder, whose considerations are yield,

profit and market share. The industrial maize grows in an agricultural factory of machines, chemicals and computers. The raw material to achieve industrial maize was generated by the old fashioned farmer breeder. Now that the raw material is endangered, the future is uncertain.

_Bl_ (Broadleaf), a genetic trait that may enhance yields by contributing to the canopy

--Galinat, WC

As an alternative to increasing yield per acre and solar energy capture by denser stands, attempts have been made to use canopy enhancement per plant at lower densities to increase yield. The dominant leafy gene (*Lfy*) suggested by Shaver increases the number of leaves above the ear from the normal of about 5 to 9 in *Lfy*. It has been widely tested and does not appear to always increase yield, at the densities tested.

The answer to both canopy enhancement and diversity supplementation may lie in the transfer of quantitative traits. The *Bl* (broad leaf) trait is one such complex factor that involves a cluster of genes representing the software regulating the course of sequential development during the flow of space-time. It may have significant value in canopy and yield enhancement per plant and possibly also in yield per acre, even at high density. It was discovered in some Choclero maize received from Victor Alamos Sr. of Jacques Seed Co., Santiago, Chile. Choclero is similar to the old Gourd Seed variety of the southeastern United States. Both have an umbrella canopy of wide leaf blades and broad husks enclosing a broad ear bearing 20 rows of shrunken kernels. The broad husks have added value as humita wrappers in Chile. Their counterparts in Mexico serve as tamale wrappers. More importantly the broad husks are associated on the same plant with broad leaf blades, although broad husks may have reduced blades, and leaves may have reduced sheaths and broad blades. This independence of sheath and blade appears to be due to regulation of targeting during development comparable to that of phase change from vegetative to floral. If the potential for fat meristem extends through the vegetative and floral phases, programming may extend the broadness to the floral bracts and to the carpels of the pericarp, resulting in wide kernels.

This developmental linkage must have evolved by means of fat enhancement in meristem size evolving from primitive levels of skinniness in teosinte, the wild ancestor. Teosinte has small (skinny) apical meristems, narrow leaf sheaths and blades, all developmentally linked together with slender two-ranked ears bearing tiny kernels.

Diversification of U.S. grain hybrids away from B73-Mo17 with some new hybrids derived from adapted exotic races

--Galinat, WC

If we are to be confined by the GEM (germplasm enhanced maize) objective of increasing diversity within the Northern Flint-Southern Dent pattern of heterosis by using Mo17 and B73 related inbreds as the recurrent parents for introgressing unknown genes from their list, LAMP (Latin American Maize) alien germplasm, there are tactical problems.

If we identified ahead of time what we are going to transfer we could do it and maintain the prescribed pattern of heterosis, especially now with the tool of biotechnology. But this would usually involve just single gene transfers and not really increase the diversity much in modern hybrid feed grain, in contrast to silage hybrids grown mostly for vegetal material and sometimes of diverse tropical pedigrees.

If the genetic diversity and different heterotic patterns represented by certain obsolete races of gigantic maize still available in germplasm banks is adapted to modern agriculture and made competitive with B73-Mo17 related hybrids, the U.S. grain hybrids will have gained the diversification that authorities claim we need to cope with sudden changes in the environment, including problems with water, weeds, insects and diseases.

The important proposal here is to adapt certain of the ungainly giant, now obsolete races of Latin American maize such as Jala, Oloton and Montana for use in modern U.S. maize agriculture by the transfer to them of a new semi-dwarf gene designated here as *rd3*. The *rd* (reduced) symbol is used because of *rd3* similarity to the phenotype of *rd1* and *rd2* (peewee) genes discovered by Singleton in C30 inbred sweet corn but non-allelic and not as potent. While *rd1* reduces plant height to about 1/3 of normal, *rd3* has a weaker reduction to only about 1/2 of normal. The *rd3* gene appeared in a 10 foot tall line of Havel's Dent (JHLE) reducing the plant down to a reasonable height of 5 feet. The height reduction is due to shorter internodes at the base of the plant. During the early growth period of reduced elongation of internodes, root development is enhanced. This increased root development may provide a degree of drought tolerance and even some Roundup herbicide tolerance.

The *rd3* gene does reduce leaf and tassel size, both of which help in adapting to high population densities. It may be helpful to also modify the tassel with the *ub* (unbranched) gene and then restore some of the tassel with a recessive tassel ramosa, *ra-D* gene. The first maize, like its wild ancestor, teosinte of now and then, must have been adapted to high population competition. It should not be all that difficult to return this trait to any maize.

Reversal of dominance and wild type during the origin of maize

--Galinat, WC

The wild type generally evolves dominance in order to maintain a high frequency for its phenotype despite the presence of a load of less adaptive mutations. Under domestication and/or a switch to a new environment, certain new phenotypes may be selected as the new wild type with the old phenotypes rejected. Selection for modifying genes that would enhance the expression of the new alleles would give dominance to single dose expression, and, therefore, increase its phenotypic frequency. As the maize alleles had greater survival value under domestication than the teosinte alleles, they acquired dominance over the millennia. The maize alleles in a teosinte and primitive maize background remained as recessive.

The identity of the key maize-teosinte alleles by use of the traditional code of upper case for dominant genes and lower case for recessive genes in segregations from teosinte-modern maize hybrids can be difficult and of little value for studies of inheritance and evolution because of the mixed background of both wild and domestic modifiers of dominance.

In teosinte by primitive maize hybrids the teosinte alleles may still behave as dominants. This is the case with Rhee Flint, Coroico and possibly with Argentine popcorn.

The symbolic identity of key trait alleles before and after a reversal of both dominance and wild type

--Galinat, WC

In analyzing the early stages on the origin of maize, one would use a teosinte background segregating the key trait alleles of maize that are symbolically coded to indicate the direction of divergence away from the wild type teosinte. These variants toward maize would be expected to be recessive and only much later to evolve a background where they could be expressed as dominants. When the background is relatively fixed, the frequency for a given phenotype may be scored under a modified type of symbol with a sub-postscript of t for teosinte or m for maize representing the background of dominance modifiers relative to the observed phenotype within the segregation as in Table 1.

Table 1. The genetic symbols for teosinte-maize key traits indicating dominance and wild type reversal.

Background genome	Variant Direction		Chromosome location	Phenotype Description	Symbol synonym
	maize	teosinte			
maize	+	rk_t	2	Teosinte two-ranked ear	(tr)
teosinte	rk_m	+	2	Maize multi-ranked ear	(mr)
maize	+	tru_t	3	Tassel replaces upper spike	(tru)
teosinte	tru_m	+	3	Ear replaces upper spike	(mru)
maize	+	pd_t	3	Teosinte single female spikelet	(pd)
teosinte	pd_m	+	3	Maize paired female spikelet	(pd)
maize	+	tga_t	4	Teosinte glume architecture	(tga)
teosinte	tga_m	+	4	Maize glume architecture	(mga)

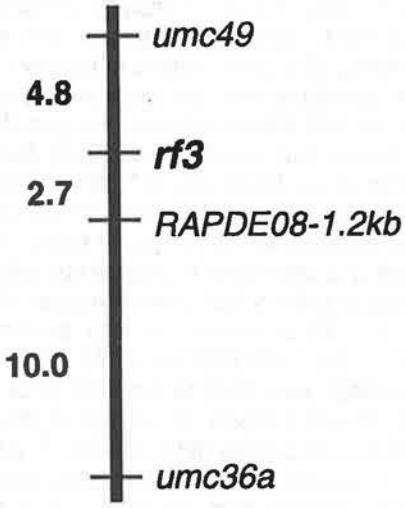


Figure 1. Region of maize chromosome 2 in the vicinity of *rf3*. Positions are shown for flanking RFLP markers (*umc49* and *umc36a*) and one RAPD markers, with map distances in cM.

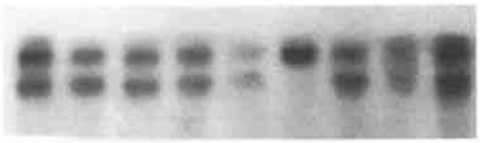


Figure 2. Southern analysis of *Hin*dIII-digested DNA hybridized with *umc36a*. (Right to left) DNAs from male-fertile individuals (*Rf3 rf3*). Lane 4 from right shows a recombinant.

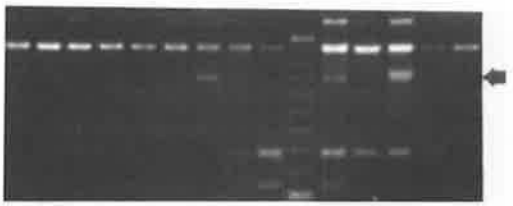


Figure 3. RAPD data for OPE08. (Right to left) Lane 1: Mo17cms-S *rf3 rf3* (parent 1); lanes 2 and 4: male-sterile bulk (*rf3 rf3*); lane 3: male fertile bulk (*Rf3 rf3*); lane 5: HZ_1N *Rf3 Rf3* (parent 2); lane 6: 100bp ladder; remaining lanes: male-sterile individuals. Lane 9 from right shows a recombinant. The arrow shows the male-fertile specific RAPD fragment.

WUHAN, CHINA
Huazhong Agricultural University

Mapping cms-S restorer gene *Rf3* with RFLPs and RAPDs

--Shi, YG; Zheng, YL; Li, JS and Liu, JL

The use of the cms inbred line as a female parent to produce maize hybrids is a cost-competitive and satisfactory technique since manual detasseling is eliminated. Three types of male-sterile cytoplasms in maize, designated as T, C and S, have been classified by specific nuclear genes that suppress the male-sterility effects of these cytoplasms and restore pollen fertility. S-cytoplasm is conditioned by interaction of the cytoplasm with a single nuclear gene and fertility is restored by a dominant nuclear gene (*Rf3*) located on the long arm of chromosome 2. It is probably a long term objective to clone the restorer gene (*Rf3*) to help us understand its function and the mechanism of fertility restoration. However, as the first step of map-based gene cloning, it is a prerequisite to construct a saturated genetic map of *rf3* with more closely linked molecular markers.

To map the *rf3* gene, a backcross, (Mo17cms-S *rf3 rf3* x HZ_1N *Rf3 Rf3*) x Mo17 N *rf3 rf3*, was used as the mapping population. Two DNA bulks were constructed from each corresponding to the 20 male-sterile and fertile individuals from this segregating population. Bulked segregant analysis (BSA)

was employed to identify RFLP and RAPD markers linked to the restorer gene (*Rf3*). For RFLP analysis, *umc36a*/*Hin*dIII and *umc49*/*Pst*I were found to cosegregate with the *rf3* allele through screening 36 probe/enzyme combinations. Furthermore, 132 random individuals from the segregating population were analyzed to calculate linkage distance. Analysis of the data with JOINMAP reveals that *umc36a* and *umc49* flank *rf3* and are separated from *rf3* by 4.8 cM and 12.7 cM, respectively (Figs. 1, 2). For RAPD analysis, 340 arbitrary 10-mer oligonucleotide primers were screened on the two paired bulks. Three primers, E08, M02 and O12 were found to produce one polymorphic DNA fragment between bulks in each case associated with the restorer allele (Fig. 3). To determine the map location of the loci represented by the 1.2kb E08 band, 174 individuals from the mapping population were taken as templates to be amplified with primer E08. Figure 1 shows the location of this RAPD allele relative to *rf3* and the flanking RFLP markers. The E08 locus lies 2.7 cM from *rf3* beyond *umc36a*. This specific RAPD E08-1.2kb fragment was extracted from the gel and then cloned in the pBluescript SK (M13-) vector. Correct inserts were released by digesting the recombinant plasmid and eventually used as a probe to hybridize with DNA blots. The preliminary result suggests that the amplified fragment should be a medium repetitive copy.

The work of searching for different types of molecular markers (RAPD, RFLP, AFLP, STS and SCARs) to saturate the genetic region near the *rf3* locus continues. When the saturated genetic map is established, it will enable us to apply these markers either in marker-assisted breeding programs or in genome walking strategies.

WUHAN, CHINA
Wuhan University

Simultaneous chromosome G-banding and in situ hybridization of RFLP markers in maize

--Song, Y; Ren, N; Mao, N; and Liu, L

The technique of simultaneous G-banding and in situ hybridization (ISH) has been developed in plants for the first time. Using this technique with RFLP markers, *umc58* was localized onto 1L3 (chromosome 1, long arm, the third band from the centromere to the end of the arm), 5L5 and 9L6; and *umc65* was localized onto 6L1 and 8L7. It was shown that *umc58* and *umc65* hybridize to

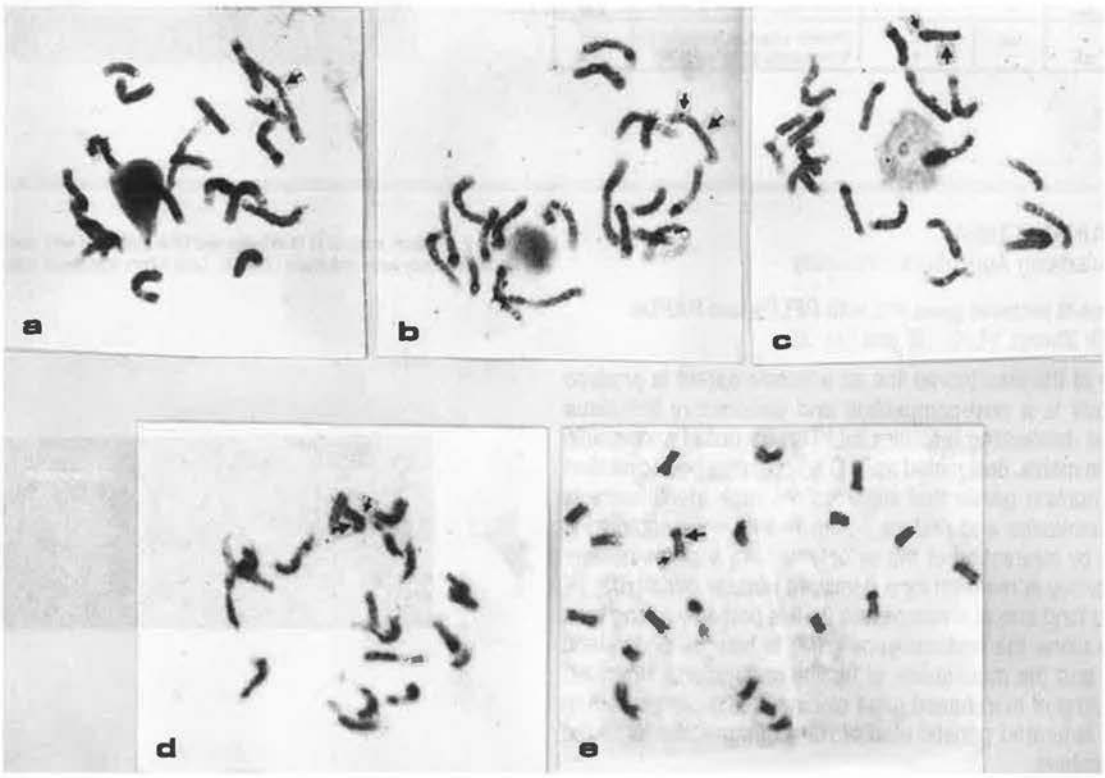


Figure 1. The mitotic chromosomes showing hybridization sites of the tested probes. In all the figures the small arrow denotes the hybridization site and the large arrow denotes the centromere. (a) Late prophase chromosomes showing a site with probe *umc58* at 1L3. (b) Late prophase chromosomes showing a site with probe *umc58* at 5L5. (c) Late prophase chromosomes showing a site with probe *umc58* at 9L6. (d) Early metaphase chromosomes showing a site with probe *umc65* at 6L1. (e) Early metaphase chromosomes showing a site with probe *umc65* at 8L7.

triplicated and duplicated sequences respectively (Figs. 1 and 2). These two markers separately showed hybridization sites near the centromere of the long arm in chromosomes 1 and 6, corresponding basically to their sites in the genetic map. It was deduced that *umc58* probably was near *Helminthosporium carbonum* susceptibility genes (*hm1* and *hm2*), as hybridization sites of *umc58* in chromosomes 1 and 9 are those at which the genes localize.

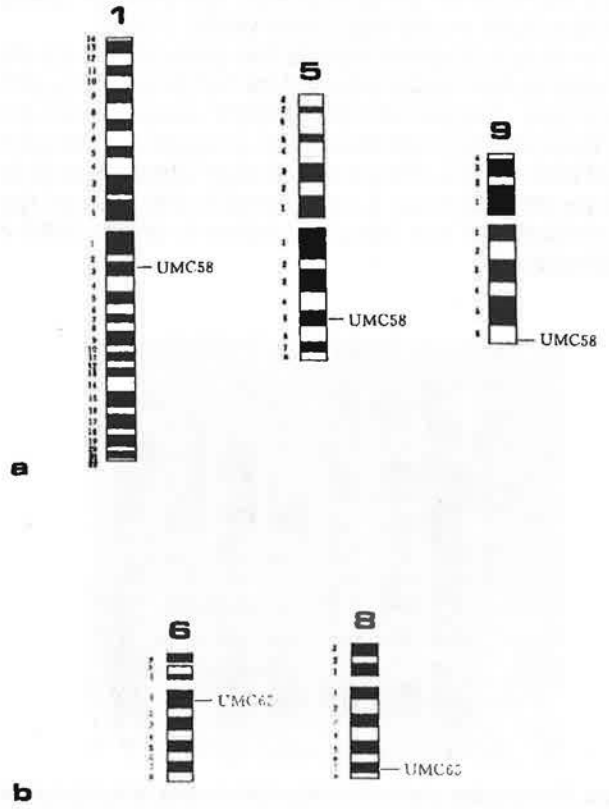


Figure 2. G-banded idiograms showing the physical location of the RFLP markers. The top numeral is the number of the chromosome. (a) G-banded idiogram of chromosomes 1, 5 and 9 showing sites with probe *umc58* at 1L3, 5L5 and 9L6 respectively. (b) G-banded idiogram of chromosomes 6 and 8 showing sites with probe *umc65* at 6L1 and 8L7 respectively.

ZEMUN-BELGRADE, YUGOSLAVIA
Maize Research Institute

Embryo salt soluble proteins as markers in research on the biological background of heterotic gene expression

--Drinic, SM; Coric, T and Konstantinov, K

A better understanding of the biochemical basis of heterotic gene expression could enhance the breeder's ability to form new maize genotypes expressing "permanent" heterosis. Several genetic models for the explanation of hybrid vigor in Mendelian terms have been suggested, including the dominance and overdominance hypotheses. The dominance hypothesis attributes the increased vigor of heterozygosity to dominant alleles and in principle should be fixable by inbreeding. The overdominance hypothesis assumes that there exist relatively rare loci at which the heterozygote is superior to either homozygote but heterosis due to overdominance or pseudo-overdominance and is not fixable by inbreeding. There are also results providing clear evidence for the role of epistasis (Russell and Eberhart, Crop Sci 10:165-169, 1970), and also indications that additive genetic effects are primarily responsible for the increase of heterosis through 5 cycles of maize selection and population crosses (Walejko and Russell, Crop Sci 17:647-651, 1977).

Maize hybrid plants expressing heterotic vigor develop from embryos consisting of 2n chromosomes which have not changed by the process of genetic recombination. Parameters derived from hybrid embryo genome expression could provide more information on the relationships between genome expression of parental lines per se and hybrid genome expression as a consequence of inbred line combinations. Salt soluble proteins, fractions of metabolically active albumin and globulin proteins, are good candidates for such studies.

A diallel set of five inbred lines, F2, ZPL120, ZPL203, W401 and EP1, excluding reciprocal crosses, has been studied at two locations, in a random block system experiment with 4 replications. Results on the heterotic effect on grain yield and soluble protein content of 10 developed F1 hybrids are presented in Table 1.

Table 1. Heterotic effect on the grain yield and soluble protein content in the embryo of all developed hybrid combinations, and index of similarity of inbred lines.

Hybrid combination	Heterosis (%)		index of similarity
	grain yield	salt soluble proteins 10^{-3} g/g fresh weight	
ZPL120 x W401	139.43**	8.28	79.2
W401 x EP1	134.30**	4.14	83.3
ZPL120 x EP1	110.52**	6.44	85.7
F2 x ZPL120	109.39**	3.44	85.2
ZPL120 x ZPL203	90.97**	4.52	86.3
ZPL203 x EP1	90.34**	0.96	85.2
ZPL203 x W401	88.48**	3.34	86.8
F2 x EP1	87.36**	0.65	87.7
F2 x W401	67.22**	-0.63	88.5
F2 x ZPL203	51.96**	0.42	88.0

** significant at the level of 0.01

In all hybrid combinations significant positive heterosis was obtained for grain yield. Low but positive heterotic effect on the salt soluble protein content in embryo tissue has been obtained in 9 out of 10 hybrids. In order to correlate grain yield heterosis and salt soluble proteins in embryo tissue several hybrid combinations were selected for high resolution polyacrylamide gel electrophoresis (PAGE) of embryo salt soluble proteins: two hybrids expressing high heterosis for grain yield and two hybrids expressing low heterosis for grain yield. In both groups, hybrids have one inbred line as a common parent. Electrophoregrams are presented in Figures 1 and 2, respectively. In the hybrid combinations expressing the highest heterosis for grain yield and salt soluble protein content (F2 x ZPL120; ZPL120 x W401) 3 hybrid-specific protein bands are identified (arrows in Fig. 1). Several male or female inbred-specific protein bands have also been identified amongst the many in common for both parents.

On the electrophoregrams of salt soluble proteins isolated from the embryo tissue of low heterotic hybrid combinations, presented in Figure 2, only one hybrid specific protein band has been identified (arrow).

By comparing electrophoregrams of hybrid combinations (F2 x ZPL120 and ZPL120 x W401; F2 x ZPL203 and F2 x W401) and coelectrophoregrams (F2 + ZPL120 and ZPL120 + W401; F2 + ZPL203 and F2 + W401) of parental lines it could be suggested that non-additive genetic effects are responsible for salt soluble protein synthesis in hybrid embryo tissue (Leonardy et al., TAG 82:552-560, 1992).

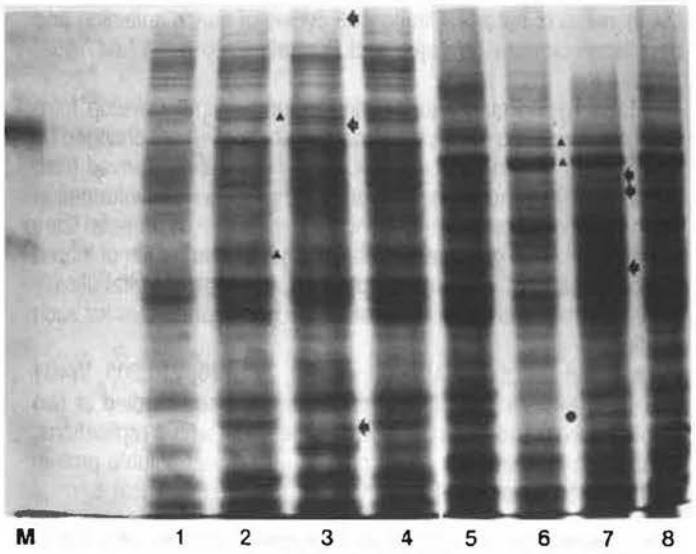


Figure 1. Electrophoregrams of embryo salt soluble proteins of two hybrids expressing high heterosis for grain yield: line 1 (F2); line 2 (ZPL120); line 3 (F2 x ZPL120); line 4 (F2 + ZPL120); line 5 (ZPL120); line 6 (W401); line 7 (ZPL120 x W401); line 8 (ZPL120 + W401).

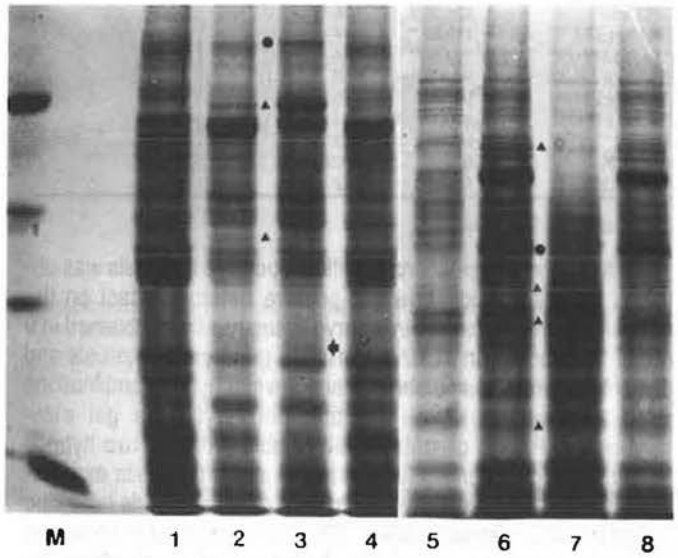


Figure 2. Electrophoregrams of embryo salt soluble proteins of two hybrids expressing low heterosis for grain yield: line 1 (F2); line 2 (ZPL203); line 3 (F2 x ZPL203); line 4 (F2 + ZPL203); line 5 (F2); line 6 (W401); line 7 (F2 x W401); line 8 (F2 + W401).

Based on the number of protein bands, their distribution according to the molecular weight, and presence or absence, the index of similarity of parent lines in hybrid combinations has been calculated and is presented in Table 1. Comparing heterosis for grain yield and protein content with index of similarity of inbred lines it could be suggested that inbreds with the lowest level of salt soluble protein similarity expressed the highest heterosis both for grain yield and content of salt soluble protein in embryo tissue.

The above data indicate that there is hybrid specific expression of certain loci in maize embryo tissue, and further biochemical experiments (i.e. isolation of poly A-mRNA specific for the protein bands synthesized only in hybrid combinations) for a better understanding of the molecular basis of heterosis are in progress.

F1 embryo proteins as valuable tools in better understanding of heterosis

--Konstantinov, K; Coric, T; Drinic, G and Drinic, SM

The creation of new and more productive maize hybrids has as a prerequisite inbred lines possessing both general and specific combining ability, determined almost entirely through studies at the phenotypic morphological level. In a companion paper are reported results on the presence of more hybrid-embryo specific proteins in higher as compared to lower yielding crosses.

This study is focused on parental lines participating in genome expression in the F1 maize embryo at the level of total and salt soluble proteins. Total and salt soluble proteins were analyzed in embryo tissue of seven single cross hybrids produced by crossing one inbred used as the female parent and seven inbreds used as the male parents. In this way it was expected to distinguish the specific contribution of each inbred line genome in genetic control of protein synthesis.

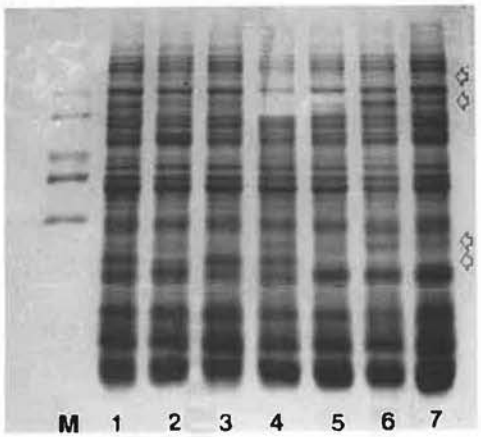


Figure 1. Electrophoregram of total proteins isolated from the maize dry embryo of different crosses: line 1 (ZPL153 x ZPL218); line 2 (ZPL153 x ZPL2/2); line 3 (ZPL153 x ZPL2/2); line 4 (ZPL153 x ZPL17); line 5 (ZPL153 x ZPL59G); line 6 (ZPL153 x ZPL655); line7 (ZPL153 x ZPL573).

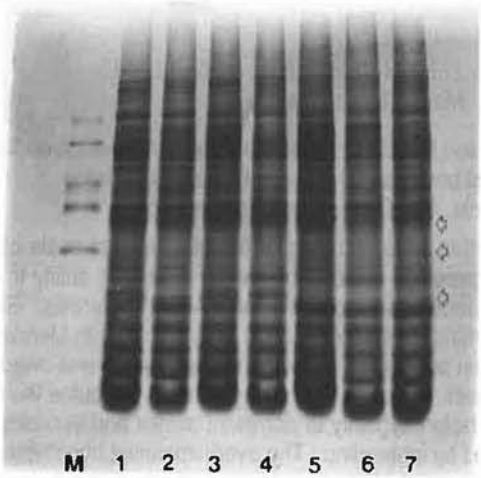


Figure 2. Electrophoregram of salt soluble proteins isolated from the maize dry embryo of different crosses. Legend is the same as in Figure 1.

A high resolution polyacrylamide gel electrophoresis (PAGE) system (Wang et al., Seed Sci. Technol. 22:51-57, 1994) was

used for protein separation according to molecular weight. Electrophoregrams of total F1 embryo proteins are presented in Figure 1 and salt soluble proteins in Figure 2.

Both quantitative and qualitative differences between analyzed crosses are obvious. Protein fractions which are candidates as markers associated with heterotic effect are indicated by arrows.

Parallel studies of embryo specific proteins and polyA-mRNAs of parental lines and hybrid combinations during kernel development after pollination are in progress. Specific fraction/fractions of protein/proteins synthesized only in particular hybrid combinations could be used as a tool for identification and characterization of the encoded gene/genes important in manifestation of heterotic vigor.

III. ADDRESS LIST

Abedon, Bruce; Dept of Agronomy; 1575 Linden Dr.; Univ of Wisconsin; Madison WI 53706; 608-262-3660; Fax: 608-262-5217
Adams, Karen R.; 2837 E. Beverly Dr.; Tucson AZ 85716-5716; 602-326-8994
Agrema, Hesham A; Agricultural Research Centre; 42 Memphis Street; Camp Caesar; Alexandria 21321; EGYPT; 203-59-70525; Fax: 203-59-63042
Ainsworth, Thomas C.; Ainsworth Seed Company; Mason City IL 62664; 217-482-3281; Fax: 217-482-3283; CORNDOCTOR@AOL.COM
Akamatsu, Toyokazu; Sakata Seed Corp; Plant Biotechnology Center; 358 Uchikoshi Sodegaura City Chiba; JAPAN; 0438-75-2369; Fax: 0438-75-2594
Albertsen, Marc C.; Pioneer Hi-Bred International; 7250 NW 62nd Ave; PO Box 1004; Johnston IA 50131-1731; 515-270-3648; Fax: 515-253-2149; ALBERTSNM@PHIBRED.COM
Alexander, Danny; Ciba Agricultural Biotech.; 3054 Cornwallis Rd.; Research Triangle Park NC 27709-2257
Alexander, Larry; Mycogen Plant Sciences; 720 St. Croix St.; Prescott WI 54021
Alfenito, Mark R.; Dept Biol Science; Stanford Univ; Stanford CA 94305-5020; 415-723-2609; Fax: 415-725-8221; alfenito@leland.stanford.edu
Alleman, Mary; 253 Mellon Hall; Duquesne University; Pittsburgh PA 15282; 412-434-1660; Fax: 412-434-5907; ALLEMAN@DUQ3.CC.DUQ.EDU
Allen, Jim; 235 Jordan Hall; Indiana University; Bloomington IN 47405
Altosaar, Illimar; Department of Biochemistry; University of Ottawa; 40 Marie Curie Private; Ottawa, Ontario K1N 6N5; CANADA; 1-613-562-5800 Ext. 6374; Fax: 1-613-562-5180; altosaar@oreo.chem.uottawa.ca
Alvey, David; 237 Myrtle Drive; W. Lafayette IN 47906; 317-567-2115; Fax: 317-567-4046
Amano, Etsuo; Joint FAO/IAEA Division, IAEA; Wagramerstrasse 5; P.O. Box 200; A-1400 Vienna; AUSTRIA; 43 1 2360 ext. 1616; Fax: (43)-1-234564
Ananiev, Evgenii; Academy of Sciences; N.I. Vavilov Inst. Gen. Genet; Gubkin Street 3; Moscow; RUSSIA
Andersen, Tim; 7300 NW 62nd Ave; Box 129; Johnston IA 50131-0129; 515-276-6541; Fax: 515-270-4312; andersent@phibred.com
Applied Biosystems; Library - Bldg. 700; 850 Lincoln Cntr. Dr.; Foster City CA 94404-1128
Area Director; Midwest Area; USDA-ARS; 1815 N. University; Peoria IL 61604; 309-685-4011; Fax: 309-671-7228
Armstrong, Charles L.; Monsanto, GG4H; 700 Chesterfield Parkway North; St. Louis MO 63198; 314-537-7229; Fax: 314-537-6567; clarms@ccmail.monsanto.com
Arnold, Jerry M.; Asgrow Seed Co.; 9866 Highway 66; Newburgh IN 47630
Arpat, Hacimurat; Ohio State University; OARDC, Dept of Agronomy; 1680 Madison Avenue; Wooster OH 44691-4096; 216-263-2882; Fax: 216-263-3658; hmarpat@magnus.acs.ohio-state.edu
Arruda, Paulo; Univ. Estadual de Campinas; Cidade Univ. Zeferino Vaz; Distrito de Barao Geraldo; Campinas - SP; BRAZIL; (192)398351; Fax: (192)394717
Arthur, Lane; Genetics Dept.; Univ. of Georgia; Athens GA 30602; (706)542-1857; arthur@dogwood.botany.uga.edu
Artim-Moore, Lori; Ciba-Ag Biotechn; PO Box 12257; Research Triangle Park NC 27709
Astwood, James D.; Dept. of Plant Science; Faculty of Agriculture; University of Manitoba; Winnipeg, Manitoba R3T 2N2; CANADA; 204-474-6064; Fax: 204-275-5128;
Atanassov, A.; Institute of Genetic Engineering; 2232 Kostinbrod 2; BULGARIA
Attewell, John; 2166 Forrest Green Drive; Decatur IL 62621; (217)422-8146
Auger, Donald L.; Biol Sci; Tucker Hall; Univ Missouri; Columbia MO 65211; ; dauger@biosci.mbp.missouri.edu
Austin, David; 1525 Agronomy; Iowa State University; Ames IA 50011; (515)294-8641; dfaustin@iastate.edu
Auyeung, Man Ting; Pioneer Overseas Corporation; 2729-1 Kohyama, Matsubase Machi; Shimomashiki-Gun; Kumamoto Pref, 869-05; JAPAN; 964-33-7666; Fax: 964-33-1677
Aycock, Harold S; 305 Montefiore St, #305; Lafayette IN 47905-5519; 317-477-7758
Ayers, John E; Dept Plant Pathology; 308 Buckhout Lab; Pennsylvania State Univ; University Park PA 16802; 814-865-7776; Fax: 814-863-7217; jea@psu.edu
Azanza, Fermin; 12 Chemin de L'Hobit; B.P. 27; Hilleshog NK; 31790 Saint-Sauveur; FRANCE; (+33) 61-37-68-09; Fax: (+33) 61-37-38-83; 100675.1167@compuserve.com
Badenhorst, Coerie; Saffola; Box 36; Boskop 2528; SOUTH AFRICA
Bai, Yongyan; Inst. of Plant Physiol.; 300 Fengling Road; Shanghai 200032; CHINA
Bailey-Serres, Julia; Botany & Plant Sciences; Batchelor Hall; Univ. Calif. Riverside; Riverside CA 92521; (714)787-3738; Fax: (714)787-4437; SERRES@UCRAC1.UCR.EDU
Bairoch, Amos; Centre Medicale Universitaire; 1211 Geneva 4; Geneva; SWITZERLAND; 41-22-784-40-82; BAIROCH@cmu.unige.ch
Baker, Raymond; 3524 Grand Avenue, Apt. 208; Des Moines IA 50312; 515-271-6803
Baker, Frank; Plant Biology Dept.; UC Berkeley; 111 Koshland Hall; Berkeley CA 94720-3102
Baker, Barbara; USDA; Plant Gene Expression Center; 800 Buchanan Street; Albany CA 94710; 510-559-5912
Balconi, C.; Ist Sper Cereal; Via Stezzano 24; 24100 Bergamo; ITALY
Ball, Dale W.; Wilson Seeds, Inc.; P.O. Box 391; Harlan IA 51537; 712-755-3841; Fax: 712-755-5261
Banuett, F.; Dept Biochem Biophys; Univ of California; San Francisco CA 94143-0448; 415-476-4985; Fax: 415-476-0943
Bar-Zur, Avri; Agricultural Research Organization; Newe Yaar Research Centre; PO Haifa 90000 31900; ISRAEL; 972-4-9833186; Fax: 972-4-9836936; EUMNEVE@technion.technion.ac.il
Barbour, Eric; Pioneer Hi-Bred Internat., Inc.; 7300 NW 62nd Ave.; PO Box 1004; Johnston IA 50131-1004
Barkan, Alice; Institute of Molecular Biology; University of Oregon; Eugene OR 97403; 503-346-5145; Fax: 503-346-5891; abarkan@molbio.uoregon.edu
Barker, Tom; Pioneer Hi-Bred Internat., Inc.; Plant Breeding Division; RR1, Box 90A; Princeton IN 47670; 812-385-2935; Fax: 812-385-8502; barkertc@phibred.com
Barnes, Wayne M.; Dept. Biochemistry 8231; Washington University Medical School; 660 South Euclid Ave.; St. Louis MO 63110
Barros, MEC; PO Box 395; Pretoria, 0001; SOUTH AFRICA; 27-12-841-3221
Baskin, Tobias; 109 Tucker Hall; Div. Biol. Sci.; University of Missouri; Columbia MO 65211; 573-882-0173; baskin@biosci.mbp.missouri.edu
Bass, Hank W.; Dept Molecular and Cell Biology; 345 LSA; Univ California-Berkeley; Berkeley CA 94720; 510-643-8277; Fax: 510-643-6791; bass@candelab.berkeley.edu
Baszczynski, C. L.; Pioneer Hi-Bred International, Inc.; 7300 N.W. 62nd Avenue; P.O. Box 1004; Johnston IA 50131-1004; (515)270-3693; Fax: (515)270-3367; BASZCZYNSKI@PHIBRED.COM
Bates, Lynn S.; Alteca Ltd.; 731 McCall Road; Manhattan KS 66502; 913-537-9773; Fax: 913-537-1800
Bayliss, Michael W.; ICI Seeds; 2369 330th St.; P.O. Box 500; Slater IA 50244; 515-685-3574; Fax: 515-685-2548
Baysdorfer, Chris; Biological Sciences; California State U; Hayward CA 94542; 510-885-3459; Fax: 510-888-4747; 72652.662@compuserve.com
Beach, Larry R.; Pioneer Hi-Bred Internatl; Specialty Grain Traits; PO Box 1004, 7300 NW 62nd Ave; Johnston IA 50131-1004; 515-270-3798; Fax: 515-270-3367; beachl@phibred.com
Beavis, W. D.; Pioneer Hi-Bred International; 7300 NW 62nd Ave.; P.O. Box 129; Johnston IA 50131-0129; 515-270-3618; Fax: 515-270-4312; beavis@phibred.com
Beckert, M.; INRA Station D'Amelioration des Plantes; 63039 Clermont Ferrand; FRANCE; (33)73 624319; Fax: (33)73 624453
Beckett, Jack; Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-2674
Becraft, Philip; Zoology & Genetics Dept.; 2116 Molecular Biology Bldg.; Iowa State University; Ames IA 50011; 515-294-2903; Fax: 515-294-6755; becraft@gnv.ifas.ufl.edu
Bedinger, Patricia; Biology Dept; Colorado State Univ.; ; Fort Collins CO 80523; 303-491-2879; Fax: 303-491-0649; bedinger@lamar.colostate.edu
Behr, Fritz; 222 W. Pearl St.; Geneseo IL 61254; (309)944-6500
Belanger, Faith; Dept of Crop Science; Cook College, Lipman Hall; Rutgers University; New Brunswick NJ 08816; 908-932-8403; Fax: 908-932-8899; belanger@mbcl.rutgers.edu
Bell, Duane; 304 Pearl St.; Blissfield MI 49228; (517)486-3520; Fax: (517)486-2631
Benito, Maria-Ines; Biology Dept.; Herrin Bldg.; Stanford University; Stanford CA 94305-5020
Benner, Michael; Science and Technology Center; Rider University; Lawrenceville NJ 08648-3099; 609-896-5096; Fax: 609-895-5782; benner@enigma.rider.edu
Bennett, Michael; Jodrell Laboratory; Royal Botanic Gardens; Kew, Richmond; Surrey, TW9 3AB; UNITED KINGDOM; 44-1181-332-5000; Fax: 44-1181-332-5310; M.Bennett@rbgkew.org.uk

Bennetzen, Jeff; Dept of Biological Sciences; Purdue University; W. Lafayette IN 47906; 317-494-4763; Fax: 317-496-1496; Maize@bilbo.bio.purdue.edu
Bensen, Robert; Pioneer Hi-Bred Int'l Inc.; 7300 NW 62nd Ave., P.O. Box 1004; Johnston IA 50131; 515-270-3645; Fax: 515-253-2149; BENSENRJ@PHIBRED.COM
Benzion, Gary; 303 W. Lanvale St.; Baltimore MD 21217; 703-308-1119; benzion@USPTO.GOV
Bergquist, Richard R.; 401 East Sixth Street; El Paso IL 61738; 309-527-6000
Bergstrom, Gary C.; Dept. Plant Pathology; 316 Plant Science Bldg.; Cornell University; Ithaca NY 14853-5908; 607-255-7849; Fax: 607-255-4471; gcb3@cornell.edu
Bergvinson, David; CIMMYT; Apdo. Postal 6-641; 06600 Mexico, DF; MEXICO; 595-544-00; Fax: 595-544-25; DBERGVINSON@ALPHAC.CIMMYT.MX
Berke, Terry; Box 42; Shanhua; Tainan, Taiwan 741; REPUBLIC OF CHINA; 8866 583 7801; Fax: 8866 583 0009; TERRY@NETRA.AVRDC.ORG.TW
Berlyn, Mary; Dept. of Biology; Yale University; New Haven CT 06520; 203-432-3536; Fax: 203-432-3854; mary@fetalpig.biology.yale.edu
Bernardo, Rex; Limagrain Genetics; 4805 West Old Chruch Rd.; Champaign IL 61821; (217)398-8968; Fax: (217)398-8976; bernardo@prairienet.org
Bernot, John; Dept. of Biological Sciences; Duquesne University; Pittsburg PA 15282
Berthaud, Julien; UR 31 Centre ORSTOM; 911, Avenue Agropolis; BP 5045; 34032 Montpellier cedex; FRANCE; 33 67 61 74 65; Fax: 33 67 54 89 00; BERTHAUD@ORSTOM.FR
Bertrand, Ralph L.; 1040 N. Nevada St.; Dept. of Biology; Colorado College; Colorado Springs CO 80903; (719)389-6402; Fax: (719)389-6940
Berville, A.; INRA; Station d'Amelior des Plantes; 2 Place Viala; 34060 Montpellier Cedex; FRANCE
Bhattramakki, Dinakar; 348 Manter Hall; PO Box 880118; University of Nebraska; Lincoln NE 68588-0118; 402-472-6243; Fax: 402-472-2083; ddh@unlinfo.unl.edu
Bianchi, Angelo; Ist Sper Cerealicoltura; Via Cassia 176; 00191 Rome; ITALY; 06-3295705; Fax: 06-3630-6022
Bigwood, Doug; National Agricultural Library; 10301 Baltimore Blvd; Beltsville MD 20705; 301-504-6689; Fax: 301-504-7473; dbigwood@gig.usda.gov
Biradar, Madhuri; 320 ERML, Crop Sci; Univ. of Illinois; 1201 W. Gregory; Urbana IL 61801
Birchler, James; Biological Sciences; Tucker Hall; University of Missouri; Columbia MO 65211; 573-882-4905; Fax: 573-882-0123; birchler@biosci.mbp.missouri.edu
Bird, Robert; CIMMYT; Lisboa 27, Apdo Postal 6-641; CP06600; Mexico, D.F.; MEXICO; 52-5-955-4400/4410; Fax: 52-5-955-4425; RBIRD@CIMMYT.MX
Bjarnason, Magni; Semences Cargill; IM Aufeld 5; D-77815 Buehl; GERMANY; +49-7227-5691; Fax: +49-7227-5691
Blakey, Cynthia Ann; Cooper Science Bldg; Dept. of Biology; Ball State University; Muncie IN 47306; 317-285-8820; Fax: 317-285-2351; 01CABLAKEY@BSUVC.BSU.EDU
Blewitt, Michael; Brookhaven National Lab; Bldg. 463; Upton NY 11973
Bodeau, John; Dept Pomology; UC-Davis; Davis CA 95616; ; Fax: (916)752-8502
Bogorad, Lawrence; Biol Labs; Harvard Univ; 16 Divinity Ave; Cambridge MA 02138; 617-495-4292; Fax: 617-495-4292; bogorad@biosun.harvard.edu
Bohn, Martin; Institut fur Pflanzenzuchtung; Universitat Hohenheim; 70593 Stuttgart; GERMANY; 0049711/459-2334; Fax: 0049711/459-2343
Bokde, S.; Telonagri International Inc.; CMC Maputo Branch; C.P. 4602; Maputu; MOZAMBIQUE; 258-1-450-109,356,316,458; Fax: 258-1-450-335,490
Bollman, Krista; Dept. of Biology; Plant Science Institute; University of Pennsylvania; Philadelphia PA 19104-6018
Bommineni, Venkat R; USDA-ARS, NCSL; State University Station; Fargo ND 58105-5677; 701-239-1311; Fax: 701-239-1369; bomminen@badlands.nodak.edu
Bongard-Pierce, Deverie K.; Dept Molec Biology; Wellman 11; Massachusetts General Hosp; Boston MA 02114; 617-726-5938; Fax: 617-726-6893; DEVERIE.BONGARD-PIERCE@MOLBIO.MGH.HARVARD.EDU
Borovskii, Genadii; Siberian Inst Plant Physiol Biochem; P.O. Box 1243; Irkutsk-33, 664033; RUSSIA; ; root@sifibr.irkutsk.su
Bosch, L.; Escola Superior d'Agricultura; Comte d'Urgell, 187; 08036 Barcelona; SPAIN; 3-4304207; Fax: 3-4192601
Boston, Rebecca S.; Box 7612; Dept Botany; North Carolina State Univ; Raleigh NC 27695-7612; (919)515-2727; Fax: (919)515-3436
Bouchard, Robert A.; College of Wooster; Biology Dept.; Wooster OH 44691; 216-263-2433; Fax: 216-263-2378; rbouchard@acs.wooster.edu
Bowen, Benjamin; Pioneer Hi-Bred Internatl; 7300 NW 62nd Avenue; P.O. Box 1004; Johnston IA 50131-1732; (515)270-3647; Fax: (515)270-3367; bowenb@phibred.com
Boyer, Charles D.; Dept. of Horticulture; Oregon State University; Ag & Life Sciences 4017; Corvallis OR 97331-7304; 503-737-5474
Brakke, M.; Box 57, Route 1; Crete NE 68333-9606; 402-826-5569; PATH010@UNLVM.UNL.edu
Brar, G. S.; Agracetus Corp; 8520 University Green; Middleton WI 53562; 608-836-7300; Fax: 608-836-9710
Braun, David; 105 Tucker Hall; Biological Sciences; University of Missouri; Columbia MO 65211; 573-882-3481; Fax: 573-882-0123; braun@biosci.mbp.missouri.edu
Brawn, Robert I.; 15 Douglas Drive; Ayr, Ontario NOB 1E0; CANADA; 519-632-7954
Breto, Paz; Pioneer Hi-Bred Int. Inc.; 7300 NW 62nd Ave.; PO Box 1004; Johnston IA 50131-1004
Brettell, Richard; CSIRO Div Plant Industry; P.O. Box 1600; Canberra City ACT 2601; AUSTRALIA; 062-46-5581; dick@pican.pi.csiro.au
Bretting, Peter K.; USDA/ARS, NCRPIS; Agronomy Building; Iowa State University; Ames IA 50011; 515-294-3255; Fax: 515-294-4880; bretting@iastate.edu
Brewbaker, James; Horticulture; Univ of Hawaii; 3190 Maile Way; Honolulu HI 96822; 808-956-7985; Fax: 808-956-3894; brewbake@Hawaii.Edu
Briggs, Steven; Pioneer Hi-Bred International; 7300 NW 62nd Ave; P.O. Box 1004; Johnston IA 50131-1004; 515-270-4143; Fax: 515-253-2149; BRIGGS@PHIBRED.COM
Briggs, Robert W.; Crow's Hybrid Corn Company; Box 306; Milford IL 60953; 815-889-4151; Fax: 815-889-5253
Briggs, Kristen; Pioneer Hi-Bred Internat Inc; Trait and Technol Development; 7300 NW 62nd Ave PO Box 1004; Johnston IA 50131-1004; 515-254-2623; Fax: 515-254-2619; BRIGGSKK@PHIBRED.COM
Brinkman, Mark; Keltgen Seed; 3720 Arch Ave.; Grand Island NE 68803; 308-381-0482; Fax: 308-381-4016
Britt, Anne Bagg; Section of Plant Biology; U of CA; Davis CA 95616; 916-752-0699; Fax: 916-752-5410; abbritt@ucdavis.edu
Brockman, Laura L.; Cargill Hybrid Seeds; 2600 W. Galena Blvd; Aurora IL 60506; 708-801-2352
Brooke, Glenn; Pioneer Hi-Bred International; 7300 NW 62nd Ave; P.O. Box 129; Johnston IA 50131-0129; (515)270-4030; Fax: (515)270-4312; brookerg@phibred.com
Brown, Douglas; Dept of Biology; Bishops University; Lennoxville J1M 1Z7 Quebec; CANADA; 819-822-9632; Fax: 819-822-9661
Brown, Sherri; Monsanto; AA2G; 700 Chesterfield Village Pkwy; St. Louis MO 63198; (314)537-7244; Fax: (314)537-6759
Brown, Steven; 2493 Pinch Road; Manheim PA 17545-9466
Brown, Robert L; USDA/ARS/SRRC; 1100 Robert E. Lee Blvd; New Orleans LA 70125; 504-286-4359; Fax: 504-286-4419; rbrown@nola.srrc.usda.gov
Brown, R. P.; 9555 Johnstown-Utica Rd; Johnstown OH 43031; 614-893-2501
Browne, Chris; Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-7616
Bruce, Wes; Pioneer Hi-Bred International, Inc.; 7300 NW 62nd Ave.; P.O. Box 1004; Johnston IA 50131; (515)270-4167; Fax: (515)270-4167; Brucewb@phibred.com
Brutnell, Thomas P.; Yale University; Dept. of Biology; Osborn Memorial Laboratories P.O. Box 6666; New Haven CT 06511-7444; 203-432-3894; Fax: 203-432-3879; bruthop@yalevm.ycc.yale.edu
Bubeck, David; Northrup King Co.; 317 330th St.; Stanton MN 55018-4308; (507)663-7666
Buckler, Edward; 105 Tucker Hall; University of Missouri; Columbia MO 65211
Buckner, Brent; Div. Science, Science Hall; Northeast Missouri State Univ.; Kirksville MO 63501; 816-785-4083; Fax: 816-785-4045; Sc12%NEMOMUS@ACADEMIC.NEMOSTATE.edu
Buescher, Pat; Custom Farm Seed; Box 160; Momence IL 60954; 815-472-2433; Fax: 815-472-3890
Bueter, Bernd; Swiss Federal Inst. Sci. (ETH) Zurich; Inst. Plant Sci.; ETH - Eschikon 33; CH - 8315 Lindau; SWITZERLAND; 41-52-33-92-83; Fax: 41-52-33-27-06; BUETERB@UNIX.DAT ACOMM.CH
Bullock, W. Paul; ICI Seeds, Inc.; Hwy 210; P.O. Box 500; Slater IA 50244
Bureau, Thomas; Dept. of Genetics; University of Georgia; Athens GA 30602
Burr, Benjamin; Biology Dept; Brookhaven National Lab; Upton NY 11973; 516-282-3396; Fax: 516-282-3407; burr@bnlux1.bnl.gov
Butler, Lou; Dept of Agronomy; Curtis Hall; Univ of Missouri; Columbia MO 65211; 573-882-7818; lou@teosinte.agron.missouri.edu
Butnaru, Gallia; Univ Stiinte Agricole A Banatului; Disciplina de Genetica; C. Post 136, O.P. 1; Timisoara 1900; ROMANIA; 40-96-14142
Byrne, Patrick; Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-0832; Fax: 573-884-7850; byrne@teosinte.agron.missouri.edu
Byrne, Mary; Cold Spring Harbor Laboratory; PO Box 100; Cold Spring Harbor NY 11724; 516-367-8827; Fax: 516-367-8369; byrne@cshl.org
Byron, Dennis; Pioneer Hi-Bred Internat Inc; 7300 NW 62nd Ave; PO Box 1004; Johnston IA 50131-1004
Cabulea, I.; Library; Agric Res Station - Turda; Str. Agriculturii 27; 3350 Turda; ROMANIA; 040-95-311680; Fax: 040-95-311134
Calderon-Urrea, Alejandro; Osborn Memorial Laboratories; Dept of Biology; Yale University, Box 6666; New Haven CT 06511-7444; (203)432-3894; Fax: (203)432-3879; Calalea@YALEVM.ycc.yale.edu

Caldwell, Elizabeth E. Oberthur; 4505 Regal Ave NE; Cedar Rapids IA 52402-2143; 319-335-8333
Callaway, Brett; P.O. Box 3131; Thomasville GA 31799
Callis, Judy; Section of Molecular and Cellular Biol.; Univ of CA; Davis CA 95616; (916)752-1015; Fax: (916)752-3085; JCallis@ucdavis.edu
Camara-Hernandez, J.; Altolaguirre 1295; Buenos Aires 1427; ARGENTINA; 54-1-521-6464; Fax: 54-1-522-1687
Camargo, Luiz; Depto. Fitopatologia -ESALQ/USP; C.P. 09; 13418-900 Piracicaba-SP; BRAZIL; 55-194-294124; Fax: 55-194-344839; leacamar@carpa.ciagri.usp.br
Campbell, Wilbur H.; Dept. of Biological Sciences; Michigan Technological Univ.; 1400 Townsend Drive; Houghton MI 49931-1295; 906-487-2214; Fax: 906-487-3355; WCAMPBEL@MTU.EDU
Camussi, Alessandro; Genetic Unit - Fac of Agriculture; Via S. Bonaventura 13; I-50129 Firenze; ITALY
Cande, Zac; Dept of Molec & Cell Biology; Box 341 LSA; Univ of California; Berkley CA 94720; (415) 642-1669; Fax: 415-643-6791
Carle-Urioste, Jose; Dept of Biological Sciences; Stanford University; Stanford CA 94305-5020
Carlson, Wayne; Botany Department; University of Iowa; Iowa City IA 52242; (319)335-1316; Fax: (319)335-3620; wrcarlsn@vaxa.weeg.uiowa.edu
Carlson, Lawrence A.; 7 North Winthrop Street; St. Paul MN 55119-4674; 612-738-8812
Carneiro, Newton; University of Arizona; Dept. of Plant Sciences; Bldg. 36; Tucson AZ 85721
Carson, Martin L.; Dept. Plant Pathology; Box 7616; NCSU; Raleigh NC 27695-7616; (919)515-3516; Fax: (919)515-7716
Carson, Chris; 105 Tucker Hall; Biological Sciences; University of Missouri; Columbia MO 65211; 573-882-4871; carson@biosci.mbp.missouri.edu
Cartinhour, Sam; Crop Biotechnology Center; Texas A&M Univ; College Station TX 77843; 409-862-3495; Fax: 409-862-4790; scartinh@coyote.tamu.edu
Carvalho, Carlos Roberto de; Depto. Biologia Geral; Universidade Federal de Vicosa; 36570.000; Vicosa - MG; BRAZIL; 31-899-2568; Fax: 31-899-2203
Causse, Mathilde; Station de Genetique Vegetale; Ferme du Moulon; 91190 Gif/Yvette; FRANCE; 33 1 6941 6727; Fax: 33 1 6941 2790; causse@moulon.inra.fr
Cavanaugh, Kevin; Beck's Superior Hybrids; 6767 E. 276th St.; Atlanta IN 46031
Chalyk, S. T.; Institute of Genetics; Lesnaya str. 20; Kishinev 277002; REPUBLIC OF MOLDOVA; 037-32-53-83-67; Fax: 037-32-55-61-80
Chan, Annette; Dept. of Plant Biology; 111 Koshland Hall; University of California; Berkeley CA 94720-3102; ; ACHAN@UCLINK3.BERKELEY.EDU
Chandler, Vicki; Department of Biology; Institute of Molecular Biology; University of Oregon; Eugene OR 97403; 503-346-5136; Fax: 503-346-5891; chandler@molbio.uoregon.edu
Chandrakanth, E.; Center for Plant Mol. Biol.; Osmania University; Hyderabad 500007; INDIA
Chang, Ming-Tang; ExSeeds Genetics L.L.C.; 1567 Food Sciences Bldg.; Iowa State Univ.; Ames IA 50011-1061; 515-294-2993; Fax: 515-294-2644
Chang, Ru-Ying; Plant Path Dept; 1453 Fifield Hall; Univ Florida; Gainseville FL 32611; 904-392-9469; rychang@iastate.edu
Chang, S. C.; 13, LN36, Chung Shan Rd.; Chiayi, ROC; TAIWAN; 05-278-4603
Chao, Shiaoman; Inst. Botany, Rm. 114; Academia Sinica; Nanking, Taipei; TAIWAN; (02) 789-9590 ext. 114; schao@ccvax.sinica.edu.tw
Char, Bharat; Plant Gene Expression Center; 800 Buchanan St.; Albany CA 94710
Charlton, Wayne; Rodney Porter Building; Dept. of Plant Sciences; University of Oxford, South Parks Road; Oxford, OX1 3RB; UNITED KINGDOM; 44-1865-275814; Fax: 44-1865-275805; WCHARLTON@GLYCOB.OX.AC .UK
Chase, Christine D.; Horticultural Sciences Dept.; 1143 Fifield Hall; Univ of Florida; Gainesville FL 32611-0690; 904-392-1928x316; Fax: 904-392-6479; ctdc@gnv.ifas.ufl.edu
Chase, Sherret S.; Chase Road; P.O. Box 193; Shokan NY 12481; 914-657-2392
Chechak, C; Stokes Seeds Limited; 39 James Street; P.O. Box 10, St. Catharines; Ontario L2R 6R6; CANADA; 905-688-4300; Fax: 905-684-3022
Chen, Rei Yang; Nankai University; Biology Division; Plant Molecular Biology Dept.; Tianjin 300071; CHINA
Chen, Shouyi; Academia Sinica; Institute of Genetics; Datun Road, Andingmen Wai; Beijing,100101; CHINA
Chen, Yun-Chia; Plant Gene Expression Center; 800 Buchanan St.; Albany CA 94710
Chen, Jychian; Institute of Molec Biol; Academia Sinica; Taipei; TAIWAN; 011-8862-789-9208; Fax: 011-8862-782-6085; mbjchen@ccvax.sinica.edu.tw
Chen, Fure-Chyi; Dept. Plant Industry; National Pingtung Polytechnic Inst; Neipu, Pingtung 91207; TAIWAN; 886-8-774-0267; Fax: 886-8-774-0264
Chen, Weicheng; Dept. of Agronomy; Henan Agric. University; ZhengZhou 450002; CHINA
Chen, Zengjian; Department of Agronomy & Plant Genetics; 411 Borlaug Hall; University of Minnesota; St. Paul MN 55108; (612)625-5793; Fax: (612)628-1268
Cheng, Kan-Sheng; Yunnan Academy of Agricultural Sciences; Kunming; Yunnan 650205; CHINA
Cheng, Wan-Hsing; Dept. of Plant Pathology; University of Florida; Gainesville FL 32611
Cheng, Ping-chin; Advanced Microscopy and Imaging Lab; Dept Elect Comp Eng, 201 Bell Hall; State University of New York at Buffalo; Buffalo NY 14260; (716)645-3868; Fax: (716)645-3868; elepcc@corn.eng.buffalo.edu
Chilton, Scott; Dept of Botany; Box 7; N. C. State University; Raleigh NC 27695-7612; (919)515-3792; Fax: (919)515-3436; joyce_bruffey@ncsu.edu
Chin, Emily; Pioneer Hi-Bred International; 7300 NW 62nd Ave; P. O. Box 1004; Johnston IA 50131-1004; (515)270-5970; Fax: (515)270-2149; chinecl@phibred.com
Choe, Bong-Ho; Agronomy Dept; College of Agriculture; Chungnam National University; Dae-Jon 305-764; KOREA; KOREA-042-821-5723; Fax: 82-42-823-8050
Choi, Keun-Jin; Dept. of Corn Breeding; Upland Crop Div.; Crop Experiment Station; Suwon; KOREA; (0331)292-3823; Fax: (0331)292-4560
Chojecki, Jan; Zeneca Seeds; Jealott's Hill Research Sta; Bracknell Berks RG12 6EY; UNITED KINGDOM; 44-1344-414814; Fax: 44-1344-414996
Chomet, Paul; DeKalb Plant Genetics; 62 Maritime Drive; Mystic CT 06355; 203-572-5224; Fax: 203-572-5240; PCHOMET@DEKALB.COM
Chongkid, Boonhong; Dept. of Agricultural Technology; Fac. of Science & Technology; Thammasat Univ., Rangsit Campus; Pathum Thani 12121; THAILAND; 5160020-39 ext. 1712, 1713; Fax: 5160963
Chopra, Surinder; 2116 Molecular Biology Building; Iowa State University; Ames IA 50011; (515)294-5054; Fax: (515)294-0345; chopra@iastate.edu
Chourey, Prem; USDA-ARS; Plant Pathology Department; University of Florida; Gainesville FL 32611-0680; 904-392-2806; Fax: 904-392-6532; PSCH@GNV.IFAS.UFL.EDU
Chrispeels, Hanya; Biology Dept.; Herrin Bldg.; Stanford University; Stanford CA 94305-5020
Christensen, Dean W.; Ciba-Geigy Seed Div.; P.O. Box 18300; Greensboro NC 27419; 919-547-1017; Fax: 919-547-1030
Chuck, George; USDA-ARS-PGEC; 800 Buchanan Street; Albany CA 94710
Chughtai, Sajjad R.; Maize Program; NARC, P.O. NIH; Islamabad; PAKISTAN; (051)241534; Fax: 51-812968
Chytry, Assunta; c/o Freeling Lab; Dept of Plant Biology; Univ of California; Berkeley CA 94720; 510-642-8058; Fax: 510-642-4995
CIMMYT Library; Lisboa #27, Apdo. Postal 6-641; Col. Juarez Deleg. Cuauhtemoc; 06600 Mexico, D. F.; MEXICO; (905)726-9091; Fax: 595 410 69
Clark, Janice K.; Dept. of Biology; University of North Dakota; Grand Forks ND 58202-9019; (701)777-2621; Fax: (701)777-2623; janclark@plains.nodak.edu
Clark, Harry; Ames Seed Farm; RR 1, Box 107A; Kelley IA 50134; 515/232-3648; Fax: 515/232-6120
Close, Timothy J.; Dept. Bot. & Plant Sci.; Univ. of California Riverside; Riverside CA 92521; 714-787-3318; Fax: 714-787-4437; TIMCLOSE@UCRAC1.UCR.EDU
Clutter, Mary; BIO/BIO; National Science Foundation Room 605N; 4201 Wilson Blvd.; Arlington VA 22230; 703-306-1400; mclutter@note.nsf.gov
Cocciolone, Suzy; Pioneer Hi-Bred International; Trait & Technology Development; 7300 NW 62d Ave Box 1004; Johnston IA 50131-1004; 515-270-3987
Coe, Ed; Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-2768; Fax: 573-884-7850; ed@teosinte.agron.missouri.edu
Colasanti, Joseph J.; Cold Spring Harbor Lab; Bungtown Rd.; P.O. Box 100; Cold Spring Harbor NY 11724; 516-367-8469; Fax: 516-367-8369; colasant@cshl.org
Colbert, Terry; PO Box 1458; ; Garden City KS 67846; 316-276-8149
Coleman, Craig; Dept. of Plant Science; 303 Forbes Bldg.; Univ. of Arizona; Tucson AZ 85721; 520-621-9154; ccoleman@ag.arizona.edu
Colless, J. M.; Agric Research Sta; Grafton, NSW 2460; AUSTRALIA; 066-420420; Fax: 066-447251
Cone, Karen C.; Biological Sciences; University of Missouri; Columbia MO 65211; 573-882-2118; Fax: 573-882-0123; Cone@biosci.mbp.missouri.edu
Consonni, Gabriella; University of Milan; Dept. of Genetics & Microbiology; Via Celoria 26; 20133 Milan; ITALY; +39-2-26605210; Fax: +39-2-2664551; tonelli@imiucca.csi.unimi.it
Cook, Allen; Montana State University; USDA-ARS; Plant Soil & Environmental Sci; Bozeman MT 59717
Cook, Bill; Biology Department; Midwestern State University; 3410 Taft Blvd.; Wichita Falls TX 76308; 817-689-4192; Fax: 817-689-4442; fcookb@nexus.mwsu.edu
Cooper, Pamela S.; Univ. of Missouri ; Div. of Biological Science; Columbia MO 65211; 573-882-1168; Fax: 573-882-0123; cooper@biosci.mbp.missouri.edu
Coors, James G.; Department of Agronomy; University of Wisconsin; 1575 Linden Drive; Madison WI 53706; 608-262-7959; COORS@MACC.WISC.EDU
Corke, Harold; 45 Highwest; 142 Pokfulam Road; Hong Kong; HONG KONG; 011 852 2859 2820; Fax: 011 852 2858 3477; harold@hkuxa.hku.hk
Cormack, Jean; DeKalb Genetics Corp.; 3100 Sycamore Rd; DeKalb IL 60115; 815-758-9682; Fax: 815-758-4106
Cornu, A.; Sta d'Amelior des Plantes; B V 1540; 21034 Dijon; FRANCE; 80-63-3159; Fax: 80-63-3263

Cowan, Kyra; University of Ottawa; 40 Marie Curie Private; Ottawa, Ontario K1N 9B4; CANADA; (613)564-5869; Fax: (613)564-9562; altosaar@acadvm1.uottawa.ca
Cowen, Neil; DowElanco Discovery Research; 9410 Zionsville Rd., CI/#245; Indianapolis IN 46268-1053; 317-337-3684; Fax: 317-337-3228
Crane, Virginia; Trait and Technology Development; Pioneer Hi-Bred International, Inc.; 7300 N. W. 62nd Ave, Box 1004; Johnston IA 50131-1004; (515)270-3645; Fax: (515)253-2149; CRANEVC@PHIBRED.COM
Creech, Roy G.; Plant & Soil Sciences; Box 9555; Mississippi State University; Mississippi State MS 39762; 601-325-2699; Fax: 601-325-8742; rgcreech@ra.msstate.edu
Cross, John; Instrumentation and Instr Devel Program; National Science Foundation; 4201 Wilson Blvd; Arlington VA 22230; ; jwcross@nsf.gov
Cuany, Robin L.; Department of Agronomy; Colorado State University; Fort Collins CO 80523; 303-491-6832; Fax: 303-491-0564
Cui, Xianqin; B420 Agronomy Hall; Iowa State University ; Ames IA 50011
Culley, David; Dept of Plant Pathology; Washington State Univ; Pullman WA 99164-6430; 509-335-3751; Fax: 509-335-9581; DCULLEY@WSUNIX.WSU.EDU
Cummings, D. P.; Dekalb Genetics Corporation; P.O. Box 367; 908 North Independence; Windfall IN 46076-0367; 317-945-7125; Fax: 317-945-7152
Currie, Randall; SWREC; 4500 E. Mary; Garden City KS 67842; 316-276-8286; Fax: 316-276-6028; RCURRIE@OZNET.KSU.EDU
Curtis, Christine A.; Dept Med & Molec Genetics, IB 264; Indiana University Medical Center; 975 W. Walnut St.; Indianapolis IN 46202; 317-274-1060
D'Halluin, Kathleen; Plant Genetic Systems N.V.; Jozef Plateaustraat 22-B 9000; Gent; BELGIUM; (32) (9)2358486; Fax: (32) (9)2240694; pgs@pgsgent.be
Dahleen, Lynn; USDA-ARS-NCSL; 1307 N. 18th St; P.O. Box 5677, S.U. Sta.; Fargo ND 58105-5677; 701-239-1384; Fax: 701-239-1369; dahleen@badlands.NoDak.edu
Damerval, Catherine; Station de Genetique Vegetale; Ferme du Moulon; 91190 Gif Sur Yvette; FRANCE; (1)69 41 67 24; Fax: 33(1)69 41 27 90
Dankov, Toma; Ivan Assen Str.-93; Sofia 1124; BULGARIA; 43-82-73
Daohong, Xie; Maize Research Institute; Jilin Acad.; 5 W. Xing Hua Street; Gongzhuling, Jilin, P.R. 136100; CHINA; (86)-04441-215179; Fax: (86)-04441-214884
Darrah, Larry; 110A Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-2349; Fax: 573-884-7850; AGROLLD1@mizzou1.missouri.edu
Das, Prem; Heartland BioTechnologies; 125 West 76th St.; Davenport IA 52806; 319-388-6422; Fax: 319-388-6158; odas@vaxa.weeg.uiowa.edu
Davis, Douglas; 117 Tucker Hall; Univ of Missouri; Columbia MO 65211; 573-882-3856; Fax: 573-882-0123; DDAVIS@BIOSCI.MBP.MISSOURI.EDU
Davis, Georgia; Curtis Hall; Agronomy Department; University of Missouri; Columbia MO 65211; 573-882-3856; Fax: 573-884-7850; gdavis@teosinte.agron.missouri.edu
Davis, David W.; Horticultural Science Dept; 286 Alderman Hall-Univ MN; 1970 Folwell Avenue; St. Paul MN 55108; (612)624-9737; Fax: (612)624-4941
Dawe, R. Kelly; Department of Botany; University of Georgia; Athens GA 30602; ; kelly@dogwood.botany.uga.edu
Day, Peter R.; Center for Ag Molec Biology; Cook College, Rutgers Univ; Foran Hall, Dudley Road; New Brunswick NJ 08903-0231; 908-932-8165; Fax: 908-932-6535; day@mbcl.rutgers.edu
De Leon, Carlos; CIMMYT; P.O. Box 9-188; Bangkok 10900; THAILAND; 662-561-4057; Fax: 662-579-4858; cimmyt@netserv.chula.ac.th
Dean, Caroline; BBSRC; John Innes Centre; Colney Lane; Norwich NR4 7UH; UNITED KINGDOM; 011-44-1603-452571; Fax: 011-44-1603-505725; ARABIDOPSIS@bbsrc.AC.UK
Deboo, Gulshan; 154 Johnson Hall; Horticulture and Landscape Architecture; Pullman WA 99164-6414
DeBroux, Steve; 700 E. Butler Ave.; Delaware Valley College; Doylestown PA 18901; 215-345-1500; Fax: 215-345-5277
Delannay, Xavier; Monsanto-Ceregen; 700 Chesterfield Pkwy North; St. Louis MO 63198; 314-537-6611; Fax: 314-537-6047; xxdela@ccmail.monsanto.com
Dellaporta, Steve; Department of Biology; 356 OML; Yale University; New Haven CT 06511; 203-432-3895; sdellap@yalevm.ycc.yale.edu
Dempsey, Ellen; 7 Prospect St; Cornwall-on-Hudson NY 12520; 914-534-5285
Dennis, Elizabeth; CSIRO; Division of Plant Industry; P.O. Box 1600; Canberra, ACT 2601; AUSTRALIA; 61-6-246-5061; Fax: 61-6-246-5000; liz@pican.pi.csiro.au
Deutsch, James A.; ICI Seeds, Inc.; RR2 ; Box 16; Marshall MO 65340; 816-886-6363; Fax: 816-886-9877
Dewald, Chester L.; ARS-USDA; 2000 18th St.; Woodward OK 73801; 405-256-7449; Fax: 405-256-1322
DH Hill Lib/Acq C; North Carolina State Univ; Box 7111; Raleigh NC 27695-7111; (919)515-2842; Fax: (919)515-7292; nancy_gibbs@library.lib.ncsu.edu
Dhillon, B. S.; CIMMYT, Maize Program; Apartado Postal 6-641; C.P. 06600 Mexico, D.F.; MEXICO; (5)726-90-91; Fax: (595)410-69
Dietrich, Chuck; B420 Agronomy Hall; Iowa State University; Ames IA 50011
Dijkhuizen, Arian; W-203 Turner Hall; 1102 South Goodwin Ave.; Urbana IL 61801; 217-244-3388; Fax: 217-333-9817; DIJKHUIZ@UX1.CSO.UIUC.EDU
Dille, John E.; Winthrop College Biology Dept; Rock Hill SC 29733; 803-323-2111; Fax: 803-323-3448; dillej@winthrop.edu
Dilworth, Machi; NSF Div BIO/IBN, Room 685S; 4201 Wilson Blvd.; Arlington VA 22230; 703-306-1423; mdilwort@nsf.gov
Dincher, Sandra; PO Box 12257; CIBV-GEIGY Corp.; Research Triangle Park NC 27709
Ding, Qun-Xing; Plant Reproductive Lab; Institute of Botany; Academia Sinica; Beijing 100093; CHINA; ; pgmlzz@mimi.cnc.ac.cn
Dodd, J. L.; Professional Seed Research, Inc; 7 South 437 Dugan Road; Sugar Grove IL 60554; 708-466-1060; Fax: 708-466-1068
Doebley, John F.; Plant Biology Department; University of Minnesota; St. Paul MN 55108; 612-625-3702; Fax: 612-625-1738; doebley@maroon.tc.umn.edu
Dogra, Anjali; 205 Curtis Hall; University of Missouri; Columbia MO 65211
Dolfini, Silvana Faccio; Dipartimento di Genetica; University of Milano; Via Celoria 26; 20133 Milano; ITALY; 39 2 266051; Fax: 39 2 2664551
Dolgykh, Yulia; Academy of Sciences; K.A. Timirjazev Inst of Plant Phys.; Botanicheskaya 35; Moscow 127276; RUSSIA; 95-903-93-92; Fax: 95-482-16-85
Dombrink-Kurtzman, Mary Ann; Natl. Ctr. for Agric. Utilization Research; USDA, ARS; 1815 N. University St.; Peoria IL 61604; (309)681-6254; Fax: (309)681-6686
Donlin, Maureen J.; 111 Koshland; c/o Freeling Lab; Univ of California; Berkeley CA 94720; (510)642-7948; Fax: (510)642-4995; donlin@nature.berkeley.edu
Dooner, Hugo K.; The Waksman Institute; Rutgers University; P.O. Box 0759; Piscataway NJ 08855; 908-445-4684; Fax: 908-445-5735; dooner@mbcl.rutgers.edu
Doring, Hans-Peter; Deutz-Kalker-St. 136; 50679 Koln; GERMANY
Dorweiler, Jane; Plant Biology Dept; 220 Bio Sciences Bldg; 1445 Gortner Ave; St. Paul MN 55108; (612)625-0271; Fax: (612)625-1738; dorwe001@maroon.tc.umn.edu
Dowd, Pat; USDA-ARS; 1815 N. University St.; Peoria IL 61614; 309-681-6242; Fax: 309-681-6686
Dowling, Edward J.; C/O Jacques Seed Co; RR #2, Box 84; Lincoln IL 62656; 217-735-2770
Dowty, Jean L.; P.O. Box 5613; Raleigh NC 27650; (919)515-2704; Fax: (919)515-3436; JLDOWTY@UNITY.NCSU.EDU
Doyle, G. G.; Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-2674
Drummond, Bruce; Pioneer Hi-Bred Internat., Inc.; 7300 NW 62nd Ave.; PO Box 1004; Johnston IA 50131-1004
Dubald, Manuel; Rhone-Poulenc Ag. Company; P.O. Box 12014; 2 T.W. Alexander Drive; Research Triangle Park NC 27709; (919)549-2459; Fax: (919)549-9175
Dudley, John W.; Crop Sciences, S112 Turner Hall; University of Illinois; 1102 S Goodwin Ave; Urbana IL 61801; 217-333-9640; Fax: 217-333-9817; jdudley@uiuc.edu
Duncan, David; Monsanto Agricultural Group GG4H; 700 Chesterfield Parkway N.; Chesterfield MO 63198; 314-537-6923; Fax: 314-537-6567; drdunc1@ccmail.monsanto.com
Durkovicova, Viera; Prachaticka 43; SK-96001 Zvolen; SLOVAK REPUBLIC
Duvick, Jonathan P.; Pioneer Hi-Bred Internatl; Dept of Biotechnology Res; 7300 N.W. 62nd Ave; Johnston IA 50131-1732; 515-270-3176; Fax: 515-253-2147
Duvick, Susan; 1501 Agronomy; Iowa State University; Ames IA 50011; 515-294-5545; SBurkhar@iastate.edu
Duvick, Donald N.; P.O. Box 446; Johnston IA 50131; 515-278-0861; Fax: 515-253-2125; duvick@phibred.com
Earle, Elizabeth D.; Dept Plant Breed & Biom; Cornell University; 252 Emerson Hall; Ithaca NY 14853-1902; 607-255-3102; Fax: 607-255-6683; ede3@cornell.edu
Eathington, Samuel R.; 910 Gaskill; Ames IA 50014; 515-685-5141; Fax: 515-685-5080
Eaton, Dana; Asgrow Seed Co; 32545 Galena Sassafras Rd; Galena MD 21635; 410-827-9240; Fax: 410-827-9763
Edwards, Marlin; Green Giant; 1201 N. 4th Street; Le Sueur MN 56058; 612-665-3515; Fax: 612-665-2682
Edwards, Keith; Cell Biol Dept; IACR-Long Ashton Res Stn; Univ Bristol, Long Ashton; Bristol BS18 9AF; UNITED KINGDOM; 44-0-1275-392181; Fax: 44-0-1275-394281; KEITH.EDWARDS@BBSRC.AC.UK
Efremov, Alexander; Max-Planck-Institute; Carl-von-Linne-Weg 10; D-50829 Koln (Vogelsang); GERMANY
Eggleston, Bill; Department of Biology; Virginia Commonwealth University; 218 Park Ave; Richmond VA 23284; 804-828-1562; Fax: 804-828-0503; weggles@cabell.VCU.edu
Egli, Margaret A.; Dept Agron & Plant Genetics; Univ of Minnesota, 411 Borlaug Hall; 1991 Buford Circle; St. Paul MN 55108; (612)625-5215/5793; Fax: (612)625-1268; peggy@biosci.cbs.umn.edu
Eichholtz, David A.; Monsanto, BB4D; 700 Chesterfield Village Pkwy; St. Louis MO 63198; 314-537-6227; Fax: 314-537-6047; DAEICH@CCMAIL.MONSANTO.COM
Eisses, John; Dept. of Biological Sciences; University of Idaho; Moscow ID 83844-30521
Elsing, Evan; Pioneer Hi-Bred Intl Inc.; Kekaha Research Sta; 1 Mile W RR50/PO Box 596; Kekaha, Kauai HI 96752-0596
England, Dan; Curtis Hall; Univ of Missouri; Columbia MO 65211; 573-882-7818

Erturk, Neval; Dept. of Biology; Virginia Polytech Inst & State Univ; Blacksburg VA 24061-0406
Esen, Asim; Dept Biology; Va Polytech Inst & State Univ; Blacksburg VA 24061; 231-5894; Fax: 231-9307; aevatan@vt.edu
Eubanks, Mary W.; 4110 Hulon Drive; Durham NC 27705; 919-490-5380; Fax: 919-684-5412; eubanks@acpub.duke.edu
Evans, Matthew; Laboratory of Genetics; 445 Henry Mall; University of Wisconsin; Madison WI 53706; 608-262-4934; Fax: 608-262-2976; mmevans@facstaff.wisc.edu
Evola, S. V.; Ciba Seeds; P.O. Box 18300; Greensboro NC 27419-8300; 910-547-1038; Fax: 910-547-1030; evolas@a1.abru.cg.com
Falbel, Tanya; Department of Horticulture; University of Wisconsin; 1575 Linden Dr.; Madison WI 53705; 608-262-1622; Fax: 608-262-4743; falbel@macc.wisc.edu
Fan, Yun-Liu; Chinese Academy of Agricultural Sciences; Biotechnology Research Center; 30 Baishiqiao Lu; Beijing 100081; CHINA
Farish, Guy; Biology Dept; Adams State College; Alamosa CO 81102; 719-589-7969; Fax: 719-589-7522; GFARISH@CC4.ADAMS.EDU
Fauron, Christiane; University of Utah; 2100 Eccles Genetics Bldg; Salt Lake City UT 84112; 801-581-4435; Fax: 801-585-7177; christiane.fauron@genetics.utah.edu
Fedoroff, Nina; Biology; 0519 Wartik Laboratory; University Park PA 16802; 814-863-5717; Fax: 814-863-1357; nvf1@psu.edu
Feix, Gunter; Institut Fur Biologie III; Universitat Freiburg; 79104 Freiburg; GERMANY; 0761-2032724; Fax: 0761-2032745; FEIX@SUN1.RUF.UNI-FREIBURG.DE
Feng, Jia Shi; Maize Research Institute Shandong; Academy of Agricultural Sciences; 11 Sang Yuan Road; Jinan, Shandong 250100, P.R.; CHINA; (0531)860329
Fennoy, Sheila; Botany & Plant Sciences; U.C. Riverside; Riverside CA 92521
Fergason, Virgil; Custom Farm Seed; P.O. Box 380; Forsyth IL 62535; 217-875-2826; Fax: 217-875-9437
Ferl, R. J.; Horticultural Sciences; Univ Florida; Gainesville FL 32611; 904-392-1928 ext 301; Fax: 904-392-4072; Robferl@NERVM.NERDC.UFL.EDU
Fincher, Robert R.; Pioneer Hi-Bred Internatl.; 7300 NW 62nd Avenue; P.O. Box 1004; Johnston IA 50131-1004; 515-270-3797; Fax: 515-253-2288; fincher@phibred.com
Flament, Pascal; Biocem; Campus Universitaire des Cezeaux; 24 Avenue des Landais; 63170 Aubiere; FRANCE; (33)73 42 79 70; Fax: (33)73 27 57 36; flament@citi2.fr
Fluminhan, Antonio Jr.; Institute of Genetic Ecology; Tohoku Univ - Katahira Campus; Katahira 2-1-1, Aoba-Ku; 980-77 Sendai; JAPAN; 81-22-227-6200x3100; Fax: 81-22-263-9845; antonio@bansui.ige.tohoku.ac.jp
Foley, Rhonda; Dept. of Biology; Univ of California - Los Angeles; 405 Hilgard Ave.; Los Angeles CA 90024-1606; ; Fax: 310-206-3987
Foley, Terry; Holden's Foundation Seeds Inc; 201 North Maplewood; P.O. Box 839; Williamsburg IA 52361; 319-668-1100; Fax: 319-668-2453; terry@holdens.com
Foreman, Daphne; 4085 Kraus Hall; Department of Biology; University of Michigan; Ann Arbor MI 48109-1048; (313)764-3579; Fax: (313)747-0884
Foster, Toshi; Plant Gene Expression Center; USDA; 800 Buchanan St.; Albany CA 94710
Fowler, John; Dept. of Biology - CB#3280; University of North Carolina; ; Chapel Hill NC 27599-3280; 919-962-0778; Fax: 919-962-0778; jfowler@uncvx1.oit.unc.edu
Fox, Tim; Pioneer Hi-Bred Internat., Inc.; 7300 NW 62nd Ave. NW; P.O. Box 1004; Johnston IA 50131
Frances, Shannon; Dept. of Genetics; Campus Box 7614; North Carolina State Univ; Raleigh NC 27695
Francis, T. R.; Northrup King Co.; R. R. 1; Arva, N0M 1C0; CANADA; 519-461-0072; Fax: 519-461-0275
Frank, Mary; Dept. of Biology; MC0116; Univ. of California - San Diego; La Jolla CA 92093-7108
Franken, P.; Max-Planck Inst Zuchtungsf; Carl-von Linne-Weg 10; D 5000 Koln 30; GERMANY
Franklin, Amie; Dept Molec Cell Biol; 345 LSA; Univ of California; Berkeley CA 94720-0001
Freeling, Michael; Dept of Plant Biology; 111 Genetics & Plant Biology Bldg; Univ of California; Berkeley CA 94720; 510-642-8058, 1107; Fax: 510-642-4995; freeling@nature.berkeley.edu
Frei, Mark; Winkelgasse 2; 4512 Bellach; SWITZERLAND; (41)65 38 17 97
Frey, Ruth; Dept. of Biological Sciences; University of Idaho; Moscow ID 83843
Frey, Monika; Lehrstuhl fur Gentechnik Hoherer Pflanzen; TUM; Lichtenbergstrabe 4; 85747 Garching; GERMANY; +49-89-3209 3532; Fax: +49-89-3209-2892; frey@c2h5oh.org.chemie.tu-muenchen.de
Freymark, Peter J.; 16 Cameron Road; P.O. Borrowdale; Harare; ZIMBABWE; 011-263-4-726061; Fax: 011-263-4-726061; FREYMARKP@PHIBRED.COM
Friedman, Robert B.; American Maize-Products Co; 1100 Indianapolis Blvd; Hammond IN 46320-1094; 219-659-2000 ext 390; Fax: 219-473-6607
Friedrich, James W.; Maize Genetic Resources, Inc; 10570 Hwy. 50 North; Angier NC 27501; 919-894-5594; Fax: 919-894-5660
Frolich, Walter; Oberriexingerstr. 32; D-74343 Sachsenheim; GERMANY
Fromm, Michael; Monsanto Co. AA2G; 700 Chesterfield Village Pkwy; St. Louis MO 63198; 314-537-6048; Fax: 314-537-6759
Frova, Carla; Dept of Genetics & Microbiology; University of Milano; Via Celoria 26; 20133 Milano; ITALY; 02/26605.201; Fax: 02/2664551; CAMELOT@IMIUCCA.CSI.UNIMI.IT
Fu, Xi-Qin; Hunan Academy of Agricultural Sciences; Hybrid Rice Research Center; Mapoling, Dong Jiao, Changsha; Hunan 410125; CHINA; 86-731-6662472; Fax: 86-731-4448877
Fuerstenberg, Susan; Plant Biology Dept - U of MN; 220 Biological Sciences Building; 1445 Gortner Avenue; St. Paul MN 55108; 612-624-2715; Fax: 612-625-5754; fuers001@maroon.tc.umn.edu
Fung, Jennifer; Dept Biochem Biophys; Box0554 HSE; UC San Francisco; San Francisco CA 94143
Furtek, D. B.; Inst. Molecular Biology Labs; Pennsylvania State Univ.; 214 Borland Lab; University Park PA 16802-2505; 814-863-7785; Fax: 814-863-6123; dbf1@psu.edu
Gabay-Laughnan, Susan; Plant Biology/265 Morrill Hall; University of Illinois; 505 S. Goodwin Avenue; Urbana IL 61801; 217-333-2919; Fax: 217-244-7246
Gaillard, Antoine; Maisadour; Route de Saint-Sever-Haut Mauco; BP 27; 40001 Mont-de-Marsan; FRANCE; 58 05 84 84; Fax: 58 05 84 99
Gale, Michael; John Innes Centre; Norwich Research Park; Colney Lane; Norwich NR4 7UH; UNITED KINGDOM
Galinat, Walton C.; Eastern Agric. Center, U. Mass.; 240 Beaver Street; Waltham MA 02154-8096; 617-891-0650; Fax: 617-899-6054
Gallie, Daniel; Dept. of Biochemistry; University of California; Riverside CA 92521; (909)787-7298; Fax: (909)787-3590; DRGALLIE@UCRAC1.UCR.EDU
Gao, Min-Wei; Zhejiang Agricultural University; Institute of Nuclear-Agric. Science; Hangzhou; Zhejiang 310029; CHINA
Garcia-Olmedo, F.; Lab Biochemistry and Molecular Biology; Dept. Biotechnology; E T S Ingenieros Agronomos; 28040-Madrid; SPAIN; 34-1-3365707; Fax: 34-1-3365757
Gardiner, Michele; Rogers NK Seed Co; 6338 Highway 20-26; Nampa ID 83687; (208)466-0319; Fax: (208)467-4559
Gardiner, Jack; Biology Building; University of Iowa; Iowa City IA 52242; 319-335-1095; Fax: 319-335-1069; zeamays@biovax.biology.uiowa.edu
Gardner, C. A. C.; Pioneer Hybrid Internatl; Highway 65 South, PO Box 218; Carrollton MO 64633; 816-542-3780
Garnaat, Carl W.; Pioneer Hi-Bred Int'l; Department of Biotechnology Research; 7300 N. W. 62nd Ave-P.O. Box 1004; Johnston IA 50131-1004; (515)253-2251; Fax: (515)270-3367; GARNAATC@PHIBRED.COM
Garwood, D. L.; Garwood Seed Company; RR 1, Box 20; Stonington IL 62567; 217-325-3715
Gavazzi, Giuseppe; Universita de Milano; Dip Fisiol Pianta Coltivate Chim Agrar; Via Celoria 2; 20133 Milano; ITALY; +39-2-70630856; Fax: +39-2-2663057
Gay, Philippe; CIBA-GEIGY Ltd; Agricultural Division; CH-4002 Basel; SWITZERLAND; 41-61-697-4457; Fax: 41-61-697-6194
Geadelmann, Jon L.; Holden's Foundation Seeds, Inc; 2440 Highway 19 Blvd; Stanton MN 55018-7220; 507-263-3476; Fax: 507-263-4839; jon@holdens.com
Gebauer, Juan E.; Corn Breeding; Casilla 190; Buin; CHILE; 011(56-2)821-1552; Fax: 011(56-2)821-3564
Geiger, Hartwig H.; Univ Hohenheim; 350 Inst Pflanzenzucht; Seed Sci and Pop Genetics; D-70593 Stuttgart; GERMANY; 49-711-459-2644; Fax: 49-711-459-2343; PZHHG@RS1.RZ.UNI-HOHENHEIM.DE
Gengenbach, Burle G.; Agron & Plant Genetics; Univ of Minnesota; 1991 Upper Buford Cir.; St Paul MN 55108; 612-625-6282; Fax: 612-625-1268; burle@molbio.cbs.umn.edu
Getschman, R. J.; Dekalb Plant Genetics; Box 408; Dayton IA 50530; 515-547-2550; Fax: 515-547-2552
Gierl, Alfons; Lehrstuhl fur Genetik; Technische Universitat Munchen; 85747 Garching; GERMANY; 49-89-3209-2890; Fax: 49-89-3209-2892; gierl@gen.chemie.tu-muenchen.de
Gilliam, Jacob; Pioneer Hi-Bred Internat Inc; Crop Protection ; 7300 NW 62nd Ave., PO Box 1004; Johnston IA 50131-1004
Gillies, Christopher; Macleay Bldg A12; Univ of Sydney; Sydney NSW 2006; AUSTRALIA; 61-2-351-2688; Fax: 61-2-351-4771; cgillies@extro.ucc.su.oz.au
Gillikin, Jeff; Dept. Botany; NCSU; Box 7612; Raleigh NC 27695-7612; 919-515-3570; Combip@unity.NCSU.edu
Giorio, Giovanni; c/o Metapontum Agrobios; SS. Ionica Km 448.2; I-75010 Metaponto (MT); ITALY; 39-835-740276; Fax: 39-835-745306; AGROBIOS@MVX36.CSATA.IT
Girard, Lisa; Plant Biology Dept; 111 Koshland Hall; UC Berkeley; Berkeley CA 94720-3102
Giroux, Michael; Dept. of Horticultural Sciences; Univ of Florida; 1255 Fifield Hall; Gainesville FL 32611; 904-392-0091
Glover, David V.; Dept of Agronomy; Purdue University; W. Lafayette IN 47907; 317-494-8067; Fax: 317-494-6508; DGLOVER@dept.agry.purdue.edu

Godshalk, E. Brent; Dekalb Genetics Corp.; 423 S. Colebrook Rd.; Manheim PA 17545-9144; 815-758-9372
Goff, Steve; CIBA-GEIGY Biotechnology; 3054 Cornwallis Road; Research Triangle Park NC 27709
Goldman, Irwin; Department of Horticulture; Univ. of Wisconsin; 1575 Linden Drive; Madison WI 53706; (608)262-7781; Fax: (608)262-4743
Goldman, Stephen; Dept of Biology; University of Toledo; Toledo OH 43606; 419-530-4197; Fax: 419-530-7737
Golubovskaya, I. N.; Dept of Genetics ; N I Vavilov Res Inst Plant Ind; Hertzen Street, 44; 190 000 St Petersburg; RUSSIA
Gong, Zuxun; Academia Sinica; Shanghai Inst. of Biochem.; 320 Yue-Yang Road; Shanghai 200031; CHINA
Gonzalez de Leon, Diego; CIMMYT, INT; Lisboa #27, APDO. POSTAL 6-641; 06600 Mexico, D. F.; MEXICO; (52)(5)955-4400/4410; Fax: (52)(5)955-4425; DGDELEON@CIMMYT.MX
Goodman, Major M.; Department of Crop Sciences; North Carolina State Univ; P.O. Box 7620; Raleigh NC 27695; 919-515-2704; Fax: 919-515-7959
Gordon, P. N.; CT Forest & Park Assoc.; 16 Meriden Rd.; Rockfall CT 06481-2961; (203)346-2372; Fax: 203-347-7463
Gordon-Kamm, William; Pioneer Hi-Bred Internat Inc; 7300 NW 62nd Ave., PO Box 1004; Johnston IA 50131-1004
Gouesnard, Brig.; INRA Centre de Montpellier; Sta Genet Amel Plantes; domaine de Melgueil; 34130 Mauguio; FRANCE; ; Fax: 67 29 39 90; gouesnar@montpellier.inra.fr
Gracen, V. E.; Cargill Hi-Bred Seed; Box 9300; Minneapolis MN 55440; 612-742-7244; Fax: 612-742-7235
Grant, David; G304 Agronomy Hall; Iowa State Univ; Ames IA 50011-1010; 515-294-1205; Fax: 515-294-2299; dgrant@mendel.agron.iastate.edu
Gray, John; Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-1412; Fax: 573-884-7850; gray@teosinte.agron.missouri.edu
Grier, Stephen L.; Rogers Seed Co.; 317 330th St.; Stanton MN 55018-4308; 507-663-7662; Fax: 507-645-7519
Griffor, Matthew; DeKalb Genetics; 62 Maritime Road; Mystic CT 06355
Grimanelli, Daniel; ORSTOM - CIMMYT; Apdo Postal 6-641; 06600 Mexico D.F.; MEXICO; (52)595-42100; Fax: (52)595-41069; dgrimanelli@cimmyt.mx
Grobman, Alexander; Semillas Penta del Peru S.A.; Apartado 270227; Lima 27; PERU; (5114)426375; Fax: (5114)425465
Gronwald, J. W.; Agronomy & Plant Genetics; Univ of Minnesota; St. Paul MN 55108
Grossniklaus, Ueli; Cold Spring Harbor Laboratory; PO Box 100; Cold Spring Harbor NY 11724
Grotewold, Erich; Cold Spring Harbor Lab; P.O. Box 100; Cold Spring Harbor NY 11724; (516)367-8827; Fax: (516)367-8369; GROTEWOL@CSHL.ORG
Gu, Ming-Hong; Jiangsu Agricultural College; Dept. of Agronomy; Yangzhou; Jiangsu 225001; CHINA
Guiltinan, Mark; Penn State Biotechnology Institute; 306 Wartik Lab; Dept of Horticulture; Univ. Park PA 16802; 814-863-7957; Fax: 814-863-6139; mjg@psupen.psu.edu
Guimaraes, Marco A; Caixa Postal 9; Via Dionisio Bortoloti Km 0.5; Santa Cruz das Palmeiras; SP 13650-970; BRAZIL; 55196-72-1917; Fax: 55196-72-2424
Guo, Jun-Yuan; Academia Sinica; South China Institute of Botany; Guangzhou 510650; CHINA
Guo, Mei; 105 Tucker; Division of Biol. Sciences; University of Missouri; Columbia MO 65211; 573-882-4871; Fax: 573-882-0123; mguo@biosci.mbp.missouri.edu
Gutierrez, Lucero; Biology Dept; Herrin Bldg; Stanford Univ; Stanford CA 94305-5020
Haag, Wayne L.; Sasakawa Global 2000; C. P. 4247; Maptuo; MOZAMBIQUE
Hadad, Robert G.; 317 Stonegate Way; Lexington KY 40503
Hake, S.; USDA-ARS-PGEC; 800 Buchanan Street; Albany CA 94710; 510-559-5907; Fax: 510-559-5678; maizesh@nature.berkeley.edu
Hakiza, J.; OARDC; Dept. of Agronomy; 1680 Madison Ave.; Wooster OH 44691
Hall, Lisa Naomi; Oxford Univ; Dept Plant Sci; South Parks Road; Oxford OX1 3RB; UNITED KINGDOM; 865-275030; Fax: 865-275147; lisa.hall@plants.ox.ac.uk
Hallauer, Arnel R.; Agronomy Building; 1505 Agronomy Hall; Iowa State University; Ames IA 50010; 515-294-3052; Fax: 515-294-3163
Hamilton, R. I.; Agriculture Canada; Plant Research Centre; Bldg # 121; Ottawa, Ontario K1A 0C6; CANADA; 613-995-3700; Fax: 613-992-7909
Han, Changdeok; Gyeongsang National University; Chinju 660-701; KOREA; 82-591-751-5188; Fax: 82-591-759-9363; cdhan@nongae.gsnu.ac.kr
Hancock, Denis C.; 213 Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-1722; Fax: 573-884-7850; dhancock@teosinte.agron.missouri.edu
Hannah, Curtis; Veg Crops Dept; Univ of Florida, IFAS; Gainesville FL 32611; 904-392-1928x315; Fax: 904-392-6479; Hannah@GNV.IFAS.UFL.EDU
Hansel, W. C.; Hansel Cons & Mgmt; Box 283; Carrollton MO 64633; 816-542-1616
Hansen, Joel; 2254 Molecular Biology Bldg.; Iowa State University; Ames IA 50011; 515-294-0347; Fax: 515-294-0453; jdhansen@iastate.edu
Hansen, Leon A. ; Rogers Seed Co.; 6338 Highway 20-26; Nampa ID 83687; 208-466-0319; Fax: 208-467-4559
Hanson, Maureen R.; Section Genetics/Develop.; Cornell Univ.; Biotech Bldg; Ithaca NY 14853; 607-254-4833; Fax: 607-255-2428
Hanten, John; Northrup King Co.; 317 330th St.; Stanton MN 55018; 507-663-7649; Fax: 507-645-7519
Hardeman, Kristine; Dept Bot Plant Path; Cordley 2082; Oregon State Univ; Corvallis OR 97331-2902
Harper, Lisa; Dept. Plant Biology; Genet. & Plant Biol. Bldg.; University of CA; Berkeley CA 94720; (415)841-1539; Fax: (415)642-7948; ligule@nature.berkeley.edu
Harris, John W.; Dept of Biology; Tennessee Tech Univ; Cookeville TN 38505; 615-372-3143; Fax: 615-528-4097
Harris, Linda J.; Plant Research Centre; Agriculture Canada; Bldg. #21, Central Exp. Farm; Ottawa, Ontario K1A 0C6; CANADA; (613)995-3700 ext.7647; Fax: (613)992-7909; harrisl@ncccot2.agr.ca
Harrison, Virginia; Dept of Science; 470 E Lockwood Av; Webster University; St. Louis MO 63119-3194; 314-968-7079; Fax: 314-968-6909
Harry, David; DataGenetics Corp; 1933 Davis St., Suite 207; San Leandro CA 94577; 510-729-0720; deh@s27w007.pswfs.gov
Hartings, H.; Ist Sper Cereal; Via Stezzano 24; 24100 Bergamo; ITALY
Havukkala, Ilkka; Rice Genome Research Program; STAFF Institute, 446-1, Ippaizuka; Kamiyokoba, Tsukuba; Ibaraki 305; JAPAN; 81-298-38-2180; Fax: 81-298-38-2245; ilkka@staff.or.jp
Hawk, James A.; Dept Plant & Soil Sciences; University of Delaware; Newark DE 19717-1303; 302-831-2531; Fax: 302-831-3651
He, Zuhua; Zhejiang Agricultural University; Biotechnology Institute; Hangzhou; Zhejiang 310029; CHINA
Heinlein, Manfred; The Scripps Research Institute; Dept. of Plant Cell Biology, MRC 7; 10666 North Torrey Pines Rd; La Jolla CA 92037; 619-554-2854; Fax: 619-554-6330; heinlein@scripps.edu
Helentjaris, Tim; Pioneer Hi-Bred Int., Inc.; Agronomic Traits/TTD; 7300 N.W. 62nd Ave. P.O. Box 1004; Johnston IA 50131-1004; 515-270-3691; Fax: 515-270-4312; helentjartg@phibred.com
Heller, Stephen R.; Bldg 005, Room 337; BARC-W; Beltsville MD 20705-2350; 301-504-6029; Fax: 301-504-6054; SRHELLER@ORIGIN.NALUSDA.GOV
Helm, James; Department of Plant Sciences; Loftsgard Hall; North Dakota State University; Fargo ND 58105; 701-231-7574; Fax: 701-231-8474; jhelm@ndsuext.nodak.edu
Herb. Library; 155 Birge Hall; 430 Lincoln Drive; Madison WI 53706-1381; 608-262-2792; Fax: 608-262-7509
Heredia-Diaz, Oscar; Mycogen Plant Sciences; RR1 Box 22A; York NE 68467; 402-362-3094; Fax: 402-362-3613; heredia@mycogen.com
Hershberger, R. Jane; Dept. of Biological Sciences; Stanford University; Stanford CA 94305-5020; (415)723-2609; Fax: (415)725-8221; janieh@leland.stanford.edu
Heslop-Harrison, J. S.; Karyobiology Group; JI Centre for Plant Science Research; Colney Lane; Norwich NR4 7UH; ENGLAND; 44-1603-452571; Fax: 44-1603-456844; HHARRISON@bbsrc.AC.UK
Hetz, Winfried; Institue of Biology; University of Freiburg; Schlanzlestr, 1; 79104 Freiburg; GERMANY
Heun, Manfred; Max-Planck Inst Zuchtungsforsch; Carl-von-Linne Weg 10; 50829 Koln; GERMANY; +49 221 5062 414; Fax: +49 221 5062 413
Hile, Glenn C.; Northrup King Co; 7113 Alt 49 East; P.O. Box 249; Arcanum OH 45304; 513-692-5164; Fax: 513-692-8256
Hill, Martha; CIBA-GEIGY; PO Box 12257; 3054 Cornwallis Rd; Research Triangle Park NC 27709-2257; 919-541-8580; Fax: 919-541-8585; HILLM@ABRU.CG.COM
Ho, David; Department of Biology; Washington University; St. Louis MO 63130; 314-935-4632; Fax: 314-935-4432; HO@WUSTLB.wustl.edu
Hodges, Tom; Botany & Plant Pathology; Agricultural research Building; Purdue University; W. Lafayette IN 47907; 317-494-4657; Fax: 317-494-5896; hodges@btny.purdue.edu
Hoegemeyer, Thomas C.; Hoegemeyer Hybrids Inc; Rt 2; Hooper NE 68031; 402-654-3399; Fax: 402-654-3342
Hoekenga, Owen; 101 Tucker Hall; University of Missouri; Columbia MO 65211
Hogan Mumm, Rita; Dekalb Plant Genetics; 2139 Country Road 2500N; Thomasboro IL 61878-9654; (217)694-4141; Fax: (217)694-4103
Hoisington, David; CIMMYT; Lisboa 27, Aptdo. Postal 6-641; 06600 Mexico, D. F.; MEXICO; 525-726-7575; Fax: 525-726-7558; DHOISINGTON@ALPHAC.CIMMYT.MX
Hole, David; Plant Soils & Biometeorology Dept.; Utah State Univ.; Logan UT 84322-4820; (801)750-2235; Fax: (801)750-3376; fahole@cc.usu.edu
Holland, Greg; Asgrow Seed Co; Box 460 Hwy 20 W; Parkersburg IA 50665; 319-347-6633; Fax: 319-347-2720
Holley, Randall; 340 Southside Dr.; Henderson KY 42420
Hollick, Jay; Institute of Molecular Biology; University of Oregon; Eugene OR 97403-1229

Hong, Guo-Fan; National Center for Gene Research; Chinese Academy of Science; 500 Cao Bao Road; Shanghai 200233; CHINA; 86-21-482-2885; Fax: 86-21-482-5775
Hong, Meng-Min; Academia Sinica; Shanghai Inst. of Plant Physiol.; 300 Fonglin Road; Shanghai 200032; CHINA; ; zkxu@fudan.ihep.ac.cn
Houchins, Kate; 302 Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-2033; Kate@teosinte.agron.missouri.edu
Howard, John; Pioneer Hi-Bred Int; 7300 NW 62nd Ave; Johnston IA 50131
Hsia, An-Ping; B420 Agronomy Hall; Iowa State University; Ames IA 50011
Hu, Gongshe; Dept Plant Path; 414 Throckmorton Hall; Kansas State Univ; Manhattan KS 66506
Hu, Jianping; Dept of Botany; University of Georgia; Athens GA 30602
Huang, Wei-Da; Fudan University; Dept. of Biochem.; Handan Road 220; Shanghai 200433; CHINA
Huang, Danian; China National Rice Research Institute; Hangzhou; Zhejiang 310006; CHINA
Huang, Anthony; Dept. Bot. & Plant Sci.; Univ. of California; Riverside CA 92521-0124; 909-787-4783; Fax: 909-787-4437; ahuang@ucrac1.ucr.edu
Huang, Bing-Quan; Biology Dept; Univ of North Dakota; Grand Forks ND 58202; 701-777-4479; Fax: 701-772-5041; bhuang@badlands.nodak.edu
Huang, Yih-Ching; Department of Agronomy; National Taiwan University; Taipei; TAIWAN; (02)363-0231 ext. 2727; Fax: (02)362-0879
Hubbard, Lauren; USDA-ARS-PGEC; 800 Buchanan St.; Albany CA 94710; 510-559-5922; Fax: 510-559-5648; LHUBBARD@Nature.Berkeley.EDU
Huffman, Gary A.; Pioneer Hi-Bred International; 7300 NW 62nd Ave.; P.O. Box 1004; Johnston IA 50131-1004; 515-270-3502; Fax: 515-270-3367; HUFFMANG@PHIBRED.COM
Hulbert, Scot; Kansas State University; Dept. of Plant Pathology; Throckmorton Hall; Manhattan KS 66506-5502; 913-532-6176; Fax: 913-532-5692; SHULBRT@KSUVM.KSU.EDU
Hultquist, Marc A; Brown University; Box 1445; Providence RI 02912; 401-274-6486
Hunsperger, John P.; P.O. Box 2217; ; ; Gilroy CA 95021-2217; (408)848-1161
Hunter, Clifford; ICI Seeds; P.O. Box 500; Slater IA 50244
Hunter, Brenda; Dept Plant Sci; Forbes Hall, Room 303; Univ of Arizona; Tucson AZ 85721
Hussey, Patrick J.; University of London; Royal Holloway New College; Dept. Biochem., Egham Hill; Egham, Surrey TW20 OEX; UNITED KINGDOM
Iida, Shigeru; Dept Biol Science & Technology; Science Univ of Tokyo; 2641 Yamazaki, Noda-shi; Chiba 278; JAPAN; 0471-24-1501 ex.4400; Fax: 0471-25-1841
Im, Kyung Hoan; Dept Plant Path; Univ of Florida; Gainesville FL 32611
Innes, R. L.; DeKalb Canada Inc.; R.R. 2; Glanworth, Ont. N0L 1L0; CANADA
Inoue, Yasuaki; National Grassland Res Inst; 768 Nishinasuno; Tochigi 329-27; JAPAN; 0287-36-0111
INTA-CICA; Instituto de Genetica "E.A. Favret"; Biblioteca; C.C.25; 1712 Castelar, Buenos Aires; ARGENTINA; 54-1-621-1876; Fax: 54-1-621-0805
Irish, Erin; Department of Biological Sciences; 312 Chemistry Bldg; University of Iowa; Iowa City IA 52242; 319-335-2582; Fax: 319-335-3620; erin-irish@uiowa.edu
Isaac, Peter; The Nickerson Seed Co Ltd; Cambridge Science Park; Milton Road; Cambridge CB4 4GZ; UNITED KINGDOM; 44-1223-423933; Fax: 44-1223-420925; mbnis@seqnet.daresbury.ac.uk
Ishige, Teruo; Ministry Agric, For, Fisheries; Kasumigaseki, Chiyodaku; Tokyo; JAPAN; 81-3-3502-8111x5051; Fax: 81-3-3507-8794; tishige@s.affrc.go.jp
Ishikawa, Ryuji; Faculty of Agriculture; Hirosaki Univ; Hirosaki Aomori 036; JAPAN; 510-642-8058; ishikawa@cc.hirosaki-u.ac.jp
Ishizaki, Mary; Mycogen Plant Sciences; 5649 East Buckeye Rd; Madison WI 53716; 608-221-5000; Fax: 608-221-5008x364; ISHIZAKI@MYCOGEN.COM
Islam-Faridi, M. Nurul; Dept Soil and Crop Sci; Texas A&M Univ; College Station TX 77843-2474
Jackson, David; USDA Plant Gene Expression Centre; 800 Buchanan St; Albany CA 94710; 510-559-5976; Fax: 510-559-5648; dJackson@nature.berkeley.edu
Jackson, Paul J.; Life Sci Div; LS2 MS M880; Los Alamos Nat Lab; Los Alamos NM 87545; 505-667-2775; Fax: 505-665-3024; JACKSON@telomere.lanl.gov
Jackson, Janet Day; Crop Sci, AW-101 Turner; University of Illinois; 1102 S. Goodwin Ave; Urbana IL 61801; 217-333-6331; Fax: 217-333-6064; j-day@uiuc.edu
James, Martha G.; Dept. of Biochemistry & Biophysics; Molecular Biology Building, Room 2152; Iowa State University; Ames IA 50011; 515-294-8202; Fax: 515-294-0453; mgjames@iastate.edu
Jampatong, Sansern; Curtis Hall; University of Missouri; Columbia MO 65211
Jarboe, Sue G.; Purdue University; Department of Agronomy; 1150 Lilly Hall of Life Sciences; West Lafayette IN 47907-1150; (317)494-4772; Fax: (317)496-1368
Jayachandran, Sanjay; Botany & Plant Sciences; UC Riverside; Riverside CA 92521
Jeffries-Griffor, Joanne; DeKalb Genetics; 62 Maritime Rd; Mystic CT 06355
Jegla, Dorothy; Dept Biol Sci; 316 CB; University of Iowa; Iowa City IA 52242
Jenkins, Bethany; Institute of Molecular Biology; University of Oregon; Eugene OR 97403
Jesiatis, Lynn; Plant Biology Dept; 111 Koshland Hall; UC Berkeley; Berkeley CA 94720-3102
Jewell, David C.; CIMMYT Maize Research Station; P.O. Box MP 163; Mount Pleasant; Harare; ZIMBABWE; (263)(4)301807; Fax: (263)(4)301327; D.Jewell@CGNET.com
Joanin, Philippe; Inst Biol Molec Plantes CNRS; Univ Louis Pasteur; 121 Rue du General Simmer; Strausbourg 67000; FRANCE
Jobling, Steve; Unilever Research; Colworth House; Sharnbrook; Bedford MK44 1LQ; UNITED KINGDOM; 44 1234 222575; Fax: 44 1234 222552; STEVE.JOBLING@URCGB.SPRINT.COM
Johal, Guri; Agronomy Dept; Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-0342; Fax: 573-884-7850; AGROGJ@MIZZOU1.MISSOURI.EDU
John Innes Centre - Library; Norwich Research Park; Colney; Norwich NR4 7UH; UNITED KINGDOM; 44-1603-452571; Fax: 44-1603-456844; LIBRARY@BBSRC.AC.UK
Johns, Mitrick A.; Dept Biological Sciences; Northern Illinois University; DeKalb IL 60115; 815-753-7836; Fax: 815-753-0461
Johnson, William K.; University of California, Davis; CEPRAP; 1930 5th Street; Davis CA 95616; 916/757-3045
Johnson, M. W.; Dept of Agronomy; Pennsylvania State Univ; University Park PA 16802; 814-865-0324; Fax: 825-863-7043
Johnson, Elmer C.; 1525 Vine St.; Belmont CA 94002
Johnson, Elizabeth; CIBA-GEIGY Corporation; P.O. Box 1830; Kaunakakai HI 96748; 808-567-6146; Fax: 808-567-6753
Johnson, Scott; Mycogen Plant Sciences; 301 Campus Dr; P.O. Box 280; Huxley IA 50124; 515-597-3284; Fax: 515-597-2875
Johri, M. M.; Molecular Biology Unit; Tata Inst Fundamental Res; Homi Bhabha Road; Bombay 400 005; INDIA; 215-2971; Fax: 091-22-215-2110; MMJOHRI@tifrvax.tifr.res.in
Jondle, Doug; Cargill Hybrid Seeds; 1502 N Gault; St. Peter MN 56082; 507-931-2940; Fax: 507-931-9691
Jones, John K.; Dept Agric Bot; University of Reading; Whiteknights; Reading RG6 2AS; UNITED KINGDOM; 44-1734-875123 EXT 7950; Fax: 44-1734-750630
Jones, Todd; E. I. DuPont de Nemours & Co; Experimental Station; P.O. Box 80402; Wilmington DE 19880-0402; 302-695-4372; Fax: 302-695-4296; jonest@esvax.dnet.dupont.com
Jones, John Edward; 8429 Meadow Green Way; Gaithersburg MD 20877
Jones, Jonathan; Sainsbury Laboratory; John Innes Centre; Colney Lane; Norwich NR4 7UH; UNITED KINGDOM; 44-1603-452571; Fax: 250024; JONESJ@bbsrc.AC.UK
Jones, Mark; Selby Hall, O.A.R.D.C, USDA-ARS; 1680 Madison Ave; Wooster OH 44691; (216)263-3838; Fax: (216)263-3841; jones.390@osu.edu
Julstrom, Paul; c/o CIMMYT; Lisboa 27, Apdo. Postal 6-641; 06600 Mexico, D.F.; MEXICO; 52 5 726 9091; Fax: 52 5 726 7558
Jun, Wei; Box 8118; Beijing 100081; CHINA
Juvik, J. A.; Dept. Nat. Res. Environ. Sci.; University of Illinois; 307 ERML; Urbana IL 61801; 217-333-1966; Fax: 217-333-4777; j-juvik@uiuc.edu
Kaeppler, Heidi F.; USDA/ARS; 344 Keim Hall P.O. Box 830937; Univ of Nebraska; Lincoln NE 68583-0937; 402-472-9640; Fax: 402-437-5254; AGRO237@UNLVM.UNL.EDU
Kaeppler, Shawn; Dept of Agronomy; University of Wisconsin; 1575 Linden Drive; Madison WI 53706; 608-262-9571; smkaeppl@facstaff.wisc.edu
Kahler, Alex; Biogenetic Services, Inc; 2308 6th Street E.; P.O. Box 710; Brookings SD 57006; 605-697-8500; Fax: 605-697-8507
Kaleikau, Ed; USDA, NRICGP; 901 D. Street, SW, Room 323; Washington D.C. 20250; 202-401-1901; Fax: 202-401-6488; EKALEIKAU@MORRILL.ESUSDA.GOV
Kalia, V.; Regional Research Station; Dhaulakuan-173001; Distt Sirmur (H. P.); INDIA
Kang, Chun-Lin; Hunan Agricultural College; Dong Jiao; Changsa; Hunan 410128; CHINA
Kang, M. S.; Department of Agronomy; Louisiana State University; Baton Rouge LA 70803; 504-388-2110; Fax: 504-388-1403
Kannenberg, L. W.; Dept of Crop Science; University of Guelph; Guelph, Ontario N1G 2W1; CANADA; 519-824-4120 EXT 2506; Fax: 519-763-8933; LKANNENB@CROP.UOGUELPH.CA
Kantety, Ramesh; Dept of Agronomy; 1150 Lilly Hall; Purdue University; West Lafayette IN 47907-1150; 317-496-2729; Fax: 317--494-6508;

RKANTETY@DEPT.AGRY.PURDUE.EDU
Karpoff, Arnold; Dept of Biology; Univ of Louisville; Louisville KY 40292; 502-852-5934; Fax: 502-852-0725; AJKARP01@ULKYVM.Louisville.edu
Kasha, K. J.; Dept of Crop Science; Univ of Guelph; Guelph, Ontario N1G 2W1; CANADA; 519-824-4120 EXT 2507; Fax: 519-763-8933
Kasim, Adamu A.; Department of Biological Sciences; Ahmadu Bello University; Zaria; NIGERIA; 069-50581 ext. 108; Fax: 234 69 50891
Kaszas, Etienne; Division of Biological Sciences; Tucker Hall; University of Missouri; Columbia MO 65211; 573-882-4871; Fax: 573-882-0123
Kato, Akio; Lab. Mutation Induct. Techn.; Inst. Radiation Breeding, NIAR; P.O. Box-3, Ohmiya-machi-Naka-gun; Ibaraki-ken, 319-22; JAPAN; 02955 (2) 1138
Kato Y., T. A.; Centro de Genetica; Colegio de Postgraduados; Chapingo 56230; MEXICO; (595)4-52-65; Fax: (595)4-57-23
Katt, Maria L.; Pioneer Hi-Bred Intl., Inc.; 7300 N.W. 62nd Avenue; P.O. Box 1008; Johnston IA 50131; 515-270-4370; Fax: 515-270-3444
Keddie, James; Plant Biology Dept; UC Berkeley; Berkeley CA 94720
Keeling, Peter; ExSeeds Genetics L.L.C.; 1567 Food Sci Bldg; Iowa State Univ; Ames IA 50011-1061; 515-294-3259; Fax: 515-294-2644; pkeeling@iastate.edu
Keim, Kent R.; Sunseeds; 1200 Anderson Corner Road; Parma ID 83660; 208-674-2208; Fax: 208-674-2372
Keith, Carlyn S.; Dept. Biol. Sciences; 105 Tucker Hall; University of Missouri; Columbia MO 65211; 573-882-8033; ckeith@biosci.mbp.missouri.edu
Kellogg, Elizabeth A.; Arnold Arboretum of Harvard University; 22 Divinity Avenue; Cambridge MA 02138; 617-496-4612; Fax: 617-495-9484; tkellogg@oeb.harvard.edu
Kendall, Tim; Pioneer Hi-Bred Internat., Inc.; 7300 NW 62nd Ave., PO Box 1004; Johnston IA 50131-1004; 515-270-5952; Fax: 515-270-3367; KENDALLTL@PHIBRED.COM
Kendra, David F.; Northrup King Company; 317 330th Street; Stanton MN 55018; 507/663-7636; Fax: 507/645-7519; dkendra@MR.Net
Kent, Beth; 220 Biological Sciences Center; 1445 Gortner Ave.; St. Paul MN 55108; (612)625-0271; Kent0021@maroon.tc.umn.edu
Kermicle, Jerry; 218 Genetics Dept; 445 Henry Mall; University of Wisconsin; Madison WI 53706; 608-262-1253; Fax: 608-262-2976
Kerstetter, Randall; Plant Gene Expression Center, USDA; 800 Buchanan Street; Albany CA 94710; (510)559-5922; Fax: (510)559-5648; RAND@NATURE.BERKELEY.EDU
Khairallah, Mireille; CIMMYT; Apdo. Postal 6-641; Mexico, D.F. 06600; MEXICO; 52(595)42100x1394; Fax: 52(5)726-7558/7559; mkhairallah@cimmyt.mx
Khavkin, Emil E.; Inst Agric Biotech; 42 Timiryazevskaya ul.; Moscow, 127550; RUSSIA; (7-095)976-6544; Fax: (7-095)977-0947; emil@agrobio.msk.su
Kiefer, Mike; Northrup King Co.; 317 330th St.; Stanton MN 55018-4308
Kim, Dyung Dong; Dept of Horticulture; College of Agric & Life Sci; Seoul National Univ; Suwon 441-744; KOREA
Kim, Insoon; Plant Biology Dept; 111 Koshland Hall; UC Berkeley; Berkeley CA 94720-3102
Kim, Soon Kwon; Internat Inst Tropical Ag; P.M.B. 5320; Ibadan; NIGERIA; ; Fax: 44-81-681-8583
Kindiger, Bryan; Southern Plains Research Stn.; 2000 18th St.; Woodward OK 73801; (405)256-7449; Fax: (405)256-1322; a03lcwoodwar@attmail.com
Kiss, Charles; 18 Avenue Gallieni; 49130 Les Ponts de Ce; FRANCE; 33-41-44-86-45; Fax: 33-41-44-98-69
Kleese, Roger; 6700 80th Ave. N.; Brooklyn Park MN 55445; 612-566-3561; Fax: 515-254-2744
Klein, Anita S.; Department of Biochemistry; Spaulding Life Science Bldg; University of New Hampshire; Durham NH 03824; 603-862-2455; Fax: 603-862-4013; klein@Colsa.UNH.EDU
Kloeckener, Barbara; Univ. of CA - Berkeley; Dept. of Plant Biology; 111 Koshland Hall; Berkeley CA 94720; 510-642-7085; Fax: 510-642-4995; bkg@nature.berkeley.edu
Knapp, Steve; Department of Crop & Soil Science; Oregon State University; Corvalis OR 97331-2902
Ko, Chris; Dept Biol Sci; Stanford Univ; Stanford CA 94305-5020
Koch, Karen E.; 2147 Fifield Hall; Horticulture Dept, Plant Molec Cell Biol; University of Florida; Gainesville FL 32611; (904)392-4711 ext 309; Fax: (904)392-5653
Kochert, Gary; University of Georgia; Department of Botany; Plant Sciences building; Athens GA 30602
Koester, Ruth; Genetic Design, Inc.; 7017 Albert Pick Rd.; Greensboro NC 27409; 919-668-1432; Fax: 919-665-3966
Kohashi, Josue; Dept of Botany; Colegio de Postgrad; Chapingo, Edo de Mex; MEXICO; (595)4-22-00 ext.5294; Fax: (595)428-73
Koinuma, Keiichi; Kyusyu Natl. Agric. Exp. Stn.; Yokoichi; Miyakonojo; Miyazaki 885; JAPAN; 0986-22-1506; Fax: 0986-23-1168
Konstantinov, Yuri; Siberian Inst Plant Phys Bioch; Russian Academy of Sciences; P.O. Box 1243; Irkutsk-33 664033; RUSSIA; 39-52-46-09-03; Fax: 7-39-52-46-16-03; root@sifibr.irkutsk.su
Konstantinov, Kosana; Maize Research Institute; P.O. Box 89; 11081 Zemun; YUGOSLAVIA; (381)11-617-434; Fax: (381)11-197-890
Kowalewski, Shirley; Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-2674; Fax: 573-884-7850; shirley@teosinte.agron.missouri.edu
Kowles, Richard V.; Biology Department - Box 10; 700 Terrace Heights; St. Mary's University of Minnesota; Winona MN 55987; 507-457-1554; Fax: 507-457-1633; DKOWLES@REX.MNSMC.EDU
Krawetz, Julie; Dept of Botany; Box 7612; North Carolina State Univ; Raleigh NC 27695; 919-515-3570; KRAWETZ@UNITY.NCSU.EDU
Krebbers, Enno; DuPont de Nemours & Co.; Agricultural Biotechnology; Experimental Station 402/2253; Wilmington DE 19880-0402; (302)695-8577; Fax: (302)695-7361; krebbers@esvax.dnet.dupont.com
Kreisman, Lori S; Dept Biol Sci; Gibb Hall; Univ of Idaho; Moscow ID 83844; ; krei9540@uidaho.edu
Krivov, Nicolai V.; Institute of Genetics, of AS RM.; Padurie str.; 20, Kishinev-277002; MOLDOVA; (0422)622068; Fax: (3732)556180; crivov@centr.moldova.su
Kriz, Al; DeKalb Plant Genetics; 62 Maritime Dr.; Mystic CT 06355-1958; (203)572-5217; Fax: (203)572-5240; alkriz@dekalb.com
Krone, Todd; Asgrow Seed Co; 634 E. Lincoln Way; Ames IA 50010; 515-232-7170; Fax: 515-232-6905;
Krueger, Roger W.; American Cyanamid Co.; Agricultural Research Division; P.O. Box 400; Princeton NJ 08543-0400; (609)799-0400; Fax: (609)799-1842; KRUEGERR@PT.CYANAMID.COM
Kubo, Ken; Institute of Molec Biol; University of Oregon; Eugene OR 97403; 503-346-5123; kubo@molbio.uoregon.edu
Kuhn, William E; Mid-Corn Belt/Specialty Res Dir.; Pioneer Hi-Bred Internatl., Inc.; 7300 NW 62d Ave., PO Box 1004; Johnston IA 50131-1004; 515-270-3362; Fax: 515-253-2288
Kumar, M.; Department of Genetics; Rajendra Agric. Univ., Bihar; Pusa (Samastipur)-848125; INDIA
Kumar, Sushil; Central Inst. of Medicinal & Aromatic Plants ; PO CIMAP; Lucknow 226015; INDIA
Kunze, Reinhard; Inst of Genetics; Univ of Munich; Maria-Ward-Str. 1a; 80638 Muenchen; GERMANY; 49-89-17 91 98-68; Fax: 49-89-17 91 98-20; UJ44208@SUNMAIL.LRZ-MUENCHEN.DE
Kuzmin, Evgeny V.; All-Union Res Inst for Agric Biotech; Pskowskaya str.; 12 bld. 4; 127253 Moscow; RUSSIA; 908-02-31; Fax: 908-0078; EVK@agrobio.msk.su
Kyetere, Denis T.; OARDC, Dept of Agronomy; 1680 Madison Avenue; Wooster OH 44691
Laccetti, Lucille B.; DeKalb Plant Genetics; 62 Maritime Park; Mystic CT 06355; 203-572-5247; Fax: 203-572-5240
Lai, Jinsheng; Lab Molec Genetics; College of Biology; Beijing Agricultural University; Beijing 100094; CHINA; 86(1)2582244x374; Fax: 86(1)2582332; chengxu@bepc2.ihep.ac.cn
Lakra, Alejandro Blanco; CINVESTAV; Apdo Postal 629; Irapuato, GTO; MEXICO; ; Fax: (462)51282
Lambert, Robert J.; Crop Science, Turner Hall; Univ of Illinois; 1102 S. Goodwin Ave.; Urbana IL 61801-4798
Lambert, Antoine; Verneuil Recherche; 33, rue de la Croix Blanche; 49630 Corne; FRANCE; 41-66-17-00; Fax: 41-45-02-61
Lamkey, Kendall; Agronomy Building; Iowa State University; Ames IA 50011; 515-294-7826; Fax: 515-294-9359; KRLAMKEY@IASTATE.EDU
Lampoh, E.; Crops Res Inst; PO Box 3785 Kumasi; Ashanti Region; GHANA; 6221
Lane, Barbara; Department of Plant Biology; 351 Koshland Hall; University of California; Berkeley CA 94720; 510-642-8058; Fax: 510-642-4995; babs@nature.berkeley.edu
Lang, Timothy; USAID/KATHMANDU/6190; Washington DC 20523
Langdale, Jane; Department of Plant Sciences; University of Oxford; South Parks Road; Oxford OX1 3RB; ENGLAND; 011-44-865-275099; Fax: 011-44-865-275147; jane.langdale@plants.ox.ac.uk
Larkin, John C.; Dept. Genetics Cell Biol.; 1445 Gortner Ave.; University of Minnesota; St. Paul MN 55108-1095; 612-624-3607; Fax: 612-625-5754; jlarkin@molbio.cbs.umn.edu
Larkins, Brian; Dept Plant Sciences; University of Arizona; Building #36; Tucson AZ 85721; (602)621-9958; Fax: (602)621-3692; LARKINS@biosci.arizona.edu
Last, Robert; Boyce Thompson Inst Plant Res, Inc.; Tower Road; Ithaca NY 14850; 607-254-1325; Fax: 607-254-1242; RLL3@cornell.edu
Laudencia-Chingcuanco, Debbie; Plant Gene Expression Center; USDA-ARS; 800 Buchanan St.; Albany CA 94710; 510-559-5968; Fax: 510-559-5678

Laurie, David; JI Centre for Plant Science Res.; Colney Lane; Norwich; Norfolk NR4 7UJ; UNITED KINGDOM; 44-1603- 52571; Fax: 44-1603-502241; LAURIED@BBSRC.AC.UK
Lawson, Emily; Plant Science Institute; Dept of Biology; Univ of Pennsylvana; Philadelphia PA 19104-6018
Lazarowitz, Sondra G.; Dept. of Microbiology; U. of Ill./131 Burrill Hall; 407 S. Goodwin Av.; Urbana IL 61801; 217-333-0390; Fax: 217-244-6697; Lazarowitz@UIUC.EDU
Leaver, Chris; Dept Plant Sciences; University of Oxford; South Parks Road; Oxford OX1 3RB; UNITED KINGDOM; 01865 275143; Fax: 01865 275144; chris.leaver@plants.ox.ac.uk
Ledger, Elizabeth; 6921 Alto Rey Ave.; El Paso TX 79912
Lee, Danny; Section of Plant Biology; Robbins Hall c/o Neelima Sinha; UC Davis; Davis CA 95616
Lee, Hsueh-Sheng; Zoology Dept; University of Texas; Austin TX 78712-1064
Lee, Warren; 4120 Dept. of Biol. Sciences; Illinois State University; Normal IL 61790-4120; 309-438-3088; Fax: 309-438-3722
Lee, Hee Bong; Dept Agronomy, Coll Agriculture; Chungnam Natl Univ; 220 Gung-Dong, Yusung-Gu; Taejon 305-764; KOREA; 82-042-821-5721; Fax: 82-042-823-8050
Lee, Michael; Department of Agronomy; Iowa State University; Ames IA 50011; 515-294-3052; Fax: 515-294-3163; mlee@iastate.edu
Lee, In-sup; Department of Biology; College of Science; Kyungsung University; Pusan, 608-736; SOUTH KOREA; 051-620-4647; Fax: 051-627-4115
Lee, Elizabeth A.; Marsh Life Sciences Bldg.; University of Vermont; Burlington VT 05405-0086; (802)656-0894; Fax: (802)656-0440; elee@moose.uvm.edu
Leland, Tim; CIBA Biotechnology Res; P.O. Box 12257; Research Triangle Park NC 27709-2257; 919-541-8680; Fax: 919-541-8557
Lemaux, Peggy; Department of Plant Biology; 111 Koshland Hall; University of California, Berkeley; Berkeley CA 94720; 510-642-1589; Fax: 510-642-7356; lemauxpg@nature.berkeley.edu
Leon, Patricia; Dept Biol Sci; Stanford Univ; Stanford CA 94305-5020
Lerner, David; Biology Dept 0116; UC San Diego; La Jolla CA 92093-0116; 619-534-2514; Fax: 619-534-7108; LERNER@JEEVES.UCSD.EDU
Leroy, Philippe; INRA; Domaine De Crouelle; 63039 Clermont-Ferrand; Cedex 2; FRANCE; 33 73 624337; Fax: 33 73 624453; leroy@valmont.clermont.inra.fr
Lesnick, Marc; Institute of Molecular Biology; University of Oregon; Eugene OR 97403
Lessard, Philip A.; Monsanto Company/AAZG; 700 Chesterfield Village Pkwy.; St. Louis MO 63198; 314-537-7102; Fax: 314-537-6759
Letovsky, Stan; 117 Woodlawn Rd; Baltimore MD 21210; 410-614-1061; letovsky@gdb.org
Levings, C. S.; Department of Genetics; North Carolina State Univ; Box 7614; Raleigh NC 27695-7614; 919-515-7115; Fax: 919-515-7116
Levites, E. V.; Inst Cytol Genetics; Novosibirsk; RUSSIA
Levy, Avraham; Plant Genetics Department; Weizmann Institute of Science; Rehovot, 76100; ISRAEL; 972-8-342421; Fax: 972-8-466966; LPLEVY@WEIZMANN.WEIZMANN.AC.IL
Li, De-Bao; Zhejiang Agricultural University; Biotechnology Institute; Hangzhou; Zhejiang 310029; CHINA
Li, Xiao-Fang; Guangdong Academy of Agric. Sciences; Rice Research Institute; Wushan, Guangzhou; Guangdong 510640; CHINA
Li, Ping; Sichuan Agricultural University; Rice Research Institute; Yaan; Sichuan 625014; CHINA
Li, Qing; China Natl. Cente Biotech. Development; P.O. Box 8118; Beijing 10008; CHINA
Li, Yuxing; 2312 Food Sciences; Iowa State Univ; Ames IA 50011
Li, Zhaohui; Lehman College, CUNY; Biology Dept; 250 Bedford Park Blvd. West; Bronx NY 10468
Li, Jiansheng; Maize Research Lab; Department of Agronomy; Huazhong Agricultural University; Wuhan, Hubei 430070; CHINA; 86-27-7815681-8545; Fax: 86-27-7815057
Li, Xianggan; 2116 MBB; Dept. of Genetics; Iowa State University; Ames IA 50011; (515)294-5054; Fax: (515)294-0345; shonlee@iastate.edu
Li, Yongzhong; Maize Inst., Jilin Acad. Agric. Sciences ; 6-West Xinghua Street; Gongzhuling; Jilin, P. R., 136100; CHINA; 04441-215179; Fax: 04441-214884
Library; Univ Philippines Los Banos; 4031 College; Laguna; PHILIPPINES
Liljegren, Sarah; Dept of Biology 0116; UC San Diego; La Jolla CA 92093-7108
Lin, Liang-Shiou; Room 323 Aerospace Bldg.; 901 D St. SW; Washington D.C. 20250-2241; 202-401-5042; Fax: 202-401-6488; llin@csrs.esusda.gov
Lin, Robert; 301 Ball St. #1110; College Station TX 77840; 409-845-1126; Fax: 409-846-9612; KHL2068@ACS.TAMU.EDU
Lin, Bor-yaw; Institute of Molecular Biology; National Chung Hsing University; Taichung 402; TAIWAN; (04)285-1885; Fax: (04)287-4879; bylin@dragon.nchu.edu.tw
Lincoln, Cindy; USDA Plant Gene Expression Center; 800 Buchanan St.; Albany CA 94710; 510-559-5968; Fax: 510-559-5648; clincoln@nature.berkeley.edu
Ling, Peng; 700 Experiment Station Road; Lake Alfred FL 33850; 813-956-1151 ext.301
Lisch, Damon; Dept of Plant Biology; University of California; Berkeley CA 94720; 501-642-7085; damon@nature.berkeley.edu
Liu, Aimin; Jiangsu Academy of Agric. Science; Institute of Agrobiol. Genet. & Physiol.; Nanjing 210014; CHINA
Liu, Xiaochuan; China National Rice Research Institute; Genetics & Breeding Dept.; Hangzhou 310006; CHINA
Liu, Liang-Shi; Zhongshan University; Biotechnology Research Center; Guangzhou 510275; CHINA
Liu, Xiangdong; South China Agricultural University; Agronomy Dept.; Wushan, Tianhe, Guangzhou; Guangdong 510642; CHINA
Liu, Yanhong; Botany Dept.; Univ. Georgia; Athens GA 30602; (706)542-1857; Fax: (706)542-1805; yanhong@dogwood.botany.uga.edu
Liu, QinQin; Dept of Biology, College Sci Eng; 317 Life Sci Bldg; 10 University Drive; Duluth MN 55812-2496; 218-726-7271; Fax: 218-726-8142; qliu1@d.umn.edu
Lonsdale, David M.; Cambridge Laboratory; IPSR; Colney Lane; Norwich NR4 7UH; UNITED KINGDOM; 44 1603 452571; Fax: 44 1603 505725; LONSDALE@bbsrc.AC.UK
Lopes, Mauricio A.; Natl. Maize & Sorghum Res. Ctr.; CNPMS/EMBRAPA; Caixa Postal 151, CEP 35 701-970; Sete Lagoas MG; BRAZIL; 011-55-31-773-2866; Fax: 011-55-31-773-9252; mauricio@cnpms.embrapa.br
Loraine, Ann; Plant Biology Dept; UC Berkeley; Berkeley CA 94720
Lorenzen Dahl, Lisa; Pioneer Hi-Bred Internat., Inc.; 7300 NW 62nd Ave; PO Box 1004; Johnston IA 50131-1004
Lorenzoni, C.; Istituto di Genetica Vegetale; Universita Cattolica; Sede di Piacenza; 29100 Piacenza; ITALY; (523)599210; Fax: (523)599283; genetica@ipcucsc.bitnet
Lorio, Julio C.; Biology Dept.; 324 Tucker Hall; University of Missouri; Columbia MO 65211
Lorz, Horst; Institut Allgemeine Botanik; Universitat Hamburg; Ohnhorststrasse 18; 22609 Hamburg; GERMANY; 49-40-82282-420; Fax: 49-40-82282-229
Loukides, Cynthia; Plant Biology Dept; 111 Koshland Hall; UC Berkeley; Berkeley CA 94720-3102
Lowe, Brenda; 204 Old Evarts Lane; Mystic CT 06355-2153; 203-572-5226; Fax: 203-572-5240; blowe@minerva.cis.yale.edu
Lu, Yong-Gen; South China Agricultural University; Guangzhou 510642; CHINA
Lu, Guihua; Pioneer Hi-Bred Internat., Inc.; 7300 NW 62nd Ave.; PO Box 1004; Johnston IA 50131-1004
Lu, Mei-Kuang; 305 Manter Hall; Univ. Nebraska; Lincoln NE 68503; (402)472-6084
Lu, Xiaowu; Dept of Horticulture; Univ of Hawaii; 3190 Maile Way; Honolulu HI 96822-2279; 808-956-2156; xiao@hawaii.edu
Lu, Yingtang; Dept. of Plant Biology; 111 Koshland Hall; Univ. of Cal.; Berkeley CA 94720; ; yingtang@nature.berkeley.edu
Ludwig, Steven; 709 E. Capitol St., S.E.; Washington DC 20003
Luebberstedt, Thomas; Inst fur Pflanzenzuchtung; Universitat Hohenheim; 70593 Stuttgart; GERMANY; ; Fax: Ge-711-4592343; luebbit@ruhaix1.rz.uni-hohenheim.de
Luo, Ming; Sichuan Agricultural University; Rice Research Institute; Yaan; Sichuan 62500; CHINA
Luo, Rui Bai; Biology Dept, Lehman College; 250 Bedford Park Blvd West; CUNY; Bronx NY 10468
Luthe, Dawn S; Dept Biochemistry; Miss State Univ; Mississippi State MS 39762; 601-325-7733; Fax: 601 -325-8664; dsluthe@ra.msstate.edu
Lutz, Sheila; Dept Agron Plant Genetics; 411 Borlaug Hall, 1991 Buford Circle; Univ of Minnesota; St. Paul MN 55108
Lynch, Margaret; 1883 21st Ave; San Francisco CA 94122
Lysikov, V. N.; Inst. of Genet. of AS RM.; st. Paudurie 20; Kishinev-277002; MOLDOVA; (0422)622068; Fax: 3732-556180
Ma, Hong; Cold Spring Harbor Laboratories; P.O. Box 100; Cold Spring Harbor NY 11724; 516-367-8309; Fax: 516-367-8369; mah@cshl.org
MacDonald, M. V.; Plant Breeding International; Maris Lane; Trumpington, ; Cambridge CB2 2LQ; UNITED KINGDOM; 01223-840411; Fax: 01223-844425
MacRae, Amy F.; Biology Dept; Univ of Missouri - St. Louis; 8001 Natural Bridge Rd; St. Louis MO 63121; 314-516-6205; Fax: 314-516-6233; SAFMACR@JINX.UMSL.EDU
Maddock, Sheila E; Pioneer Hi-Bred Int Inc.; 7300 NW 62nd Ave.; PO Box 1004; Johnston IA 50131-1004; 515-270-4047; Fax: 515-270-3444
Maddox, Joyce; Pioneer Hi-Bred Internat Inc; Crop Protection, PO Box 1004; 7300 NW 62nd Ave.; Johnston IA 50131-1004; 515-270-3636; maddoxj@phibred.com
Magill, Clint; Texas A & M University; Dept. of Plant Pathology; College Station TX 77843; 409-845-8250; Fax: 409-845-6483; CWM5354@VENUS.tamu.edu

Maguire, Marjorie; Zoology Department; University of Texas; Austin TX 78712-1064; 512-471-7451; Fax: 512-471-9651
Maheshwari, J. K.; National Botanical Res Inst; H.I.G.-130, Sector 'E'; Aliganj Extension, Aliganj; 226 020, U.P. - Lucknow; INDIA; 72655; Fax: 244330
Maillet, Dan; Dept Plant Sciences; Univ of Western Ontario; London, Ontario N6A 5B7; CANADA
Maluf, Mirian; Crop Science; Turner Hall, 1102 S. Goodwin Ave.; University of Illinois; Urbana IL 61801
Mangano, Mary Lou; DeKalb Genetics Corp.; 62 Maritime Dr.; Mystic CT 06355
Manjunath, Sivalinganna; Dept Bot & Plant Sci; Batchelor Hall; Univ California; Riverside CA 92521-0124; 909-787-6376; manju@ucrac1.ucr.edu
Manzocchi, Lucia A.; Consiglio Nazionale Ricerche; Istituto Biosintesi Vegetali; Via Bassini 15; 20133 Milano; ITALY; 0039-2-70600170; Fax: 0039-2-2362946; luman@icm.mi.cnr.it
Marillonnet, Sylvestre; Dept of Botany; 2502 Plant Sciences; Univ of Georgia; Athens GA 30602-7271; 706-542-1857; Fax: 706-542-1805; MARILLONNET@BSCR.UGA.EDU
Marocco, Adriano; Universita Cattolica S. Cuore; Istituto Di Genetica Vegetale; Via E. Parmense 84; 29100 Piacenza; ITALY
Marshall, Lori; Holden's Foundation Seeds, Inc.; P.O. Box 839; 201 N. Maplewood Ave; Williamsburg IA 52361; 319-668-1100; Fax: 319-668-2453
Martienssen, R. A.; Cold Spring Harbor Labs; P.O. Box 100; Cold Spring Harbor NY 11724-2212; 516-367-8322; MARTIENS@CSHL.ORG
Martin, Michael J.; ICI Seeds; P.O. Box 500; Slater IA 50244; (515)685-3574; Fax: (515)685-3828
Martin Sanchez, J. A.; UdL-IRTA Centro R S D; Alcalde Rovira Roure 177; 25006 Lerida; SPAIN; 34-73-702569; Fax: 34-73-238301
Mascarenhas, Joseph P.; Department of Biol Sci; State University of New York; Albany NY 12222; 518/442-4388; Fax: 518/442-4354; jm558@cnsunix.albany.edu
Mascia, Peter N.; Cargill Hybrid Seeds; RR 3, Box 751; Aurora IL 60506; 708-801-2304; Fax: 708-801-2345; PNMA@aol.com
Mather, Diane E.; Plant Sci Dept - Macdonald Col; McGill Univ - 21111 Lakeshore; Ste-Anne-de-Bellevue; Quebec H9X 3V9; CANADA; (514) 398-7851x7854; Fax: (514)398-7897; MATHER@AGRADM.LAN.MCGILL.CA
Mathern, Julie; USDA-ARS-PGEC; 800 Buchanan Street; Albany CA 94710; (510)559-5907; Fax: (510)559-5678; jmathern@nature.berkeley.edu
Mathur, D. S.; Div. of Genetics; Indian Agr Res Inst; New Delhi-110012; INDIA; 581481
Matias, Dayana; Lehman College, CUNY; Biology Dept c/o Elli Wurtzel; 250 Bedford Park Blvd West; Bronx NY 10468
Matthews, Paul; Lehman College, CUNY; 250 Bedford Park Blvd West; Bronx NY 10468
Matz, Eileen C.; Dept of Biology; Building 463; Brookhaven National Laboratory; Upton NY 11973; (516)282-3396; Fax: (516)282-3407; matz@bnlux1.bnl.gov
Mawgood, Ahmed L. Abdel; 31 Saada St; Karmous; Alexandria; EGYPT; (203)492-1718; mawgood@Alex.eun.eg
Mazoti, Luis B.; Carlos Croce 145; 1832 Lomas de Zamora; ARGENTINA
Mazur, Barbara J.; DuPont Agr Products; Biotechnol Res & Devel; Experimental Sta E402/3226; Wilmington DE 19880-0402; 302-695-3700; Fax: 302-695-7361; mazur@esvax.dnet.dupont.com
McCarthy, Susan A.; National Agricultural Library; 10301 Baltimore Blvd; Beltsville MD 20705; 301-504-6875; Fax: 301-504-7098; SMCCARTH@ASRR.ARSUSDA.GOV
McCarty, Donald R.; Vegetable Crops Department; 1255 Fifield Hall; University of Florida; Gainesville FL 32611; 904-392-9087
McConnell, R. L.; Research & Product Development; Pioneer Hi-Bred International; Box 85; Johnston IA 50131; (515)270-3363; Fax: (515)253-2125; McConnelR@phibred.com
McConnell, D. J.; Genetics, Trinity College; University of Dublin; Dublin 2; IRELAND; 353-1-7021140; Fax: 353-1-714968
McCormick, Sheila; USDA-ARS-PGEC; 800 Buchanan Street; Albany CA 94710; 510-559-5906; Fax: 510-559-5678; sheilamc@mendel.berkeley.edu
McCullough, Andrew; Dept. of Biochemistry; Baylor College of Medicine; Houston TX 77030; 713-798-4622; andrewm@bcm.tmc.edu
McCurdy, Leroy; P.O. Box 77; McCurdy Seed Co; Fremont IA 52561; 515-933-4291
McElver, John; Pioneer Hi-Bred Internat Inc; 7300 NW 62nd Ave.; PO Box 1004; Johnston IA 50131-1004
McFerson, John; Asgrow Seed Co.; 634 E. Lincoln Way; Ames IA 50010; (515)232-7170; Fax: (515)232-6905
McLaren, James S.; AgReSource; 2214 Stoneridge Terrace Court; St. Louis MO 63017-7120; 314-530-6943; Fax: 314-530-6945; jamesM66@aol.com
McMullen, Michael; Agronomy Dept; Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-7606; Fax: 573-884-7850; mcmullen@teosinte.agron.missouri.edu
McWhirter, K. S.; 127 Victoria Road; West Pennant Hills NSW 2125; AUSTRALIA; 02-484-7417
Mead, Doug; Northrup King Co.; 317 330th St.; Stanton MN 55018-4308; (507)663-7623; Fax: (507)645-7519
Meeley, Robert; Trait and Technology Dev.; Pioneer Hi-Bred Int'l; 7300 NW 62nd Ave. - Box 1004; Johnston IA 50131-1004; 515-270-3770; Fax: 515-253-2149; MeeleyRB@phibred.Com
Meghji, Moez; CIBA-GEIGY Corp; RR13/Box166; Rt 51 S at Hendrix Rd; Bloomington IL 61704; 309-823-8578; Fax: 309-823-9468; meghjim@AM.abru.cg.com
Mei, Mantong; South China Agricultural University; Genetic Engineering Laboratory; Guangzhou 510642; CHINA
Melchinger, Albrecht E.; Universitat Hohenheim; Institut fur Pflanzenzuchtung; Postfach 70 05 62 (350/1); D-70593 Stuttgart; GERMANY; 0711-459-2334; Fax: 0711-459-2343
Melia-Hancock, Susan; Curtis Hall - Agronomy; University of Missouri; Columbia MO 65211; 573-882-2674; Fax: 573-884-7850
Mello-Sampayo, Tristao; R. Padre Francisco 16, 5.F.; 1300 Lisboa; PORTUGAL
Mena, Montana; UC San Diego; Dept of Biology, 0116; La Jolla CA 92093-7108
Messing, Jo; Rutgers, The State Univ; Waksman Institute; P.O. Box 759; Piscataway NJ 08855-0759; 908-445-4256; Fax: 908-445-0072; messing@mbcl.rutgers.edu
Messmer, M. M.; Universitat Hohenheim; Instiutu fur Pflanzenzuchtung; Postfach 70 05 62 (350/1); D-7000 Stuttgart 70; GERMANY
Mettler, I. J.; Northrup King Co.; 317 330th Street; Stanton MN 55018-4300; 507-663-7643; Fax: 507-645-7519; mettler@mr.net
Meyer, Terry; Pioneer Hi-Bred International; 7300 N.W. 62nd Avenue; P. O. Box 1004; Johnston IA 50131-1004; 515-270-3962; Fax: 515-270-3367; MEYERTE@PHIBRED.COM
Meyerowitz, Elliot; Biology Dept 156-29; California Inst Tech; Pasadena CA 91125; 818-395-6889; Fax: 818-449-0756; meyerowitze@starbase1.caltech.edu
Michelini, Luiz Antonio; R. Ayrton Playsant, 21; Ponta Grossa; Parana 84100-550; BRAZIL; 55-42-223-2774; Fax: 55-42-223-2774
Michiels, Frank; Plant Genetic Systems; Jozef Plateaustraat 22; Gent B-9000; BELGIUM; 32-9-2358475; Fax: 32-9-2240694; FRAL@PGSGENT.BE
Micu, V. E.; Scientific Res Inst Maize & Sorghum; Pashcani; Criuleni; 278336 Moldova; MOLDOVA; (3732)-22-24-78; Fax: (3732)-22-73-02
Mies, David; Northrup King; 306 Meadow Drive - Box 710; St. Joseph IL 61873; 217-469-2746; Fax: 217-469-2407
Mihm, John A.; French Agricultural Research; RR2, Box 294; Lamberton MN 56152; 507-752-7274; Fax: 507-752-6132; JMihm@Prairie.lakes.com
Miksche, J. P.; USDA NPS; Bldg 005, Rm 331C, BARC-W; Beltsville MD 20705; 301-504-6029; Fax: 301-504-6231; jmiksche@origin.nalusda.gov
Mikula, Bernard C.; Defiance College; 901 College Drive; Defiance OH 43512; 419-784-4010 EXT 426; Fax: 419-784-0426
Milach, Sandra; 1991 Buford Circle; Room 411 Borlang Hall; St. Paul MN 55108; (612)625-6223; Fax: (612)625-1268
Miles, Donald; Tucker Hall; Div. Biological Sciences; University of Missouri; Columbia MO 65211; 573-882-7933; miles@biosci.mbp.missouri.edu
Millard, Mark; USDA-ARS-NCRP; State and Mortensen Rd.; Ames IA 50010; 515-292-6502; Fax: 515-292-6690; nc7mm@sol.ars-grin.gov
Min, Shao-Kai; China National Rice Research Institute; Genetics and Breeding; 171 Ti Yu Chang Road, Hangzhou; Zhejiang 310006; CHINA
Ming, Reiguang; Dept Soil Crop Sci; Texas A&M Univ; College Station TX 77843; 409-862-2459; Fax: 409-845-0456; reiguan@tam2000.tamu.edu
Miranda, L. T. de; Instituto Agronomico; Caixa Postal 28; 13.100 Campinas SP; BRAZIL; 0192-415188 R326
Miranda, Luiz Eugenio C de; Av B de Itapura 1481; Cx Postal 28; Campinas 28 SP 13180; BRAZIL
Miura, Y; Maize Breeding Station; Hokkaido Natl. Agr. Exp. Stn.; Hitsujigaoka; Sapporo 062; JAPAN
Miyoshi, K.; Sakata Seed Corp.; Kakegawa Breed. STN; Yoshioka 1743-2; Kakegawa City, Shizuoka City 436-01; JAPAN
Modena, Stephen; Dept. of Crop Science; North Carolina State Univ.; Box 7620; Raleigh NC 27695-7620; 919-515-2246; Fax: 919-515-7959; ab4el@Cybernetics.NET
Molina, M. C.; Del Valle Iberlucea 3711; 1826 Remedios de Escalada; Buenos Aires; ARGENTINA
Montagu, Jonathan; Cold Spring Harbor Lab; PO Box 100; Cold Spring Harbor NY 11724
Mooney, Mark; UC Berkeley; Plant Biology Dept; 111 Koshland Hall; Berkeley CA 94720-3102
Moore, Paul H.; USDA ARS PWA; Experiment Station HSPA; P.O. Box 1057; Aiea HI 96701; 808-487-5561; Fax: 808-486-5020
Moore, Kathy; Molec & Cell Biol Dept; LSS 444; University of Arizona; Tucson AZ 85721; (602)621-3381; Fax: (602)621-3709
Moose, Stephen P.; c/o Dr. Robert J. Schmidt; Dept. of Biology 0116; Univ. of California - San Diego; La Jolla CA 92093; ; smoose@jeeves.ucsd.edu
Moreira-Filho, Carlos A.; Dept. de Imunologia do ICP-USP; Av. Prof. Lineu Prestes, 2415; 05508-900 Sao Paulo S. P.; BRAZIL
Moreno, Maria Angela; Yale Univ - Dept Biology; P.O. Box 6666; New Haven CT 06511; 203-432-3894; mormarf@Yalevm.ycc.yale.edu

Mori, Naoki; Dept Agron Plant Genetics; Univ of Minnesota, 411 Borlaug Hall; 1991 Buford Circle; St. Paul MN 55108; 612-625-9261; Fax: 612-625-1268; morix002@gold.tc.umn.edu
Moro, Gloverson Lamego; Dept. of Plant Sciences; University of Arizona; Tucson AZ 85721; (520)621-9154; Fax: (520)621-3692; gmoro@ag.arizona.edu
Morrow, Sasha; Cargill Hybrid Seeds; 2600 W. Galena Blvd; Aurora IL 60506
Mottinger, John; Department of Botany; University of Rhode Island; Kingston RI 02881; 401-792-2625; Fax: 401-792-5974; johnmott@uriacc.uri.edu
Motto, M.; Ist Sper Cereal; Via Stezzano 24; 24100 Bergamo; ITALY; 39-35-313132; Fax: 39-35-316054
Mourad, George; Department of Biology; Indiana-Purdue University; Fort Wayne IN 46805-1499; 219-481-5704; Fax: 210-481-6880; mourad@smtplink.ipfw.indiana.edu
Mozoub, Daniel; Lehman College, CUNY; Biology Dept, c/o Elli Wurtzel; 250 Bedford Park Blvd West; Bronx NY 10468
Muehlbauer, Gary; UC Berkeley; Plant Biology Dept; 111 Koshland Hall; Berkeley CA 94720-3102
Muenchrath, Deborah A.; Dept Agronomy; Iowa State Univ.; Ames IA 50011; 515/294-4951; Fax: 515/294-8146; mnchrath@iastate.edu
Mulcahy, David; Botany Department; Univ of Massachusetts; Amherst MA 01003; 413-545-2238; Fax: 413-545-3243
Mulligan, Timothy P.; P. O. Box 523; Cold Spring Harbor NY 11724; 516-367-8829; Fax: 516-367-8369; MULLIGAN@CSHL.ORG
Mungoma, Catherine; Mt. Makulu Research Station; P. B. 7; P.O. Box 30563; Chilanga; ZAMBIA; 260-1-278008; Fax: 260-1-249127
Muniz, J. F. Vazquez; Departamento de Genetica; E. T. S. Ing. Agronomos; Univ. Politecnica, Ciudad Universitaria; 28040-Madrid; SPAIN
Murigneux, Alain; BIOCEM-Groupe Limagrain; Lab Biol Cell Molec, Campus Univ Cezeaux; 24 av des Landais; 63170 Aubiere; FRANCE; 73-42-79-70; Fax: 73-27-57-36; murigneux@cicc.univ-bpclermont.fr
Murphy, C. F.; USDA NPS; Bldg 005, Rm. 239; BARC-W; Beltsville MD 20705; 301-504-5560; cmurphy@asrr.arsusda.gov
Murray, Michael G.; Mycogen Plant Sciences; 5649 E Buckeye Rd; Madison WI 53716; 608-221-5000
Musket, Theresa; Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-2033; Fax: 573-884-7850; musket@teosinte.agron.missouri.edu
Mustell, Robert A.; National Corn Growers Assoc.; 1000 Executive Parkway, Suite 105; St. Louis MO 63141; 314-275-9915x113; Fax: 314-275-7061
Muszynski, Michael G.; Pioneer Hi-Bred Intl.; 7300 NW 62nd Ave.; POB 1004; Johnston IA 50131-1004; 515-254-2637; Fax: 515-254-2619; muszynskimg@phibred.com
Myers, A. M.; Dept of Zoology and Genetics; Molecular Biology Building, Room 2204; Iowa State University; Ames IA 50011
Nagle, B. J.; Dekalb Plant Genetics; Box 33; Mason City IL 62664; 217-482-3213
Nakagawa, Yoichi; Takii & Company LTD; P.O. Box 7; Kyoto C. P. O.; JAPAN; (075)365-0123; Fax: (075)365-0110
Nan, Ren; College of Life Science; Wuhan University; Wuhan 430072; CHINA
Naranjo, Carlos; Inst Fitotecnico de Santa Catalina (UNLP); C.C.4 (1836) Llavallol; Buenos Aires; ARGENTINA
Natti, Thomas A.; Harris Moran Seed Co.; 1832 Garrity Blvd.; P.O. Box 980; Nampa ID 83653; 208-467-6341; Fax: 208-466-8188
Negrotto, David; CIBA-Geigy Corp; 3054 Cornwallis Rd; Research Triangle Park NC 27709-2257
Nel, P. M.; Dept of Genetics; Univ of The Witwatersrand; P.O. WITS; Transvaal 2050; SOUTH AFRICA; 011-716-2154; Fax: 011-716-8030
Nelson, Jennifer; UC Berkeley; Plant Biology Dept; 111 Koshland Hall; Berkeley CA 94720-3102
Nelson, Oliver E.; Department of Genetics; 445 Henry Hall; University of Wisconsin; Madison WI 53706; 608-265-4636; Fax: 608-262-2976; nelsonoe@macc.wisc.edu
Nelson, Timothy; Department of Biology; PO Box 208104; Yale University; New Haven CT 06520-8104; 203-432-3860; Fax: 203-432-5632; TIMOTHY.NELSON@YALE.edu
Nemeth, J; Gabonater Kutatointezet; Also Kikoto sor 9; Szeged; HUNGARY; 62-54-555; Fax: 62-54-588
Neuffer, M. G.; 202 Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-7735; Fax: 573-884-7850; Gneuffer@aol.com
Newhouse, Keith; ICI Seeds; Highway 210, P.O. Box 500; Slater IA 50244; 515-685-3574; Fax: 515-685-2548
Newman, T. S.; Wyffels Hybrids, Inc; P.O. Box 246; Atkinson IL 61235; 309-936-7833; Fax: 309-936-7930
Newman, Thomas C; MSU-DOE Plant Res Lab; Plant Biology Bldg; East Lansing MI 48824-1312; 517-353-0854; Fax: 517-353-9168; 22313TCN@IBM.CL.MSU.EDU
Newton, Kathleen; Dept Biol Sci; University of Missouri; Columbia MO 65211; 573-882-4049; Newton@biosci.mbp.missouri.edu
Nguyen, Henry T.; Dept of Plant & Soil Science & Inst for Biotech; Texas Tech University; Lubbock TX 79409-2122; 806-742-1622; Fax: 806-742-0775; bwhtn@ttacs1.ttu.edu
Nguyen, Mai Ngoc; 105 Tucker Hall; University of Missori; Columbia MO 65211; 573-882-4871; Fax: 573-882-0123
Nickerson, N. H.; Department of Biology; Tufts University; Medford MA 02155; 617-627-3544; Fax: 617-627-3805
Nikolau, Basil; Dept. Biochem. & Biophys.; Iowa State Univ.; Ames IA 50010; 515-294-9423; dimmas@iastate.edu
Noble Jr., Stephen W.; Dept of Corn Breeding; Pioneer Hi-Bred Int'l Inc; P.O. Box 385; Johnston IA 50131-0385; 515-270-3318; Fax: 515-270-4314; NOBLES@PHIBRED.COM
Norton, Robert A.; USDA, ARS, NCAUR Mycotoxin R.U.; 1815 N. University; Peoria IL 61604; 309-681-6251; Fax: 309-671-7814
Notani, N. K.; Bhabha Atomic Res Centre; Biology Division, Mod Lab; Trombay, Bombay 400085; INDIA; 5510323; Fax: 91-22-5560750
Nowell, David C; Pannar (Pty) Ltd; PO Box 19; Greytown 3500; SOUTH AFRICA; 27-334-31131; Fax: 27-334-71208; dnowell@iafrica.com
Nutter, Robert; Pioneer Hi-Bred; 7300 NW 62nd Street; Johnston IA 50131-1004; (515)270-3349; Fax: (515)270-3367
Ober, Eric; 1-87 Agriculture Bldg.; University of Missouri; Columbia MO 65211; 573-882-6832; Fax: 573-882-1469; agroeric@mizzou1.missouri.edu
Ogle, Charles W.; P.O. Box 484; Sugar Grove IL 60554; 312-466-4742
Ohta, Y.; Kasuga 2-5-1-301; Tsukuba 305; JAPAN
Oishi, Karen; Molec & Cell Biol Dept; University of Arizona; Tucson AZ 85721; 602-621-3381
Okagaki, Ron; Dept Environm Hort; UC Davis; Davis CA 95616; 916-752-6202; RJOKAGAKI@UCDAVIS.EDU
Okuno, Kazutoshi; National Inst of Agrobiol Resources; 2-1-2 Kannondai; Tsukuba; Ibaraki 305; JAPAN; 81-298-38-7458; Fax: 81-298-38-7408; okusan@abr.affrc.go.jp
Oldroyd, Giles; UC Berkeley; Plant Biology Dept; 111 Koshland Hall; Berkeley CA 94720-3102
Olhoft, Paula; Dept Agron & Plant Genetics; 1991 Buford Circle; 411 Borlaug Hall, Univ of Minnesota; St. Paul MN 55108
Orr, Alan R.; Department of Biology; University of Northern Iowa; Cedar Falls IA 50614; 319/273-2150; Fax: 319/273-2893; ORR@UNI.EDU
Osterman, John C.; School of Life Sciences; University of Nebraska-Lincoln; Lincoln NE 68588; 402-472-5129; Fax: 402-472-2083; josterman@unl.edu
Ostrander, Brad; Dept of Agronomy; Univ of Wisconsin; 1575 Linden Drive; Madison WI 53706; 608-262-5087; OSTRANDE@CALSHP.CALS.WISC.EDU
Ottoboni, Laura; CBMEG Inst. Biol.; UNICAMP/Caixa Postal 6109; CEP 13083-970; Campinas SP; BRAZIL; 55-192-397030; Fax: 55-192-39-4717; OTTOBONI@TURING.UNICAMP.BR
Pace, Gary M.; Ciba-Geigy; POB 12257; 3054 Corn Wallis Road; Research Triangle Park NC 27709; 919-541-8582; paceg@am.abru.cg.com
Padilla, Chris; UC San Diego; Dept of Biology, 0116; La Jolla CA 92093-7108
Paez, Alix V.; Genetic Enterprises Int'l; 6165 Crabapple Lane; Johnston IA 50131; 515-278-1170; Fax: 515-276-9360
Pages, Montserrat; Jordi Girona Salgado 18-26; 08034 Barcelona; SPAIN; 34-3-2040600; Fax: 34-3-2045904;
Palmer, K. E.; Dept. of Microbiology; University of Cape Town; Private Bag; Rondebosch 7700; SOUTH AFRICA; 21-650-3269; Fax: 21-650-4320; KENNETH@MOLBIOL.UCT.AC.ZA
Palmer, Reid; USDA-ARS-MWA; Iowa State University; Agronomy Department, Room G301; Ames IA 50011
Pan, Caixian; Chinese Academy of Agrucultural Sciences; 30 Baishiqiao Road; West Suburb Beijing; Beijing; CHINA
Pareddy, Dayakar R.; DowElanco; R&D Building, 306/B-1; 9330 Zionsville Road; Indianapolis IN 46268; (317)337-3646; Fax: 317-337-3228
Parlov, Dragomir; Inst Breeding & Prod Field Crops; Marulicev trg 5; 41000 Zagreb; YUGOSLAVIA; 041-750-311; Fax: 41-750-523
Parsons, Ronald; UC San Diego; Dept of Biology, 0116; La Jolla CA 92093-7108
Partas, E. C.; Maize and Sorghum Res. Inst.; Pashcani; Criuleni; 278336 Moldova; MOLDOVA
Passas, Hilli; Dept of Biology; University of Pennsylvania; Philadelphia PA 19104-6018; 215-898-8916; Fax: 215-898-8780; HPASSAS@SAS.UPENN.EDU
Pataky, Jerald K.; Crop Science, Turner Hall; 1102 S. Goodwin Ave; University of Illinois; Urbana IL 61801; 217-333-6606; snook@vmd.cso.uiuc.edu
Paterson, Andrew H; Dept Soil & Crop Sci; Texas A&M Univ; College Station TX 77843-2474; 409-845-3773; Fax: 409-845-0456; ahp2343@bioch.tamu.edu
Patil, M. S.; Agric. Research Station; Gulburua 585101; INDIA; 21120; Fax: 091-08472-21120
Patterson, Earl; Crop Sci, S-118 Turner Hall; University of Illinois; 1102 S. Goodwin Avenue; Urbana IL 61801; 217-333-6631; Fax: 217-333-6064; maize@uiuc.edu
Paul, Anna-Lisa; Dept Horticultural Sciences; 1255 Fifield Hall; Univ Florida; Gainesville FL 32611; 904-392-4711x313; Fax: 904-392-6479; ALP@NERVM.NERDC.UFL.EDU
Pawar, S. E.; Nuclear Agriculture Division; Bhabha Atomic Research Center; Trombay Bombay 400085; INDIA; 5563060 ext 2638; Fax: 9122-556-0750

Paxson, Julia; Biology Dept c/o Tim Nelson; PO Box 208104; Yale University; New Haven CT 06520-8104; ; JPAXSON@MINERVA.CIS.YALE.EDU
Payne, Thomas; Dept. of Biology; 110 Tucker Hall; Univ of Missouri; Columbia MO 65211
Peacock, W. J.; Division of Plant Industry; CSIRO; Canberra ACT 2601; AUSTRALIA; 062-465250
Peng, Jinzhi; State Science & Tech. Commission; China Natl. Ctr. Biotech. Development ; 54 Sanlihe Road; Beijing; CHINA
Penzes, Eva; Dept Molec Cell Biol; 345 LSA; UC Berkeley; Berkeley CA 94720-0001
Pereira de Souza, Anete; CBMEG Inst. Biol.; UNICAMP/Caixa Postal 6109; CEP 13083-970; Campinas SP; BRAZIL; ; Fax: 55-192-39-4717; anete@ccvax.unicamp.br
Perez, Pascual; Biocem - Groupe Limagrain; 24 Av. Des Landais; 63130 Aubiere; FRANCE; (33) 73427977; Fax: (33) 73275736; perezcim@citi2.fr
Perich, Andreas D.; Kaneda Corporation; Asahi Shimbun Bldg.; 2-4, 3-Chome, Nakanoshima, Kita-Ku; Osada 530; JAPAN; 06(226)5044; Fax: 06(226)5144
Peschke, Virginia M.; Plant Sciences, GG6A, Monsanto Co.; 700 Chesterfield Village Parkway; St. Louis MO 63198; (314)537-7426; Fax: (314)537-6950; vmpesc@ccmail.monsanto.com
Peterson, Peter A.; Dept of Agronomy; Iowa State University; Ames IA 50011; 515-294-9652; Fax: 515-294-2299; pap@iastate.edu
Peterson, Thomas A.; Dept. of Zoology & Genetics; 2206 Molecular Biology; Iowa State Univ.; Ames IA 50011; 515-294-6345; Fax: 515-294-0345; t_peterson@molebio.iastate.edu
Pham, Hiep; Cargill Seed Research; P.O. Box 774; Grinnell IA 50112; (515)236-4911; Fax: (515)236-3607
Phelps, Tara; Tucker Hall; University of Missouri; Columbia MO 65211
Phillips, Ronald; Agronomy & PI Genetics; 411 Borlaug Hall; University of Minnesota; St. Paul MN 55108; 612-625-1213; Fax: 612-625-1268; Phill005@maroon.tc.umn.edu
Phinney, Bernard O.; Dept. of Biology; 405 Hilgard Avenue; UCLA; Los Angeles CA 90024-1606; (310)825-3177; Fax: (310)825-3177; IBB9PHI@MVS.OAC.UCLA.EDU
Piastuch, William C.; NASA/Dynamac Corp.; Mail Code DYN-3; Kennedy Space Center FL 32899; (407)853-4158; Fax: (407)853-4220; william.piastuch-2@kmail.ksc.nasa.gov
Pioneer Genetique; ATT: Gatien Arnault; Chemin De L'Enseigure BP N 5; 31840 Aussonne; FRANCE
Pixley, Kevin V; PO Box MP 163; Mount Pleasant; Harare; ZIMBABWE; 263-4-301807; Fax: 263-4-301327; k.pixley@cgnet.com
Plehn, Steve J.; Cargill Hybrid Seeds; P.O. Box 762; Mt. Vernon IN 47620; (812)838-5218; Fax: (812)838-8864
Plett, Stanley; Brandon Research Station; Agriculture Canada; P.O. Box 1000A RR #3; Brandon, Manitoba R7A 5Y3; CANADA; 204-726-7650; Fax: 204-728-3858; splett@em.agr.ca
Plunkett, Dave; Green Giant Company, M.S. 9921; 330 University Ave. S.E.; Minneapolis MN 55408; 612-330-8007; Fax: 612-330-8064
Podolskaya, Anna P.; N. I. Vavilov All Union Inst Plant Industry; 44 Herzen Street; 190000, St. Petersburg; RUSSIA; 311-99-45; Fax: 311-8762
Poethig, R. Scott; Biology Department; Leidy Labs, Univ Penn; Philadelphia PA 19104-6018; 215-898-8780; SPOETHIG@MAIL.SAS.UPENN.EDU
Poggio, Lidia; Inst Fitotecnico de Santa Catalina (UNLP); C.C.4 (1836) Llavallol; Buenos Aires; ARGENTINA
Polacco, Mary; Curtis Hall; University of Missouri; Columbia MO 65211; 573-884-7873; Fax: 573-884-7850; maryp@teosinte.agron.missouri.edu
Poljoprivredni Institut; Odjel Za Oplem.Kukuruza; Ulica Svete Ane 82 a; 31000 Osijek; CROATIA; 385 41 42 43 41; Fax: 385 41 42 04 12
Pollacsek, M.; Station Amelior PI-INRA; 63039 Clermont Ferrand; FRANCE; 73-62-43-01; Fax: 73-62-44-53; jaques.bordes@clermont.inra.fr
Pollak, Linda; USDA-ARS; Dept. Agronomy; Iowa State Univ.; Ames IA 50011; 515-294-7831; Fax: 515-294-9359; lmpollak@iastate.edu
Pollmer, W. G.; Universitat Hohenheim; Egilolfstr. 25; D-70599 Stuttgart; GERMANY; 0711-451315; Fax: 0711-4569008
Poneleit, Charles G.; Agronomy; University of Kentucky; Lexington KY 40546-0091; 606-257-4934; Fax: 606-258-1952; AGR021@UKCC.UKY.EDU
Porter, Hedera L.; RR 1; Box 81; Revere MN 56166; 507-752-7012; Fax: ;
Prasanna, B.M.; Division of Genetics; Indian Agricultural Research Institue; New Delhi-110 012; INDIA
Pratt, Richard C.; Dept. Hort. & Crop Science; OSU/OARDC; 1680 Madison Avenue; Wooster OH 44691; 216-263-3972; Fax: 216-263-3887; pratt.3@osu.edu
Price, Carl; Waksman Inst; Rutgers University; Piscataway NJ 08855-0759; 908-445-2920; Fax: 908-445-5735; Price@mbcl.rutgers.edu
Prigge, Michael; Institute Molec Biol; Univ of Oregon; Eugene OR 97403
Pring, Daryl R.; Dept of Plant Pathology; 1453 Fifield Hall; University of Florida; Gainesville FL 32611; 904-392-3638; Fax: 904-392-6532; DRPG@ICBR.IFAS.UFL.EDU
Prioli, Laudenir M.; Depto. Genetica; IB/CBMEG, Univ Estad Campinas; CP 6109; Campinas 13083-970; BRAZIL; 55-192-397030; Fax: 55-192-394717; LAUDENIR@CCVAX.UNICAMP.BR
Prioul, Jean-Louis; IBP Bat 630; Universite de Paris-Sud; 91405 Orsay Cedex; FRANCE; 33169336373; Fax: 33169336424; prioul@ibp.u-psud.fr
Prosen, Dennis; Harris Moran Seed Co.; 100 Breen Rd.; San Jun Bautista CA 94045; (408)623-4323; Fax: (408)623-2260
Prostko, Michael; Dept Biol Sci; Univ of Wisconsin; Kenosha WI 53141
Pryor, Tony; Plant Industry CSIRO; PO Box 1600; Canberra ACT 2601; AUSTRALIA; (61)(6)2465494; Fax: 2465000; poss@pican.pi.csiro.au
Puigdomenech Rosell, Pedro; Centro de Investigacion y Desarrollo; c/ Girona Salgado, 18-26; 08034 Barcelona; SPAIN; 400-61-29; Fax: 204-59-04
Purugganan, Michael; Dept of Biology - 0116; UC San Diego; La Jolla CA 92093
Qin, Lu; Institute of Genetics and Crop Breeding; Fuzhou 0591; CHINA
Qin, Minmin; USDA-ARS-PGEC; 800 Buchanan Street; Albany CA 94710
Qiu, Lijuan; G403 Agronomy Hall; Iowa State Univ; Ames IA 50011
Qu, Feng; Institute of Genetics; Lab No. 801; Beijing 100101; CHINA
Quaker Oats Company; Sam Weaver; 617 West Main St.; Barrington IL 60010-4199; 708-304-2135; Fax: 708-304-2166
Qualset, Calvin O.; Genetic Resources Cons Program; Univ of California; Davis CA 95616-8602; 916-757-8921; Fax: 916-757-8755; coqualset@ucdavis.edu
Quarrie, Steve; Cambridge Lab; John Innes Centre; Colney Lane; Norwich NR4 7UJ; UNITED KINGDOM; 44-1603-452571; Fax: 44-1603-502241
Quayle, Tom; Dept. of Biological Sciences; 900 Wood Road, Box 2000; University of Wisconsin-Parkside; Kenosha WI 53141-2000; 414-595-2172; Fax: 414-595-2056; quayle@cs.uwp.edu
Quebedeaux, Bruno; Horticulture Dept.; Univ of MD; College Park MD 20742; 301-405-4336; Fax: 301-314-9308; BQ1@umail.umd.edu
Qun Hui, Lin; Fujian Agricultural College; Dept. of Agronomy; Jingshian, Fuzhou; Fujian 350002; CHINA
Raboy, Victor; USDA/ARS; Plant & Soil Science Dept; MT State University; Bozeman MT 59717; 406-994-5054; Fax: 406-994-2011; ruavr@msu.oscs.montana.edu
Rabson, Robert; Div. of Energy Bioscience; Office of Basic Energy Sci; U.S. Dept of Energy, ER-17 GTN; Washington DC 20545; 301-903-2873; Fax: 301-903-1003;
Racchi, Milvia L.; Genetics Unit; Univ of Florence; Via San Bonaventura 13; 50145 Firenze; ITALY; 55-573201; Fax: 55-580341; gene_agr@cesit1.unifi.it
Radicella, Pablo; Room 56-730; Department of Biology; Massachusetts Institute of Technology; Cambridge MA 02139; (617)253-4724
Ragot, Michel; Ciba-Geigy Limited; R-1096.2.17; CH-4002 Basel; SWITZERLAND; 41(61)697 8621; Fax: 41(61)697 4256; RAGOTM@ABRU.CG.COM
Raizada, Manish; Dept Biol Sci; Stanford Univ; Stanford CA 94305-5020
Ralston, Ed; DNA Plant Technology Corp; 6701 San Pablo Avenue; Oakland CA 94608; 510-547-2395; Fax: 510-547-2817; ralston@dnap.com
Ramsey, Ann; RR2, Box 15; Rochester IL 62563; 217-498-9374
Rao, P. N.; Dept of Botany; Andhra University; Visakhapatnam 530003; INDIA; 54871 ext 390
Rapp, William; Department of Biology; Univ. of Missouri-St. Louis; 8001 Natural Bridge Rd.; St. Louis MO 63121-4499; 314-553-6225; Fax: 314-553-6233; swdrapp@umslvma.umsl.edu
Rattray Arnold Research Stn; P. O. Box CH 142; Chisipite; Harare; ZIMBABWE; 263-74-407; Fax: 263-74-407
Rayburn, A. Lane; Crop Sci, 320 ERML; 1201 W. Gregory; Univ of Illinois; Urbana IL 61801; (217)333-4777; Fax: (217)333-9817; arayburn@uiuc.edu
Reardon, Ellen; Waksman Institute; Piscataway NJ 08855-0759; 908-445-3512; Fax: 908-445-5735; reardon@mbcl.rutgers.edu
Reddy, G. M.; Department of Genetics; Osmania University; Hyderabad-500007; INDIA; 868951 Ext. 375; Fax: 91-0842-868087
Reddy, A. R.; School of Life Sci; Univ of Hyderabad; Hyderabad-500001; INDIA; 253901, ext. 226
Redinbaugh, Margaret; USDA-ARS; Utah State Univ; Forage & Range Research Lab; Logan UT 84322-6300
Reid, L. M.; Bldg 121; Plant Research Centre; Agriculture Canada; Ottawa, Ontario K1A 0C6; CANADA
Retief, AE; Dept of Genetics; Univ of Stellenbosch; Stellenbosch 7600; SOUTH AFRICA; 027-21-808-4769; Fax: 027-21-808-4336; AER@MATIES.SUN.AC.ZA
Reynolds, James O.; Department of Biological Sciences; University of Idaho; Moscow ID 83843; 208-885-7477; Fax: 208-885-7905
Rhee, Seung; Carnegie Institution of Washington; 290 Panama St.; Stanford CA 94305
Rhodes, C. A.; 219 Bay Tree Rd.; San Carlos CA 94070; 415-598-9469; Fax: 415-857-1125
Ribaut, Jean-Marcel; CIMMYT; Apdo. Postal 6-641; 06600 Mexico D.F.; MEXICO; 595-54400/54410; Fax: 595-54425; JRIBAUT@ALPHAC.CIMMYT.MX

Rice, Doug; Pioneer Hi-Bred Internat Inc; 7300 NW 62nd Ave; PO Box 22; Johnston IA 50131-1004
Rice, Thomas B.; DeKalb Plant Genetics; 3100 Sycamore Road; DeKalb IL 60115
Richards, Eric; Biology Dept.; Washington University; St. Louis MO 63130; 314-935-7196; richards@biodec.wustl.edu
Richter, Todd E.; Plant Path. Dept.; Throckmorton Hall; Manhattan KS 66506; (913)532-6176; Fax: (913)532-5692; trichter@ksuvm.ksu.edu
Riera-Lizarazu, Oscar; Dept. Agronomy & Plant Genetics; Univ. Minnesota; 411 Borlaug Hall, 1991 Buford Circle; St. Paul MN 55108-6026; (612)625-6223; Fax: (612)625-1268; rier0001@gold.tc.umn.edu
Rinehart, Karl; Box 187; Marshalltown IA 50158; 515-752-2170
Rivin, Carol; Dept. of Botany; Cordley 2082; Oregon State University; Corvallis OR 97331-2902; 503-737-5281; rivinc@cgrb.orst.edu
Robbins Jr., W. A.; P.O. Box 158; Ag. Alumni Seed Imp. Assn.; Romney IN 47981; 317-538-3145; Fax: 317-538-3600
Roberts, Jean L.; DowElanco Discovery Research; P.O. Box 68955; 9330 Zionsville Road/D1; Indianapolis IN 46268-1053; 317-337-3126
Robertson, Donald S.; 1707 Woodhaven Circle; Ames IA 50010-4198; 515-232-2892; Fax: 515-294-0453
Robison, Glenn; DeKalb Plant Genetics; 3100 Sycamore Road; DeKalb IL 60115; 815-758-9531; Fax: 815-758-4106
Rocheford, Torbert R.; Crop Sci, AW-100 Turner Hall; University of Illinois; 1102 S. Goodwin Av.; Urbana IL 61801; 217-333-9643; Fax: 217-333-9817; rochefor@uxh.cso.uiuc.edu
Rocky, Sally; USDA, NRICGP; 901 D. Street, SW, Room 323; Washington D.C. 20250
Rodermel, S.; Department of Botany; Bessey Hall; Iowa State University; Ames IA 50011; 515-294-8890; Fax: 515-294-1337; S1SRR@ISUVAX.BITNET
Roebbelen, G.; Tuckermannweg 9; D-37085 Goettingen; GERMANY; 0049-551-394361; Fax: 0049-551-394601
Rogers, Suzanne; Salem-Teikyo University; Salem WV 26426-0520
Rogowsky, Peter; RCAP; ENS-Lyon; 46 Allee d'Italie; F-69364 Lyon cedex 07; FRANCE; +33 72 72 86 07; Fax: +33 72 72 86 00; Peter.Rogowsky@popserver.ens-lyon.fr
Romero-Severson, Jeanne; Linkage Genetics; PO Box 157; Mazomanie WI 53560; 608-767-3237; Fax: 608-795-4563; romeros@mailbag.com
Ronchi, Angela; University of Milan; Dept. of Genetics & Microbiology; Via Celoria 26; 20133 Milan; ITALY; +39-2-26605235; Fax: +39-2-2664551; tonelli@imiucca.csi.unimi.it
Rood, Tracy; Pioneer Hi-Bred Internat Inc; 7300 NW 62nd Ave.; PO Box 1004; Johnston IA 50131-1004
Rosato, S. Caprice; 1220 Oak Villa Road; Dallas OR 97338
Rosichan, Jeffrey L.; Northrup King Co.; Research Center; 317 330th St.; Stanton MN 55018-4308; 507-663-7642; Fax: 507-645-7519
Rosielle, A.; Asgrow Seed Co; 634 E. Lincoln Way; Ames IA 50010; 515-232-7170; Fax: 515-232-6905
Roth, Brad; Pioneer Hi-Bred Internat, Inc.; 7300 NW 62nd Ave.; Box 1004; Johnston IA 50131-1004; (515)270-3789; Fax: (515)270-3367; rothba@phibred.com
Roura, Lluis Bosch; Departament d'Agronomia; Escola Superior d'Agricultura; Urgell 187; 08036 Barcelona; SPAIN; 34-3-4304207; Fax: 34-3-4192601
Rubenstein, Irwin; 220 Bioscience Center; Dept Plant Biology; University of Minnesota; St Paul MN 55108; (612)624-2755
Rubinstein, Amy; Dept. of Biology; Colorado State Univ; Ft Collins CO 80521; 303-491-3348; rubins@lamar.colostate.edu
Rufener, Keith; ICI Seeds; Hwy 210; P.O. Box 500; Slater IA 50244
Ruff, Thomas G.; Monsanto-Ceregen; 700 Chesterfield Pkwy North; AA3E; St. Louis MO 63198; 314-537-7023; Fax: 314-537-6759; tgruff@ccmail.monsanto.com
Russell, Kelly; Institute of Molec Biol; University of Oregon; Eugene OR 97403
Russell, Doug; Agracetus, Inc.; 8520 University Green; Middleton WI 53562; 608-836-7300; Fax: 608-836-9710; darussll@gead.doit.wisc.edu
Saab, Imad; Crop Sci, Turner Hall; 1102 S. Goodwin Ave.; Univ of Illinois; Urbana IL 61801; ; i-saab@uiuc.edu
Sachan, J. K. S.; Division of Genetics; I.A.R.I.; New Delhi-110012; INDIA; 91-011-5783077; Fax: 91-011-5752006
Sacher, Robert; Hunt-Wesson; Research and Development; 1645 W. Valencia Drive; Fullerton CA 92634; 714-680-2811; Fax: 714-449-5166
Sachs, Marty; USDA/ARS; S108 Turner Hall; 1102 S. Goodwin Ave; Urbana IL 61801; (217)244-0864/333-9743lab; Fax: (217)333-6064; msachs@uiuc.edu
Saedler, Heinz; Max-Planck Inst Zuchtungsf; Carl-von Linne-Weg 10; D 50829 Koln 30; GERMANY; 221-5062-100; Fax: 221-5062-113
Saghai Maroof, M. A.; CSES Department; VPI & SU; Blacksburg VA 24061; 540-231-9791; Fax: 540-231-3431; SMAROOF@VT.EDU
Sainz, Manuel; Institute of Molecular Biol; Univ of Oregon; Eugene OR 97403-1229; (503)346-5123; Fax: (503)346-5891; sainz@molbio.uoregon.edu
Salamini, Francesco; Max Planck Inst Zuchtungsf; Abt Pflanzenz Ertragsphysiol; D-50829 Koln; GERMANY; 49-221-5062400; Fax: 0049-221-5062413
Salerno, Juan C.; Instituto de Genetica; INTA; C.C. 25 1712-; Castelar; ARGENTINA; 54-1-621-1876; Fax: 54-1-621-0805 1876; POSTMASTER%Castelar@secyt.gov.ar
Salimath, S. S.; Plant Biology Div; PO Box 2180; The S.R. Noble Foundation; Ardmore OK 73402; 405-221-7349; salimath@noble.org
Salvador, Ricardo J.; Iowa State University; Dept. of Agronomy; 1126 Agronomy Hall; Ames IA 50011-1010; 515-294-9595; Fax: 515-294-8146; RJSALVAD@IASTATE.EDU
San Miguel, Phillip; HANS 339; Dept. of Biological Sciences; Purdue University; West Lafayette IN 47907; (317)494-4919; pmiguel@bilbo.bio.purdue.edu
Santos, M. A.; Dept Genetica Molecular; Centro Invest Desarrollo; Gorge Girona 18-24; 08034 Barcelona; SPAIN; 34-3-4006100; Fax: 34-3-2045904
Sarkar, Kumud R.; Division of Genetics; Indian Agric Res Inst; New Delhi 110012; INDIA; 91-011-5783077; Fax: 91-011-5752006
Sasaki, Takumi; Rice Genome Research Program; STAFF Institute, 446-1, Ippaizuka; Kamiyokoba, Tsukuba; Ibaraki 305; JAPAN; 81-298-38-2199; Fax: 81-298-38-1780
Satarova, Tatjana N; Research Institute of Maize; Dzerzhinskaya st., 14; Dniepropetrovsk; UKRAINE
Saura, Fulgencio; Dpto Tecnologia; Univ. Nacional Lujan; CC 221-6700 Lujan(Bs As); ARGENTINA
Savidan, Yves H.; APONET/CIMMYT; Aptdo. Postal 6-641; 06600 Mexico D.F.; MEXICO; (52)5-726.90.91; Fax: (52)5-7267558; ysavidan@alphac.cimmyt.mx
Scandalios, John; Dept. of Genetics; North Carolina State Univ.; Box 7614; Raleigh NC 27695-7614; (919)515-7079; Fax: (919)515-3355
Scanlon, Mike; Dept of Plant Biology; 111 Genetics & Plant Biology Bldg; Univ of California; Berkeley CA 94720; ; mjscanlo@nature.berkeley.edu
Scheffler, Brian E.; Inst. Allgem. Bot.; Angew. Molek.; Pflanzen, AMP I, Ohnhorststrafie 18; D-2000 Hamburg 52; GERMANY; (49) 40 822 82 381; FB5A112@rrz-cip-1.rrz.uni-hamburg.de
Schichnes, Denise E.; Dept of Plant Biology; 111 Koshland Hall; Univ California Berkeley; Berkeley CA 94720; (510)642-8058; Fax: (415)642-4995; Schichne@nature.berkeley.edu
Schiefelbein, John W.; 4085 Natural Science Bldg.; University of Michigan; Ann Arbor MI 48109; 313-764-3579; Fax: 313-747-0884; John_Schiefelbein@UM.CC.UMICH.EDU
Schillinger, John; Asgrow Seed Company; 9672-190-16; 7000 Portage Rd.; Kalamazoo MI 49001
Schmidt, Robert J.; Univ of California-San Diego; Dept of Biology 0116; San Diego CA 92093; 619-534-1636; Fax: 619-534-7108; rschmidt@ucsd.edu
Schnable, Patrick; Dept of Agronomy; G302 Agronomy Hall; Iowa State Univ; Ames IA 50011; (515)294-0975; Fax: (515)294-2299; Schnable@iastate.edu
Schneeberger, Richard G.; Dept. of Plant Biology; 111 Koshland Hall; University of California; Berkeley CA 94720-3102; 510-642-7948; Fax: 510-642-4995; schnee@nature.berkeley.edu
Schneerman, Martha C; Illinois State University; 4120 Biological Sciences; Normal IL 61790-4120; 309-438-3088; Fax: 309-438-3722; MCSCHNEE@ilstu.edu
Schnicker, Bruce; Cornnuts; 1000 S. Edgewood Ave.; P.O. Box 830; Urbana OH 43078; 513-652-1321; Fax: 513-653-3675
Scholl, Randy; Arabidopsis Biol Resource Center; Ohio State; 1735 Neil Ave.; Columbus OH 43210; 614-292-0603; Fax: 614-292-0603; scholl.1@osu.edu
Schramke, Mary; Bio-Rad Laboratories, Life Sciences Group; 2000 Alfred Nobel Drive; Hercules CA 94547; 510-741-6717; Fax: 510-741-1051
Schulman, Alan H.; Univ Helsinki; Institute of Biotechnology; P.O. Box 56, Viikinkaari 9; 00014 Helsinki; FINLAND; 358-0-708-59422; Fax: 358-0-708-59366; schulman@operoni.helsinki.fi
Schultes, Neil; Dept Biochem & Genetics; Conn Agric Exper Sta; 123 Huntington St; New Haven CT 06511; 203-789-6912; Fax: 203-789-7232; NPSCHULT@PCNET.COM
Schwall, Michael; Suedwestdeutsche Saatzucht; Im Rheinfeld 1-13; 76437 Rastatt; GERMANY; 49-7222-7707-0; Fax: 49-7222-770777; schwall@sun1.ruf.uni-freiburg.de
Schwartz, Drew; Biology Dept; Indiana University; Bloomington IN 47405; 812-855-6060; Fax: 812-855-6705; Schwartz@bio.indiana.edu
Schwer, Joseph F.; Mycogen Plant Sciences; 5649 E. Buckeye Road; Madison WI 53716
Scott, Lu Ann; Dept Biol Sci; University of Idaho; Moscow ID 83844-3051
Selinger, David; Institute Molec Biol; University of Oregon; Eugene OR 97403-1229
Selzer, Gerald; Room 615; National Science Foundation; 4201 Wilson Blvd.; Arlington VA 22230

Sendo, Shigeyuki; Hokkaido Plant Genet Res S Ctr; 363-2 Minami Takinokawa; Takikawa City 073; Hokkaido; JAPAN; 0125-23-3195; Fax: 0125-24-3877
Senechal, Neil; 507B First St.; College Station TX 77840; (409)846-4352
Senior, Lynn; USDA-ARS; N. C. State University; Box 7620; Raleigh NC 27695-7620; (919)515-4087; Fax: (919)515-7959; marker@unity.ncsu.edu
Seo, Beom-Seok; G412 Agronomy Dept; Iowa State Univ; Ames IA 50011
Setter, Tim L.; Department of Soil Crop and Atm. Sci.; 519 Bradfield Hall; Cornell University; Ithaca NY 14853; 607-255-1701; Fax: 607-255-2644; tls1@Cornell.edu
Settles, Mark; Cold Spring Harbor Lab; PO Box 100; Cold Spring Harbor NY 11724; 516-367-8827; Fax: 516-367-8369; settles@cshl.org
Sevilla P., Ricardo; Programa de Maiz; Univ Nacional Agraria; Aptdo 456, La Molina; Lima; PERU
Shadley, Jeff and Gwen Krill-; 7018 Chestnut St.; Milwaukee WI 53213-2742
Shamina, Zlata; Academy of Sciences; K. A. Timiryazev Inst. Plant Phys.; Botanicheskaya 35; 127276 Moscow; RUSSIA
Shands, Henry L.; USDA-ARS-NPS; Bldg 005 BARC-W; Beltsville MD 20705; 301-504-5059; Fax: 301-504-6699; shands@ars-grin.gov
Shao, Qi-Quan; Academia Sinica; Genetics Institute 917 Bldg.; Datun Road, Andingmen Wai; Beijing 100101; CHINA
Sharp, Peter; Plant Breeding Institute; University of Sydney; Cobbitty Road; Cobbitty NSW 2570; AUSTRALIA; 61-46-512-600; Fax: 61-46-512-578; pbic00@angis.su.oz.au
Shaver, Donald L; Plant Br Dept, Cornnuts; 24 Winham St; Salinas CA 93901; 408-424-1023; Fax: 408-424-5091
Shcherbak, V. S.; Corn Breeding Dept; Krasnodar Res Inst Agric; 350012 Krasnodar; RUSSIA
Sheen, Jen; Dept. of Molecular Biology; Wellman 11, MGH; Boston MA 02114; 617-726-5916; Fax: 617-726-6893; sheen@frodo.mgh.harvard.edu
Shen, Daleng; Fudan University; Inst. of Genetics; Shanghai 200433; CHINA
Shen, Yu-Wei; Zhejiang Agricultural University; Institute of Nuclear-Agric. Science; Hangzhou; Zhejiang 310029; CHINA
Shen, Zong-Tan; Zhejiang Agricultural University; Dept. of Agronomy; Hangzhou; Zejiang 310029; CHINA
Shen, Jennie; P.O. Box 80402, E402/4255; DuPont Co.; Wilmington DE 19880-0402; (302)695-1246; Fax: (302)695-4296; shenjb@esvax.dnet.dupont.com
Sheridan, William; Biology Department; Univ of North Dakota; PO Box 9019 Univ Station; Grand Forks ND 58202; 701-777-4479 or -4705; Fax: 701-777-2623
Shiga, Toshio; Sakata Seed Corp; Plant Biotechnology Center; 358 Uchikoshi; Sodegaura Chiba Pref. 299-02; JAPAN
Shigemori, I.; Chusin Agr. Exp. Stn.; Sooga Shiojiri; Nagano 399-64; JAPAN
Short, Kent E.; Carnia Seed (Pty) Ltd.; P.O. Box 7424; Petit 1512; SOUTH AFRICA; (011)965-1905; Fax: (011)965-1906
Shotwell, Mark A; Dept of Biology; 123 Vincent Science Hall; Slippery Rock Univ; Slippery Rock PA 16057-1326; 412-738-2476; Fax: 412-738-2188; MAS@SRUVM.SRU.EDU
Siddiqui, Khushnood A.; Plant Genetics Division; A.E.A.R.C.; Tandojam Sind; PAKISTAN; 40468 02233-837; Fax: 02233-284
Sidorenko, Lyuda; 2292-1 Molec Biol; Iowa State Univ; Ames IA 50011
Silva, WJ da; Univ Estadual Campinas; Inst Biol; Caixa Postal 6109; BF-13081-970 Campinas, SP; BRAZIL; ; dasilva@turing.unicamp.br
Simcox, Kevin; OARDC/OSU Dept Hort Crop Sci; 216 Williams Hall; 1680 Madison Ave; Wooster OH 44691; 216-263-3682; Fax: 216-263-3887; simcox.3@osu.edu
Sims, Lynne E.; Trait & Technology Development; Pioneer Hi-Bred Internatl; 7300 NW 62nd Ave/P.O. Box 1004; Johnston IA 50131-1732; 515-270-3652; Fax: 515-270-3367; SIMSL@PHIBRED.com
Singh, Karam; Dept Mol, Cell & Devel Biol; 405 Hilgard Avenue; UCLA; Los Angeles CA 90095-1606; 310-206-8259; Fax: 310-206-3987; Ksingh@ucla.edu
Sinha, Neelima; Section of Plant Biology; Division of Biological Sciences; University of California; Davis CA 95616; 916-754-8441; Fax: 916-752-5410; NRSINHA@UCDAVIS.EDU
Sinibaldi, Ralph; 1780 Acacio Ct.; Fremont CA 94536; 510-794-6410
Sisco, Paul; USDA-ARS, Dept. Crop Science; North Carolina State Univ; P.O. Box 7620; Raleigh NC 27695-7620; (919)515-2704; Fax: (919)515-7959; Sisco@ncsu.edu
Sleper, David A.; Agronomy Dept; 210 Waters Hall; University of Missouri; Columbia MO 65211; 573-882-7320; Fax: 573-882-1467
Smith, Steve; Pioneer Hi-Bred Internatl; P.O. Box 1004; 7300 N.W. 62nd Ave.; Johnston IA 50131-1004; 515-270-3353; Fax: 515-270-4312; SMITHS@PHIBRED.COM
Smith, Alan G.; Dept Horticultural Science; 356 Alderman Hall, Univ. of MN; 1970 Folwell Av.; St Paul MN 55108; 612-624-9290; alan@molbio.cbs.umn.edu
Smith, Oscar S.; Pioneer Hi-Bred International; 7300 NW 62nd Ave.; P.O. Box 85; Johnston IA 50131-0129; 515-270-3539; Fax: 515-270-4312; SMITHO@Phibred.com
Smith, Laurie G.; Dept of Biology - Coker Hall; University of North Carolina; Chapel Hill NC 27599-3280; 919-962-6943; Fax: 919-962-1625
Smith, James D.; PO Box 2132; Department Soil & Crop Sci; Texas A & M University; College Station TX 77843; 409-845-8276
Smith, Margaret E.; Cornell Univ; 252 Emerson Hall; Dept of Plant Breeding; Ithaca NY 14853; 607-255-1654; Fax: 607-255-6683; mes25@cornell.edu
Snape, John W.; Cambridge Laboratory; JI Centre for Plant Science Research; Colney Lane; Norwich NR4 7UJ; UNITED KINGDOM; 44-1603-452571; Fax: 44-1603-502270
Sokolov, Victor A.; Institute of Cytology and Genetics; Russian Academy of Sciences; Lavrentjev str., 10; Novosibirsk 630090; RUSSIA; 3832-355-713; Fax: 3832-356-558; sokolov@cgi.nsk.su
Soller, M.; Department of Genetics; The Hebrew University; Jerusalem 91 904; ISRAEL; 972-2-585104; Fax: 972-2-586975; SOLLER@HUJIVMS.Bitnet
Somers, David A.; Dept Agron & Plant Genet; University of Minnesota; 1991 Upper Buford Cir.; St. Paul MN 55108; 612-625-5769; Fax: 612-625-1268; somer001@maroon.tc.umn.edu
Somerville, Chris; MSU/DOE Plant Research; Michigan State U; East Lansing MI 48824; ; 21847CRS@MSU.edu
Song, Xiangfu; China National Rice Research Institute; 171 Tiyuchang Road; Hangzhou 310006; CHINA
Song, Yunchun; Life Science College; Wuhan University; Wuhan 430072 P.R.O.; CHINA; (027)7822712-4505; Fax: 7813833
Songstad, David; Pioneer Hi-Bred Int'l; 7300 NW 62nd Ave; P.O. Box 1004; Johnston IA 50131-1004; 515-270-3642; Fax: 515-270-3444; SONGSTADDD@PHIBRED.COM
Sotomayor-Rios, A.; Tropical Agric Res Stn; P.O. Box 70; Mayaguez PR 00709
Southgate, E. M.; Plant Genetic Manipulation Group; Department of Life Science; Univ of Nottingham; Nottingham NG7 2RD; UNITED KINGDOM; 44-1602-515151 ext. 847314; Fax: 44-1602-513251
Sprague, George F.; Washington Abbey; 494 West 10th St.; ; Eugene OR 97401; 503-465-8920
Spray, Clive R.; Dept. of Biology; 405 Hilgard Av; UCLA; Los Angeles CA 90024-1606; 310-825-3177; Fax: 310-825-3177; IBB9PHI@MVS.OAC.UCLA.EDU
Springer, Patricia; Cold Spring Harbor Lab; P.O. Box 100; Cold Spring Harbor NY 11724; (516)367-8827; Fax: (516)367-8369; SPRINGER@CSHL.ORG
Srinivasan, Ganesan; CIMMYT Maize Program; Lisboa 27, Aptdo Postal 6-641; 06600 Mexico, D. F.; MEXICO; 52-5-726-9091 Ext. 1116; Fax: 52-5-726-7558/59; GSRINIVASAN@ALPHAC.CIMMYT.MX
St. Clair, Grace; Pioneer Hi-Bred Internat Inc; Trait & Technology Dept; 7300 NW 62nd Ave, PO Box 1004; Johnston IA 50131-1004
Stack, Stephen; Department of Biology; Colorado State University; Fort Collins CO 80523-1878; 970-491-6802; Fax: 970-491-0649; sstack@lamar.colostate.edu
Staebell, Mark S; Pioneer Hi-Bred Internat Inc; 7300 NW 62nd Ave; PO Box 1004; Johnston IA 50131-1004; 515-253-2148; Fax: 515-254-2619; staebellm@phibred.com
Staiger, Chris; Dept. of Biological Sciences; Purdue University; 321A Hansen Bldg.; West Lafayette IN 47907; 317-496-1769; Fax: 317-496-1496; CSTAIGER@BILBO.BIO.PURDUE.EDU
Stapleton, Ann E.; Dept. of Biological Sciences; Stanford University; Stanford CA 94305-5020; ; Fax: 415-725-8221; ANNMAIZE@LELAND.STANFORD.EDU
Start, William; DeKalb Genetics; 62 Maritime Drive; Mystic CT 06355; 860-572-5223; Fax: 860-572-5240; dekalb@conix.com
Steffensen, D. M.; 506 Morrill Hall, Cell Biol; 505 S. Goodwin Ave; University of Illinois; Urbana IL 61801; 217-333-3087; Fax: 217-244-1648
Stein, Nils; Univ Hohenheim; Plant Breeding Biotech Inst; D70593 Stuttgart; GERMANY
Stelly, David M.; Dept Soil & Crop Science; Texas A & M Univ; College Station TX 77843-2474
Stern, David B.; Boyce Thompson Inst. Plant Res. Inc.; Tower Road; Ithaca NY 14853-1801; (607)254-1306; Fax: (607)254-1242; ds28@cornell.edu
Stettner, Cornelia; LS Gentechnik Hoherer Pflanzen; Tu-Munchen; Lichtenbergstrasse 4; 85747 Garching; GERMANY
Stiles, J. I.; Dept. of Pl & Molec Physiology; Univ. Hawaii at Manoa; Honolulu HI 96822; 808-956-7354; Fax: 808-956-3542; stiles@hawaii.edu
Stinard, Philip; USDA/ARS; S123 Turner Hall; 1102 S. Goodwin Ave.; Urbana IL 61801-4798; (217)333-6631; Fax: (217)333-6064; pstinard@uiuc.edu
Strom, Daniel; Dept Bot Plant Path; Cordley 2082; Oregon State Univ; Corvallis OR 97331-2902
Stuber, Charles W.; Dept of Genetics; North Carolina State Univ Box 7614; 3513 Gardner Hall; Raleigh NC 27695-7614; 919-515-5834 ; Fax: 919-515-3355; cstuber@ncsu.edu
Stucker, Robert; Agronomy & Plant Genetics; 411 Borlaug Hall; Univ of Minnesota; St. Paul MN 55108; 612-625-2738; Fax: 612-625-1268

Styles, E. D.; Biology; Univ of Victoria; Victoria; British Columbia V8W 2Y2; CANADA; 604-721-7101
Subbaiah, Chalivendra; University of Illinois; Crop Sci, S-27 Turner Hall; 1102 S. Goodwin Ave.; Urbana IL 61801; ; subbaiah@uiuc.edu
Subramanian, Alap Raman; Dept Biochemistry; BioScience West; Univ of Arizona; Tucson AZ 85721-0001; 49 30 8413-1332; Fax: 49 30 8413-1383; SUBRAMANIAN@MPIMG-BERLIN-DAHLEM.MPG.DE
Sudupak, Mehmet Ali; Illinois Institute of Technology; Life Sciences - Dept. of Biology; 3101 S. Dearborn #286; Chicago IL 60616; ; SUDUMEH@karl.iit.edu
Sughroue, Jay; Great Lakes Hybrids; 2201 229th Place; Boone IA 50036; 515-292-1957; Fax: 515-292-7010
Sul, Ill-Wan; Biol Sci; 324 Tucker Hall; Univ of Missouri; Columbia MO 65211
Sullivan, Sue; ICI Seeds; 2369 330th St.; Slater IA 50244; 515-685-3574; Fax: 515-685-2548; TDSULLVN@MACC.WISC.EDU
Sullivan, Tom; Laboratory of Genetics; 445 Henry Mall; University of Wisconsin; Madison WI 53706; 608-262-4934; Fax: 608-262-2976; tdsullvn@vms2.macc.wisc.edu
Sun, Chongrong; Fudan University; Dept. of Biochem.; Handan Road 220; Shanghai 200433; CHINA
Sun, Zongxiu; China National Rice Research Institute; Genetics and Breeding Dept.; Tiyuchang Road 171; Hangzhou 310006; CHINA
Sundaresan, V.; Cold Spring Harbor Lab; P.O. Box 100; Cold Spring Harbor NY 11724; 516-367-8467
Sundberg, Marshall D.; Department of Botany; 502 Life Science Bldg; Louisiana State University; Baton Rouge LA 70803-1705; 504-388-8563; Fax: 504-388-8459; BTMARSH@LSUVM.LSU.EDU
Sung, Tong Ming; Dept of Agronomy; Beijing Agric Univ; 912 Research Building; Beijing 100094; CHINA; 2582223-0274; Fax: 2582332
Suprasanna, P.; Plant Biotechnology Division; Bhabha Atomic Research Centre; Trombay, Bombay 400 085; INDIA; 91-22-556-3060x2349/3276; Fax: 91-22-556-0750
Suresh, Jayanti; Dept. of Agronomy; 513 Borlaug Hall; 1991 Buford Cr.; St. Paul MN 55108; (612)625-1208
Sussex, Ian M.; Dept Plant Biology; Univ of California; Berkeley CA 94720; 510-642-7759; Fax: 510-642-4995; SUSSEX@NATURE.BERKELEY.EDU
Suttie, Janet; CIBA; PO Box 12257; 3054 Cornwallis Rd; Research Triangle Park NC 27709-2257
Sutton, Teresa R.; Pioneer Hi-Bred; 7250 NW 62nd Ave; P.O. Box 1004; Johnston IA 50131-1004; (515)270-3319; Fax: (515)270-4312
Swiecicki, W.K.; Polish Academy of Sciences; Institute of Plant Genetics; ul. Strzeszynska 34; 60-479 Poznan; POLAND; 233-511; Fax: (48-61)221-122
Sylvester, Anne W.; Dept of Biological Sciences; University of Idaho; Moscow ID 83843; 208-885-7477; Fax: 208-885-7905; annes@uidaho.edu
Szick, Kathy; Bot Plant Sci; UC Riverside; Riverside CA 92521
Tadmor, Yaakov; Dept of Horticulture; 1201 Gregory; University of Illinois; Urbana IL 61801-4798; 217-244-3388; Fax: 217-333-9817
Tagliani, Laura; Pioneer Hi-Bred Internat Inc; PO Box 1004; Johnston IA 50131-1004; 515-270-4188; Fax: 515-270-3367; TAGLIANILA@PHIBRED.COM
Tan, C. C. (Jia Zheng); Fudan University; Inst. of Genet.; Shanghai 20043; CHINA
Tang, Xi-Hua; Academic Sinica; Shanghai Inst. of Plant Physiol.; 300 Fonglin Road; Shanghai 200032; CHINA
Tanksley, Steven D.; Dept. Plant Breeding; Cornell University; 252 Emerson Hall; Ithaca NY 14853
Tao, Quanzhou; 320 Yue-Yang Road; Shanghai 200031; CHINA; 86-21-4374430; Fax: 86-21-4378357
Taramino, Graziana; PO Box 80402; E.I. DuPont deNemours & Co.; Agric Prod Exper Sta, Bldg. 402; Wilmington DE 19880-0402; 302-695-8328; Fax: 302-695-4296
Taylor, R. D.; Department of Biological Sciences; Stanford University; Stanford CA 94305-5020; (415)723-2413; Fax: (415)723-6132; TAYLORR@Leland.stanford.edu
Taylor, Loverine P.; Hort. and Landscape Architecture; Washington State University; Pullman WA 99164-6414; 509-335-3612; Fax: 509-335-8690
Taylor, Brian H.; Dept of Biology; Texas A&M Univ; College Station TX 77843-3258; 409-845-7754; Fax: 409-845-2891;
Taylor, W. C.; CSIRO; Division of Plant Industry; G.P.O. Box 1600; Canberra ACT 2601; AUSTRALIA; (61-6)246-5223; Fax: (61-6)246-5000; bt@pican.pi.csiro.au
Thatiparthi, V. R.; 412 Agronomy; Iowa State University; Ames IA 50010
Thelen, Jay; Biol Sci; 118 Tucker Hall; Univ of Missouri; Columbia MO 65211
Thompson, R. D.; Max Planck Inst Zuchtungsf; Abt Pflanzenz Ertragsphysiol; D-50829 Koeln; GERMANY; +49-221-5062-440/441; Fax: +49-221-5062-413; thompson@mpiz-koeln.mpg.de
Thompson, Steven A.; United Agriseeds; 103 Tomaras Ave; Savoy IL 61874
Thornbury, David W.; S-305 Ag Science Center N; Dept Plant Path; University of Kentucky; Lexington KY 40546; 606-257-4819; Fax: 606-323-1961; THORN@UKCC.UKY.EDU
Thornsberry, Jeffry; Biol Sci; 324 Tucker Hall; Univ of Missouri; Columbia MO 65211
Tierney, Mary L.; Marsh Life Sciences Bldg.; University of Vermont; Burlington VT 05405-0086; 802-656-0434; mtierney@moose,uvm.edu
Tiffany, Doug; Corn Research; Pioneer Hi-Bred, Int.; Rt. 8, Box 113A; Mankato MN 56001; (507)625-3252; Fax: (507)625-6446; TIFFANYD@PHIBRED.COM
Till, Bradley; Inst Molec Biol; Univ of Oregon; Eugene OR 97403
Timmermans, Marja; Waksman Inst; Rutgers Univ; PO Box 759; Piscataway NJ 08855-0759
Ting, Yu-Chen; Biology, Boston College; Chestnut Hill 67; Boston MA 02167; 617-552-2736; Fax: 617-552-2011
Tingey, Scott V.; Du Pont Company; P.O. Box 80402; Wilmington DE 19880-0402; (302)695-7252; Fax: (302)695-4296; TINGEYSV@ESVAX.DNET.DUPONT.COM
Toennissen, Gary; The Rockefeller Foundation; New York NY 10018
Tomes, Dwight T.; Pioneer Hi-Bred Intl; 7300 NW 62nd Ave; Johnston IA 50131-1004; 515-270-3646; Fax: 515-270-3444; tomesd@phibred.com
Tonelli, Chiara; University of Milan; Dept. of Genetics & Microbiology; Via Celoria 26; 20133 Milano; ITALY; 39-2-26605210; Fax: 39-2-2664551; tonelli@imiucca.csi.unimi.it
Tossberg, John; Pioneer Hi-Bred Internat Inc; Reid Research Center; 7300 NW 62nd Ave, PO Box 1004; Johnston IA 50131-1004
Tracy, William; Department of Agronomy; 1575 Linden Drive; University of Wisconsin; Madison WI 53706; 608-262-2587; wftracy@facstaff.wisc.edu
Trimnell, Mary; Pioneer Hi-Bred International; 7300 NW 62nd Ave.; P.O. Box 1004; Johnston IA 50131-1731; 515-270-3657; Fax: 515-270-3667; trimnellm@phibred.com
Troxell, Cynthia; Dept. MCD Biology; Campus Box 347; University of Colorado; Boulder CO 80309-0347; 303-492-8534; Fax: 303-492-7744; troxell@beagle.colorado.edu
Troyer, A. Forrest; Cargill Hybrid Seeds; Blackberry Creek Facility; 2600 W. Galena Blvd; Aurora IL 60506; 708-801-2302; Fax: 708-801-2345
Tsai, C. Y.; Dept Bot Plant Pathol; Purdue University; W. Lafayette IN 47907; 317-494-4640
Tu, Zeng-Ping; Guangdong Acad. of Agric. Sciences; Rice Research Institute; Wushan, Guangzhou; Guangdong 510640; CHINA
Tuerck, Jutta; ATC; 210 Science Park; Milton Road; Cambridge CB4 4WA; UNITED KINGDON; 44-1223-420284; JAT@mole.bio.cam.ac.uk
Tuttle, Ann Marie; CIBA-Geigy Corp; PO Box 12257; Research Triangle Park NC 27709-2257
Tyers, Randall; Plant Biol Dept; 111 Koshland Hall; UC Berkeley; Berkeley CA 94720-3102
Tymov, Valery; Genetics Dept; 83 Astrakhanskaya Str; Saratov State University; Saratov 410071; RUSSIA
Uhr, David V.; Northrup King Co.; 340 Southside Drive; Henderson KY 42420; (502)827-5787; Fax: (502)827-5703
Ujiie, Katsuhiro; HOKUREN Naganuma Res. Stn.; Minami-2, Higashi-9; Naganuma-Cho, Yuubari-Gun; Hokkaido 069-13; JAPAN; 01238-8-3330; Fax: 01238-8-3200
Ulrich, Valentin; P.O. Box 451; Morgantown WV 26506; 304-292-5262
Usami, Satoru; Plant Brdg Genetics Res Lab; Japan Tobacco Inc; 700 Higashibara Toyoda-cho; Iwata-gun Shizuoka ken438; JAPAN; 81-538-32-7111; Fax: 81-538-32-8700
Vain, Philippe; Cent. Rech. Plantes Physiol. Veg. Molec.; B'aiment 430; Universit'e de Paris Sud; 91 405 Orsay Cedex; FRANCE; 33-1-69-41-77-08; Fax: 33-1-69-85-37-15; quetier@citi2.fr
Valdez, Gregorio; Lehman College CUNY; Biology Dept c/o Elli Wurtzel; 250 Bedford Park Blvd West; Bronx NY 10468
Vallejos, Ruben H.; CEFOBI; Suipacha 531; 2000 Rosario; ARGENTINA
Van Heeckeren, Wim; Inst Molec Biol; Univ of Oregon; Eugene OR 97403-1229
Van Montagu, M.; Lab Genetics; K L Ledeganckstr 35; B-9000 Gent ; BELGIUM; 32-91-645170; Fax: 32-91-645349; jecop@gengenp.rug.ac.be
van Nocker, Steve; Dept Horticulture; Univ of Wisconsin; Madison WI 53706
Van Schaik, N.; Dept Genetics/U Witwatersrand; PO Wits 2050; SOUTH AFRICA; (011) 716-2125; Fax: 27-11-403-1733
Vanderslice, Olin L.; Vanderslice Enterprises; RD #3, Box 194; Gallatin MO 64640; 816-663-2946
Vantoai, Tara T.; USDA Agronomy; 590 Woody Hayes Dr; Columbus OH 43210; 614-292-9806; Fax: 614-292-9448; tvantoai@magnus.acs.ohio-state.edu
Varagona, Rita; Department of Biology; Box 30001/Dept 3AF; NMSU; Las Cruces NM 88003-0001; (505)646-7963; Fax: (505)646-5665; MVARAGON@NMSU.EDU
Vasal, S. K.; CIMMYT; Lisboa 27; Apartado Postal 6-641; Mexico 6, D.F.; MEXICO; 52-5-726-9091x1206; Fax: 52-5-726-7558; SVASAL@ALPHAC.CIMMYT.MX
Vasil, Indra K.; Laboratory of Plant Cell & Molecular Biol; 1143 Fifield Hall; University of Florida; Gainesville FL 32611; 904-392-1193; Fax: 904-392-9366

Vega, Shifra; Dept Biol; Plant Sci Inst; Univ of Pennsylvania; Philadelphia PA 19104-6018
Veit, Bruce; Dept of Biology 0116; Univ of California-San Diego; La Jolla CA 92093-0116; 619-534-7298; bveit@jeeves.ucsd.edu
Veldboom, Lance; PO Box 839; Holden's Foundation Seeds, Inc.; Williamsburg IA 52361; 319-668-1100; Fax: 319-668-2453; lance@holdens.com
Verbeke, Judith A.; Developmental Mechanisms Program; National Science Foundation; 4201 Wilson Boulevard; Arlington VA 22230
Vergne, Phillippe; RCAP; ENS-Lyon; 46 Allee d'Italie; 69364 Lyon cedex 07; FRANCE; +33/72-72-86-08; Fax: +33/72 72 86 00; Philippe.Vergne@ens-lyon.fr
Vermerris, Wilfred; Dept. Crop Science; Box 7620; North Carolina State Univ; Raleigh NC 27695-7620; 919-515-2704; Fax: 919-515-7959; weverme1@unity.ncsu.edu
Vierling, Richard; Indiana Crop Improvement; 3510 U.S. 52 South; Lafayette IN 47905; 317-474-3494; Fax: 317-474-8959; Vierling@mace.cc.purdue.edu
Violic, Alejandro D.; Vital Apoquindo 180; Santiago (Las Condes); CHILE; (562)229-0685; Fax: (562)735-5892
Viotti, Angelo; Ist Biosintesi Vegetali; Via Bassini 15; 20133 Milano; ITALY; 39 2 706.001.70/309.85; Fax: 39 2 2362946; AVIOTTI@vm.cnuce.cnr.it
Vodkin, Lila Ott; 384 PABL, Dept Crop Sci; Univ Illinois; 1201 W. Gregory; Urbana IL 61801; 217-244-6147; Fax: 217-333-9817; vodkin@UX1.CSO.UIUC.EDU
Voelker, Rodger; Inst Molec Biol; Univ of Oregon; Eugene OR 97403
Vogel, Julie; E. I. DuPont de Nemours; Ag. Products; E402/4247; Wilmington DE 19880-0402; (302)695-7980; Fax: (302)695-4296; VogelJM@ESVAX.DNET.DuPONT.COM
Vollbrecht, Erik; Dept. of Plant Biology; University of California; Berkeley CA 94720; 510-559-5922; Fax: 510-559-5648; erikv@uclink2.berkeley.edu
Von Bulow, J. F. W.; Rua Sa Ferreira, 172; Apt. 601; 22071-100 Rio de Janeiro, RJ; BRAZIL
Von Wettstein, D.; Carlsberg Lab; Gamle Carlsbergvej 10; DK-2500 Copenhagen Valby; DENMARK; 45 31 22 10 22; Fax: 45 33 27 47 66; CARLFYS@BIOBASE.AAU.DK
Voytas, D.; Dept. of Botany; Iowa State University; Ames IA 50011; ; voytas@iastate.edu
Waines, J. Giles; Dept of Botany/Plant Sciences; University of California; Riverside CA 92521; 909-787-3706; Fax: 909-787-4437
Walbot, V.; Dept Biol Sci; Stanford Univ; Stanford CA 94305-5020; 415-723-2227; Fax: 415-725-8221; walbot@leland.stanford.edu
Walden, D. B.; Dept of Plant Sciences; Univ of Western Ontario; London N6A 5B7; CANADA; 519-661-3103; Fax: 519-661-3935
Walker, Nigel; Plant Biol Dept; 111 Koshland Hall; UC Berkeley; Berkeley CA 94720-3102
Walker, Elsbeth L.; 11 Greenwood Ln.; So. Hadley MA 01075; ; Fax: 413-538-2327; ewalker@mhc.mtholyoke.edu
Walker, John; Biol Sci; 308 Tucker Hall; Univ of Missouri; Columbia MO 65211; 573-882-3583; Fax: 573-882-0123; jcw@biosci.mbp.missouri.edu
Walko, Richard; Pharmacia LKB Biotechnology; Alameda CA 94501
Walsh, Justine; Plant Biology Dept; 111 Koshland Hall; UC Berkeley; Berkeley CA 94720-3102
Walsh, Laura C.; Mycogen Plant Sciences; 720 St. Croix Street; Prescott WI 54021; 800-321-2867; Fax: (715)262-3996
Walton, Jonathan; DOE Plant Research Lab; Michigan State University; East Lansing MI 48824; 517-353-4885; Fax: 517-353-9168; jdwalton@msu.edu
Wan, Yuechun; Monsanto Agricultural Group; 700 N Chesterfield Pkwy - GG4H; St. Louis MO 63198; 314-537-6734; yywan@ccmail.monsanto.com
Wang, Ya-hui; Academia Sinica; Inst. of Cell Biol.; 320 Yo-Yang Road; Shanghai 200031; CHINA
Wang, Bin; Academia Sinica; Institute of Genetics; Beijing 100101; CHINA
Wang, Qinnan; National Natural Science Foundation; Dept. of Life Science; Beijing 100083; CHINA
Wang, Xun; Pioneer Hi-Bred Internat Inc; 7300 NW 62nd Ave; PO Box 1004; Johnston IA 50131-1004
Wang, Zhendong; Waksman Institute; Rutgers Univ; PO Box 759; Piscataway NJ 08855-0759
Wanous, Michael; Biol Sci; 117 Tucker Hall; Univ of Missouri; Columbia MO 65211; 573-882-4871; Fax: 573-882-0123; mwanous@biosci.mbp.missouri.edu
Warner, Todd; Northrup King Co; 317 330th St; Stanton MN 55018-4308
Warren, Jana; Pioneer Hi-Bred Internat Inc; 7300 NW 62nd Ave; PO Box 1004; Johnston IA 50131-1004
Weaver, Sam; Quaker Oats Company; 617 W. Main St.; Barrington IL 60010-4199; 708-304-2135; Fax: 708-304-2166
Weber, David; Illinois State Univ; 4120 Biological Sciences; Normal IL 61761; 309-438-2685; Fax: 309-438-3722; dfweber@rs6000.cmp.ilstu.edu
Weber, Gerd; Institut fur Pflanzenzuchtung; Universitat Hohenheim; D 70593 Stuttgart; GERMANY; 49 (711)459 2341; Fax: 49 (711)459 2343; weberg@rs1.rz.uni-hohenheim.de
Weck, Edward A.; IAEA; POB 100; 1400 Vienna; AUSTRIA; 43-1-2060-21626; Fax: 43-1-20607; weck@ripo1.iaea.or.at
Weil, Cliff; Dept. of Biological Sciences; University of Idaho; Moscow ID 83843; (208)885-6370; Fax: (208)885-7905; cweil@crow.csrv.uidaho.edu
Wen, Tsui-Jung; B422 Agronomy Hall; Iowa State University; Ames IA 50011; 515-294-1659; Fax: 515-294-2299; TJWEN@IASTATE.EDU
Wendel, Jonathan F.; Department of Botany; Bessey Hall; Iowa State University; Ames IA 50011; 515-294-7172; Fax: 515-294-1337; jfw@iastate.edu
Wenxiong, Lin; Fujian Agricultural College; Dept. of Agronomy; Jingshan, Fuzhou; Fujian 350002; CHINA
Werr, Wolfgang; Institut Fur Entwicklungsbiologie; Universitat zu Koln; Gyrhofstr 17; 50931 Koln 41; GERMANY; +49 221 470 2619; Fax: +49 221 470 5164; Wower@Gen1.Genetik.Uni-Koeln.de
Wessells, Catherine P. B.; 28015 Stonehenge Lane; Eugene OR 97402; (503)344-3290
Wessler, Sue; University of Georgia; Dept of Genetics; Life Sciences Bldg; Athens GA 30602; 706-542-1870; Fax: 706-542-3910
West, Dennis R.; Dept Plant and Soil Sci; Univ of Tennessee; Knoxville TN 37901-1071; 423-974-8826; Fax: 423-974-7997; DWEST@UTK.EDU
Westhoff, Peter; Ins. Ent. Mol. Bio. Pflanzen; Heinrich-Heine-Univ Dusseldorf; D-40225 Dusseldorf ; GERMANY; 49-211-311-2338; Fax: 49-222-311-4871; West@Uni-Duesseldorf.de
Wetzel, Carolyn; Dept of Botany; Bessey Hall; Ames IA 50011; 515-294-7724; Fax: 515-294-1337; cmwetzel@iastate.edu
Whalen, R. H.; Dept of Biology; South Dakota State Univ; Brookings SD 57007; 605-688-4553
White, Shawn; Dept of Botany; University of Georgia; Athens GA 30602; (706)542-1857; Fax: (706)542-1805; whites@bscr.uga.edu
Whitwood, W.; Robson Seed Farms; 1 Seneca Circle; Hall NY 14463; 716-526-5879
Widholm, Jack M.; Crop Science; Univ of Illinois; PABL, 1201 W. Gregory; Urbana IL 61801; 217-333-9462; Fax: 217-333-4777; Widholm@UIUC.EDU
Widstrom, Neil W.; Coastal Plain Exp Sta; PO Box 748; Tifton GA 31793; 912-387-2341; Fax: 912-387-2321; nwidstro@tifton.cpes.peachnet.edu
Wienand, Udo; Inst. Allge. Bot.; Angew. Molek.; Pflanzen, AMP I, Ohnhorststrasse 18; D-22609 Hamburg ; GERMANY; (49)40 822 82 501; Fax: (49)40 882 82 503; FB5A114@RRZ-CIP-1.RRZ.UNI-HAMBURG.DE
Wilkes, H. Garrison; Biology-College II; Univ of Mass/Boston; 100 Morrissey Blvd; Boston MA 02125-3393; 617-287-6600; Fax: 617-287-6650; WILKES@UMBSKY.CC.UMB.EDU
Willcox, Martha; CIMMYT; Apartado Postal 6-641; Mexico, D.F. 06600; MEXICO; 52(5)726-9091 ext.1128; Fax: 52(5)726-7559; MWillcox@CIMMYT.MX
Williams, Rosalind; Plant Biology Dept; 111 Koshland Hall; UC Berkeley; Berkeley CA 94720
Williams, Terrill E.; Pioneer Hi-Bred Internatl; P.O. Box 128; New Holland PA 17557; 717-354-6044; Fax: 717-355-2445; Williamste@phibred.com
Williams, W. Paul; Crop Sci Res Lab; PO Box 9555; Miss. State MS 39762; 601-325-2735; Fax: 601-325-8441
Williams, Claire G.; Texas A&M Univ; Dept of Forest Science; College Station TX 77843-2135; 409-845-6049; Fax: 409-862-3745; claire_williams@tamu.edu
Williams, Mark; DuPont de Nemours & Co Agric Biotech; Stine-Haskell Res Cent 210N/253; 1090 Elkton Rd; Newark DE 19714; 302-366-5102; Fax: 302-451-4832; WILLIAME@ESVAX.DNET.DUPONT.COM
Williams, Robert E.; PO Box 294; Pittsfield IL 62363; 217-285-2530
Willman, Mark R.; Hunt-Wesson Inc; 463 U.S. Hwy. 30 East; Valparaiso IN 46383; 219/477-2233; Fax: 219/477-2232
Wing, Rod; Department of Soil and Crop Sciences; Texas A&M University; College Station TX 77843; ; rodwing@tamvm1.tamu.edu
Winkler, Rodney G.; University of Arizona; Plant Science (C795424); Forbes Bldg Rm 303; Tucson AZ 85721; 602-621-9567; Fax: 602-621-7186; RWINKLER@AG.ARIZONA.edu
Winter-Vann, Ann Marie; CIBA Ag Biotech; PO Box 12257; Research Triangle Park NC 27709-2257
Wise, Roger; USDA-ARS; Dept. Plant Pathology; Iowa State Univ.; Ames IA 50011-1020; 515-294-9756; Fax: 515-294-9420; rpwise@iastate.edu
Wolfe, Kenneth; Dept. of Genetics; University of Dublin; Trinity College; Dublin 2; IRELAND; 353-1-702-1253; Fax: 353-1-679-8558; KHWOLFE@VAX1.TCD.IE
Woo, Claudine; 2667 Parker St; Berkeley CA 94704
Woodman, Wendy; Dept. of Agronomy; Iowa State Univ.; Ames IA 50011; 515-294-3635; Fax: 515-294-3163; wlwoodma@iastate.edu
Woodruff, Dorde; 6366 Cobblerock Lane; Salt Lake City UT 84121-2304; 801-277-5526
Woodward, Wendy; Biol Sci; Tucker Hall; Univ of Missouri; Columbia MO 65211
Woody, Laura; Biol Sci; 110 Tucker Hall; Univ of Missouri; Columbia MO 65211

Wright, James; Pioneer Hi-Bred Internat Inc; PO Box 245; ; Wilson NC 27894-0245
Wright, Allen; ExSeed Genetics L.L.C.; 1573 Food Science Bldg.; Iowa State University; Ames IA 50011; (515)294-8395; Fax: (515)294-9359
Wright, S.; Linkage Genetics; 1515 West 2200 South, Suite C; Salt Lake City UT 84119; (801) 975-1188; Fax: (801)975-1244
Wrobel, Russell; Box 7612; Dept. of Botany; North Carolina State University; Raleigh NC 27695-7612; ; qwerty@unity.NCSU.edu
Wurtzel, Eleanore; Dept Biol Sci; Davis Hall, Lehman College; City Univ New York; Bronx NY 10468; 718-960-4994, -8643; Fax: 718-960-8236; etwlc@cunyvm.cuny.edu
Xia, Zhen-Ao; Academia Sinica; Shanghai Inst. of Plant Physiol.; 300 Fonglin Road; Shanghai 200433; CHINA
Xia, Yiji; B420 Agronomy Hall; Iowa State Univ; Ames IA 50011
Xiao, Yongli; 2292-1 Molecular Biology Bldg; Iowa State University; Ames IA 50010; 515-294-3277; yxiao@iastate.edu
Xie, You-Ju; College of Biology; China Agricultural University; Beijing 100094; CHINA; 86 (10) 62631895; Fax: 0086-1-2582332
Xiong, Chenmin; China National Rice Research Institute; Ti Yu Chang Road 171; Hangzhou; Zhejiang 310006; CHINA
Xu, Yun-Bi; Zhejiang Agricultural University; Dept. of Agronomy; Hangzhou; Zhejiang 310029; CHINA
Xu, Zhi-Hong; Shanghai Inst. of Plant Physiol.; 300 Fenglin road; Shanghai 200032; CHINA
Xu, Zeng-Fu; Zhongsan Univ.; Biotechnology Res. Center; 135 West Xingang Road, Guangzhou; Guangdong 510275; CHINA
Xu, Xiaojie; B420 Agronomy Hall; Iowa State Univ; Ames IA 50011
Xu, Guilin; Agronomy Dept.; 302 Curtis Hall; University of Missouri; Columbia MO 65211; 573-882-2033
Xu, Wenwei; Plant Molecular Genetics Laboratory; Mail Stop 2122; Texas Tech Univesity; Lubbock TX 79409; (806)742-2831; Fax: (806)742-0775; BWWXU@TTACS1.TTU.EDU
Yaklin, Paul; Pioneer Hi-Bred Internat Inc; Trait & Technol Devel; 7300 NW 62nd Ave, PO Box 1004; Johnston IA 50131-1004
Yamada, Minoru; STAFF; Sankaido Bldg. 7F; Akasaka 1-9-13, Minato-ku; Tokyo 107; JAPAN; (03)3586-8644; Fax: (03)3586-8277
Yamaguchi, Judy; Plant Gene Expression Center; USDA-ARS; 800 Buchanan St; Albany CA 94710
Yamato, Tom; Biol Sci; 324 Tucker Hall; Univ of Missouri; Columbia MO 65211
Yang, Jin Shui; Fudan University; Institute of Genetics; Shanghai 200433; CHINA
Yang, Yuesheng; South China Agricultural University; Experimental Center; Guangzhou; Guangdong 510642; CHINA
Yang, Ren-Cui; Fujian Agricultural College; Heterosis Utilization Lab.; Chinmen, Fuzhou; Fujian 350002; CHINA
Yang, Hong; Chinese Academy of Agric. Sciences; Biotech. Research Centre; Beijing 100081; CHINA
Yano, Masahiro; Rice Genome Research Program; Nat. Inst. Agrobiol. Resources; 2-1-2, Kannondai; Tsukuba, Ibaraki 305; JAPAN; 81-298-38-7441,2199; Fax: 81-298-38-7468,2302; myano@abr.affrc.go.jp
Yatou, Osamu; Crop Science Division; Kagoshima Agricultural Experiment Station; 5500 Kamifukumoto-cho; Kagoshima, 891 - 01; JAPAN; +81-992-68-3231; Fax: +81-992-68-9268; GFE01254@NIFTYSERVE.OR.JP
Ye, Sheng-Yu; Shanghai Inst. of Biochem.; 320 Yue Yang Road; Shanghai 200031; CHINA
Ye, Ke-Nan; Zhongsan University; Biotechnology Research Centre; Guangzhou 510642; CHINA
Yi, Bu-Young; Nat Agric Sci & Technol Inst; RDA; SEO DUN DONG 249; Suwon 441-707; KOREA; 82-331-296-9436; Fax: 82-331-294-1072
Yoder, John; Dept of Vegetable Crops; Univ of California, Davis; Davis CA 95616; 916-752-1741; Fax: 916-752-9659; JIYODER@UCDAVIS.EDU
Yoganathan, Arulmolee; Department of Biology; Lehman College/CUNY; Bedford Park Blvd. West; Bronx NY 10468; 212-960-8235; Fax: 212-960-8227
Yong, Gao; Liaoning Academy of Agric. Sciences; Rice Research Institute; Sujiatun; Shenyang 110101; CHINA
Yoon, Elizabeth; Dept Bot Plant Path; Oregon State Univ; Cordley 2082; Corvallis OR 97331-2902
You, Chong-biao; Chinese Academy of Agric. Sciences; IAAE, Dept. of Biotechnology; P.O. Box 5109; Beijing 100094; CHINA
Young, Todd; Botany Dept; UC Riverside; Riverside CA 92521-0129
Yu, Li; China National Rice Research Institute; Library; Tiyuchang Road No. 171, Hangzhou; Zhejiang 310006; CHINA
Yu, Di-qiu; Zhongsan(Sun Yat-Sen)University; Biotechnology Research Center; Guangzhou; Guangdong 510275; CHINA
Yu, Jia; Dept. Biological Science; Lehman College; 250 Bedford Park Blvd. West; Bronx NY 10468; 212-960-4994; Fax: 212-960-8227
Yu, Yuhua; Souh China Inst. Bot.; Academia Sinica; Guangzhou 510650; CHINA
Yu, Yong Gang; CSES VPI & SU; Blacksburg VA 24061-0404; (703)231-3701; YGYU@VTVM1.CC.VT.EDU
Zabala, Gracia; Plant Biol/265 Morrill Hall; Univ Illinois; 505 S. Goodwin Avenue; Urbana IL 61801; 217-333-3736; Fax: 217-244-7246; Gracia.Zabala@Qms1.Life.uiuc.edu
Zaitlin, David; 4112 Yuma Drive; Madison WI 53711; 510-729-0720; Fax: 510-562-9215
Zavalishina, Alexandra; Genetics Dept; Saratov State University; 83, Astrakhanskaya St.; 410071, Saratov; RUSSIA; ; Fax: 845-2-240446; POSTMASTER@SCNIT.SARATOV.SU
Zehr, Brent; Purdue University; Dept of Agronomy; Lilly Hall of Life Sciences; West Lafayette IN 47907-1150; (317)494-8088; Fax: (317)494-6508; bzehr@dept.agry.purdue.edu
Zeng, Zhaomei; Washington University; Dept. of Biology; Campus Box 1137; St. Louis MO 63130; 314-935-6826
Zeng, M. Q.; Institute of Genetics; Academia Sinica; Datun Rd.; 100101 Beijing; CHINA; 4917283; Fax: (001 861)4914896
Zhang, Deyu; Jiangsu Academy of Agricultural Sci.; Inst. of Genet. and Physiol.; Nanjing 210014; CHINA
Zhang, Gui-Quang; South China Agricultural University; Dept. of Agronomy; Guangzhou 510642; CHINA
Zhang, Jianbo; 2288 Molecular Biology Building; Iowa State University; Ames IA 50010; (515)294-2922; jzhang@iastate.edu
Zhang, Peifen; 2288 Molecular Biology Bldg; Iowa State University; Ames IA 50011; 515-294-2922; zpf@iastate.edu
Zhang, Fan; Department of Botany; Box 7612; NCSU; Raleigh NC 27695-7612; ; Fax: 919-515-3570; Fan_Zhang@ncsu.edu
Zhang, Qifa; Huazhong Agricultural University; Biotechnology Center; Shizishan, Wuchang; Hubei 430070; CHINA; 86-27-7816734; Fax: 86-27-7815057
Zhao, Qiquan; Zhejiang Agricultural University; Dept. of Tea Science; Hangzhou; Zhejiang 32100; CHINA
Zhao, Zuo-Yu; Biotechnology Research; Pioneer Hi-Bred Int'l; 7300 NW 62nd Ave. P.O. Box 1004; Johnston IA 50131-1004; 515-270-3644; Fax: 515-270-3444; zhaoz@phibred.com
Zhen, Zhu; Academia Sinica; Institute of Genetics; Beijing 100101; CHINA
Zheng, Kangle; China National Rice Research Institute; 171 Ti Yu Chang Road; Hangzhou 310006; CHINA
Zhixian, Liu; 11 Sangyuan Road; Maize Research Inst; Shandong Academy of Agri. Science; Jinan, 250100; CHINA; (0531)8963721-313; Fax: (0531)862303
Zhong, Zhen-Ping; Fujian Agricultural College; Dept. of Agronomy; Fuzhou; Fujian 350002; CHINA
Zhou, Kaida; Sichuan Agricultural University; Rice Research Institute; Yaan; Sichuan 625014; CHINA
Zhou, Zhaolan; Chinese Academy of Sciences; Institute of Genetics; Group 601; Beijing 100101; CHINA
Zhou, Li; Dept Molec Biol; Wellman 11, MGH; Boston MA 02114; 617-726-5916; Fax: 617-726-6893; zhou@frodo.mgh.harvard.edu
Zhou, Hongsheng; Institute of Crop Breeding and Cultiv; Chinese Acad Agric Sci; 30, Bai Shi Qiao Lu; Beijing 100081; CHINA; 86-1-8351731; Fax: 86-1-8316545
Zhu, Li-Hong; Nanjing Agric. University; Dept. of Agronomy; Nanjing; Jiangsu 210014; CHINA
Zhu, Z. P.; Shanghai Inst. of Plant Physiol.; 300 Fengling Road; Shanghai 200032; CHINA
Zhu, Ying-Guo; Wuhan University; Genetics Dept; Wuchang; Hubei 430072; CHINA; 27-7822712-4560; Fax: 27-7812661
Zhu, Li-huang; Academia Sinica; Institute of Genetics; Datun Road, Andingmen Wai; Beijing 100101; CHINA; 86-1-2033491; Fax: 86-1-4913428
Zhu, Xiaoyang; Curtis Hall; University of Missouri; Columbia MO 65211
Zimmer, Elizabeth; Lab of Molecular Systematics MRC 534; Support Ctr. Nat'l Museum Nat. History; Smithsonian Inst; Washington DC 20560; 301-238-3025; Fax: 301-238-3059; zimmer@onyx.si.edu

Maize Genetics Cooperation • Stock Center

USDA/ARS/MWA - Plant Physiology and Genetics Research Unit
&
University of Illinois at Urbana/Champaign - Department of Crop Sciences

S-123 Turner Hall
1102 South Goodwin Avenue
Urbana, IL 61801-4798

(217) 333-6631 [*phone*]
(217) 333-6064 [*fax*]
maize@uiuc.edu [*internet*]
http://www.uiuc.edu/ph/www/maize [*URL*]

During 1995, 2012 seed samples have been supplied in response to 264 requests. Of these, a total of 60 requests were received from 20 foreign countries. Approximately two thirds of our requests were received by electronic mail or through our order form on the World-Wide Web.

Spring rains caused a delay of planting and then soil crusting; this was followed by a very hot and dry summer followed by an early killing frost. In addition to this, our plants' root systems were compromised by rootworms. About 5 acres of nursery were grown. Despite the weather and pests, and with the help of irrigation, good increases were obtained of numerous stocks that were in low supply and new stocks from the collections of Marcus Rhoades, Donald Robertson, Ed Coe, Hugo Dooner, Barbara McClintock, Jerry Neuffer, and Nina Fedoroff. Special plantings were made of several categories of stocks, with special attention given to the collection of reciprocal translocations developed by A. E. Longley and E. G. Anderson. Some tests for allelism were made within groups of mutants of similar phenotype. We had a spotty winter nursery at the USDA facility in Isabela, Puerto Rico last year due to a problem with the soil. However, soil tests did not reveal any specific toxicity or deficiency. Our winter crop in Puerto Rico looks excellent this year, so far.

We have obtained additional stocks from the collections of Jerry Neuffer, Ed Coe, Jerry Kermicle, Kevin Simcox, Donald Robertson, William R. Findley, Karen Cone, Robert Brawn, and John Laughnan. Through the help of Rob Martienssen and Paul Chomet, we obtained stocks from the collection of Barbara McClintock. We selected mutant stocks from McClintock's collection that we will maintain, the rest were sent to NSSL for archival purposes. We have pedigree information in electronic form for McClintock's stocks. This and information about other donated collections is available at URL: <ftp://ftp.agron.missouri.edu/pub/mgcsc/>. We expect to receive several additional large accessions of stocks from maize geneticists within the upcoming year. We strongly urge all cooperators with mutants (old or new) that are not presently in our collection, to contribute seeds to us. This will insure that mutants you have will be maintained and shared with the maize research community.

We set up a WWW home page in March of 1995 that allows us to receive requests over the 'Web' from users with software such as Mosaic or Netscape. We are continuing to enter data into our internal database. In addition to information about our stocks, we also have the reprint collections of M. M. Rhoades, G. F. Sprague and E. G. Anderson. Information about these reprints is accessible from our growing internal database.

We have been continuing our collaboration with Ed Coe's efforts in the growing Maize Genome Database (MaizeDB). This is part of the Plant Genome Database (PGD) effort being sponsored by the National Agricultural Library. Information about our stocks is presently in MaizeDB (and therefore also with the PGD at NAL) allowing users access to information about available maize genetic stocks. Available maize genetic stocks have also been listed in GRIN (with links to detailed information contained in MaizeDB and PGD). Stock information is accessible from our web site.

A list of available stocks will continue to be published annually as part of the *Maize Genetics Cooperation • Newsletter.* This year the stock list has many new additions. When making requests please give both the stock number and the genotype.

Marty Sachs
Director

Philip Stinard
Curator

Janet Day Jackson
Research Specialist

CHROMOSOME 1

101A sr1 zb4 P1-ww
101B sr1 P1-wr
101C sr1 P1-ww
101D sr1 P1+rr
101F sr1 ts2 P1+rr
102F ms28
103D vp5
103DA vp5-mu3076
103DB vp5-86GN4
103DC vp5-86GN3
103DD vp5-86GN6
103DE vp5-86GN11
103DF vp5-Mumm#1
103E zb4 ms17 P1-ww
105A zb4 P1-ww
105B zb4 P1-wr
105C zb4 P1-ww br1
105E ms17 P1-wr
105F ms17 P1-ww
106A zb4 P1-ww bm2
106B ts2 P1+rr
107A P1-cr
107B P1+rr
107D P1-cw
107E P1-mm
107F P1-vv::Ac
107G P1-or
107H P1-ww
109D P1+rr ad1 bm2
109E P1-wr br1 f1
110A P1-wr an1 Kn1 bm2
110D P1-wr an1 bm2
110E P1-wr ad1 bm2
110F P1-wr br1 Vg1
110H P1-wr br1 f1 bm2
110K P1-wr br1
111G P1-wr rs2
111H Les5-N1449
112E as1
112H P1-ww br1
112K an1 gs1 bm2
113A as1 br2
113B rd1
113C br1 f1
113E br1 f1 Kn1
113K hm1; hm2
113L Hm1; hm2
114C br1 bm2
114D Vg1
114F br2 hm1
114G br2 hm1; hm2
115C v22-8983
115CA v22-055-4
115J bz2-m::Ds; A1 A2 C1 C2 Pr1 R1
116A bz2-m::Ds; A1 A2 Ac C1 Pr1 R1
116C an1 bm2
116D an1-bz2-6923; A1 A2 Bz1 C1 C2 Pr1 R1
116G an1
116I bz2 gs1 bm2 Ts6; A1 A2 Bz1 C1 C2 R1
117A br2
117D tb1
117DA tb1-8963
117E Kn1
118B Kn1 bm2
118C lw1
118I bm2 Ts6
119A Adh1+1S; Adh2-1P
119B vp8
119C gs1
119D gs1 bm2
119E Ts6
119F bm2
119H Adh1-FkF(gamma)25; Adh2+N
120A id1
120B nec2
120C ms9
120D ms12
120E v22-055-4 bm2
120F Mpl1-Sisco
120G Mpl1-Freeling
121A ms14
121B br2-mi8043
121C D8
121D lls1
121E ty*-8446
121G ct2
121GA ct2-rd3
122A TB-1La
122B TB-1Sb (1S.05; BL.2)
122C P1-wr; R1-nj TB-1Lc Y1
124A v*-5688
124B j*-5828
124C w*-8345
124D v*-5588
124E w*-018-3
124F w*-4791
124H w*-8054
124I v*-032-3
124J v*-8943
124K yg*-8574
124L w*-6474
125A Les2-N845A
125B Mpl1-Jenkins
126A bz2 gs1 bm2; A1 A2 Bz1 C1 C2 R1
126F o13
126G P1-vv::Ac bz2-m::Ds; A1 A2 Bz1 C1 C2 R1 TB-1Sb (1S.05; BL.2)
126H P1-vv::Ac bz2-m::Ds
126I P1-vv::Ac
126J P1-ww-1112
126K P1-ovov-1114
126L P1+rr-4B2
126M P1-vv-5145
127A bz2 zb*-N101 bm2
127B dek1-N792
127C dek2-N1315A
127D dek22-N1113A
127E f1
127G Tlr1-N1590
127I gt1
128A ij2-N8
128B l16-N515
128C l17-N544
128D pg15-N340B
128E pg16-N219
128F v25-N17
129A w18
129B wl*-N266A
129C zb*-N101
130A o10-N1356

CHROMOSOME 2

201F ws3 lg1 gl2 b1
203B al1
203BA al1-Brawn
203BB al1-y3
203D al1 lg1
203G al1-y3 gl2
205A al1 lg1 gl2
205B lg1
205C lg1 gl2
205G al1 gl2 B1
206A lg1 gl2 B1
208B lg1 gl2 B1 sk1
208C lg1 gl2 B1 sk1 v4
208D lg1 gl2 B1 v4
208E lg1 gl2 b1
208H gl2
209E lg1 gl2 b1 sk1
211A lg1 gl2 b1 fl1
211H gl2 wt1
212B lg1 gl2 b1 fl1 v4
212D lg1 gl2 b1 v4
213B lg1 gl2 wt1
213F lg1 B1-V Ch1
213H lg1 gl2 B1-V
214B lg1 b1 gs2
214C d5
214D gl11 B1
214E B1 ts1
214J B1 sk1
214L lg1 gl2 mn1
215A gl14
215B gl11
215C wt1
215D mn1
215E fl1
215EA fl1-o4
215G fl1 v4
215H wt1 gl14
216A fl1 v4 Ch1
216D fl1 w3
216E fl1 v4 w3
216G fl1 v4 w3 Ch1
217A ts1
217B v4
217G v4 Ch1
217H ba2 v4
218A w3
218C w3 Ch1
218D Ht1-GE440
218DA Ht1-Ladyfinger
218E ba2
218G B1+Peru; A1 A2 C1 C2 r1-r
218H w3-8686
218I w3-86GN12
219A B1+Peru; A1 A2 C1 C2 r1-g
219B b1; A1 A2 C1 C2 r1-g
219C Ch1
219G B1+Bolivia-706B; A1 A2 C1 C2 r1-g
219H B1+Bolivia; A1 A2 C1 C2 Pl1 Pr1 r1-g
219I B1+I; A1 A2 C1 C2 Pl1+Rhoades r1-r
219J B1+I; A1 A2 C1 C2 Pl1+Rhoades r1-g
220A Les1-N843
220B ws3 lg1 gl2; T2-Tripsacum
220F os1
221A gs2
221C wlv1 Ch1
221G wlv1
222A TB-1Sb-2L4464
222B TB-3La-2S6270
223A trisomic 2
224A w*-4670
224AB w*-017-14-A
224B v*-5537
224H whp1; A1 A2 C1 c2 R1
224I ws3-7752
224J ijmos*-7335
224K glnec*-8495
224L ws3-8949
224M ws3-8991
224N ws3-8945
225A TB-3La-2L7285 (2L.26; 3L.1)
225B TB-1Sb-2Lc (1S.77; 2L.33)
227A dek3-N1289
227C dek16-N1414
227D dek23-N1428
227E Les4-N1375
227I nec4-N516B
228A l18-N1940
228B spt1-N464
228C v26-N453A
228E B1-Bh
229A rf3 Ch1
229B v24-N424
229C w3 rf3 Ch1

CHROMOSOME 3

301A cr1
302A d1-6016
302B d1 rt1
302E d1-tall
303F g2
303FA g2-pg14::I
303FB g2-v19
303FC g2-Funk
303FD g2-56-3034-14
303FE g2-59-2097
303FF g2-94-1478
303G g2 d1
304A d1 ys3
304F d1 Lg3-O ys3
304G Lg3-O Rg1
304I d1 h1
305A d1 Lg3-O
305B d1 Lg3-O gl6
305D d1 Rg1
305J d1 h1 Lg3-O
305K d1 cl1; Clm1-4
306B d1 gl6
306D d1 Rg1 ts4
307A d1 pm1
307C pm1
308B d1 ts4
308E ra2
309D ra2 Rg1 lg2-R
310C ra2 lg2-R
310D Cg1
311A cl1
311B cl1; Clm1-2
311C cl1; Clm1-3
311E rt1
311F ys3
311G Lg3-O ys3
312D Lg3-O
313A gl6
313D ms3
313E Lg3-O gl6
314A gl6 lg2-R A1; A2 C1 C2 R1
314C gl6 lg2-R a1-m et1; A2 C1 C2 Dt1 R1
314F Rg1 gl6 lg2-R
314G gl6 lg2-R
315B Rg1 gl6
315C Rg1
315D A1-b(P415); A2 C1 C2 R1
315H gl6 a1-m; A2 C1 C2 dt1 R1
316A ts4
316H gl6 lg2-R a1-m et1; A2 C1 C2 R1
316I gl6 lg2-R a1-m et1; A2 C1 C2 Dt1 R1
317F gl6 ts4 lg2-R
318A ig1
318B ba1
318C y10-7748
318H vp1-Mc#2
318I y10-8624
319A lg2-R A1-b(P415) et1; A2 C1 C2 Dt1 R1
319C lg2-R a1-m et1; A2 C1 dt1 R1
319D lg2-R a1-m et1; A2 C1 Dt1 R1
319F lg2-R a1-st et1; A2 C1 C2 Dt1 R1
320A lg2-R
320C lg2-R na1
320E et1
320F A1 sh2; A2 b1 C1 pl1 R1
321A A1-d31; A2 C1 R1
321B lg2-R a1; A2 C1 C2 dt1 R1
321C lg2-R A1-b(P415) et1; A2 C1 C2 dt1 R1
321D a1-m4::Ds; A2 C1 C2 R1
321E a1-rUq; A2 C1 C2 R1
321F a1-Mum1; A2 C1 C2 R1
321G a1-Mum2; A2 C1 C2 R1
321H a1-Mum3; A2 C1 C2 R1
322A A1-d31 sh2; A2 C1 dt1 R1
322B A1-d31 sh2; A2 C1 Dt1 R1
322F a1-m; A2 b1 C1 dt1 pl1 R1

322G a1; A2 C1 C2 R1
323A a1-m; A2 C1 Dt1 R1
323D a1-m sh2; A2 C1 C2 Dt1 R1
323E a1-m et1; A2 C1 C2 Dt1 R1
323H a1-st; A2 C1 C2 dt1 Mrh R1
323I a1-m1::rDt (Neuffer); A2 C1 C2 dt1 R1
324A a1-st; A2 C1 Dt1 R1
324B a1-st sh2; A2 C1 C2 Dt1 R1
324E a1-st et1; A2 C1 Dt1 R1
324G a1-st; A2 C1 dt1 R1
324H a1 et1; A2 C1 C2 dt1 R1
324I a1-st et1; A2 C1 C2 R1
324J a1-sh2-del::Mu1; A2 C1 C2 R1
325A a1-p et1; A2 C1 dt1 R1
325B a1-p et1; A2 B1 C1 Dt1 Pl1 R1
325C a1-x1
325D a1-x3
325E A1 ga7; A2 C1 C2 R1
325G a3
325I a1-p; A2 C1 C2 Dt1 R1
325J a1-p; A2 C1 Pr1 R1
325K a1-m3 sh2-m1::Ds; A2 Ac C1 C2 R1
326A sh2
326B vp1
326BA vp1-mum3
326C Rp3
326D te1-1
326DA te1-Forester
327A TB-3La
327B TB-3Sb
327C TB-3Lc
327D TB-3Ld
328A trisomic 3
329A v*-9003
329B v*-8623
329C w*-022-15
329D yd2
329E w*-8336
329F yg*-W23
329G w*-062-3
329H v*-8609
329HA v*-8959
329I pg2
329K yel*-8630
329L yel*-5787
330A h1
330C d1 h1 Lg3-O
330G a1-mrh; A2 C1 C2 Mrh R1
330H A1-b(P415) Ring 3; A2 C1 C2 R1
330I a1-Mum2; A2 C1 C2 MuDR R1
330J a1-Mum2; A2 C1 C2 R1
330K a1 sh2; A2 C1 C2 dt1 R1
330L a1-mrh; Mrh
331A TB-1La-3L5267
331B TB-1La-3L4759-3
331C TB-1La-3L5242 (1L.2; 3L.65)
331E TB-3Lf
331F TB-3Lg
331H TB-3Ll
331I TB-3Lj
331J TB-3Lk
331K TB-3Ll
332B dek5
332C cp*-N1283
332D Wrk1-N1020
332G dek6-N627D
332H dek17-N330D
332I Lxm1-N1600
332J ms23
332L brn1-R
332M Spc1-N1376
332N wlu1-N28
332P g2 brn1-R
332Q brn1-R cr1
332R brn1-R ra2 lg2-R
332S Mv1

CHROMOSOME 4

401B Ga1
401C Ga1 su1
401D Ga1-S
401I ga1 su1
401J Ga1-M
401K Ga1-S su1
402A st1
402C fl2 st1
402D Ts5
403A Ts5 fl2
403B Ts5 su1
405B la1
405D la1 su1 gl3
405G la1 su1 gl4
406C fl2
406D fl2 su1
407D su1
407E su1-am
407F su1-am; du1
408B bm3-1 su1
408C su1 zb6
408E bm3-1
408J su1 ra3
408K su1; se1
409A su1 zb6 Tu1
410D su1 zb6 gl3
411A su1 gl4 j2
411B su1 gl4 o1
411F su1 v17 gl7
412C su1 gl3
412E su1 j2 gl3
412G su1 gl4 Tu1
413A su1 o1
413B su1 gl4
413D su1 C2-Idf1(Active-1); A1 A2 C1 R1
413F su1 de*-414E
413G v23 Su1 gl3
414A bt2
414AA bt2-Williams
414AB bt2-60-158
414B gl4
414BA gl4-Stadler
414BB gl4-gl16
414C gl4 o1
414D gl4 j2
414E de*-414E
414F bm3-1 gl4
415A j2
416A Tu1
416B Tu1-I(1st)
416C Tu1-I(2nd)
416D Tu1-d
416E Tu1-md
416F Tu1 gl3
417A j2 gl3
417B v8
417C gl3
417D o1 gl3
418A gl3 dp1
418B c2; A1 A2 C1 R1
418D C2-Idf1(Active-1); A1 A2 C1 R1
418E dp1
418F o1
418G v17
419A v23-8914
419E gl7
419F Dt6 gl3; a1-m A2 C1 R1
419H c2-m1::Spm; A1 A2 C1 R1
420A su1 Dt4; a1-m A2 C1 R1
420B TB-9Sb-4L6504
420C nec*-rd
420CA nec*-016-15
420D yel*-8457
420F dp*-4301-43
420G w*-9005
420H Dt4 C2; a1-m A2 C1 R1
420I TB-9Sb-4L6222
421A TB-4Sa
421B TB-1La-4L4692
421C TB-7Lb-4L4698
422A trisomic 4
423A TB-4Lb
423B TB-4Lc
423C TB-4Ld
423D TB-4Le
423E TB-4Lf
427A cp2-o12
427AA cp2-dek7
427AB cp2
427B dek25-N1167A
427C Ysk1-N844
427D orp1-N1186A; orp2-N1186B
427E dek8-N1156
427F dek10-N1176A
427G Ms41-N1995
427H dek31-N1130
427I Sos1-ref
428A gl5 Su1; gl20
428C nec5-N642
428D spt2-N1269A
428F lw4; Lw3
428G bx1
428H gl5 su1; gl20

CHROMOSOME 5

501A am1 a2; A1 C1 R1
501B lu1
501D ms13
501E gl17
501G gl17 a2; A1 C1 C2 R1
501I am1
502B A2 ps1-vp7 pr1; A1 C1 R1
502D A2 bm1 pr1; A1 C1 R1
502F Nl2-N1445
503A A2 bm1 pr1 ys1; A1 C1 C2 R1
504A A2 bt1 pr1; A1 C1 R1
504C A2 bm1 pr1 zb3; A1 C1 R1
504E A2 bt1; A1 C1 C2 R1
505B A2 pr1 ys1; A1 C1 R1
505C A2 bt1 pr1 ga*-Rhoades; A1 C1 R1
506A A2 v3 pr1; A1 C1 R1
506B A2 pr1; A1 C1 R1
506C A2 pr1 v2; A1 C1 R1
506D na2 A2 pr1; A1 C1 R1
506F A2 pr1 v12; A1 C1 R1
506L A2 br3 pr1; A1 C1 R1
507A a2; A1 C1 R1
507AA a2-Mus2; A1 C1 C2 R1
507AB a2-Mus3; A1 C1 C2 R1
507B a2 bm1 bt1 bv1 pr1; A1 C1 C2 R1
507F a2 bm1 bt1 ga*-Rhoades; A1 C1 C2 R1
507G a2 bm1 bt1; A1 C1 C2 R1
507H A2 bt1 pr1; A1 C1 C2 R1
508A a2 bm1 bt1 pr1; A1 C1 C2 R1
508C a2 bt1 bv1 pr1; A1 C1 R1
508F a2 bm1 pr1 ys1; A1 C1 R1
510A a2 bm1 pr1 v2; A1 C1 R1
510G a2 bm1 pr1 eg1; A1 C1 R1
511C a2 bt1 pr1; A1 C1 R1
511F a2 bt1 Pr1; A1 C1 C2 R1
511H a2 bt1; A1 C1 C2 R1
512B a2 v3 pr1; A1 C1 R1
512C a2 bt1 pr1 ga*-Rhoades; A1 C1 R1
513A a2 pr1; A1 C1 R1
513C a2 pr1 v2; A1 C1 R1
513D A2 pr1 sh4; A1 C1 C2 R1
513E a2 pr1 v12; A1 C1 R1
515A vp2
515AB a2 vp2-green mosaic; A1 C1 C2 R1
515C ps1-vp7
515CA ps1-8776
515CB ps1-881565-2M
515D bm1
516B bt1-R
516BA bt1-Elmore
516BB bt1-C103
516BC bt1-Singleton
516BD bt1-sh3
516C ms5
516D td1 ae1
516G A2 bm1 pr1 yg1; A1 C1 R1
517A v3
517AB v3-8982
517B ae1
517E ae1 pr1 gl8
518A sh4
518B gl8
518C na2
518D lw2
519A ys1
519AA ys1-W23
519B eg1
519C v2
519D yg1
519E A2 pr1 yg1; A1 C1 R1
519F A2 pr1 gl8; A1 C1 R1
519G zb3
520B v12
520C br3
520F A2 Dap1; A1 C1 C2 R1
520G A2 pr1 Dap1; A1 C1 C2 R1
520H Dap1-2
521A nec3
521B Nec*-3-9c
521C nec*-8624
521D nec*-5-9(5614)
521E nec*-7476
521F nec*-6853
521G nec*-7281
521H nec*-8376
521I v*-6373
521J yg*-8951
521K lw3; lw4
521L w*-021-7
521N lnec*-5931
521P lw3; lw4
522A TB-5La
522B TB-5Lb
522C TB-5Sc
527A dek18
527B dek9-N1365
527C dek26-N1331
527D dek27-N1380A
527E grt1
527F nec7-N756B
527H Msc2-N1124B
527I ppg1-N199
527J nec6-N493
528A Hsf1-N1595
528B wgs1-N206B
528C anl1-N1643
528D TB-1La-5S8041

CHROMOSOME 6

601C rgd1 y1
601D rgd1 Y1
601F po1-ms6 y1 pl1
602A po1-ms6 wi1 y1
602C y1
602J y1-w-mut
602K y1-gbl
602L y1-pb1
602M y1-8549
602N y1-Caspar
602O y1-0317
603A y1 l10
603AA y1 l10-1359
603B y1 l11-4120
603C y1 l12-4920
603D w15-8896 y1
603H mn3-1184 y1
604D y1 l15
604F y1 si1-mssi
604H y1 ms1
604I Y1 ms1
605A wi1 y1 Pl1
605C y1 pg11; pg12 wx1
605E wi1 Y1 Pl1
605F wi1 Y1 pl1
606A Y1 pg11; pg12 Wx1
606AA pg11-8925; pg12-8925
606AC pg11-8563; pg12-8563

606AD pg11-8322; pg12-8322
606B y1 pg11; pg12 wx1
606C Y1 pg11; pg12 wx1
606E y1 pl1
606F y1 Pl1
606I y1 pg11 su2; pg12 Wx1
607A y1 Pl1-Bh1; A1 A2 c1 R1 sh1 wx1
607C y1 su2
607E y1 pl1 su2 v7
607H y1 Pl1-Bh1; A1 A2 c1 C2 R1 sh1 Wx1
608B Y1 I12
608F y1 pl1 w1
608G Y1 I11
609A Y1 pb4
610B Dt2 Pl1; a1-m A2 C1 R1
610C pl1 sm1; P1+rr
610F Y1 pl1 su2 v7
610H Y1 Dt2 pl1; a1-m A2 C1 R1
610I Y1 Pl1 su2 v7
611A Pl1 sm1; P1+rr
611D Pt1
611E Y1 pl1 w1
611EA w1-7366
611I sm1 py1; P1+rr
611K Y1 Pl1 w1
611L w1; I1
611M afd1
612A w14
612B po1
612BA po1-ms6
612C I*-4923
612D oro1
612DA oro1-6474
612I py1
612J w14-8657
612K w14-8050
612L w14-6853
612M w14-025-12
612N w14-1-7(4302-31)
613A 2NOR; A1 a2 bm1 C1 pr1 R1 v2
613D vms*-8522
613F w14-8613
613H pg11-6853; pg12-6853
613I tus*-5267
613L w*-8954
613M yel*-039-13
613N yel*-7285
613P yel*-8631
613T pg11-6656; pg12-6656
614A TB-6Lb
614B TB-6Sa
614C TB-6Lc
615A trisomic 6
627A dek28-N1307A
627B dek19-N1296A
627C vp*-5111
627D hcf26
627E Dt2; a1-m A2 C1 C2 R1 TB-6Lc

CHROMOSOME 7

701B In1-D
701C In1-D gl1
701D o2
701F Hs1
702A v5 o5
702B o2 v5 ra1 gl1
702I In1-Brawn
703A o2 v5 gl1
703D o2 ra1 gl1
703J Rs1-O
703K Rs1-Z
704A o2 ra1 gl1 ij1
704B o2 ra1 gl1 sl1
705A o2 gl1
705B o2 gl1 sl1
705D o2 bd1
706A o2 sl1
707A y8 v5 gl1
707B in1; A1 A2 C1 pr1 R1
707C in1 gl1; A1 A2 C1 C2 pr1 R1
707D v5
707E vp9
707EA vp9-3111
707EB vp9-86GN9
707EC vp9-86GN15
707F y8 gl1
707G In1 gl1; A1 A2 C1 C2 Pr1 R1
708A ra1
708G y8
709A gl1
709C gl1-m
710A gl1 Tp1
710B gl1 mn2
710E o5 gl1
710H ms7 gl1 Tp1
711A Tp1
711B ij1-ref::Ds
711G ts*-br
712A ms7
712B ms7 gl1
712D ij1 bd1
713A Bn1
713E Bn1 bd1
713H Bn1 ij1
713I bd1 Pn1
714A Pn1
714B o5
714D va1
715A Dt3; a1-m A2 C1 R1
715C gl1 Dt3; a1-m A2 C1 R1
716A v*-8647
716B yel*-7748
716F Les9-N2008
717A TB-7Lb
718A trisomic 7
719A TB-7Sc
720A Dt3; a1-m TB-7Lb
727A dek11-N788
727B wlu2-N543A
727E gl1-cgl
727G Rs1-O o2 v5 ra1 gl1
728A Px3-6
728B ptd2-Mu3193
728C cp1
728D sh6-8601
728E sh6-1295

CHROMOSOME 8

801A gl18-gl23
801B v16
801I yel*-024-5
801K v16 ms8
802G ms43
803A ms8
803B nec1-025-4
803D gl18 ms8
803F nec1-7748
803G nec1-6697
804A v21-A552
804B dp*-8925
804D wh*-053-4
804E w*-017-14-B
804F w*-034-16
804G w*-8635
804H w*-8963
805A fl3
805C gl18 v21-A552
805D fl3 ms8 j1
805E el1
805G ms8 j1
806A TB-8La
806B TB-8Lb
807A trisomic 8
808A ct1
808B Lg4-O
809A TB-8Lc
810A v16 j1; I1
810B j1
810C gl18 v21-A552 j1
827A dek20-N1392A
827B dek29
827C Bif1-N1440
827D Sdw1-N1592
827E Clt1-N985
827J wlu3-N203A
827K pro1
827L pro1-Tracy

CHROMOSOME 9

901B yg2 C1 sh1 bz1; A1 A2 C2 R1
901C yg2 C1 sh1 bz1 wx1; A1 A2 C2 R1
901E yg2 C1 bz1 wx1; A1 A2 R1
901H yg2 C1 Bz1; A1 A2 C2 R1
901I yg2 C1 sh1 Bz1 wx1 K9S-I; A1 A2 C2 R1
902A yg2 c1 sh1 bz1 wx1; A1 A2 R1
902B yg2 c1 sh1 wx1; A1 A2 R1
902C yg2 c1 sh1 wx1 gl15; A1 A2 R1
902D yg2 C1 sh1 Bz1 wx1 K9S-s; A1 A2 C2 R1
903A C1 sh1 bz1; A1 A2 R1
903B C1 sh1 bz1 wx1; A1 A2 R1
903D C1-I sh1 bz1 wx1; A1 A2 R1
904B C1 sh1; A1 A2 R1
904C C1 sh1 wx1; A1 A2 C2 R1
904D C1 wx1 ar1; A1 A2 R1
904F C1 sh1 bz1 gl15 bm4; A1 A2 C2 R1
905A C1 sh1 wx1 K9S-I; A1 A2 C2 R1
905C C1 bz1 Wx1; A1 A2 R1
905D C1 sh1 wx1 K9S-I; A1 A2 C2 K10 R1
905E C1 sh1 wx1 v1; A1 A2 C2 R1
905G C1 bz1 wx1; A1 A2 C2 R1
905H c1 sh1 wx1; A1 A2 b1 C2 R1-sc:m2
906A C1 wx1; A1 A2 C2 Dsl Pr1 R1 y1
906B C1 wx1; A1 A2 C2 Dsl pr1 R1 Y1
906C C1-I Wx1; A1 A2 C2 Dsl R1
906D C1-I; A1 A2 C2 R1
907A C1 wx1; A1 A2 C2 R1
907E C1-I wx1; A1 A2 C2 R1 y1
907H c1-n; A1 A2 b1 C2 pl1 R1
907I C1-S wx1
908A C1 Wx1 da1 ar1; A1 A2 C2 R1
908B C1 wx1 v1; A1 A2 C2 R1
908D C1 wx1 gl15; A1 A2 C2 R1
908F C1 wx1 da1; A1 A2 C2 R1
908H C1 wx1; A1 A2 C2 R1 y1
909A C1 wx1 Bf1-ref; A1 A2 C2 R1
909B c1 bz1 wx1; A1 A2 C2 R1
909C c1 sh1 bz1 wx1; A1 A2 C2 R1 y1
909D c1 sh1 wx1; A1 A2 C2 R1
909E c1 sh1 wx1 v1; A1 A2 C2 R1
909F c1 sh1 wx1 gl15; A1 A2 C2 R1
910B c1 sh1 wx1 gl15 Bf1-ref; A1 A2 C2 R1
910D c1; A1 A2 C2 R1
910G C1 sh1-bz1-x2 Wx1; A1 A2 C2 R1
910H C1 sh1-bz1-x3; A1 A2 C2 R1
911A c1 wx1; A1 A2 C2 R1 y1
911B c1 wx1 v1; A1 A2 C2 R1
911C c1 wx1 gl15; A1 A2 C2 R1
912A sh1
912AA sh1-1746
912AB sh1-9026-11
912B sh1 wx1 v1
912E lo2
912H lo2 wx1
913C sh1 I7
913D sh1 I6
913E baf1
914A wx1 d3-N660B
914K Wc1-ly; Y1
915A wx1
915B wx1-a
915C w11
915E wx1-Alexander
916A wx1 v1
916C wx1 bk2
916E wx1 v1 gl15
917A wx1 Bf1-ref
917C v1
917D ms2
917E gl15-Sprague
917EA gl15-Lambert
917F d3
917FF d3-d2-Harberd
918A gl15 Bf1-ref
918B gl15 bm4
918C bk2 Wc1
918D Wc1
918F Wx1 Bf1-ref
918G Wc1 Bf1-ref bm4
918GA Wc1-Wh Bf1-ref bm4
918K bk2 v30
918L wx1 Wc1
919A bm4
919B Bf1-ref bm4
919C I6
919D I7
919G I6; I1
920A yel*-034-16
920B w*-4889
920C w*-8889
920E w*-8950
920F w*-9000
920G Df3; Tp3-9
920L ygzb*-5588
920M wnl*-034-5
920N pyd1
921A TB-9La
921B TB-9Sb
921C TB-9Lc
922A trisomic 9
922B Wc1; TB-9Lc
922C C1-I; TB-9Sb
922D TB-9Sd
923A wx1-a
923B wx1-B
923C wx1-B1
923D wx1-B2::TouristA
923E wx1-B3::Ac
923F wx1-B4::Ds2
923G wx1-B6
923H wx1-B7
923I wx1-B8
923J wx1-BL2
923K wx1-BL3
923L wx1-C
923M wx1-C1
923N wx1-C2
923O wx1-C3
923P wx1-C4
923Q wx1-C31
923R wx1-C34
923S wx1-F
923T wx1-90
923U wx1-H
923V wx1-H21
923W wx1-I
923X wx1-J
923Y wx1-M
923Z wx1-M1
923ZA wx1-M6R
923ZB wx1-M6NR
923ZC wx1-M8
923ZD wx1-P60
923ZE wx1-R
923ZF wx1-Stonor
924A wd1 Wd1+ C1 C1-I Ring 9S; A1 A2 C2 R1
924B C1-I Ring 9S; A1 A2 C2 R1
924C yg2
924D wd1
925A bz1-m1::Ds wx1-m9::Ac
925B wx1-m9::Ds; Ac
925C bz1-m2::Ac
925E bz1-m2(DII)::Ds wx1-m6
925F C1 sh1 bz1 wx1-m8::Spm-I8
925G wx1-m7::Ac7; a2-m4::Ds
925H bz1-m2(DI)::Ds wx1; R1-sc
927A dek12-N873
927B dek13-N744
927C dek30-N1391
927D Les8-N2005

927E Zb8-N1443
927H C1 Dt7; a1-r A2 C2 R1
927I G6-N1585
928A v28-N27
928B wlu4-N41A
928G c1-m5::Spm wx1-m8::Spm-I8; A1 A2 C2 R1
928H wx1-m7::Ac7
928I C1 bz1-mut::Mut; A1 A2 Bz2 C2 R1
929A TB-9 isochromosome Type 1
929B TB-9 isochromosome Type 2
929C T9-B(La); T9-B(Sb)
929D TB-9 isochromosome (original)
929E Dp9
929F T9-B (La + Sb)
929G T9-8(4453); TB-9Sb
929H T9-3(6722); TB-9Sb
929I TB-9Sb-1866
929J TB-9Sb-1852
929K TB-9Sb-2150
929L TB-9Sb-14
929M TB-9Sb-2010

CHROMOSOME 10

X01A oy1-Anderson
X01AB oy1-8923
X01B oy1 R1; A1 A2 C1
X01C oy1 bf2
X01E oy1 bf2 R1; A1 A2 C1
X02C oy1 zn1 R1; A1 A2 C1 C2
X02E oy1 du1 r1; A1 A2 C1 C2
X02G oy1 zn1
X03A sr3
X03B Og1
X03D Og1 R1; A1 A2 C1 C2
X03E oy1 y9
X04A Og1 du1 R1; A1 A2 C1
X04B ms11
X04D bf2
X05A zn1 bf2
X05E bf2 sr2
X06A bf2 r1 sr2; A1 A2 C1 C2
X06C nl1 g1 R1; A1 A2 C1 C2
X06F bf2 R1 sr2; A1 A2 C1 C2
X07A nl1 g1 r1; A1 A2 C1 C2
X07C y9
X07D nl1
X08F li1
X08FA li1-IL90-243Tco
X09B li1 g1 R1; A1 A2 C1 C2
X09EA g1-g4
X09EB g1-56-3004-24
X09EC g1-1-7(X-55-16)
X09ED g1-68-609-13
X09EE g1-ws2
X09F ms10
X09G li1 g1 r1; A1 A2 C1 C2
X10A du1
X10D du1 g1 r1; A1 A2 C1 C2
X10F zn1
X10FA zn1-N25
X10G du1 v18
X11A zn1 g1
X11C zn1 g1 r1; A1 A2 C1 C2
X11D Tp2 g1 r1; A1 A2 C1 C2
X11E g1 R1 sr2; A1 A2 C1 C2
X11F g1 r1; A1 A2 C1 C2
X11H zn1 R1-r; A1 A2 C1 C2
X11I Tp2 g1 sr2
X12A g1 r1 sr2
X12C g1 R1-g sr2; A1 A2 C1 C2
X12E g1 R1; A1 A2 C1 C2
X13D g1 r1-r sr2; A1 A2 C1 C2
X14A r1-r Isr1-Ej; A1 A2 C1 C2
X14F v18 r1; A1 A2 C1 C2
X15B l1 r1 sr2; A1 A2 C1 C2
X15C R1-g; A1 A2 C1 C2
X15D r1-ch; A1 A2 C1 C2 Pl1
X15F Isr1 R1-g Sr2
X15G isr1 r1-g sr2
X16B r1; A1 A2 abnormal-10 C1
X16C R1-ch; A1 A2 B1 C1 C2 Pl1
X16D r1 sr2; A1 A2 C1 C2
X16F R1 K10-II; A1 A2 C1 C2
X17A r1-g; A1 A2 C1 C2
X17B r1-r; A1 A2 C1 C2
X17C R1-mb; A1 A2 C1 C2
X17D R1-nj; A1 A2 C1 C2
X17E R1-r; A1 A2 C1 C2
X18A R1-Isk; A1 A2 C1 C2
X18B R1-sk:nc-2; A1 A2 C1 C2
X18C R1-st; A1 A2 C1 C2
X18D R1-sk; A1 A2 C1 C2
X18E R1-st Mst1
X18G R1-sc:m2; A1 A2 bz2 C1 C2
X18H R1-nj; A1 A2 bz2 C1 C2
X18I r1; A1 A2 C1 C2
X19B w2
X19BA w2-Burnham
X19C l1 w2
X19D o7
X19F r1 w2
X20B l1
X20C v18
X20F yel*-8721
X20H yel*-5344
X20HA yel*-8793
X20HB yg*-8962
X21A TB-10La
X21B TB-10L19
X22A TB-10Sc
X22B T1La-B-10L18
X22C TB-10Lb
X22D T10S-B-10L18a
X23A trisomic 10
X24A cm1
X24B lep*-8691
X25A R1-sc:m2; a1-st A2 C1 C2
X25B R1-sc:m2; A1 A2 C1 c2
X25C R1-sc:m122; A1 A2 C1 C2 pr1
X25D R1-sc:m2; A1 a2 C1 C2
X25E R1-sc:m2; A1 A2 c1 C2
X26A R1 r1-X1; A1 A2 C1 C2
X26B R1-sc:m2; A1 A2 C1 C2
X26C R1-sc122; A1 A2 C1 C2
X26D R1-sc*5691; A1 A2 C1 C2
X26E R1-sc:m2; A1 A2 C1 C2 pr1 wx1
X26F R1-sc:m2; A1 A2 C1 C2 In1-D
X26G R1-sc:m2; A1 A2 C1 c2-m2::dSpm
X26H R1-sc:m2; wx1 A1 A2 C1 C2
X27A dek14-N1435
X27B dek15-N1427A
X27C w2-N1330
X27D Les6-N1451
X27E gl21-N478B; gl22-N478C
X27F Vsr1-N1446
X27G Oy1-N700
X27H orp2-N1186B; orp1-N1186A
X27I I19-N425
X27J I13-N59A
X27K v29
X28B R1-sc:m2; a1-m1::rDt (Neuffer)
X28C R1-nj (Cudu); A1 A2 C1 C2
X28D Vsr*-N716
X28E Les3
X28F cr4-6143
X28G R1-nj (Chase); A1 A2 C1 C2
X28I R1-sc:m2; a1-m1-5719::dSpm A2 C1 C2
X30A TB-10L1
X30B TB-10L2
X30C TB-10L3
X30D TB-10L4
X30E TB-10L5
X30F TB-10L6
X30G TB-10L7
X31B TB-10L9
X31C TB-10L10
X31D TB-10L11
X31E TB-10L12
X31G TB-10L14
X31H TB-10L15
X31I TB-10L16
X31J TB-10L17
X32C TB-10L20
X32D TB-10L21
X32H TB-10L25
X32I TB-10L26
X32J TB-10L27
X32K TB-10L28
X33A TB-10L29
X33B TB-10L30
X33D TB-10L32
X33E TB-10L33
X33G TB-10L35
X33H TB-10L36
X34A TB-10L37
X34B TB-10L38

UNPLACED GENES

U140C I4
U140E I3
U140F Fas1
U140G ms22
U140H ms24
U240A Les7-N1461
U240B vp10
U240BA vp10-86GN5
U240BB vp10-TX8552
U240C v13
U240D o11
U340B zb1
U340C zb2
U340D g1-ws2-Pawnee; ws1-Pawnee
U340E y11
U340F y12
U340G oro2
U340H oro4
U440A o9
U440B gl13
U440C zn2
U440D ub1-76C
U440E frz1
U440F mg1-Sprague
U540A dv1
U540B dy1
U640A dsy1-Doyle
U640C pam1

MULTIPLE GENE

M141A A1; A2 B1 C1 C2 Pl1 Pr1 R1-g
M141D A1; A2 b1 C1 C2 pl1 R1-g
M241A A1; A2 B1 C1 C2 Pl1 Pr1 r1-g
M341D A1; A2 B1 c1 C2 Pl1 Pr1 R1-r
M341F A1; A2 b1 C1 C2 pl1 Pr1 R1-r
M441D A1; A2 B1 C1 C2 Pl1 Pr1 r1-r
M441E A1; A2 B1 c1 C2 Pl1 Pr1 r1-r
M441F A1; A2 b1 C1 C2 pl1 Pr1 R1-g wx1
M641B A1; A2 b1 C1 C2 pl1 Pr1 R1 wx1
M641C A1; A2 b1 C1 C2 pl1 Pr1 R1 wx1
M641D A1; A2 C1 C2 Pr1 r1 wx1 y1
M641E A1; A2 C1 C2 r1-g wx1 y1
M741A A1; A2 b1 C1 C2 pl1 Pr1 r1-g wx1
M741F Stock 6 A1; A2 C1 C2 pl1 R1-g y1
M741G Stock 6 A1; A2 C1-I C2 pl1 R1-g wx1 y1
M741H Stock 6 A1; A2 B1 C1 C2 Pl1 R1-nj
M841A A1; A2 C1 C2 pr1 R1 su1
M841C colored scutellum A1; A2 C1 C2 Pr1 R1
M941A A1; A2 c1 C2 Pr1 R1 wx1 y1
MX40A bm2 lg1 a1 su1 pr1 y1 gl1 j1 wx1 g1 (Mangelsdorf's tester)
MX40D gl1; wx1 y1
MX40E gl8; wx1 y1
MX41A A1 A2 C1 C2 R1 pr1 y1 wx1 gl1
MX41B A1; A2 C1 C2 gl1 pr1 R1 su1 wx1 y1
MX41C a1; a2 bz1 bz2 c1 c2 pr1 r1 wx1 y1
MX41D a1; A2 C1 C2 gl1 pr1 R1 su1 wx1 y1
MX41E a1-m1-n::dSpm; A2 C1 C2 R1 wx1-m8::Spm-I8

B-CHROMOSOME

B542A Black Mexican Sweet, B chromosomes present
B542B Black Mexican Sweet, B chromosomes absent

TETRAPLOID

N102A A1; A2 Autotetraploid B1 C1 C2 Pl1 Pr1 R1
N102C a1-m; A2 Autotetraploid C1 C2 Dt1 R1
N102D A1; A2 Autotetraploid C1 C2 R1
N102E Autotetraploid; B chromosomes present
N102EA Autotetraploid; B chromosomes present
N102F A1; a2 Autotetraploid C1 C2 R1
N103A Autotetraploid; P1+rr
N103B Autotetraploid; P1-vv::Ac
N103C Autotetraploid; P1-ww
N103D Autotetraploid; P1-wr
N103E Autotetraploid; P1-mm
N103F Autotetraploid; bz2
N104A Autotetraploid; su1
N104B A1; A2 Autotetraploid C1 pr1 R1
N105B Autotetraploid; wx1 y1
N105D A1; a2 Autotetraploid bt1 C1 C2 R1
N105E Autotetraploid; bt1
N106C Autotetraploid; wx1
N107B W23 Autotetraploid
N107C Synthetic B Autotetraploid
N107D N6 Autotetraploid

CYTOPLASMIC STERILE/RESTORER

C736A R213 Rf1; rf2
C736B Ky21 Rf1; Rf2
C736C B37 rf1; Rf2
C736D N6 rf1; Rf2
C736E Tr rf1; rf2
C736F W23 rf1; Rf2
C736G B73 rf1; Rf2
C836A Wf9 cms-T; rf1 rf2
C836B N cytoplasm rf1; rf2

CYTOPLASMIC TRAIT

C337A NCS2
C337B NCS3

TOOLKIT

T318AA ig1; lg1 TB-3Ld; R1-nj
T318AB cms-L; ig1 R1-nj
T318AC cms-MY; ig1 R1-nj
T318AD cms-ME; ig1 R1-nj
T318AE cms-S; ig1 R1-nj
T318AF cms-SD; ig1 R1-nj
T318AG cms-VG; ig1 R1-nj
T318AH cms-CA; ig1 R1-nj
T318AI cms-C; ig1 R1-nj
T318AJ cms-Q; ig1 R1-nj
T940A Hi-II Parent A (for producing embryogenic callus cultures)
T940B Hi-II Parent B (for producing embryogenic callus cultures)
T940C Hi-II A x B (for producing embryogenic callus cultures)
T940D KYS (for chromosome

observations in pachytene microsporocytes)

T3307A trAc8178; T2-9b (2S.18; 9L.22) wx1
T3307B trAc8178; T2-9c (2S.49; 9S.33) wx1
T3307C trAc8178; T2-9d (2L.83; 9L.27) wx1
T3307D trAc8163; T3-9(8447) (3S.44; 9L.14) wx1
T3307E trAc8163; T3-9c (3L.09; 9L.12) wx1
T3307F trAc8183; T3-9(8447) (3S.44; 9L.14) wx1
T3307G trAc8183; T3-9c (3L.09; 9L.12) wx1
T3308A trAc8200; T4-9g (4S.27; 9L.27) wx1
T3308B trAc6076; T5-9a (5L.69; 9S.17) wx1
T3308C trAc6076; T5-9c (5S.07; 9L.1) wx1
T3308D trAc8175; T5-9c (5S.07; 9L.1) wx1
T3308E trAc8193; T5-9c (5S.07; 9L.1) wx1
T3308F trAc8179; T5-9a (5L.69; 9S.17) wx1
T3308G trAc8181; T5-9a (5L.69; 9S.17) wx1
T3308H trAc8186; T5-9a (5L.69; 9S.17) wx1
T3309A trAc8196; T5-9a (5L.69; 9S.17) wx1
T3309B trAc6062; T6-9b (6L.1; 9S.37) wx1
T3309C trAc6063; T6-9b (6L.1; 9S.37) wx1
T3309D trAc8172; T6-9b (6L.1; 9S.37) wx1
T3309E trAc8184; T6-9b (6L.1; 9S.37) wx1
T3310A trAc8161; T7-9(4363) (7ctr; 9ctr) wx1
T3310B trAc8173; T7-9(4363) (7ctr; 9ctr) wx1
T3310C trAc8173; T7-9a (7L.63; 9S.07) wx1
T3310D trAc8190; T7-9(4363) (7ctr; 9ctr) wx1
T3310E trAc8194; T7-9(4363) (7ctr; 9ctr) wx1
T3310F trAc8185; T7-9a (7L.63; 9S.07) wx1
T3311A trAc8162; T8-9d (8L.09; 9S.16) wx1
T3311B trAc8182; T8-9d (8L.09; 9S.16) wx1
T3311C trAc8182; T8-9(6673) (8L.35; 9S.31) wx1
T3311D trAc6059; T9-10b (10S.4; 9S.13) wx1
T3311E trAc6059; T9-10(8630) (10L.37) wx1
T3311F trAc8180; T9-10b (10S.40) wx1
T3311G trAc8180; T9-10(8630) (10L.37) wx1

INVERSION

I143B Inv1c (1S.3-1L.01)
I143C Inv1d (1L.55-1L.92)
I143D Inv1k (1L.46-1L.82)
I243A Inv2b (2S.5-2L.15)
I243B Inv2h (2L.13-2L.51)
I343A Inv3a (3L.38-3L.95)
I343B Inv3b (3L.19-3L.72)
I343C Inv3c (3L.09-3L.81)
I344A Inv9a (9S.7-9L.9)
I443A Inv4b (4S.1-4L.12)
I443B Inv4c (4S.8-4L.62)
I444A Inv2a (2S.7-2L.8)
I543A Inv4e (4L.16-4L.81)
I743A Inv5(8623) (5S.6-5L.69)
I743B Inv6d (6S.7-6L.33)
I743C Inv6(3712) (6S.7-6L.63)
I843A Inv6e (6S.8-6L.32)
I943A Inv7f (7L.17-7L.61)
I943B Inv7(8540) (7L.12-7L.92)
I943C Inv7(3717) (7S.3-7L.3)
IX43A Inv8a (8S.3-8L.15)
IX43B Inv9b (9S.05-9L.87)

RECIPROCAL TRANSLOCATION (wx1 and Wx1 marked)

wx01A T1-9c (1S.48; 9L.22); wx1
wx01B T1-9(5622) (1L.1; 9L.12); wx1
wx02A T1-9 4995 (1L.19; 9S.20); wx1
wx03A T1-9(8389) (1L.74; 9L.13); wx1
wx04A T2-9c (2S.49; 9S.33); wx1
wx05A T2-9b (2S.18; 9L.22); wx1
wx06A T2-9d (2L.83; 9L.27); wx1
wx07A T3-9(8447) (3S.44; 9L.14); wx1
wx08A T3-9c (3L.09; 9L.12); wx1
wx10A T4-9e (4S.53; 9L.26); wx1
wx11A T4-9g (4S.27; 9L.27); wx1
wx12A T4-9(5657) (4L.33; 9S.25); wx1
wx13A T4-9b (4L.9; 9L.29); wx1
wx15A T5-9(4817) (5L.06; 9S.07); wx1
wx16A T5-9d (5L.14; 9L.1); wx1
wx17A T5-9a (5L.69; 9S.17); wx1
wx18A T6-9(4778) (6S.8; 9L.3); wx1
wx20A T6-9b (6L.1; 9S.37); wx1 y1
wx21A T6-9(4505) (6L.13; 9ctr); wx1
wx22A T7-9(4363) (7ctr; 9ctr); wx1
wx23A T7-9a (7L.63; 9S.07); wx1
wx24A T8-9d (8L.09; 9S.16); wx1
wx25A T8-9(6673) (8L.35; 9S.31); wx1
wx26A T9-10(8630) (10L.37; 9S.28); wx1
wx28A T5-9(8386) (5L.87; 9S.13); wx1
Wx30A T1-9c (1S.48; 9L.22); Wx1
Wx30B T1-9(4995) (1L.19; 9S.2); Wx1
Wx30C T1-9(8389) (1L.74; 9L.13); Wx1
Wx31A T2-9c (2S.49; 9S.33); Wx1
Wx31B T2-9b (2S.18; 9L.22); Wx1
Wx32A T3-9(8447) (3S.44; 9L.14); Wx1
Wx32B T3-9(8562) (3L.65; 9L.22); Wx1
Wx32C T3-9c (3L.09; 9L.12); Wx1
Wx33A T4-9e (4S.53; 9L.26); Wx1
Wx33B T4-9(5657) (4L.33; 9S.25); Wx1
Wx33C T4-9g (4S.27; 9L.27); Wx1
Wx34B T5-9(4817) (5L.06; 9S.07); Wx1
Wx34C T4-9b (4L.9; 9L.29); Wx1
Wx35A T5-9(8386) (5L.87; 9S.13); Wx1
Wx35B T5-9a (5L.69; 9S.17); Wx1
Wx35C T5-9d (5L.14; 9L.1); Wx1
Wx36A T6-9(4778) (6S.8; 9L.3); Wx1
Wx37A T6-9(8768) (6L.89; 9S.61); Wx1
Wx37B T7-9(4363) (7ctr; 9ctr); Wx1
Wx37C T6-9(4505) (6L.13; 9ctr); Wx1
Wx38A T7-9a (7L.63; 9S.07); Wx1
Wx38B T8-9d (8L.09; 9S.16); Wx1
Wx38C T8-9(6673) (8L.35; 9S.31); Wx1
Wx39B T9-10b (10S.4; 9S.13); Wx1

We received the following request
:-)

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>Date: Mon, 29 Jan 96 23:17:16 -0600
>To: maize@uiuc.edu
>Subject: FORM ORDER
>
>Apparently-from: [Mozilla/1.0N (Windows)]@annex2-57.dial.umd.edu
>At: 23:17:15 On: 29 Jan 1996
>
>
>Requests:
>Please e-mail or send me info. about quarter earnings, and
>potential for financial growth with your company.
>----------

V. MAIZE GENOME DATABASE
http://www.agron.missouri.edu/

The Maize Genome Database or MaizeDB is curated as a Sybase database at the University of Missouri, Columbia, MO. Information content is dynamic and updated daily. Accesses to the database at the Missouri location have approximately doubled over the past year from 20,000 to 40,000/month, after subtracting an approximately equal number of accesses from commercial indexing services and local accesses. Over 3.5 megabytes of information have been transferred over the Web in the past 2 years to some 38,000 different machines around the world. These accesses do not include records curated in other databases, such as sequence (GenBank), other genomes (yeast) and germplasm (GRIN), for which specific records may be seamlessly retrieved by users from within MaizeDB. Currently, 3,322 records in MaizeDB have 25,396 links to any of 18 external databases. SwissProt (Switzerland), Entrez(GenBank) and GRIN use links, as curated by the MaizeDB staff, to connect back to MaizeDB information. MaizeDB continues to provide four distinct front-ends for accessing the data electronically: gopher, World Wide Web, APT and ACEDB; a guest login account provides telnet access to all formats, in the event users do not have their own WWW or gopher browsing software. June 1996 records include 327 genetic maps, which form the basis for the integrated chromosome maps ; 7331 mapped loci, including 400 quantitative trait loci; 4295map data entries, both recombination and map score data; 4658 probes; 2169 genetic/cytogenetic stocks; 20828 locus variations; allozyme typing for 21 loci and 437 elite stocks; 4662 stock pedigrees; 8276 selected bibliographic references, indexed to other database objects including agronomic traits; 3280 researchers with address entries.

New Data

Total new records increased by 18% to over 118,000. Special WWW files of new data are maintained on the What's New page. Major new additions are high-lighted on the top line of our home page as they occur. Many of the files will also be listed and updated on the 'Of Interest to Maize Cooperators" page. Major new data include:

1. Images : 2924 images of 1685 mutants in the Neuffer collection; hundreds of traits and pathogens/pests. We thank Gerry Neuffer, Lou Butler and Beth Bennett for their efforts with mutant images and CIMMYT for making their slides of traits, pathogens and pests available. These images will not be published in the 1996 edition of Mutants of Maize. Look for enhanced annotation of the images over the upcoming year. According to one commercial source, Infoseek, *http://guide.infoseek.com/*, MaizeDB is an "Amazing archive of images of mutant ears of corn".

2. SSR's : 177 PCR primer mapping-pairs to detect simple sequence repeats (SSR). We are grateful for the careful compilations provided pre-publication by Lynn Senior (ARS, NC State), Emily Chin (Pioneer Hi-Bred), Julie Vogel (DuPont), and Mark Walton (Linkage Genetics). Information includes the primer sequences, the loci probed, with bin locations, and where provided, gel patterns, raw mapscores and annealing conditions. SSR map data are available for several previously unlocated genes, including *fdx1, gln4, gst1, mtl1, nac1, ohp2, ole2, tlk1.*

3. 1996 Maize Genetics Conference Abstracts are part of the reference additions in the database, thanks to electronic submissions by the cooperators and especially, Paul Chomet, Bill Sheridan and Brenda Schilling.

4. Genetic stocks: updated and new descriptions of 2169 seed stocks available from the Maize Genetics Cooperation Stock Center are entered into MaizeDB directly by Marty Sachs, who also facilitates links from GRIN to MaizeDB genetic stocks.

5. Molecular markers are largely updated with thanks to Theresa Musket for preparation of electronic files with information about 3278 molecular probes available from the UMC RFLP laboratory.

6. Continuing areas of update include (1) selected new references with indexing to MaizeDB objects; (2) record-to-record pointers to information in external databases that include SwissProt, GenBank, dbEST, Enzyme and GRIN; (3) raw map data, current and retrospective; (4) QTL experiments; (5) addresses of maize researchers.

New Connections

The Plant Genome Database (PGD), *http://probe.nalusda.gov:8300/* , now links back to the up-to-the-minute record, typos-and-all, at the Missouri server; use the "[MaizeDB-Sybase]" button at the top of each PGD record. PGD permits full-text queries across all plant species and provides a snapshot of the MaizeDB data as last extracted at Missouri into ACEDB format.

Entrez, a frontend of GenBank, *http://www3.ncbi.nlm.nih.gov/Entrez/*, now links to PGD(AGIS) records, based on the links established at Missouri.

Contacts

The e-mail address for the database folks is db_request@teosinte.agron.missouri.edu. In general, technical matters are handled by Denis Hancock; all else by any of a small group that includes: Ed Coe, Pat Byrne, Georgia Davis, Mary Polacco, and Marty Sachs.

Mary Polacco

VI. MAIZE PROBE BANK

CLONE DISTRIBUTION FROM THE UMC/ARS-USDA RFLP LABORATORY

The Maize Probe Bank at the University of Missouri/ARS-USDA, Columbia, Missouri, curates, maintains and distributes DNA probes for maize. Over 4500 probes are maintained in secured storage. Sequences for approximately 2500 are available in GenBank and other sequence databases. Probes are distributed upon request free of charge, limited to 30 probes in a 6-week period. Exception is made for the 90-probe "Core Marker" set, which contains probes for spaced loci covering the entire nuclear genome. Probes are provided as stabs. Following are the collections available for distribution:

Clone Set	Abbreviation	No. Distributable
Asgrow	asg	85
Brookhaven National Lab.	bnl	109
California State University	csu	1197
Iowa State University	isu	136
Mycogen Plant Genetics	agr	413
Pioneer Hi-Bred International	php	161
Pioneer Hi-Bred International	npi (#'s greater than 96)	236
University of Arizona	uaz (5C, 6C, 7C)	1920
University of Missouri	umc	238
University of Missouri-Tripsacum	tda	20

Within these categories of clones we may not have or are not permitted to distribute all clones of that designation. We do not distribute npi clones with numbers less than 100, nor certain umc clones that were sent to us with restrictions. We distribute specific defined-function clones on a case-by-case basis. We do not have uaz clones in the 1C, 2C, and 3C series, and are unable to provide these at this time. To be certain that a particular clone is available note the "Available From" line on the probe form of the maize database -- clones available from the UMC RFLP Laboratory will show T. Musket, who is the clone distribution coordinator. Clicking on T. Musket will give address and e-mail information. The easiest method to request clones is to use the probe request form directly from the maize database WWW homepage:

URL http://teosinte.agron.missouri.edu.

Please be certain to enter information in each field on the request form to aid our processing of your request. If you are unable to use the World Wide Web, send your request to Theresa A. Musket (address, phone and email in this Newsletter; FAX is 573-884-7850). Please provide your name, full mailing address, and email address if available.

Over the last 2-3 years the number of clones for which we have responsibility has grown from a few hundred to greater than four thousand. Our resources, both personnel and financial, for maintenance and distribution of clones are very limited. For this reason we must limit requests to 30 probes in a 6-week period, and ask that you request only those clones necessary for your experiments. Because of concurrent research commitments we have difficulty answering clone requests as rapidly as we (and you) would like and would appreciate receiving requests for clones as far in advance of need as possible. Turnaround time is usually 2-4 weeks, depending upon the request load.

During 1995, 203 requests were received from 21 countries, for over 5400 clones, including 35 core sets.

Asgrow Seeds, Mycogen Plant Genetics and Pioneer Hi-Bred International have made generous donations of probes to the maize research community. The cooperation of individuals in making defined-function clones available is equally appreciated. We are grateful for partial support for the Probe Bank from the USDA-Agricultural Service, International Atomic Energy Agency, Asgrow Seed Co., Mycogen Plant Genetics, CIMMYT, and DeKalb Genetics Corp.

VII. NEW GENES - NEWLY MAPPED GENES -NEW MARKERS

GENELIST: The genelist table in MNL 69:191-229 is supplemented below with a table of new, recently documented, and newly mapped genes, drawn up from the Maize Genome Database (MaizeDB - Section V). The table includes the symbol for the locus; the location in 'bins' (Working Maps - Section VIII); the locus name with a brief phenotypic description; and references to first reports or publications central to the designation of the locus. These references are given in a list following the Genelist, and are prefixed with "g" for genelist.

The genelist is dynamic, and is increasingly refined and expanded in MaizeDB. The number in the following list is 297, and the total number of defined genes (in the broad sense including chromosome segments and transposable elements, among other entities) is nearly 1200. New loci identified by directly visible mutations, and new loci defined by sequences from clones with specific known functions, both contribute to this growth. Of the 297 listed, 142 have been mapped or have been placed to linkage group, bringing the total mapped to 833.

Stocks of variants may be obtained from the Maize Genetics Cooperation Stock Center, as described in Section IV. Many variations (e.g., cob color; endosperm color; isozymes) occur naturally among generally available strains. For an increasing number of genes there is no present definition of variations in a gene product or trait identified to that gene, beyond RFLP polymorphisms. See Section VIII in this issue, Working Maps, for criteria used in designating genes based upon DNA evidence. By way of contrast, one impressive class of polymorphisms, the position shift loci (*psl*) for polypeptides identified on 2D-PAGE, has been mapped by the INRA group and is being analyzed to define their functions.

Ed Coe and Mary Polacco

SYMBOL	BIN	NAME, PHENOTYPE	REF
1L3	1.06	G-band 3 on 1L, cytological structure	135
5L5	5.06-5.07	G-band 5 on 5L, cytological structure	135
6L1	6.01-6.03	G-band 1 on 6L, cytological structure	135
8L7	8.06-8.09	G-band 7 on 8L, cytological structure	135
9L6	9.07-9.08	G-band 6 on 9L, cytological structure	135
aba1		abscisic stress protein homolog, root cDNA, sequence similar to plant abscisic acid stress and ripening proteins	5
abc1		ABC(yeast) homolog1, endosperm cDNA 5C05H02(uaz263) similar to yeast ABC1 protein, may encode chaperonin, mitochondrial cytochrome b	55
abph1	2.03	aberrant phyllotaxy1, decussate leaves and ear shoots (opposite at nodes) frequent; variable, recessive	50, 51, 61
Ac9		Activator9, isolated from *wx-m9*; 4563bp	93, 101
adc1	8.02-8.03	amino deoxychorismate synthesis homolog1, leaf cDNA csu329, single copy, similar to bacterial folate biosynthesis enzyme, may encode p-aminobenzoate synthase glutamine amidotransferase, CII	14
adf1		actin depolymerizing factor1, pollen cDNA similar to yeast cofilin, may encode actin depolymerizing factor	116
aec1		aminoethyl-L-cysteine resistant1, dominant *Aec1* resistant to lysine analog; elevated lysine content	7
aec5		aminoethyl-L-cysteine resistant5, recessive *aec5* resistant to lysine analog; elevated lysine content	7
apx1		ascorbate peroxidase homolog, leaf cDNA csu238, partial 5' sequence similar to plant ascorbate peroxidase, may encode ascorbate peroxidase	14
apx2		ascorbate peroxidase2, leaf cDNA, similar to plant cytosolic ascorbate peroxidase; sequence distinct from *apx1*, may encode ascorbate peroxidase	146
arf1		ADP-ribosylation factor homolog1, cDNA similar to ARF family of GTP binding proteins, may encode GTP-binding, ARF family	150
asn1		*Zea* asparagine synthetase homolog1, cDNA sequence 70% identical to asparagine synthetase from Pisum sativum, encodes asparagine synthetase	30
atp3		ATP synthase3, vegetative meristem cDNA 7C02A03, encodes ATP synthase, mitochondrial, delta subunit	56
bar		Basta resistance, transgene, confers resistance to phosphinothricine (PPT, Basta); single or multiple copy transformants, encodes phosphinothricin acetyl transferase	72
barnase		transgene, contains anther-specific promoter and encodes for enzyme barnase, which disrupts normal cell activity resulting in male sterility, corrected by *barstar*	147
barstar		transgene, contains anther-specific promoter (as in *barnase* transgene) and a gene that inactivates barnase, rendering plant male fertile	147
ben2		bentazon resistance2, dominant *Ben2* with *Ben1* confers resistance to bentazon herbicide	20
betl1	2.09	basal endosperm transfer layer1, (aka *bet1*) tissue specific cDNA; multiple copies, single map site, 17 amino acid extensin-like signal peptide, ser-(pro)4 motif, encodes BETL-1	60
betl2	4.04-4.05	basal endosperm transfer layer2, cDNA, multiple copies, distinct from *betl1* sequence, encodes BETL-2	160
betl3		basal endosperm transfer layer3, like *betl1*, but not specific to basal endosperm transfer layer	160
blk1		bladekiller1, progressive elimination of leaf blade, successive younger leaves most affected; generally tasselless	121
bsd2		bundle sheath development2, bundle sheath chloroplasts disrupted	24
bvp1	7.04	bovine virus protein homolog1, endosperm cDNA 5C04D07 (uaz207), similar to a bovine virus protein, may encode transcription factor	54
caat1	8.04	CAAT box binding protein1, cDNA 5C05F12 similar to binding protein; single copy, may encode NF-YB, CCAAT-box binding protein subunit B	55, 130
cap1		calcium pump1, anoxic root cDNA, may encode calcium ATPase	139

car30		chilling acclimation response30, cDNA from cold-acclimated seedlings	4
car757		cold acclimation response757, cDNA from cold acclimated seedlings	4
cbp2		calmodulin binding protein2, partial root tip cDNA; fusion protein binds calmodulin; wind-induced; 1-2 copies, encodes calmodulin binding protein	113
cdpk2		calcium dependent protein kinase2, genomic and cDNA clones; genomic sequence similar to plant CDPK; pollen-specific expression; possibly two copies (Southern blot); antisense oligonucleotides disrupt pollen tubes, encodes calcium dependent, calmodulin independent protein kinase	41
Cin4		Cinteotl4, member of the class LINE-like non-viral retrotransposon elements, 50-100 copies, preferentially located in regions approximately 44% GC	27, 85
ck2	2.08	casein kinase2, partial cDNA has three regions of identity to all other known casein kinase 2 alpha subunit genes, encodes casein kinase	37
colonist1		colonist1, family of elements containing reverse transcriptase domain (*LINE*-like); originally found in ACCase B1 and B2 genes; high sequence identity to largest (1.8kb) intron of *sh2*	85
colonist2		colonist2, family of elements containing reverse transcriptase sequence (*LINE*-like), similar to *Cin4*; 100-500 copies in genome; originally found in ACCase genes B1 and B2 (as an insertion in colonist1)	85
cpn10		chaperonin10 candidate, etiolated leaf cDNA 6C02E06(uaz222) similar to microbial and plant chloroplast chaperonin 10 or groES protein, may encode chaperonin 10	55
crs1		chloroplast RNA splicing1, chloroplast atpF RNA splicing	9
crs2		chloroplast RNA splicing2, generally required for chloroplast RNA splicing, in contrast to *crs1*	9
csa1		contact site A glycoprotein homolog1, leaf cDNA csu184 similar to *Dictyostelium* contact site A glycoprotein, may encode glycoprotein	14
cyp2	4.01	cytochrome P450 2, seedling-specific; cDNA and genomic clones; gene-specific probe, encodes cytochrome P450 CYP71	44
cyp3	4.01	cytochrome P450 3, cDNA, gene specific probe, encodes cytochrome P450 CYP71	44
cyp4	4.01	cytochrome P450 4, seedling specific cDNA CYP71C3 (mpik7), gene-specific probe, encodes cytochrome P450 CYP71	44
cyp5	4.01	cytochrome P450 5, seedling specific, cDNA CYP71C4 (mpki8), gene specific probe, encodes cytochrome P450 CYP71	44
cyp6	7.02	cytochrome P450, leaf cDNA 6C06B11 (uaz338) similar to eggplant protein, SSR *phi034*, may encode cytochrome P450	55, 127
cys1		cysteine synthase1, vegetative meristem cDNA 7C02B02, may encode cysteine synthase, plastid	56
dba1	4.10	DNA binding activity1, cDNA pAS10 with binding activity, similar to E5 protein; gene specific	138
dba2	8.05-8.06	DNA binding activity2, cDNA pAS12 has binding activity; gene specific	138
dba3	10.07	DNA binding activity3, cDNA pAS13 has binding activity; gene specific	138
dba4	9.06	DNA binding activity4, cDNA pAS14 has strong binding activity and similarity to zinc finger proteins, single copy	138
dek34	6.00-6.01	defective kernel34, reduced kernel	108
dks8	2.02	defective kernel shootless8, from Mu screening; eliminates the development of the shoot pole during embryogenesis, encodes coproporphyrinogen III oxidase	134
doppia		duplicate, (Latin: to duplicate) discovered at the *r1* locus, lies between *S1* and *S2* in the *S* complex; appears to have contributed to the formation of *q* and *S2* from *P* element	155
Dp9	9.00-9.03	Duplication 9, duplicated segment bearing *c1 sh1 wx1* loci, repeated in reversed order	92
Ds1		Dissociation1, isolated from *Adh1-Fm335*; deletion of virtually all of *Ac* except the 11bp inverted sequence at ends, which determines response to *Ac* and excision	104, 141
Ds2		Dissociation2, isolated from *Adh1-2F11;* 1319bp	38, 39, 98
Ds6		Dissociation6, isolated from *wx-m6*; deletion of 2521 bp of *Ac*	38, 42, 94
Ds9		Dissociation9, derived from *wx1-m9*; 4369bp, deletion of 194bp from *Ac9*	38, 93
DsA		DissociationA, transgenic, artificial *Ds*-like element	140
Ef1	10.04	endosperm factor1, segment affecting endosperm development by paternal imprinting	78, 79
Ef2	10.04	endosperm factor2, segment affecting endosperm development by paternal imprinting	78, 79
Ef3	10.04	endosperm factor3, segment affecting endosperm development by paternal imprinting	78, 79
Ef4	10.06-10.07	endosperm factor4, segment affecting endosperm development by paternal imprinting	79
eif2		elongation initiation factor2, etiolated leaf cDNA 6C02E11(uaz224) similar to eIF-2 gamma chain, may encode eucaryotic initiation factor 2, gamma subunit	55
eif4		eucaryotic initiation factor4, cDNA; one of two with map sites on chr 5 and chr 6, encodes eucaryotic initiation factor 4A	88
Enl102		Enhancerl102, non-autonomous transposition, deletion derivative of *En1*	125
eoh1	10.03	*E. coli* origin of replication homolog1, genomic sequence pAS3 similar to *E. coli* origin ; gene specific probe	138
ers1		enhancer of rough sheath1, enhances *Rs1-0* phenotype; alone affects leaf dimensions (shorter, more lanceolate) but no effect on ligule or lateral veins	16
fat1		fatty acyl thioesterase1, leaf cDNA csu817 similar to plant fatty acid metabolism protein, may encode acyl-(acyl carrier protein) thiolesterase	15

fdx1	6.00	ferredoxin1, chloroplast, light induced, N-terminal amino acid sequence of mature protein, cDNA sequence, SSR *phi075*, encodes ferredoxin	53, 127
fht1	2.01-2.02	flavanone 3-hydroxylase1, (aka *f3h*) single copy cDNA similar to Antirrhinum homolog, may encode flavanone 3-hydroxylase	34
gbf1		G-box binding factor, anoxia induced, nuclear, basic-region leucine zipper protein; low copy number; cDNA clone, encodes G-box binding factor	33
gef1		glossy early flowering1, recessive *gef1* eliminates first leaves	149
gfa1		glucosamine fructose-6-phosphate aminotransferase1, endosperm cDNA 5C01G05 (uaz309) similar to rate limiting enzyme of hexosamine synthesis, may encode glucosamine fructose-6-phosphate aminotransferase	55
gl25	5.00-5.04	glossy25, like *gl1* but seedlings small, twisted	123
gl26		glossy26, like *gl1*	123
gl7	4.00-4.05	glossy7, (was *gl12*) like *gl1*	40, 136
gln2	1.09-1.10	glutamine synthetase2, cytosolic, GS1-2 isoform, root specific, gene specific cDNA probe, 6-member nuclear gene family, encodes glutamate-ammonia ligase, cytosol	76, 118, 133
gln4	5.07	glutamine synthetase4, cytosolic GS1-3 isoform, major species in both root and leaf, gene specific cDNA probes, 6-member nuclear gene family; SSR *phi085,* encodes glutamate-ammonia ligase, cytosol	118, 133
gln5	4.04-4.06	glutamine synthetase5, cytosolic GS1-4 isoform, major species in both leaf and root, gene specific cDNA probe, 6-member nuclear gene family, encodes glutamate-ammonia ligase, cytosol	118, 133
gln6	1.01-1.02	glutamine synthetase6, cytosolic GS1-1 isoform, gene specific cDNA probe, 6-member nuclear gene family, encodes glutamate-ammonia ligase, cytosol	118, 133
glu2		beta-glucosidase2, cDNA produces higher activity in transgenic tobacco; shares 20 amino acids with an N-terminal sequence reported for membrane-bound beta-glucosidase, encodes beta glucosidase, p60	25
gly1		glycine1, leaf cDNA 7C04A02 similar to a fungal and *E. coli* enzyme used in glycine metabolism, may encode glycine hydroxymethyltransferase	56
gol1	4.08	goliath homolog1, leaf cDNA csu216 single copy, similar to *Drosophila* Goliath protein, may encode transcription factor	14
gos2	7.03-7.04	homolog to rice *gos2*, leaf cDNA csu209, single copy, 5' sequence similar to constitutive rice *gos2*, may encode translation factor, SUI1 family	14
gst2		glutathione S-transferase2, safener-induced; heterodimer, encodes glutathione S-transferase II, 27 kDa subunit	58
gst4	3.05	glutathione-S-transferase4, cDNA sequence, transgenic expression, single or low copy gene, sequence in conflict with earlier sequence reported for *gst3* (possible allele of *gst3*), SSR *phi073*, encodes glutathione S-transferase	52, 127
gtr1		glutamyl-tRNA reductase1, leaf cDNA csu839, plastid porphyrin biosynthesis, encodes glutamyl-tRNA reductase	15
gzr1	7.05-7.06	gamma zein modifier1, enhances gamma-zein accumulation; possibly identical to *o15*; with other loci, modifies hardness of *o2* endosperm	81
hca1	7.04	histocompatibility antigen homolog1, endosperm cDNA 5C04C07 (uaz199), similar to human histocompatibility antigen, single copy, may encode glycoprotein	54
hmg1		high mobility group protein1, cDNA sequence isolated by immunoscreening, homologous to vertebrate HMG1 family, single or low copy gene, encodes high mobility group a protein	49
hmp1	1.00-1.04	humpback1, proliferation of sheath just beneath auricle results in bulged sheath, more apparent above the ear node	124
Hopscotch		Hopscotch, copia-like retrotransposon in *wx1-K* with single open reading frame	159
hox3	3.07	homeobox3, cDNA ZmHox2a, meristem specific, duplicate of *hox4*, based on sequence and expression; sequence distinct from knotted related homeobox genes, encodes HOX2a, transcription factor candidate	67
hox4	8.09	homeobox4, cDNA Zmhox2b, meristem specific, duplicate of *hox3* based on sequence and expression, encodes HOX2b, transcription factor candidate	67
hsk1	9.03	high-sulfur keratin homolog1, endosperm cDNA 5C04B04 (uaz144), similar to high-sulfur keratin; relation to *uaz144a* (bin 4.06) and *uaz144b* (bin 5.06) unclear, encodes high sulfur keratin homolog	54
ht4	1.03-1.06	*Helminthosporium turcicum* response4, chlorotic halo on infection by *Exserohilum turcicum*	28
idc1		iron deficiency candidate1, endosperm cDNA 2C02A04 (uaz80) similar to barley sequences D10058, D37796	55
IGS	6.01	intergenic spacer in NOR, spacer region between transcribed rDNA units; interacts with high-mobility group (HMG) nuclear proteins	59
imd1		isopropylmalate dehydrogenase1, vegetative meristem cDNA 7C03E11 similar to potato sequence X67310, with less similarity to various mammalian isocitrate dehydrogenases, may encode isopropylmalate dehydrogenase	56
incw1	5.04	cell wall invertase1, full-length cDNA, similar to tobacco and carrot cell-wall invertase; Northerns specific to cell suspension and developing endosperm 28-32 DAP; expressed protein cross-reacts with antibodies to carrot cell-wall invertase; low copy number, encodes invertase, cell wall	129
ivr1		invertase1, cDNA, genomic clones similar to soluble plant invertase, encodes invertase	162
ivr2	5.03	invertase2, cDNA for soluble invertase, single band on Southerns, encodes invertase	68

K10	10.07	abnormal 10, heterochromatic alternative end of long arm of chromosome 10 found in some strains; neocentric activity distorts segregation of knobs and of genes linked to them	80
K3L	3.07	knob on 3L, heterochromatic structure found in most strains, varies in size	35
knox1	1.00-1.01	knotted related homeobox1, class 2 root homeobox; cDNA and genomic clones; gene-specific probe	65
knox10	5.02-5.03	knotted related homeobox10, class I homeobox, gene-specific probe; cDNA and genomic clones	65
knox11	8.05	knotted related homeobox11, class I homeobox; cDNA and genomic clones; sequence and expression similar to *lg3* and *knox5*	65
knox2	9.03	knotted related homeobox2, sequence similar to knox6 and knox7; gene specific probe; cDNA and genomic clones	65
knox5	8.05	knotted related homeobox5, class I homeobox; cDNA and genomic clones; gene-specific probe; sequence and expression similar to *lg3* and *knox11*	65
knox6	5.04	knotted related homeobox6, similar to *knox2* in sequence and expression; cDNA and genomic clones; gene specific probe	65
knox7	4.09-4.10	knotted related homeobox7, sequence and expression similar to *knox6*; gene specific probes	65
knox8	1.10-1.11	knotted related homeobox8, cDNA, shoot meristem and developing stem specific, similar in sequence and expression pattern to *kn1*	62, 65
kpp1		kinase associated protein phosphatase1, cDNA similar to *Arabidopsis* KAPP sequence, encodes kinase associated protein phosphatase	21
les28		lesion mimic28, dominant *Les28*, leaf lesions enhanced by strong sunlight and cold	90
lhca1		light harvesting complex A1, leaf cDNA csu800 similar to photosystem I antenna protein, encodes chlorophyll a/b binding protein type II LHCI	15
lhcb4	5.07	light harvesting complex a/b protein4, leaf cDNA csu227, single site, encodes light-harvesting chlorophyll a/b binding protein	14
LINE		Long Interspersed Nuclear Elements, non-viral retrotransposon family (includes *Cin4, colonist1 & 2)*	85
lss1	4.10	lanosterol synthase1, leaf cDNA csu265, encodes oxidosqualene-lanosterol cyclase	14
ltf1	5.03-5.04	lysr transcription factor homolog1, endosperm cDNA 5C02B05 (uaz275) single copy, similar to lysr family of transcription regulators, may encode lysr transcription factor	54
Maize 1		copia-like retrotransposon isolated by PCR, may encode reverse transcriptase	154
Maize 2		copia-like retrotransposon, isolated by PCR, may encode reverse transcriptase	154
MARZadh1	1.10	matrix associated region, near *adh1*, DNA region at 5' end of *adh1*, distal to the promoter region with high affinity for the nuclear matrix, prepared from nuclei of young maize seedlings	6
met1		methionine synthase homolog1, leaf cDNA csu194 similar to *E. coli metE*, may encode methionine synthase	14
mha2		plasma-membrane H+ATPase2, cDNA sequence similar to plant plasma-membrane [H+]-ATPase and distinct from mha1, encodes H(+)-ATPase, plasma membrane	128
mhl1		macrohairless1, reduced complement of macrohairs on adaxial surface of leaf blade; with *Rld1-O*, abaxial macrohairs characteristic of *Rld1* are absent	71
mrl1		midribless1, loss of midrib in juvenile leaves, occasionally in adult leaves	105
ms25		male sterile25, tapetal cells abnormal, contain lipid bodies; microspores vacuolate prematurely after release from the tetrad, then collapse	84
ms26		male sterile26, tapetal cells abnormal, die early; microspores vacuolate early and abort after the tetrad stage	84
ms27		male sterile27, description pending	2, 17
ms45	9.00-9.08	male sterile45, abnormal microspore wall formation, tassel specific, cDNA clone, may encode strictosidin synthase	3
msf1		mRNA splicing factor homolog1, leaf cDNA csu363 similar to animal mRNA splicing factor, may encode mRNA splicing factor U2AF	14
msh1		male sterile homolog1, etiolated leaf cDNA 6C02E02(uaz195) similar to *Arabidopsis* male sterile locus, *ms2*	55
mss1		MSS1 homolog, leaf cDNA csu834 similar to human protease, may encode ATP-dependent protease, MSS1	15
mta1	1.09-1.10	mouse transplantation antigen homolog1, endosperm cDNA 5C04D09 (uaz208) single copy, similar to *Arabidopsis* homolog of a mouse transplantation antigen, may encode glycoprotein	54
mtl1	4.01	metallothionein homolog1, genomic clone, transcriptional and translation start sites mapped, Northern blots, similar to other class-I metallothioneins, root specific; SSR *phi072*, may encode metallothionein	32
mtl2		metallothionein2, seed cDNA sequence similar to wheat sequence (SwissProt P30569) and distinct from *mtl1*, may encode Ec metallothionein class II protein	158
mtr1		methyltryptophan resistant1, dominant variation conveys resistance to 5-methyl tryptophan	63
Mu2		Mutator2, contains an additional 385 bp insertion not found in *Mu1*	19
Mu3		Mutator3, terminal inverted repeats have 80-90% identity with TIRs of *Mu1*, but no sequence similarity internally with other *Mu* elements	102
Mu7		Mutator7, cloned by homology to *Mu1* termini	19
MuA		MutatorA, isolated by homology to *Mu1* TIRs	142
nac1	10.04	NaCl stress protein1, endosperm cDNA 5C01G10 (uaz250, SSR *phi084*), similar to wheat salt-stress peptide, may encode salt stress protein	54

nad2		NADH dehydrogenase2, vegetative meristem cDNA 7C02A11, encodes NADH:ubiquinone oxidoreductase, PSST subunit	56
NCS7		nonchromosomal stripe7, aborted kernel sectors; photosystem I deficient; maternally inherited	143
ndk1	7.03-7.04	nucleotide diphosphate kinase1, leaf cDNA csu269 single copy, encodes nucleotide diphosphate kinase I	14
nfy2		NF-YB homolog, single PCR-isolated sequence with strong homology to CCAAT-box binding protein subunit, encodes NF-YB, CCAAT-box binding protein subunit B	77
nii2		nitrite reductase2, cDNA homologous to spinach gene, induced by nitrate, putative chloroplast transit peptide, two copies, encodes ferredoxin--nitrite reductase	70
odo1		alpha keto dehydrogenase candidate1, etiolated leaf cDNA 6C02A09 (uaz215) similar to microbial TCA cycle enzyme, may encode alpha-ketoglutarate dehydrogenase	55
oec17		oxygen evolving complex, 17kDa homolog, leaf cDNA csu229 similar to plant OEC17, encodes oxygen evolving complex, 17kDa subunit	14
ohp2	5.00	opaque2 heterodimerizing protein2, cDNA sequence, SSRs *nc007*, *phi024*, encodes *o2* heterodimerizing protein	109, 126
ole1	2.04-2.05	oleosin1, major protein from lipid bodies, cDNA and genomic clones, encodes oleosin, 16 kDa	74, 148
ole2	5.02	oleosin2, embryo lipid body protein; peptide, cDNA and genomic sequences; SSR *phi113*, encodes oleosin, 17 kDa	74, 75
ole3	5.03-5.04	oleosin3, embryo lipid body protein, peptide, cDNA and genomic sequences, encodes oleosin, 18 kDa	74, 75, 110
oro4		orobanche4, like *oro1*	86
ost1		oligosaccharide transferase1, vegetative meristem cDNA 7C02F04 similar to an integral endoplasmic reticulum protein, may encode dolichyl-diP-oligosaccharide protein glycosyl transferase	56
pal1	5.05	phenylalanine ammonia lyase candidate, leaf cDNA csu156 similar to rice phenylalanine ammonia lyase, single copy, encodes phenylalanine ammonia lyase	64
pat		phosphinothricin acetyl transferase, synthetic gene sequence derived from the *Streptomyces viridochromogenes* gene; Mendelian segregation of transformants, encodes phosphinothricin acetyl transferase	103
pcna1		proliferating cell nuclear antigen1, full-length cDNA; predicted protein shows high similarity to rice, human, others, encodes proliferating cell nuclear antigen	83
pcr1		protochlorophyllide reductase1, leaf cDNA csu349 similar to plant protochlorophyllide reductase, encodes NADPH protochlorophyllide oxidoreductase	14
pdk1	6.05	pyruvate, orthophosphate dikinase1, cDNA, genomic and peptide sequences; microsatellite mapped (SSRs *phi025*, *phi078*, *phi081*; *nc012*); cytosolic or plastidic, dependent on transcript processing, encodes pyruvate, orthophosphate dikinase	46, 126
pex2		pollen, extensin-like2, clone like *pex1*, encodes hydroxyproline-rich glycoprotein	117
pfk1		phosphofructose kinase1, vegetative meristem cDNA 7C02A06, encodes 6-phosphofructose-1-kinase, beta subunit	56
pgd1	6.01	6-phosphogluconate dehydrogenase1, electrophoretic mobility, null alleles occur; cytosolic; dimeric, intra/interlocus hybrid bands occur; cDNA csu262 single copy, encodes 6-phosphogluconate dehydrogenase	14, 48
pks1		polyketide synthesis homolog1, vegetative meristem cDNA 7C02F01 similar to an acyl CoA condensing enzyme, may encode 6-deoxyerythronolide B synthase I	56
pld1		phospholipase D1, cDNA clone, amino acid sequence 90% similar to rice PLD, encodes phospholipase D	145
pls1		phospholipid synthesis1, endosperm cDNA complements *E. coli* temperature sensitive mutant in *plsC*, encodes 1-acyl-sn-glycerol-3-phosphate acyltransferase	23
pop1	1.04-1.05	putative organelle permease1, endosperm cDNA 5C02F05 (uaz 282)single copy, similar to yeast putative mitochondrial carrier protein, may encode organellar permease	54
ppo1		polyphenol oxidase1, vegetative meristem cDNA 7C02D02, may encode polyphenol oxidase	56
ppp1	5.07	pyrophosphate-energized proton pump1, endosperm and leaf cDNA's 5C02E08 (uaz280), zcsu220; single copy; similar to plant vacuolar pyrophosphate-energized ATPase, may encode pyrophosphate-energized proton pump, vacuolar	14, 54
prc1	9.02	proteasome C9 homolog1, endosperm cDNA 5C02A05 (uaz237), similar to proteasome subunit, may encode proteasome (endopeptidase) component C9	54
prc2		proteasome component2, vegetative meristem cDNA 7C02B10, may encode proteasome component C11	56
psei2		cystatin2, cDNA expressed in *E. coli* inhibits cysteine proteinases; sequence and gene product activity distinct from psei1, encodes cysteine proteinase inhibitor II	1
psl1	2.07	position shift locus1, psl1 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl3	9.02	position shift locus3, psl3 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl4	3.05	position shift locus4, psl4 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl5	3.01-3.03	position shift locus5, psl5 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31

psl6	1.06-1.07	position shift locus6, psl6 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl7	5.03	position shift locus7, psl7 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl8	5.04-5.05	position shift locus8, psl8 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl9	10.03	position shift locus9, psl9 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl10	3.04	position shift locus10, psl10 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl11	2.04-2.06	position shift locus11, psl11 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl13	1.12	position shift locus13, psl13 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl15	6.02-6.03	position shift locus15, psl15 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl16	3.06	position shift locus16, psl16 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl18	1.06	position shift locus18, psl18 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl19	8.04-8.05	position shift locus19, psl19 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl20	5.03	position shift locus20, psl20 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl21	5.05	position shift locus21, psl21 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl22	9.04	position shift locus22, psl22 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl23	7.03	position shift locus23, psl23 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl24	1.10	position shift locus24, psl24 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl25	1.04	position shift locus25, psl25 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl26	4.11	position shift locus26, psl26 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl27	7.03-7.04	position shift locus27, psl27 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl28	3.05	position shift locus28, psl28 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl29	6.04-6.05	position shift locus29, psl29 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl31	2.05-2.06	position shift locus31, psl31 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl32	2.07	position shift locus32, psl32 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl33	1.12	position shift locus33, psl33 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl35	4.03-4.04	position shift locus35, psl35 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl38	8.02	position shift locus38, psl38 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl39	5.04-5.05	position shift locus39, psl39 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl42	8.01	position shift locus42, psl42 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl43	5.03	position shift locus43, psl43 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl44	1.11	position shift locus44, psl44 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl45	4.03-4.05	position shift locus45, psl45 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl46	9.07	position shift locus46, psl46 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl47	3.02-3.04	position shift locus47, psl47 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31

psl48	10.07	position shift locus48, psl48 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
psl75	4.09-4.10	position shift locus75, psl75 polypeptide altered, revealed by 2-dimensional polyacrylamide gel electrophoresis	31
pur1		pollen ubiquitin regulator1, dominant regulator of ubiquitin level	96
px10		peroxidase10, anodal; active in scutella, seedling roots, tassel spikelets, pollen, encodes peroxidase	22, 66
px12		peroxidase12, root-specific in planta; occurs in callus tissues and somaclones, encodes peroxidase	22, 66
q	10.06	non-functional *r1* component, in the *S* complex, structure *q-1S-S2* (i.e., *S1* and *S2* elements are in reverse orientation); synapses with *P, S1, S2*	115
rab15	5.03	responsive to abscisic acid15, nucleolar; cDNA and genomic sequence, cDNA isolated from dry embryo; SSR *phi008*, encodes MA16 RNA binding protein	47
rab28	5.03	abscisic acid-responsive28, cDNA and genomic clones, inducible by ABA in embryos and young leaves and by water-stress in leaves; similar to cotton *LeaD-34*	107
rad1		RAD1 DNA repair protein homolog, endosperm cDNA 5C10D10 similar to yeast *RAD1*, may encode DNA repair protein, RAD1 homolog	55
rad51		recombination and DNA repair51, cDNA similar to yeast *RAD51*, may encode RAD51	97
rap1		retinoblastoma-associated protein homolog1, etiolated leaf cDNA 6C02C02 (uaz191) similar to human cell cycle protein, may encode retinoblastoma protein (RB) family member	55
rf8		restorer of fertility8, dominant *Rf8* substitutes for *Rf1* in fertility restoration	36
ring 3	3.08-3.09	ring carrying *A1-b, Sh2, W19*; losses in endosperm or seedling tissue are recognizable by phenotypic losses of these dominants	137
ring 9S	9.00-9.01	ring carrying *Wd1, Yg2, and C1-I;* frequent losses recognizable in endosperm in presence of *C1*, in plants if *wd1* or *yg2*	95, 114
rip2	7.04	ribosome-inactivating protein2, cDNA; genomic sequence produces RIP protein in *E. coli*, encodes ribosome inactivating protein	11
rnp1	2.08	chloroplast RNA binding protein1, leaf cDNA csu17, similar to RNA binding proteins, encodes chloroplast RNA binding protein	12
rpa40		acidic ribosomal protein P40, vegetative meristem cDNA 7C02D05 similar to cytoplasmic ribosomal protein, may encode 40S ribosomal protein, P40	56
rpl15		60S ribosomal protein L15, leaf cDNA csu364 similar to eucaryotic 60S ribosomal protein L15 (L10, YL10), may encode ribosomal protein L15, 60S	14
rpl16		ribosomal protein L16, precursor mRNA stored in embryo axes, encodes ribosomal protein L16	18
rpl3		ribosomal protein L3, precursor mRNA stored in embryo axes, encodes ribosomal protein L3	18
rpl44		ribosomal protein L44, vegetative meristem cDNA 7C02A07, encodes 60S ribosomal protein L44	56
rps12		ribosomal proteinS12 (homolog), endosperm cDNA 5C08C03 similar to rodent ribosomal protein, may encode ribosomal protein S12	55
rps21		40S ribosomal protein S21, endosperm cDNA, similar to rice 40S ribosomal protein S21, encodes 40S ribosomal protein S21, cytoplasmic	55
rps27		ribosomal protein S27, endosperm cDNA 5C09A02, may encode 40S ribosomal protein S27	55
rps28		ribosomal protein S28, endosperm cDNA 5C01A05(uaz146) similar to animal 40S ribosomal protein S28, encodes 40S ribosomal protein S28, cytoplasmic	55
rps4		ribosomal protein S4, vegetative meristem cDNA 7C02E04 similar to cytoplasm ribosomal protein, encodes 40S ribosomal protein S4	56
rps6		ribosomal proteinS6, mature mRNA stored in embryo axes, encodes 40S ribosomal protein S6, cytoplasmic	18
rtcs1		root deficient1, root system drastically reduced, solely to a primary root, yet plants can be carried to seed	57
S1	10.06	subcomponent of *S* region of *r1 S* complex, arranged *q-1S-S2* (*S1* reversed relative to *S2*); synapses with *P, q, S2*	155
S2	10.06	subcomponent of *S* complex of *r1*, arranged *q-1S-S2* (*S1* and *S2* in reverse order); synapses with *P, q,* and *S1*	155
sam1	10.04-10.05	S-adenosylmethionine decarboxylase1, single copy leaf cDNA csu217; aka csu6b, may encode S-adenosylmethionine decarboxylase	14
sbp1		sedoheptulose bisphosphatase1, leaf cDNA csu813 similar to plant Calvin cycle enzyme, may encode sedoheptulose bisphosphatase	15
se1	2.10	sugary-enhancer1, high sugar content with *su1*; light yellow endosperm; freely wrinkled in Ill677a	43
sed1		senescence-diminished1, mRNA differentially diminished in early- vs. late-senescing lines; similarity to ATP sulfurylase mRNA of *Arabidopsis*, may encode sulfate adenyltransferase	132
sed2		senescence-diminished2, mRNA differentially diminished in early- vs. late-senescing lines	132
see1		senescence-enhanced1, mRNA differentially enhanced in late- vs. early-senescing lines; similarity to rice oryzain gamma (cysteine protease), may encode cysteine protease	132
see2		senescence-enhanced2, mRNA differentially enhanced in late- vs. early-senescing lines; similarity to castor bean vacuolar processing enzyme (cysteine protease), may encode protease, vacuolar processing	132
see3		senescence-enhanced3, mRNA differentially enhanced in late- vs. early-senescing lines; similarity to maize pyruvate, o-phosphate dikinase, may encode pyruvate, orthophosphate dikinase	132

see4		senescence-enhanced4, mRNA differentially enhanced in late- vs. early-senescing lines; similarity to maize ferredoxin I, may encode ferredoxin	132
sem1	9.00-9.03	semaphore1, small kernels with reduced germination; plants brachytic with leaves that droop at maturity	119, 120
ser1		seryl-tRNA synthetase1, etiolated leaf cDNA 6C02G11 (uaz236) similar to yeast tRNA ligase, may encode seryl-tRNA synthetase	55
sigma		sigma subcomponent of *S* complex of *r1*, region between *S1* and *S2*, unrelated to them or to *P* but showing some homology to *doppia*	155
Sleepy		Sleepy, element of 328bp, found as an insertion into an exon in *d3-4*	161
snr14		small nucleolar RNA1, nucleolar; possible polycistronic cluster of U14 units; sequence similar to yeast and mouse counterparts, encodes U14 small nucleolar RNA	73
spr1		signal recognition particle receptor homolog1, endosperm cDNA 2C07F04(uaz8) similar to alpha subunit of animal signal recognition particle receptor, may encode signal recognition particle receptor, alpha subunit	55
sps2	3.05	sucrose phosphate synthase2, leaf cDNA csu328, sequence similar to *sps1*, encodes sucrose-phosphate synthase	14
taf1		transcription associated factor1, low copy, leaf cDNA csu38 similar to human transcription initiation factor subunit, may encode TFIID subunit	12
tap1		translocon-associated protein homolog1, vegetative meristem cDNA 7C02D06, similar to endoplasmic reticulum protein, may encode RAP, delta subunit	56
tct1		translationally controlled tumor1, vegetative meristem cDNA 7C02C06 similar to protein conserved in yeast, plants and mammals, encodes TCT1	56
tha1	3.04	thylakoid assembly1, reduced polypeptides of photosystem II, photosystem I, cytochrome bf; normal coupling factor, normal RUBISCO; missing polypeptides appear to be synthesized normally	8
tha3		thylakoid assembly, like *tha2*, presumed not allelic	10
thr1	3.08	threonine synthase homolog1, leaf cDNA csu189 similar to bacterial threonine synthase; single copy, may encode threonine synthase	14
tlk1	6.07	tousled protein kinase1, endosperm cDNA 5C04A03 (uaz130; SSR *phi070*), similar to *Arabidopsis* protein kinase, TOUSLED, encodes Lea Group 3 protein MLG3	54, 127, 157
tnpA		transposase A, positive and negative regulator and transposition elicitor of *Spm*, encodes TnpA	122
tola1		tola protein homolog1, endosperm cDNA 5C05A03 (uaz254) similar to *E. coli* TOLA protein, an inner membrane, colicin transport protein, may encode membrane permease	55
TouristA		TouristA, elements with frequent 5'-GGATT-3' repeats, generally small, 133 bp average	163
TouristB		TouristB, elements similar to *TouristA* but also contain internal domain I, subterminal poly(A).poly(T) tract and one copy of 5'-TCACATCGAAT-3' located 39-50 bp from a terminus	26
TouristC		TouristC, elements similar to *TouristB* but have an additional domain, I'	26
TouristD		TouristD, elements with a distinct, although related, terminal inverted repeat and with variable length	26
trm1		thioredoxin M1, cDNA with conserved active site, encodes thioredoxin M	144
trp1		tryptophan synthase1, genomic sequence; pith preferential cDNA, complements *E. coli trpA*, encodes tryptophan synthase alpha subunit	69
tru1	3.04-3.10	tassels replace upper ears1, upper ear branches tassel-like, tillers bear ears	131
tsl1		twin shoot line1, twin shoots, heritability low and variable, apparently normal number of chromosomes, dormant embryo has twin apical meristem, but single root primordium	45
tua4	5.01-5.02	alpha tubulin4, belongs to alpha tubulin subfamily I, with *tua1* and *tua2*; gene specific cDNA probe, encodes alpha tubulin	151
tua6	7.04	alpha tubulin6, alpha tubulin subfamily II, gene specific cDNA probe, encodes alpha tubulin	151
tub6	3.06	beta tubulin6, cDNA sequence, gene specific probe, encodes beta tubulin	152
tub7	9.04	beta tubulin7, cDNA sequence, gene specific probe, encodes beta tubulin	152
tubg1		gamma-tubulin1, full-length cDNA; deduced amino acid sequence shows high similarity to this tubulin of *Arabidopsis* and others, encodes gamma tubulin	82
uce1	1.08	ubiquitin conjugating enzyme1, endosperm cDNA 2C06C11 (uaz102), similar to plant ubiquitin conjugating enzymes, encodes ubiquitin conjugating enzyme	54
ugp1	2.07	UDP-glucose pyrophosphorylase1, endosperm cDNA 5C02H07 (uaz194), similar to potato UDP-glucose pyrophosphorylase, encodes UDP-glucose pyrophosphorylase	54
vp13	10.04-10.07	viviparous13, viviparous embryo, necrotic seedling	91
vpp2		vacuolar proton pump2, etiolated leaf cDNA, 5' sequence similar to plant vacuolar ATPase, subunit B, encodes vacuolar (H+)-ATPase, subunit B	55
vsp1	9.03	vegetative-specific protein homolog1, endosperm cDNA 5C01C06 (uaz246), similar to slime mold vegetative protein, may encode vegetative-specific protein	54
xet1	5.03	xyloglucan endotransglycosylase homolog1, cDNA clone (cultivar Berkeley Fast); continuous anaerobic accumulation of mRNA through 72 h, may encode xyloglucan endotransglycosylase	106
z1c(zp22)	4.02	zein cluster, 22 kDA alpha zein cluster defined by single *SalI* restriction fragment, encodes zein-1 (alpha zein)	29
ZEAR		*Zea* specific repeat, family of 253 bp elements, specific to the genus *Zea*, with about 2500 copies in both maize and teosinte	112
zem1		*Zea* endosperm MADS box1, genomic clone; distinct leaf and endosperm transcripts attributed to alternative splicing; contains *zag1*-like MADS box, may encode transcription factor (MADS box)	99

zim1		*Zea* IM30 protein homolog1, leaf cDNA csu159 similar to pea IM30 protein, may encode chloroplast membrane targeting protein	13
zlfy1		*Zea* leafy homolog1, genomic sequence similar to *Arabidopsis* floral meristem determining locus, *lfy1*	156
zlp1		zeamatin-like protein1, cDNA selected with *Arabidopsis* thaumatin-like protein clone; antifungal; mRNA and protein highest in endosperm at 4 weeks; one band in Southerns, expressed in transgenic *Arabidopsis* and tomato; closely similar to alpha-amylase/trypsin inhibitor, encodes thaumatin-like protein	87
ZLRS		*Zea* long repetitive sequence, *Zea* specific, 9kbp repetitive elements with 1350-1700 copies/haploid genome	112
zp19/22(pms2)	4.05	alpha zein pms2, genomic sequence pMS2, SSR *phi096*, encodes zein-1 (alpha zein)	111, 127
zp22(zA1)	4.09-4.11	zein cluster zA1, 22 kDa alpha zein cluster, encodes zein-1 (alpha zein)	153
zp22.1	4.04	zein protein 22.1, cDNA pZ22.1, SSR *phi074*, encodes zein-1 (alpha zein)	89, 127
zrp2		*Zea* root protein2, cDNA expressed in roots and stems	100

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Following are two tables, **A RANDOM SET OF MAIZE SIMPLE SEQUENCE REPEAT MARKERS**, provided by Graziana Taramino and Scott Tingey of DuPont (see Genome 39:277-287), and a **COMBINED TABLE OF SSR LOCI** ,developed from information of Taramino and Tingey; of Senior et al., MNL 70:50-54; and of Burr and Walton, in order by approximate bin locations. These data are maintained in MaizeDB.

A RANDOM SET OF MAIZE SIMPLE SEQUENCE REPEAT MARKERS

--Graziana Taramino* and Scott Tingey, DuPont Agricultural Products, P.O. Box 80402, Wilmington, DE 19880-0402
*to whom correspondence should be addressed -- Current address: Dipartimento di Genetica e Biologia Dei Microrganismi, Universita' degli Studi di Milano, Via Celoria 26, I-20133 Milano, Italy. Telephone: +39226605201 FAX: +3922664551 email: camelot@imiucca.csi.unimi.it

Simple sequence repeats (SSRs), also known as microsatellites, are a relatively new class of DNA markers that are based on short runs of tandemly repeated sequences, present in high abundance in many eukaryotic genomes. A high rate of variation in the number of repeat units between individuals or genotypes translates into a high degree of polymorphism that can be revealed by SSR-based markers. SSR markers are convenient, PCR-based, codominant markers that are easily transferable between populations, and often represent a highly informative set of universal markers for a particular species.

The table below reports specific information for 34 randomly selected SSR sequences from a large set that we isolated and characterized from the maize inbred, B73. This information is sufficient to apply these SSRs as potential markers in any maize population. Amplification of a specific product from the maize genome for each SSR is performed using a single set of conditions:

Microsatellite amplifications are performed in a 20 µl volume containing 25 ng of DNA, 5 picomoles of each primer, 200 µM each dNTP, 90mM Tris-HCl pH 9, 20mM $(NH_4)_2 SO_4$, 2.5mM $MgCl_2$ and 0.75 unit of AmpliTaq polymerase (Perkin Elmer Cetus, Norwalk, CT USA). Amplifications conditions are: 94 C for 4 min (1 cycle); 94 C for 1 min, 56 C (or alternate- see specific primer data for ideal annealing temperature) for 1min, 72 C for 1 min (30 cycles); 72 C for 7 min (1 cycle). A single annealing temperature of 56 C can be used as a general condition for all of these SSRs. Products are visualized on 6% denaturing polyacrylamide gels for single-base resolution, or viewed on 2%-4% metaphor agarose (FMC) gels. This set represents the 34 maize SSRs developed by Graziana Taramino and Scott Tingey at DuPont, described in greater detail in: Taramino, G. and Tingey, S.V., Simple Sequence Repeats For Germplasm Analysis and Mapping In Maize, Genome, in press

In an initial mapping trial, we used the CM37 x T232 recombinant inbred population from Ben Burr. Using a 3.5% metaphor agarose gel/ethidium bromide detection system, 18 produced easily scorable polymorphisms, and therefore these 18 SSRs were mapped in this particular population. Below we report the chromosome arm assignments for these loci. The specific map positions, and the entire dataset of information about these SSRs, can be accessed through the Maize Genome Database (http://www.agron.missouri.edu). Although we have not currently done so, we expect that the remainder of these SSRs can be mapped using additional maize populations.

Description of the Table fields:

Locus Name: the unique locus identifier assignments that correspond directly to map position designations on public and published maps.

SSR Identifier: the arbitrary unique identifier we have given to each cloned SSR. The name of the clone also denotes the general type of repeat for which screening was done.

Type of Repeat: the core repeat as contained in the B73-derived clone that was sequenced.

Primer Sequence: the 5'-->3' sequence of each of two primers for each SSR. Each pair of primers is specific to the unique flanking region sequence of the designated SSR and therefore defines that SSR.

PCR Product Size: the size in nucleotides of the PCR product amplified from the B73 allele.

Anneal Temp: the temperature we recommend for the annealing phase of the PCR cycling. In general, amplifications for all 34 primer pairs can be done using a universal 56 C annealing temperature with no loss of information.

Map: the chromosome arm assignment for the 18 SSRs that could be mapped in the CMxT RI population. Specific map positions are available from the Maize Genome Database.

H (Expected Heterozygosity): this is the calculated probability that any two maize genotypes tested will be polymorphic for this SSR locus. This value was calculated with the formula, $H = 3D1-\Sigma(p_i)^2$, where p_i is the frequency of the ith allele in the population studied for each SSR locus. The allele assignments were made using high-resolution polyacrylamide gels, from a set of 12 maize lines that we have determined to represent 87% of the RFLP allele diversity among hundreds of diverse maize lines.

Locus Name	SSR identifier	Repeat Type	Primer Sequence	Anneal Temp	PCR Prod Size (B73)	Map	H
dupssr1	MAC.E00B03	(CA)32	TGT TCT CAA CAA CCA CCG CGT TTA GCG ATA TCA TTT TCC	56 C	148	5S	0.85
dupssr2	MAC.T03B03	(CA)10	GCT AAA TGA TCA GTC ATC CAT G CCA TGT CGC TCA CAC ATC	56 C	158		0.78
dupssr3	MAC.E01C08	(CA)10	TTT AAA ACC TCT TTA TGA CTT TTG CTG ATA CCA TAT CCA GCA TCA	56 C	123	8L	0.53
dupssr4	MAC.T02E08	(AC)4 G (CA)6 T (CA)3 TA (CA)3 TA (CA)3	CGA TAC TAA TGG AAG CCC TAA ATG GCC CAT TAA GTT TAT CAC	56 C	121		0.48
dupssr5	MAC.E01E07	(CA)16	GGC AAT CAA GCT AAG GAA G GCA GTG CAG ATG TTT AGA AGA	56 C	134		0.64
dupssr6	MAC.T02B08	(CA)6 (A)5 (CA)9	GAT CCT ACC AAA ATC TTA TAG GC ACA GCT AGC CAA GAT CTG ATT	56 C	112	9S	0.84
dupssr7	MAC.T02H12	(CA)25	GAA GCT TAA TCT GGA ATC TGG TGT TGC TTC CTT GTA AAA TCT	56 C	138		0.72
dupssr8	MAC.T02B10	(TA)3 (CA)17	AAA TAG TCC AGA AAA AAA TAG TGT G ACC TCT TGT TTT CCA CAG TTC	56 C	107		0.61

dupssr9	MAC.E01G01	(AC)26	GAT GTC GTG TGA GTG ACC TG GTG TTG CTA TTG CAG TGA GAC	56 C	137	7L	0.80
dupssr10	MAC.E01A03	(AC)22	AGA AAA TGG TGA GGC AGG TAT GAA ATC TGC ATC TAG AAA TTG	56 C	167	5S	0.81
dupssr11	MAC.E01C02	(AC)17	AGG CAA GGC TTT CTT CAT AC CGG ACG ACG ACT GTG TTC	56 C	72	7L	0.76
dupssr12	MAC.E01F06	(AC)15	CAG GTA CTA CGT GCC GTG CTA GAG ACA AAC GAG GCT AGG	56 C	131	1L	0.71
dupssr13	MAC.E01F07	(CA)12	TCG TTC GGT CCA TGA AAT CAA ATA TCT CTC ATC TTT GCT GAC	56 C	143	7L	0.78
dupssr14	MAC.E01C01	(CT)3 T (CT)6 (CA)16	AGC AGG TAC CAC AAT GGA G GTG TAC ATC AAG GTC CAG ATT T	56 C	95	8L	0.78
dupssr15	MAC.T02E01	(CA)30	GAA GTC GAT CCA TCC ACC GGG GTA GTG GAG ATA ACT AGT G	56 C	147	6L	0.82
dupssr16	MAG.B01	(TA)35 (GA)14	TTC TTT AAC TAT TGG AAG CCC A GCG CAA TAT TCT CTC TAT ATT GAA	58 C	186		0.84
dupssr17	MAG.1C05	(AG)24	AGA AGA AAG CGA GCA GAC AG GAG ACA CAT CAC ACC CTA AGT TC	57 C	182		0.83
dupssr18	MAG.G02	(AG)20	AAT TTG AGG ATT TCC GCG A ACA TCA CAC GCA GAG CTA ATC	60 C	111		0.40
dupssr19	MAG.E01	(AG)20	GCT GAA GGA CTA AAG AAA CCG CCT CCA AGG TTG GTA CTG TC	58 C	100	9S	0.86
dupssr20	MAG.C04	(AG)20	TGT TCA TGT ATG ATT TGC CAA TCC TGG CAC TAG TTT TTC TTT T	58 C	146		0.69
dupssr21	MAG.E05	(AG)10	GTG CAA ACT AAT CCA AAG CAA ATG TAG GGA CAA AGG AAT AAA TCA	58 C	112	2L	0.79
dupssr22	MAG.D01	(GA)29	CTC TCC CCC CCT CTC CCT GTG TAT GTC TCC AAC ACG CG	63 C	113		0.76
dupssr23	MAG.1A03	(GA)2 TA (GA)19	TGA TCA TCA TAA GCA CAC CG CCA ATG TGA AGC AAG AGA GAA	58 C	104	3L	0.82
dupssr24	MAG.1A01	(GA)16	ACT GCA CTG CAC CTC TCT C ACA CAA CGG CTT CTA ACC TT	57 C	110	2L	0.89
dupssr25	MAG.1F03	(GA)18	TGT TCA CTT GTC CAC CAC TG GGA AGC ACA TAA ACT ATC TCG G	58 C	145	2L	0.83
dupssr26	MAG.1E07	(GA)23	GTC GGA GCA CTC CAA GAC CTT CTC GCT CAT CAG CTT AAA	56 C	142		0.71
dupssr27	MAG.T01D04	(TG)13 (AG)29	CTA TAG TTG CCA CCA CAT CC ACC CTT TGT GTA ACT TTT CA	56 C	140		0.86
dupssr28	MAG.T01H07	(GA)28	GAA GGA AGC CTT TGT TAC AAG T CTG GAG TGC TGG TCT TGT TAT	56 C	116	4L	0.87
dupssr29	MAG.T01D06	(GA)24	CAG CGA ATA CTG AAT AAC GC TGT TGG ATG AGC ACT GAA C	56 C	121	9L	0.87
dupssr30	MAG.T01C02	(AG)25	TGA TAG TTT ATG GTA GCA ACT CG CAT TGT GCG GGT AAT GCT	56 C	109		0.84
dupssr31	MTTC.D01	(TTC)80	GAT AGG AGT GCT GAC GCT AA ATC CTG CTA TAG AGT CCA GAC TT	56 C	400		0.84
dupssr32	MTTC.G01	(TTC)65	AGG CCT GTT TAT TTG GCG TCA GTT CCT AGC CCA GGC	56 C	215		0.89
dupssr33	MTTG.H02	(TTG)14	GTG CTT GGG ACA AAA AGG AGT CCA CTC CAG AGG ATG	56 C	100		0.69
dupssr34	MTTG.B02	(TTG)14	TCA GTG CTT TCA TTG TAA CGA ATA AAC ATC TTG CCA GCA AA	56 C	155	4L	0.73

COMBINED TABLE OF SSR LOCI
(primers are available from Research Genetics)

Bin	Locus	SSR Probe	PCR Primer Pairs
1.00-1.05	*bngl147*	p-bngl147(ZCA147)	AGGAAGCTTTGGTCAAGTCTTA
		(Alternative location 7.01)	GCTCACTCGATTTGTTGTGCTA
1.00-1.05	*bngl149*	p-bngl149(ZCA149)	CATCCTCCAAAAGCACTACGT
			CAGCTGTCCGACACTTATTCTGTA
1.01	*tub1*	p-phi056	ACGCCCAGATCTGTTCCTTCTC
			ATGGCGGCAGGCCGATTGTT
1.01	*tub1*	p-phi097	TGCTTCACATTCAGTCACCGTCAG
			CCACGACAGATGATTACCGACC
1.02	*bngl109*	p-bngl109(ZAG109)	GCCAGCTGATGTCTGATGAACAGCACA
			GATCGGGCCAGATTTCTCAAGTCGTCA
1.03	*bngl176*	p-bngl176(ZCA176)	AGTTCACGTCCAGCTGAATGACAG
		(Alternative location 6.04)	CGCGCATCGCATGCTTATCCTA
1.03	*bngl182*	p-bngl182(ZCT182)	AGACCATATTCCAGGCTTTACAG
			ACAACTAGCAGCAGCACAAGG
1.03	*bngl439*	p-bngl439(ZCT439)	TTGACATCGCCATCTTGGTGACCA
			TCTTAATGCGATCGTACGAAGTTGTGGAA
1.03	*p1*	p-phi095	CCGATCGGCTTTATCACTGTTTAGC
			ATGCACCATTCTAGCACTATAGCAACACT
1.03	*ts2*	p-phi001	TGACGGACGTGGATCGCTTCAC
			AGCAGGCAGCAGGTCAGCAGCG
1.04	*bngl652*	p-bngl652(ZCT652)	CGCACGTCGGGAGAGAGGGAGA
			GCCGCAAACATAGCCGCCAAAAAT
1.05	*bngl421*	p-bngl421(ZCT421)	GGGGCAAGGACTTGTCGGT
			AGCCAGTTGCCCAGCATCT
1.06-1.12	*bngl400*	p-bngl400(ZAG400)	AGCTGTGACTGTGAAGGGAAAA
			CGTCACACCGCTGTTTCTTG
1.06	*bngl615*	p-bngl615(ZCT615)	CTTCCCTCTCCCCATCTCCTTTCCAA
			GCAACCTGTCCATTCTCACCAGAGGATT
1.07	*bngl100*	p-bngl100(ZAG100)	TGCACGCACGGGCACTGAAC
			TAAGACATCTATGGCCACCGGAG
1.08	*dupssr12*	p-dupssr12(MAC.E01F06)	CAGGTACTACGTGCCGTG
			CTAGAGACAAACGAGGCTAGG
1.09	*glb1*	p-phi055	GAGATCGTGTGCCCGCACC
			TTCCTCCTGCTCCTCAGACGA
1.09	*glb1*	p-phi094	AAAGAGGAGGAACGCGAAGGAC
			TCACATCCTGGCGGTCACCA
1.09	*glb1*	p-phi011	GAGCTTCAGCAAGAGCATCCAG
			CAACGCGATCGATGTGAGCACA
1.11	*bngl131*	p-bngl131(ZCT131)	CTCTGCGCTACCTTTCTGAGTC
			GCGGAATCCTTGTGTTCTTG
1.11	*bngl504*	p-bngl504(ZCA504)	CGGCAGCTCCAGCACCGGCAT
			AGTGTCCACATACCGCCACACACGTTT
1.11	*phi064*	p-phi064	CCGAATTGAAATAGCTGCGAGAACCT
			ACAATGAACGGTGGTTATCAACACGC
1.12	*bngl257*	p-bngl257(ZCAA257)	TCGAGAGACGAGCGTTTGAATGCT
			GCTCTGAGGTTTTCATACGGGGTT
2.02	*bngl469B*	p-bngl469(ZCA469)	(See 9.03)
2.03	*bngl125*	p-bngl125(ZAG125)	CTGCTCTCACTGAGCTTGATGGAAAGG
			TGCAAATCAATGGCAAGGGACCTCGTAGTT
2.03	*bngl381*	p-bngl381(ZCA381)	TCCCTCTTGAGTGTTTATCACAAA
			GTTTCCATGGGCAGGTGTAT
2.03	*bngl480*	p-bngl480(ZCA480)	GACATTTCCAATGGCGGCTTTCC
		(Alternative location 6.02)	TCTAGTTATTCCAAGCCCTGGGC
2.04	*bngl108*	p-bngl108(ZAG108)	GCACTCACGCGCACAGTTCA
			CGCCTGCCAAGGTACATCAC
2.04	*bngl121*	p-bngl121(ZCT121)	AGTTCTACAGGCTTCTTGTCCAA
			CTATAAAGAAGGTAACTGGTTGCTC
2.04	*bngl166*	p-bngl166(ZCT166)	GCCAACGTTTCCAGCCTGA
			CTCCGTTTGCCCGAGTCC

2.04	*bngl420*	p-bngl420(ZCT420)	CTTGCGCTCTCCTCCCCTT GGCCAGCTCACTGCTCACT
2.04	*prp3*	p-phi083	CAAACATCAGCCAGAGACAAGGAC ATTCATCGACGCGTCACAGTCTACT
2.05	*bngl180*	p-bngl180(ZCT180)	CTAGAGCCTTCGTCGCAGAG AACGGCGGCGAGATAAAAT
2.05-2.10	*bngl371*	p-bngl371(ZCA371)	CAACGCGAAGCAGAGATAAAA TCGTCGCATGACCATAGTAGC
2.05-2.06	*dupssr21*	p-dupssr21(MAG.E05)	GTGCAAACTAATCCAAAGCAA ATGTAGGGACAAAGGAATAAATCA
2.08	*bngl198*	p-bngl198(ZCT198)	GTTTGGTCTTGCTGAAAAATAAAA GCTGGAGGCCTACATTATTATCTC
2.08	*dupssr24*	p-dupssr24(MAG.1A01)	ACTGCACTGCACCTCTCTC ACACAACGGCTTCTAACCTT
2.08	*dupssr25*	p-dupssr25(MAG.1F03)	TGTTCACTTGTCCACCACTG GGAAGCACATAAACTATCTCGG
3.04	*bngl602*	p-bngl602(ZCT602)	CCCGATAGCCAAGCTCTCGCCAA AGCTCGTGGACCGAACAAGCCCA
3.04	*tpi4*	p-nc030	CCCCTTGTCTTTCTTCCTCC CGATTAGATTGGGGTGCG
3.04	*tpi4*	p-phi029	TTGTCTTTCTTCCTCCACAAGCAGCGAA ATTTCCAGTTGCCACCGACGAAGAACTT
3.05	*gst4*	p-phi073	TTACTCCTATCCACTGCGGCCTGGAC GCGGCATCCCGTACAGCTTCAGA
3.06	*dupssr23*	p-dupssr23(MAG.1A03)	TGATCATCATAAGCACACCG CCAATGTGAAGCAAGAGAGAA
3.07	*bngl197*	p-bngl197(ZCT197)	GCGAGAAGAAAGCGAGCAGA CGCCAAGAAGAAACACATCACA
3.08	*bngl150*	p-bngl150(ZCA150) (Alternative location 5S)	GAAAAACCCCCTCCCCATAT AATGGCCGAACACAATTCAA
4.00-4.04	*bngl372*	p-bngl372(ZCA372)	TTCACATGCCATCCTCCTATAT TATCCCTCTCTGATCACGTTGG
4.01	*mtl1*	p-phi072	ACCGTGCATGATTAATTTCTCCAGCCTT GACAGCGCGCAAATGGATTGAACT
4.03	*adh2*	p-nc004	TGCGAAGAAGCAGTAGCAAA TGGAGGTAGAAGACGCACG
4.03	*adh2*	p-phi021	TTCCATTCTCGTGTTCTTGGAGTGGTCCA CTTGATCACCTTTCCTGCTGTCGCCA
4.04	*bngl252*	p-bngl252(ZAG252)	CGTTCTCCGTACAGCACAGACCAACGT CTCAGATGAACTCCTCAGCAGCTGTAGCCT
4.04	*bngl490*	p-bngl490(ZCA490)	GCCCTAGCTTGCTAATTAACTAACA ACTGTAAGGGCAGTGGACCTATA
4.04	*bngl667*	p-bngl667(ZCT667)	CGTGGATGTAAGGGGGCGCGCT GGCCGCTGCTCAACACAGGCAG
4.04	*zp22.1*	p-phi074	CCCAATTGCAACAACAATCCTTGGCA GTGGCTCAGTGATGGCAGAAACT
4.05	*gpc1*	p-nc005	CCTCTACTCGCCAGTCGC TTTGGTCAGATTTGAGCACG
4.05	*gpc1*	p-phi079	TGGTGCTCGTTGCCAAATCTACGA GCAGTGGTGGTTTCGAACAGACAA
4.05	*gpc1*	p-phi026	TAATTCCTCGCTCCCGGATTCAGC GTGCATGAGGGAGCAGCAGGTAGTG
4.05	*zp19/22(pms2)*	p-phi096	CAACAATGTCGTCGTCGCTCTATC GACGACCGTTGAAACTGGTGCTTT
4.06-4.07	*dupssr34*	p-dupssr34(MTTG.B02)	TCAGTGCTTTCATTGTAACGA ATAAACATCTTGCCAGCAAA
4.08	*bngl292B*	p-bngl292(ZAG292)	(See 9.06)
4.08	*dupssr28*	p-dupssr28(MAG.T01H07)	GAAGGAAGCCTTTGTTACAAGT CTGGAGTGCTGGTCTTGTTAT
4.08	*ssu1*	p-phi092	GTGGGGGAGCCTACTACAGG GACGAGGCCATCATCACGGT
4.08	*ssu1*	p-phi093	AGTGCGTCAGCTTCATCGCCTACAAG AGGCCATGCATGCTTGCAACAATGGATACA
4.09	*bngl589*	p-bngl589(ZAG589)	GGGTCGTTTAGGGAGGCACCTTTGGT GCGACAGACAGACAGACAAGCGCATTGT

4.11	*cat3*	p-phi006	AGGCGGCGTGCTGAACACCT CGCTTCATCTCCCGTGACAATG
4.11	*cat3*	p-phi076	TTCTTCCGCGGCTTCAATTTGACC GCATCAGGACCCGCAGAGTC
4.11	*cat3*	p-phi019	TCCGCCTTTGTACCAATACAAGCCA ATCCATCTTCAGGTAGCAGGGGT
5.00	*ohp2*	p-nc007	ACTGTTCCACCAAACCAAGC CTCCATGGAGAAGACGCG
5.00	*ohp2*	p-phi024	ACTGTTCCACCAAACCAAGCCGAGA AGTAGGGGTTGGGGATCTCCTCC
5.00-5.03	*bngl150*	p-bngl150(ZCA150) (Alternative location 3.08)	GAAAAACCCCCTCCCCATAT AATGGCCGAACACAATTCAA
5.01	*bngl143*	p-bngl143(ZCA143)	GCACTGCCGGAGTGCCTTCT ATGCCGTGATCTGTGACATCTAACC
5.01	*dupssr1*	p-dupssr1(MAC.E00B03)	TGTTCTCAACAACCACCG CGTTTAGCGATATCATTTTCC
5.02	*bngl105*	p-bngl105(ZAG105)	GACCGCCCGGGACTGTAAGT AGGAAAGAAGGTGACGCGCTTTTC
5.02	*bngl565*	p-bngl565(ZAG565)	TAAGAACGACGAACGGTAACTG GCTCACTGCACGCCAACAC
5.02	*ole2*	p-phi113	GCTCCAGGTCGGAGATGTGA CACAACACATCCAGTGACCAGAGT
5.03	*bngl557*	p-bngl557(ZAG557)	TCACGGGCGTAGAGAGAGA CGAAGAAACAGCAGGAGATGAC
5.03	*rab15*	p-phi008	CGGCTACGGAGGCGGTG GATGGGCCCACACATCAGTC
5.04	*bngl603*	p-bngl603(ZCT603)	CTGAGCTGGCCCCTGTGAATGGTG CGCCCTCCGCTGCGCTTCTCT
5.04	*bngl653*	p-bngl653(ZCT653)	CGCATTGCCATGGATGAAGAACTGG GCAAGCGCCTCACAAGGTATGCACA
5.04	*dupssr10*	p-dupssr10(MAC.E01A03)	AGAAAATGGTGAGGCAGG TATGAAATCTGCATCTAGAAATTG
5.06	*bngl278*	p-bngl278(ZAG278)	CATGCATCAACGTAACTCCCT CATGTCACGCGTTCCACTTG
5.06	*bngl609*	p-bngl609(ZCT609)	GCTCGTTCTCGCCAGTGTGCCG GGCCCGAGCCATCTCTGCTGC
5.07	*gln4*	p-phi085	CGAGACCACCATCATCTGGAAG TTTGCAATCGCTTCGGGGACC
5.08	*bngl118*	p-bngl118(ZCT118)	CTTCCAGCCGCAACCCTC CCAACAACGCGGACGTGA
5.08	*bngl389*	p-bngl389(ZCT389)	GGTCACCCTCCCTTTGCAG ATTGCCTACACAGTTTGATTGG
5.09	*bngl386*	p-bngl386(ZAG386)	CACCCTCCCTTTGCAGGTA TGGTTTATCAGATAACGATTCAGC
6.00	*fdx1*	p-phi075	GGAGGAGCTCACCGGCGCATAA AAAGGTTACTGGACAAATATGCGTAACTCA
6.01	*bngl107*	p-bngl107(ZAG107)	AGCAATGCATTATCTTTTGGGACAAACCCCA CAACAACAAGTGGCTGGCTAGGGTGAA
6.01	*bngl161*	p-bngl161(ZCT161)	GCTTTCGTCATACACACACATTCA ATGGAGCATGAGCTTGCATATTT
6.01	*bngl238*	p-bngl238(ZAG238)	CTTATTGCTTTCGTCATACACACACATTCAT GAGCATGAGCTTGCATATTTCTTGTGG
6.01	*bngl249*	p-bngl249(ZAG249)	CCGGTCGCAGTTAGTAGATGAT TCGGCGTTGATTTCGTCAGTA
6.01	*bngl391*	p-bngl391(ZCAA391)	CAGATATCACAGCATCAGAAGATCA AAAATGTAAGAACTTGTTTGGGATT
6.01	*bngl426*	p-bngl426(ZCT426)	TGCATTAATTAGAAGGCTATCAAA GGTTTGGTGACTGGACTGACTT
6.01	*phi077*	p-phi077	GAGAAGAGGATCAGGTTCGTTCCA CGCGTTGTACATCTTGCCTGCTT
6.02	*bngl480*	p-bngl480(ZCA480) (Alternative location 2.03)	GACATTTCCAATGGCGGCTTTCC TCTAGTTATTCCAAGCCCTGGGC
6.04	*pl1*	p-nc010	TGAGCTGACGACGAGCAG CATTATCTGTTCGGCCCG
6.04	*pl1*	p-nc009	CGAAAGTCGATCGAGAGACC CCTCTCTTCACCCCTTCCTT

6.04	*pl1*	p-phi031	GCAACAGGTTACATGAGCTGACGA CCAGCGTGCTGTTCCAGTAGTT
6.04	*bngl176*	p-bngl176(ZCA176) (Alternative location 1.03)	AGTTCACGTCCAGCTGAATGACAG CGCGCATCGCATGCTTATCCTA
6.05	*bngl345*	p-bngl345(ZCT345)	CGAAGCTAGATGTAGAAAACTCTCT CTTACCAACCAACACTCCCAT
6.05	*pdk1*	p-nc012	TAATTTAAACACCACACCACCG ACACACGCCAAAGAAAAACC
6.05	*pdk1*	p-phi081	AAGGAACTGGTGAGAGGGTCCTT AGCCCGATGCTCGCCATCTC
6.05	*pdk1*	p-phi078	CAGCACCAGACTACATGACGTGTAA GGGCCGCGAGTGATGTGAGT
6.05	*pdk1*	p-phi025	GCAACATCCTGGAGAGCCACTACAAGG ACAGCCTGTTTTCCTGGACAGTGAACTC
6.06	*dupssr15*	p-dupssr15(MAC.T02E01)	GAAGTCGATCCATCCACC GGGGTAGTGGAGATAACTAGTG
6.07	*tlk1*	p-phi070	GCTGAGCGATCAGTTCATCCAG CCATGGCAGGGTCTCTCAAG
7.01	*o2*	p-phi057	CTCATCAGTGCCGTCGTCCAT CAGTCGCAAGAAACCGTTGCC
7.01	*o2*	p-phi112	TGCCCTGCAGGTTCACATTGAGT AGGAGTACGCTTGGATGCTCTTC
7.01	*bngl147*	p-bngl147(ZCA147) (Alternative location 1S)	AGGAAGCTTTGGTCAAGTCTTA GCTCACTCGATTTGTTGTGCTA
7.02	*bngl398*	p-bngl398(ZAG398)	CGTCGGCCAACAGGGTATC CTCGCACGCGGTCTTCTTC
7.02	*oec17*-Z26824*	p-phi114	CCGAGACCGTCAAGACCATCAA AGCTCCAAACGATTCTGAACTCGC
7.03-7.06	*bngl339*	p-bngl339(ZCT339)	CCAACCGTATCAGCATCAGC GCAGAGCTCTCATCGTCTTCTT
7.03	*bngl434*	p-bngl434(ZCT434)	GTGCAAAGGGGAGAGAGGAA TCGCCGTTCTTCGCCTTAG
7.03-7.06	*bngl572*	p-bngl572(ZAG572)	ACTGGACTGTCCTCGTGCCTA CAAAAAAAGATTCGTTCGGAGTAA
7.03	*bngl657*	p-bngl657(ZCT657)	TCTGAGGATGCCCAATCATGCGC CGTTTCCGTTCGTCACCAGCTCG
7.03	*dupssr11*	p-dupssr11(MAC.E01C02)	AGGCAAGGCTTTCTTCATAC CGGACGACGACTGTGTTC
7.03-7.04	*dupssr9*	p-dupssr9(MAC.E01G01)	GATGTCGTGTGAGTGACCTG GTGTTGCTATTGCAGTGAGAC
7.04	*bngl155*	p-bngl155(ZCT155)	ACCGAGTAGCCGAGACACG AGAGTCCTGGAGCCACATGAG
7.04	*dupssr13*	p-dupssr13(MAC.E01F07)	TCGTTCGGTCCATGAAAT CAAATATCTCTCATCTTTGCTGAC
7.06	*bngl469C*	p-bngl469(ZCA469)	(See 9.03)
7.06	*uaz230(gfu)*	p-phi082	CACAGCACAGGCAGTTCG CGCGGCAAAAGATCTTGAACACCT
8.01	*bngl669*	p-bngl669(ZCT669)	GCACGCACCAGCAGTCGGCAGT CGGCCTAGTGGGCATGGAGCCT
8.02	*bngl119*	p-bngl119(ZCT119)	AGGTGAGGAGAGGAAAGGTTGT GCCACTCCGCATCCGAGC
8.02	*bngl666*	p-bngl666(ZCT666)	AAAAGGCAAGTAGCTAGCATGCATTTGCAG GGCTCACGTCCGTATCCAAACCAACA
8.02	*dupssr3*	p-dupssr3(MAC.E01C08)	TTTAAAACCTCTTTATGACTTTTG CTGATACCATATCCAGCATCA
8.03	*bngl162*	p-bngl162(ZCA162)	ACTAGCAGCAGTAAAACCTAATAAAGGGA CAAGTAGCTAGCAGTCATTTGCAGTGT
8.04	*act1*	p-phi115	CTAGTGGGCGAACAACTGGTAAG AAAGAGACCGTGTCAGGATTGCC
8.04	*bngl240*	p-bngl240(ZAG240)	AAGAACAGAAGGCATTGATACATAA TGCAGGTGTATGGGCAGCTA
8.04	*rip1*	p-phi060	ACATGCAGAAGCTTGGCATCAAGG GCTGAGCGATCAGTTCATCCAG
8.04	*rip1*	p-phi014	AGATGACCAGGGCCGTCAACGAC CCAGCTTCACCAGCTTGCTCTTCGTG

8.08	*dupssr14*	p-dupssr14(MAC.E01C01)	AGCAGGTACCACAATGGAG GTGTACATCAAGGTCCAGATTT
8.08	*gst1*	p-phi080	CACCCGATGCAACTTGCGTAGA TCGTCACGTTCCACGACATCAC
8.08	*gst1*	p-phi015	GCAACGTACCGTACCTTTCCGA ACGCTGCATTCAATTACCGGGAAG
9.01-9.02	*dupssr6*	p-dupssr6(MAC.T02B08)	GATCCTACCAAAATCTTATAGGC ACAGCTAGCCAAGATCTGATT
9.01	*sh1*	p-phi033	ATCGAAATGCAGGCGATGGTTCTC ATCGAGATGTTCTACGCCCTGAAGT
9.01	*sh1*	p-phi028	TCTCGCTGTCCTTCGATTAGTACGG AATGCAGGCGATGGTTCTCCGGCCT
9.01	*sh1*	p-phi044	TTATTGGTCCCTCTCCCGTCCCAGA AGCATACCCCAATGGTCAACAGGGA
9.02	*bngl244*	p-bngl244(ZAG244)	GATGCTACTACTGGTCTAGTCCAGA CTCCTCCACTCATCAGCCTTGA
9.02	*bz1*	p-phi017	CGTTGGCGACCAGGGTGCGTTGGAT TGCAACAGCCATTCGATCATCAAAC
9.03	*bngl127*	p-bngl127(ZCT127)	CATGTATACGAGAAGCACCCTAT ATCGTAACTCAGCGGTTTGTG
9.03	*bngl430*	p-bngl430(ZCT430)	CTTATCGAGCATCTTCCTTCTCTCC TCCGGTGATGCTCCAGCGAC
9.03	*bngl469A*	p-bngl469(ZCA469)	AGGGTGTACAGGTCCAAGTCCAA AATGTGGGTCGTCAGCCATCAG
9.03	*dupssr19*	p-dupssr19(MAG.E01)	GCTGAAGGACTAAAGAAACCG CCTCCAAGGTTGGTACTGTC
9.03	*pep1*	p-phi065	AGGGACAAATACGTGGAGACACAG CGATCTGCACAAAGTGGAGTAGTC
9.03	*wx1*	p-phi022	TGCGCACCAGCGACTGACC GCGGGCGACGCTTCCAAAC
9.03	*wx1*	p-phi027	CACAGCACGTTGCGGATTTCTCT GCGTACGTACGACGAAGACAC
9.03	*wx1*	p-phi061	GACGTAAGCCTAGCTCTGCCAT AAACAAGAACGGCGGTGCTGATTC
9.04	*sus1*	p-phi032	CTCCAGCAAGTGATGCGTGAC GACACCCGGATCAATGATGGAAC
9.04	*sus1*	p-phi016	TTCCATCATTGATCCGGGTGTCG AAGGAGCAACATCCCATCCAGGAA
9.04	*sus1*	p-phi042	ATGTGGCCATCATTCAATGCTGTAGAC ACACATGCAGGTGCAGCCAGA
9.06	*bngl128*	p-bngl128(ZCT128)	CACCTGGAGGGACCCATTCC AGGACCACAGGATCCATCATCCT
9.06	*bngl279*	p-bngl279(ZAG279)	GCATGCGTACCTTCAAGCTA TGTGTTCATCGGCAATTTTG
9.06	*bngl292A*	p-bngl292(ZAG292)	TGGTAGGACCTTACAATGGGA CGGGAGTACTGCTACACACGA
9.06	*bngl619*	p-bngl619(ZCT619)	ACCCATCCCACTTTCCACCTCCTCCT GCTTTCAGCGAATACTGAATAACGCGGA
9.06-9.07	*dupssr29*	p-dupssr29(MAG.T01D06)	CAGCGAATACTGAATAACGC TGTTGGATGAGCACTGAAC
10.02	*phi059*	p-phi059	AAGCTAATTAAGGCCGGTCATCCC TCCGTGTACTCGGCGGACTC
10.02	*phi063*	p-phi063	GGCGGCGGTGCTGGTAG CAGCTAGCCGCTAGATATACGCT
10.03	*bngl210*	p-bngl210(ZAG210)	GCCTCGCACCAAGACATAATA TGCCCCATTTGAGTAGACTTC
10.03	*bngl640*	p-bngl640(ZCT640)	TGCGGATCCAACACGGACTGTCC GCAGGCTCTCCGCCCACACCTC
10.04	*bngl137*	p-bngl137(ZCA137)	AGACAACTACCCCCACCCA CCAGGTTACCGTGAAATGCT
10.04	*hsp90**	p-phi071	GGAGTTCATCAGCTACCCCATCT TTCTGCTTGTTGATCTGCACCCAC
10.04	*mgs1*	p-phi062	CCAACCCGCTAGGCTACTTCAA ATGCCATGCGTTCGCTCTGTATC
10.04	*nac1*	p-phi084	AGAAGGAATCCGATCCATCCAAGC CACCCGTACTTGAGGAAAACCC

10.06	*bngl153*	p-bngl153(ZCT153)	TCCACTGCTCCTCCACTGC
			CACTTCAAACTGTCAAATCTCCA
10.06	*bngl236*	p-bngl236(ZAG236)	CGCTTTGCAGTACCAGTACACAC
			GACGACAACTGCAGAGTACCAGA
10.06	*bngl594*	p-bngl594(ZAG594)	CGAGCGCTTTGCGAGTACCAGTACACA
			CTGCGTGCGTCCAGCCTCCACT
	dupssr16	p-dupssr16(MAG.B01)	TTCTTTAACTATTGGAAGCCCA
			GCGCAATATTCTCTCTATATTGAA
	dupssr17	p-dupssr17(MAG.1C05)	AGAAGAAAGCGAGCAGACAG
			GAGACACATCACACCCTAAGTTC
	dupssr18	p-dupssr18(MAG.G02)	AATTTGAGGATTTCCGCGA
			ACATCACACGCAGAGCTAATC
	dupssr2	p-dupssr2(MAC.T03B03)	GCTAAATGATCAGTCATCCATG
			CCATGTCGCTCACACAT
	dupssr20	p-dupssr20(MAG.C04)	TGTTCATGTATGATTTGCCAA
			TCCTGGCACTAGTTTTTCTTTT
	dupssr22	p-dupssr22(MAG.D01)	CTCTCCCCCCCTCTCCCT
			GTGTATGTCTCCAACACGCG
	dupssr26	p-dupssr26(MAG.1E07)	GTCGGAGCACTCCAAGAC
			CTTCTCGCTCATCAGCTTAAA
	dupssr27	p-dupssr27(MAG.T01D04)	CTATAGTTGCCACCACATCC
			ACCCTTTGTGTAACTTTTCA
	dupssr30	p-dupssr30(MAG.T01C02)	TGATAGTTTATGGTAGCAACTCG
			CATTGTGCGGGTAATGCT
	dupssr31	p-dupssr31(MTTC.D01)	GATAGGAGTGCTGACGCTAA
			ATCCTGCTATAGAGTCCAGACTT
	dupssr32	p-dupssr32(MTTC.G01)	AGGCCTGTTTATTTGGCG
			TCAGTTCCTAGCCCAGGC
	dupssr33	p-dupssr33(MTTG.H02)	GTGCTTGGGACAAAAAGG
			AGTCCACTCCAGAGGATG
	dupssr4	p-dupssr4(MAC.T02E08)	CGATACTAATGGAAGCCCTAA
			ATGGCCCATTAAGTTTATCAC
	dupssr5	p-dupssr5(MAC.E01E07)	GGCAATCAAGCTAAGGAAG
			GCAGTGCAGATGTTTAGAAGA
	dupssr7	p-dupssr7(MAC.T02H12)	GAAGCTTAATCTGGAATCTGG
			TGTTGCTTCCTTGTAAAATCT
	dupssr8	p-dupssr8(MAC.T02B10)	AAATAGTCCAGAAAAAAATAGTGTG
			ACCTCTTGTTTTCCACAGTTC

VIII. WORKING MAPS

The **Genetic Working Maps** presented in MNL 69:247-256 contain the most recent complete synthesis of known gene mapping information, built on an RFLP map framework. They were prepared by compiling information from all available sources of mapping data. The RFLP maps in this issue are substantially enhanced, updated and expanded, developed during the past year as part of the Maize Mapping Project.

The **Maize Mapping Project**, UMC/USDA-ARS, seeks to develop organized, functional knowledge and mapping data on genetic content and relationships in the nuclear genome of maize. Insofar as priorities and resources permit, we are continuing to map RFLP markers. Our current priorities include mapping of (1) functionally defined clones that we request following reports in the literature or that we receive voluntarily from research scientists; (2) the remaining sequenced *csu* cDNA clones produced and evaluated by Dr. Chris Baysdorfer; (3) cDNA anchor sets from other grass species. At the same time we are mapping phenotypic and morphological mutants relative to molecular markers with the goal of identifying potential cDNA/mutant allelic pairs. Association of a cDNA sequence with a phenotype provides a powerful tool to enhance our understanding of biochemical pathways, regulatory functions, and quantitative trait expression. Identification of gene functions by either cDNAs or phenotypes that correspond to QTL regions may permit dissection of the trait and enhance our understanding of the effects of specific genes relative to traits of interest.

To locate large numbers of mutants relative to molecular markers, including DNA sequences of known function, several resources are needed. The first is a solid, high resolution map containing a large number of sequenced cDNAs. The second is a "Core Marker" set of simple, evenly spaced RFLP markers that forms a framework for grouping mutants, cDNAs and QTLs to chromosome region. The third is a rapid, cost-effective means of dealing with the large number of mapping populations needed to place the myriad of already documented and new, phenotypically characterized mutants into bins.

OBJECTIVES

1. Produce a well defined genetic map with a preponderance of sequenced cDNAs using the Tx303 x CO159 Immortalized F2 population (this report is an update).
2. Define an appropriate set of core markers to facilitate localization of genes defined by mutants or by cDNAs, and of QTLs, into "bins" (MNL 69:247-256).
3. Develop and implement a simple, rapid, and cost-effective strategy for large-scale mapping of mutants (manuscript in preparation).

METHODS AND PROGRESS

1. High Resolution Map: The mapping population consists of 54 Immortalized F2 individuals from a cross of Tx303 x CO159 (Gardiner et al., 1993). Hybridization and washing procedures were conducted according to the protocols given in the University of Missouri RFLP Laboratory Manual (copies are available by writing the UMC RFLP Lab or by request from musket@teosinte.agron.missouri.edu). All hybridizations were carried out using ^{32}P oligolabelled probes. All probes were screened for polymorphism with CO159 and Tx303 using *Eco*RI, *Hin*dIII, *Eco*RV, *Bam*HI, *Dra*I, *Xba*I, *Bgl*II, and *Sst*I. The enzyme with the best fragment separation between the two lines was chosen for mapping. In some cases more than one enzyme was used to map multi-copy probes.

Data collection and map construction: During the past 18 months, we have made a particular effort to review and to enhance the quality of the data. All autoradiograms were scored independently by two readers. Markers with more than 3 missing data points were discarded. Chromosomes were constructed using MAPMAKER for UNIX, Version 3 on a Sun SPARC Server 1000. The 10 maize chromosomes were defined with the 'make chromosome' function and the 90 core markers were anchored to chromosomes. Initial framework orders were assigned for the core markers for each chromosome. The remaining markers were attached to linkage group with the 'assign' command. Additional markers were added to the framework, first at LOD3 then at LOD2, 10-15 markers at a time with the 'build' command. Remaining markers assigned to each linkage group were added with the 'place' command. Marker loci with more than three double crossovers based on the 'genotype' function were deleted. Chromosome maps were extracted to postscript files and edited with the UNIX text editor. The resulting form of the maps is similar to those presented by Matz, Burr and Burr (MNL 69:257-267).

The 1995 UMC map contained approximately 600 loci. The 1996 map contains about 1000 loci, with the most substantial increase in the number of cDNA and defined-function loci (over 240 loci are detected by csu cDNAs, isolated and sequenced by Chris Baysdorfer; these are part of a targeted group of approximately 1000 csu clones we are mapping in this collaboration).

2. Core Markers: Core markers are as on the 1995 map except for the replacement of umc163 with the more suitable umc259 at the same location on chromosome 10. In some cases an acronym for candidate function has been added to the name of the probed site, based upon information following sequencing. Core markers were selected as follows. Markers that had simple fragment patterns and were distributed along the chromosome every 20 to 30 cM were selected as potential core markers. Markers that were not among the previous set of cores identified by Gardiner et al., 1993, were screened against A619, A632, B73, Mo17, CO159, and Tx303 using *Eco*RI, *Hin*dIII, *Eco*RV, *Bam*HI, *Dra*I, *Xba*I, *Bgl*II, and *Sst*I to determine whether they were polymorphic enough to be designated as core markers. Several substitutions last year were made due to low levels of polymorphism or high fragment pattern complexity. Subsequently, all the previous core markers were screened in the same manner. Final choices were based on even spacing, simple fragment patterns, and high degrees of polymorphism.

Locus names for clones have been assigned according to the following criteria:

1. Gene, function defined. If a clone has been sequenced and found to have high similarity (typically BlastX score of at least 80) to a previously defined functional protein or gene, and detects a single site in a number of lines with multiple enzymes, the locus is named as a gene with a suitable acronym, according to the Maize Nomenclature Standards (MNL 69:182-184; Web location http://www.agron.missouri.edu/maize_nomenclature.html).

2. Gene candidate. If a clone has high similarity to a previously defined functional molecule or gene, but detects multiple sites, each mapped locus is named as a probed site with a suitable acronym in parenthesis, e.g., *csu179a(hsp70)*. This designation reflects the potential function of this site, pending evidence for a function of a gene specifically at this location. Relevant information such as GenBank number and potential product or function may be retrieved from MaizeDB using the locus name.

3. Gene, function unknown. If a cDNA has no significant similarity and detects a single site, the mapped locus is named as a probed site, e.g. *csu320*. Addition of the acronym *gfu*, e.g. *csu320(gfu)*, for "gene, function unknown", has been deferred.

4. Probed site. If a clone has no significant similarity or has not been examined for similarity, and detects more than one site, loci detected are named as probed sites, e.g., *csu315c*.

Categories 2, 3, and 4 may be upgraded at any time pending additional information from the literature or updated similarity searches. Changes are reflected regularly in MaizeDB in both the locus names and in the maps themselves. Previous designations are maintained as synonyms to facilitate searching.

Acronyms in parentheses, for probed sites on maps, identify the candidate function at that site, based on high sequence similarity but showing multiple sites (see criterion 2 above). These acronyms, and the name of the gene product or function, follow.

a1	anthocyaninless1
aba	abscisic stress protein homolo
acc	acetyl-coenzyme A carboxylase1
act	actin
adc	amino deoxychorismate synthesis
adh2	alcohol dehydrogenase2
aga	alpha-galactosidase
agp1	ADP glucose pyrophosphorylase1
agp2	ADP glucose pyrophosphorylase2
ahh	adenosyl homocysteine hydrolase
alr	aleurain
als1	acetolactate synthase1
als2	acetolactate synthase2
alt	alanine amino transferase
amyBS2	beta amylase
anp1	anaerobic protein1
ant	adenine nucleotide translocator
ap	apetala
ars1	autonomously replicating sequence
atp	ATP synthase
atpb	ATP synthase beta subunit, mitochondrial
b32a	aka rip, ribosome inactivating protein
b32b	aka rip, ribosome inactivating protein
b32c3a	aka rip, ribosome inactivating protein
b32c3b	aka rip, ribosome inactivating protein
b70a	heat shock protein, 70kDa
b70b	heat shock protein, 70kDa
bre1	branching enzyme1
Bs1	barley stripe, transposable element
bt2	brittle endosperm2
bZip	bZip motif
cab,	chlorophyll a/b binding protein
cac	calcium chanel protein
cah	carbonic anhydrase
cat1	catalase1
cat3	catalase3
cdc2	cell division control protein2
cdc2a	cell division control protein2
cdc2b	cell division control protein2
cdc2c	cell division control protein2
cdc48	cell division protein48
cdj	chaperone DNA J
cdpk	calcium dependent protein kinase
cgn	collagen
chi	chalcone flavanone isomerase
chn	chitinase
chs1a	chitin synthase
chs1b	chitin synthase
cin4	cin4, transposable element
ck	casein kinase
clp	CLP protease
clx	calnexin
cppgk	phosphoglycerate kinase, chloroplast
csa	contact site A glycoprotein
cts	citrate synthase
dba	DNA binding activity
dcm1	deoxycytidine methylase
dcso	disconnected protein, DISCO
DH7	cytochrome P450
dts	aspartyl-tRNA synthetase
eif	eucaryotic initiation factor
eif2	eucaryotic initiation factor2
eif5A	eucaryotic initiation factor 5
elf	elongation factor
elf1	elongation factor
EMu	endogenous Mu, transposable element
end	early nodulin
ets	ets-family transcription factor
ext	extensin
F-bA	fructose-bisphosphate aldolase
fdx	ferredoxin
fer	ferritin
gab1	gibberellin
gag	GAG polyprotein
gast	gibberellin stimulated transcript
gbp	GTP-binding protein
glb	globulin
GlDh	glutamate dehydrogenase
gne	guanine nucleotide exchange
gpc	glyceraldehyde 3-phosphate dehydrogenase
gpc1	glyceraldehyde-3-phosphate dehydrogenase1
gpr	G protein subunit
grf	general regulatory 14-3-3 protein
grp	glycine-rich protein
grx	glutaredoxin
gss	starch synthase
gts	glutaminyl-tRNA synthetase
hfi	Hageman factor inhibitor
his2a	histone H2A
his2b	histone H2B
his2B1	histone H2B1
his3	histone 3

hmd	homeodomain protein
hox	homeobox
hsp	heat shock protein
hsp18	heat shock protein 18kDa
hsp70	heat shock protein, 70kDa
hsp90	heat shock protein, 90 kDa
incw	invertase, cell wall
inv1A	invertase
iron	iron deficiency
ivr	invertase
ivr2a	invertase, soluble
kapp	kinase associated protein phosphatase
kri	ketol-acid reductoisomerase
lan	laminin (glycoprotein)
lbr	
ldl	LDL lipoprotein
lfyA	leafy
lfyB	leafy
lhcb	chlorophyll a/b light harvesting
lox	lipoxygenase
lts	leucine tRNA synthetase
maf	MAF, avian sarcoma
mah9	responsive to abscisic acid15
map	microtuble associated protein
me	NADP malic enzyme1
me2	NADP malic enzyme3
met	methionine synthase
ms	male sterile
msd	methylmalonate-semialdehyde dehydrogenase
mta	mouse transplantation antigen
myb	myb protein
nabp1	nucleic acid binding protein1
nad	NADH ubiquinone oxidoreductase
ndk	nucleotide diphosphate kinase1
nia1	nitrate reductase
nia2	nitrate reductase
nia3	nitrate reductase
nia4	nitrate reductase
nia5	nitrate reductase
nr	nitrate reductase
nrA	nitrate reductase
nrB	nitrate reductase
ntc	Notch
ntm9	neurotoxin M9
obf3A	octopine synthase binding factor
obf3B	octopine synthase binding factor
obf6	octopine synthase binding factor
odo	alpha keto dehydrogenase
oec	oxygen evolving complex
ohp	opaque2 heterodimerizing protein
orp	orange pericarp
orp1	orange pericarp1
orp2	orange pericarp2
P450	cytochrome P450
pac	
pal2	phenylalanine ammonia lyase
pal3	phenylalanine ammonia lyase
pck	phosphoenolpyruvate carboxykinasw
pcr	protochlorophyllide reductase1
pdc1	pyruvate decarboxylase1
pdk	pyruvate, orthophosphate dikinase
pdk2	pyruvate, orthophosphate dikinase
pds	
pds2	
pds3	
PDsI	protein disulfide isomerase
pep	phosphoenolpyruvate carboxylas
pext	pistil extensin
phy	phytochrome1
phyB1	phytochrome
phyB2	phytochrome
plB	
plt	phospholipid transfer protein
pmr15	phosphoenolpyruvate carboxylase
pog1a	globulin processing protein
pog1b	globulin processing protein
pog1c	globulin processing protein
pop	putative organelle permease
ppi	peptidyl-prolyl isomerase
ppp	pyrophosphate-energized proton pump
prc	proteasome C9
prh	protein phosphatase
prk	phosphoribulokinase
prl	protease PrlC1
psaN	photosystem I, subunit N
psei	cystatin
ptk	protein kinase
px	peroxidase
r1	colored1
rab30	responsive to abscisic acid30
rap	retinoblastoma-associated protein
rip	ribosome-inactivating protein
rnp	chloroplast RNA binding protein
rpL10	ribosomal protein L10e
rpL19	ribosomal protein L19
rpL5	ribosomal protein L5
rpL7	ribosomal protein L7
rpS11	ribosomal protein S11
rpS12	ribosomal protein S12
rpS22	ribosomal protein S22
rpS6	ribosomal protein S6
rpS8	ribosomal protein S8
S10	
sam	S-adenosylmethionine decarboxylase
sar	SAR1
sbe	starch branching enzyme
sbe1	starch branching enzyme
sca	short chain alcohol dehydrogenase
sci	subtilisin-chymotrypsin inhibitor
SDAg	Sm-D nuclear antigen
sdh	sorbitol dehydrogenase
ser	serine tRNA synthetase
ser	proteasome C9 subunit
sod	superoxide dismutase
sod2	superoxide dismutase
sod3a	superoxide dismutase
sod3b	superoxide dismutase
sod3c	superoxide dismutase
sod4	superoxide dismutase
sod4a	superoxide dismutase
sod4b	superoxide dismutase
spr1	signal recognition particle re?????
srp	RNA polymerase suppressor
ssu	ribulose bisphosphate carboxylase, small subunit
ssu1a	ribulose bisphosphate carboxylase, small subunit
ssu1b	ribulose bisphosphate carboxylase, small subunit
taf	transcription associated factor
tas1a	telomere associated sequence
tas1b	telomere associated sequence
tas1c	telomere associated sequence
tas1e	telomere associated sequence
tas1g	telomere associated sequence

tas1h	telomere associated sequence
tas1j	telomere associated sequence
tas1l	telomere associated sequence
tas1m	telomere associated sequence
tas1n	telomere associated sequence
tas1o	telomere associated sequence
tas1p	telomere associated sequence
tas2b	telomere associated sequence
tas2g	telomere associated sequence
tas3a	telomere associated sequence
tas4j	telomere associated sequence
tas4k	telomere associated sequence
tas4l	telomere associated sequence
tau	tau protein
tgd	dTDP-glucose dehydratase
thp	thiol protease
thr	threonine synthase
tlk	tousled protein kinase
tpi	triose phosphate isomerase
tpi5	triose phosphate isomerase5
ts2	tassel seed2
tua	alpha tubulin
tyk30	tyrosine protein kinase
ubf9	ubiquitin fusion protein
ubi	polyubiquitin
uce	ubiquitin conjugating enzyme
ugu	UDP-glucose pyrophosphorylase
vfa	vessicle fusion ATPase
vp2274a	viviparous
vp2274b	viviparous
vpp	vacuolar proton pump
vsp	vegetative-specific protein
zag	Zea agamous
zag1	Zea agamous
zag2	Zea agamous
ze40	
zp19	alpha zein
zp22	alpha zein
zpE2	alpha zein

We gratefully acknowledge the generosity of the organizations listed in the map legend, and numerous individual scientists, for providing the probes used in producing the high density map. Special thanks is given to Chris Baysdorfer for providing sequence information for the clones in his library. This research was supported by USDA-ARS and the NRI Competitive Grants Program.

If you have cloned a gene that you would like to have mapped, please send it as a stab if at all possible (otherwise plasmid DNA - we cannot accept clones supplied as insert only), along with a completed clone information sheet (in this issue of MNL, or available electronically at http://www.agron.missouri.edu) to the UMC Maize RFLP Laboratory, ATTN: Theresa Musket, 302 Curtis Hall, University of Missouri, Columbia, MO 65211.
There is no charge for this mapping. All clones submitted for mapping will be included on the public map and in MaizeDB. You will be notified by mail of the location of your clone. If you have questions regarding the status of a clone that you have submitted for mapping, please use the Clone Mapping Query Form in MaizeDB.

Most of the probes for loci listed on this map are publicly available from the University of Missouri-Columbia RFLP Laboratory, as described in Section VI of this issue. See the listing in MaizeDB, "Available From", for particulars, and for information about how to request clones.

Georgia Davis, Mike McMullen, Ed Coe, and Mary Polacco

Quote without comment--

"The Maize Genome Project to identify all corn genes is well underway, and corn seed companies have a strong understanding of their crops...."

"First, and most obvious, traits that would increase the value of an ingredient must be identified...."

"Second, there must be a precise understanding of what elements of plant metabolism might bring about the desired functionality...."

"Third, simple and easy-to-use tests must be developed to identify expression of a plant's 'chemotype.'...."

"Fourth, the information from screening experiments must be collected in such a way as to illuminate the genetic control of characteristics of interest. The Maize Genome Project is well on the way to complete mapping of starch genetic structure. Commercial efforts to identify and understand specific mutants are also underway. Information management systems are designed to easily capture field information and relate it to theoretical models of inheritance...."

--A. C. Stockwell, 1995. Some current developments in technology-assisted breeding. Cereal Foods World 40:7-10.

MAP LEGEND

Markers are listed to the right of the map. Marker sets were provided by:

agr	Mycogen Plant Sciences
asg	Asgrow Seeds
bnl	Brookhaven National Laboratory
csu	California State University-Hayward
isu	Iowa State University
npi	Native Plants Inc. & Pioneer Hi-Bred International
php	Pioneer Hi-Bred International
uaz	University of Arizona
umc	University of Missouri-Columbia

Numerous individual cDNA donors

The large numbers (i.e. 1.01) to the left of the chromosome identify the **bin**, bounded by **Core Markers** located at the horizontal lines. Small numbers immediately to the left of the chromosome indicate cM distances between the markers using Haldane's correction. **Bold** markers are set to the framework, on which order is assured first at LOD 3.0 (occasionally at LOD 2.0). Markers in lighter type are placed at a 2-point LOD of 3.0. Such markers are firmly placed in this part of the map, but order relative to the framework sites cannot be defined. Distance from the framework site is shown preceding the marker or series of markers.

Please refer to the list of new genes in this issue, and to the genelist in MNL 69, for information about individual genes in these maps.

Amazing Maize Maze comes to Ames

by KRISTIN KERNEN
Daily Staff Writer

Imagine acres of corn with people wandering about on twisting paths. No, it's not the Field of Dreams — it's the Amazing Maize Maze.

Volunteers are currently working to finish the "world's largest maze," which will be located in a seven acre field of corn. The paths, which will vary in width from five to 15 feet, will twist and turn around various designs associated with Iowa and the state's sesquicentennial celebration.

The main design for the paths is the symbol that was previously used with the promotional slogan "Iowa - A Place to Grow." The word "Iowa" and "150" also will be spelled out in the maze.

Iowa State architectural student Lori Berglund assisted with the design of the maze and headed the design committee. The Ankeny Lutheran Church, of which Lori is a member, is sponsoring the project.

The field of corn was cross-planted in order to make it very thick, and the paths where the corn is to be removed were marked. After all the paths are marked, an aerial photo shot will be taken to make sure the paths line up correctly. Volunteers are planning to use a roto tiller to clear the corn.

More than two miles of paths make up the maze, which could baffle some visitors for many hours. But there is a trick to reaching the end of the maze with ease — just brush up on Iowa history before going to the maze. Iowa history clues can be found throughout the maze to assist those less fortunate in finding the exits. Several numbered posts with walkie talkies are located around the maze and can be used "in desperation," said Paul Christoffers, who directs the project. Directions will be given to the next numbered post or the exits.

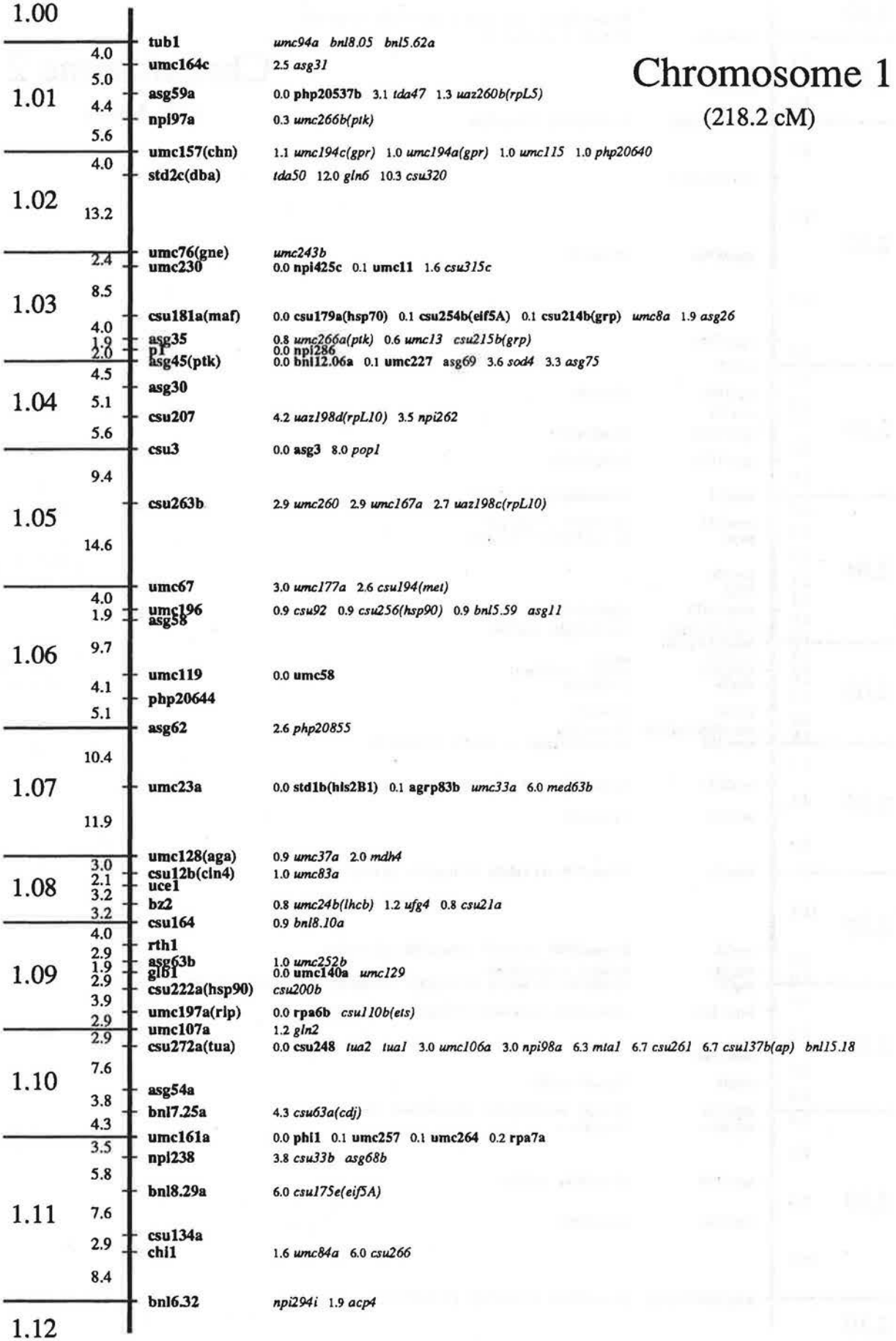
Of course, there is a benefit in finding the dead ends. Christoffers said he hopes to place promotional clues at the dead ends, and offer some sort of prize to people who can correctly identify a certain number of clues after exiting the maze.

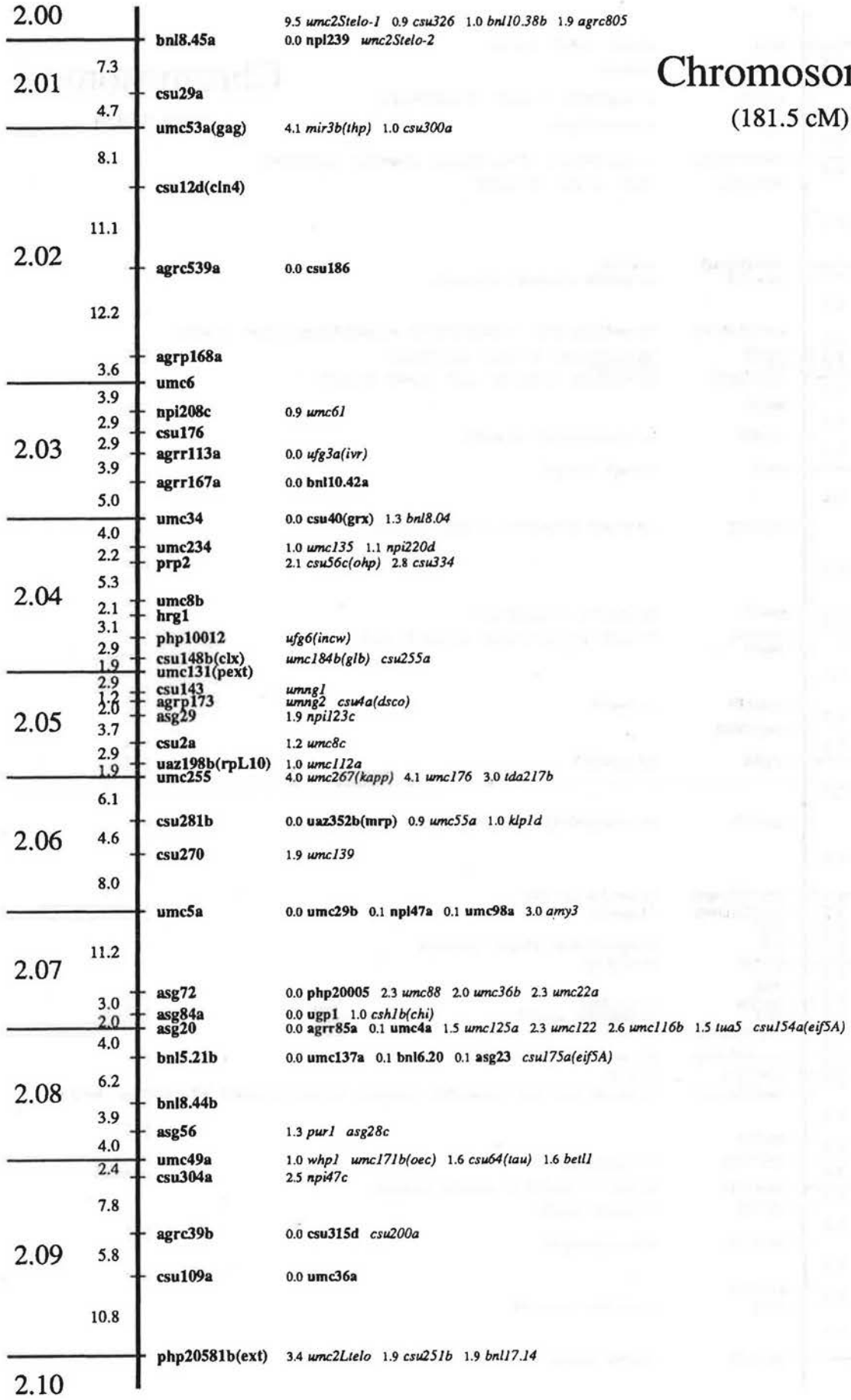
For a real challenge, visitors should wait to visit after the corn has grown to maximum height, which should occur around July 15. At the opening on July 4, the corn will probably have grown only to waist-level.

The main purpose of the project is to raise funds for non-profit organizations. A group can earn money by selling tickets to the maze, by volunteering to work at the grounds, or both.

The Amazing Maize Maze is scheduled to open on July 4 and will remain open to the public every weekend into September. Hours will be from 10 a.m. to 6 p.m. and admission will be $6 per person. All proceeds will go to non-profit organizations. There are still openings for groups that would like to use the fund raising opportunity. Contact John Christoffers at 1-800-965-9921.

Iowa State "Daily", 6-18-96


Chromosome 1
(218.2 cM)
1.00
tub1 umc94a bnl8.05 bnl5.62a
4.0
umc164c 2.5 asg31
5.0
1.01
asg59a 0.0 php20537b 3.1 tda47 1.3 uaz260b(rpL5)
4.4
npi97a 0.3 umc266b(ptk)
5.6
umc157(chn) 1.1 umc194c(gpr) 1.0 umc194a(gpr) 1.0 umc115 1.0 php20640
4.0
std2c(dba) tda50 12.0 gln6 10.3 csu320
1.02
13.2
umc76(gne) umc243b
2.4
umc230 0.0 npi425c 0.1 umc11 1.6 csu315c
8.5
1.03
csu181a(maf) 0.0 csu179a(hsp70) 0.1 csu254b(eif5A) 0.1 csu214b(grp) umc8a 1.9 asg26
4.0
1.9
asg35 0.8 umc266a(ptk) 0.6 umc13 csu215b(grp)
2.0
pt 0.0 npi286
asg45(ptk) 0.0 bnl12.06a 0.1 umc227 asg69 3.6 sod4 3.3 asg75
4.5
asg30
1.04
5.1
csu207 4.2 uaz198d(rpL10) 3.5 npi262
5.6
csu3 0.0 asg3 8.0 pop1
9.4
csu263b 2.9 umc260 2.9 umc167a 2.7 uaz198c(rpL10)
1.05
14.6
umc67 3.0 umc177a 2.6 csu194(met)
4.0
1.9
umc196 0.9 csu92 0.9 csu256(hsp90) 0.9 bnl5.59 asg11
asg58
1.06
9.7
umc119 0.0 umc58
4.1
php20644
5.1
asg62 2.6 php20855
10.4
1.07
umc23a 0.0 std1b(his2B1) 0.1 agrp83b umc33a 6.0 med63b
11.9
umc128(aga) 0.9 umc37a 2.0 mdh4
3.0
csu12b(cln4) 1.0 umc83a
2.1
1.08
uce1
3.2
bz2 0.8 umc24b(lhcb) 1.2 ufg4 0.8 csu21a
3.2
csu164 0.9 bnl8.10a
4.0
rth1
2.9
asg63b 1.0 umc252b
1.9
1.09
gl61 0.0 umc140a umc129
2.9
csu222a(hsp90) csu200b
3.9
umc197a(rip) 0.0 rpa6b csu110b(ets)
2.9
umc107a 1.2 gln2
2.9
csu272a(tua) 0.0 csu248 tua2 tua1 3.0 umc106a 3.0 npi98a 6.3 mta1 6.7 csu261 6.7 csu137b(ap) bnl15.18
7.6
1.10
asg54a
3.8
bnl7.25a 4.3 csu63a(cdj)
4.3
umc161a 0.0 phi1 0.1 umc257 0.1 umc264 0.2 rpa7a
3.5
npi238 3.8 csu33b asg68b
5.8
bnl8.29a 6.0 csu175e(eif5A)
1.11
7.6
csu134a
2.9
chi1 1.6 umc84a 6.0 csu266
8.4
bnl6.32 npi294i 1.9 acp4
1.12

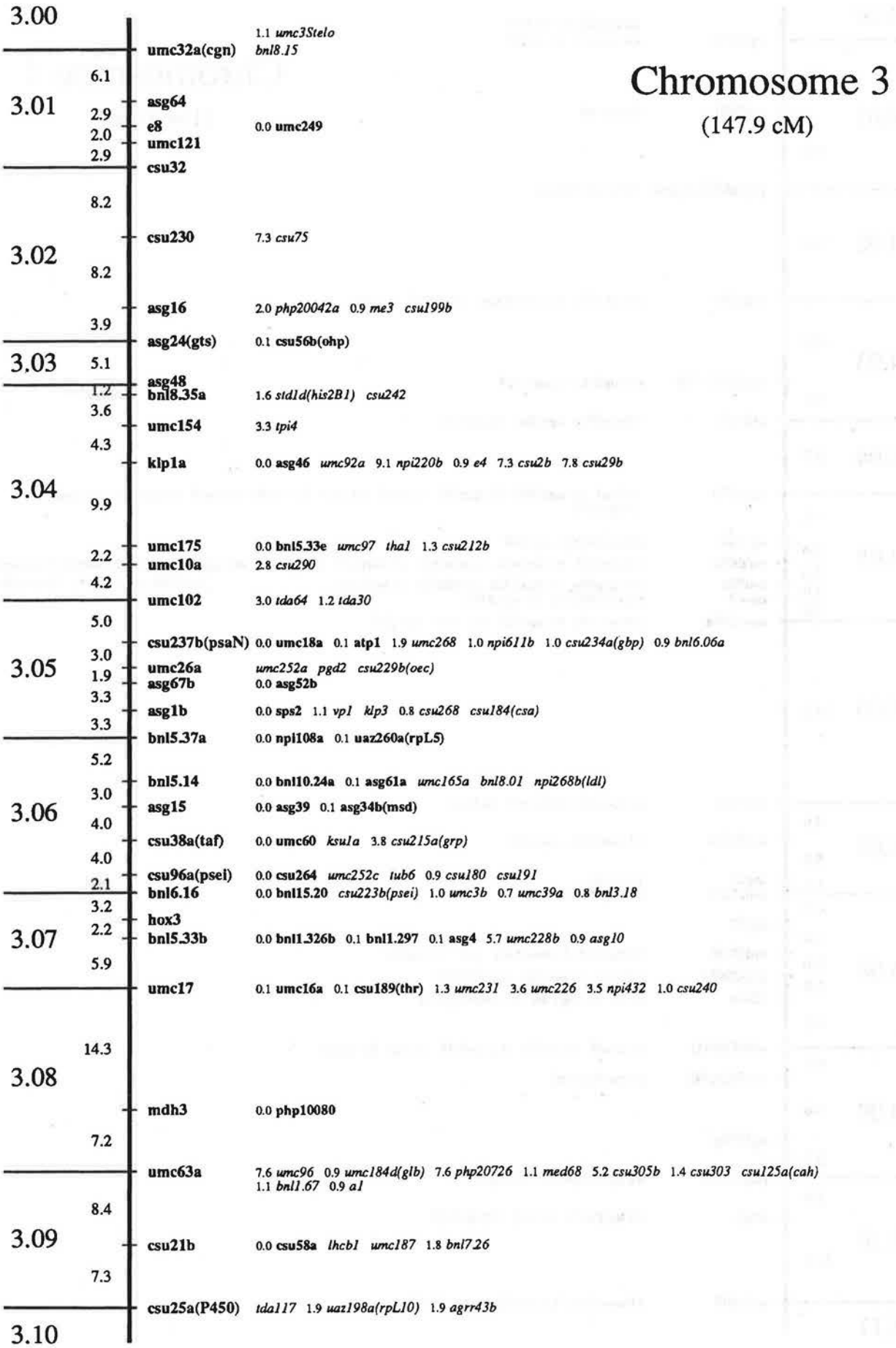


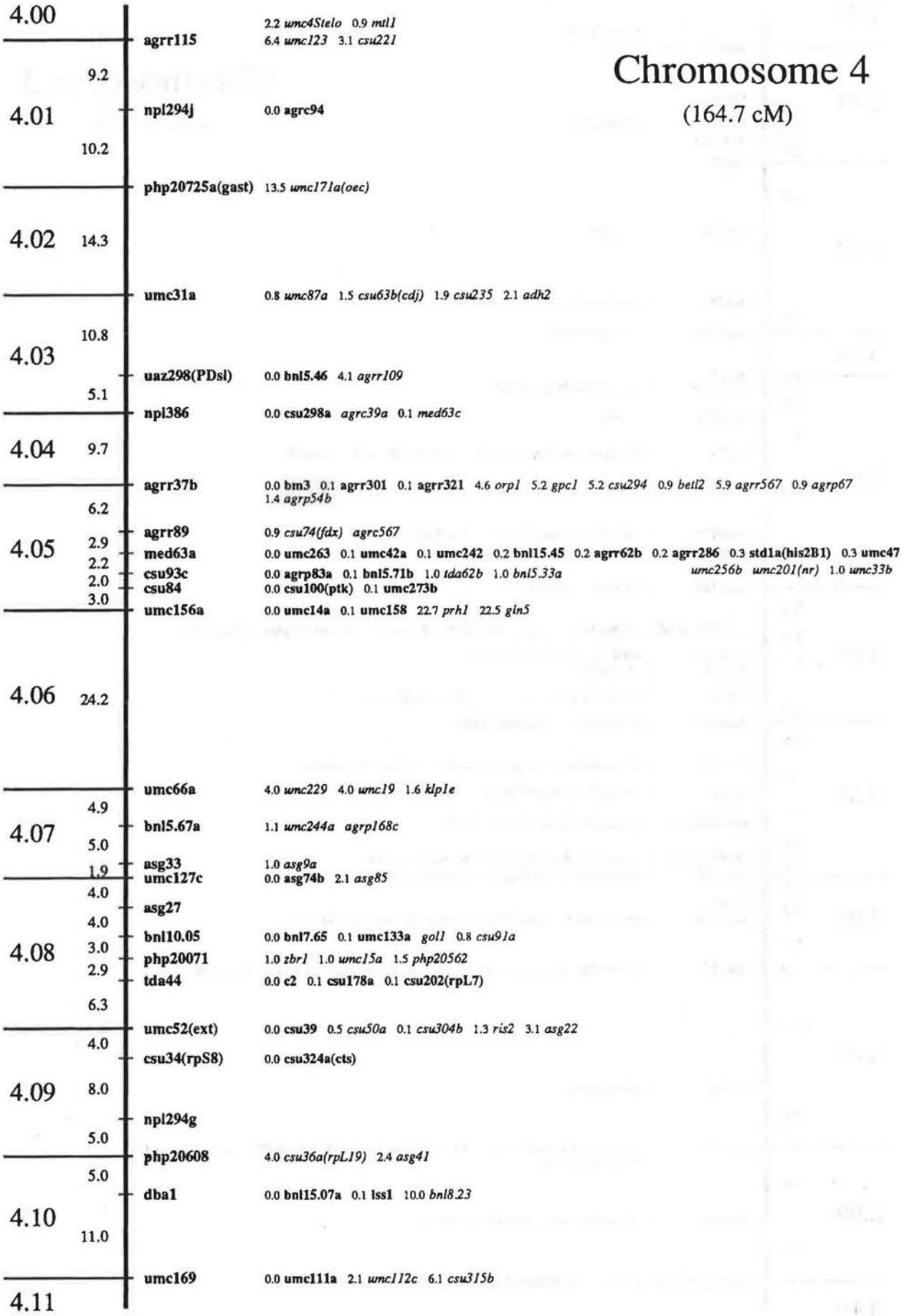
Chromosome 2

(181.5 cM)

Chromosome 3

(147.9 cM)



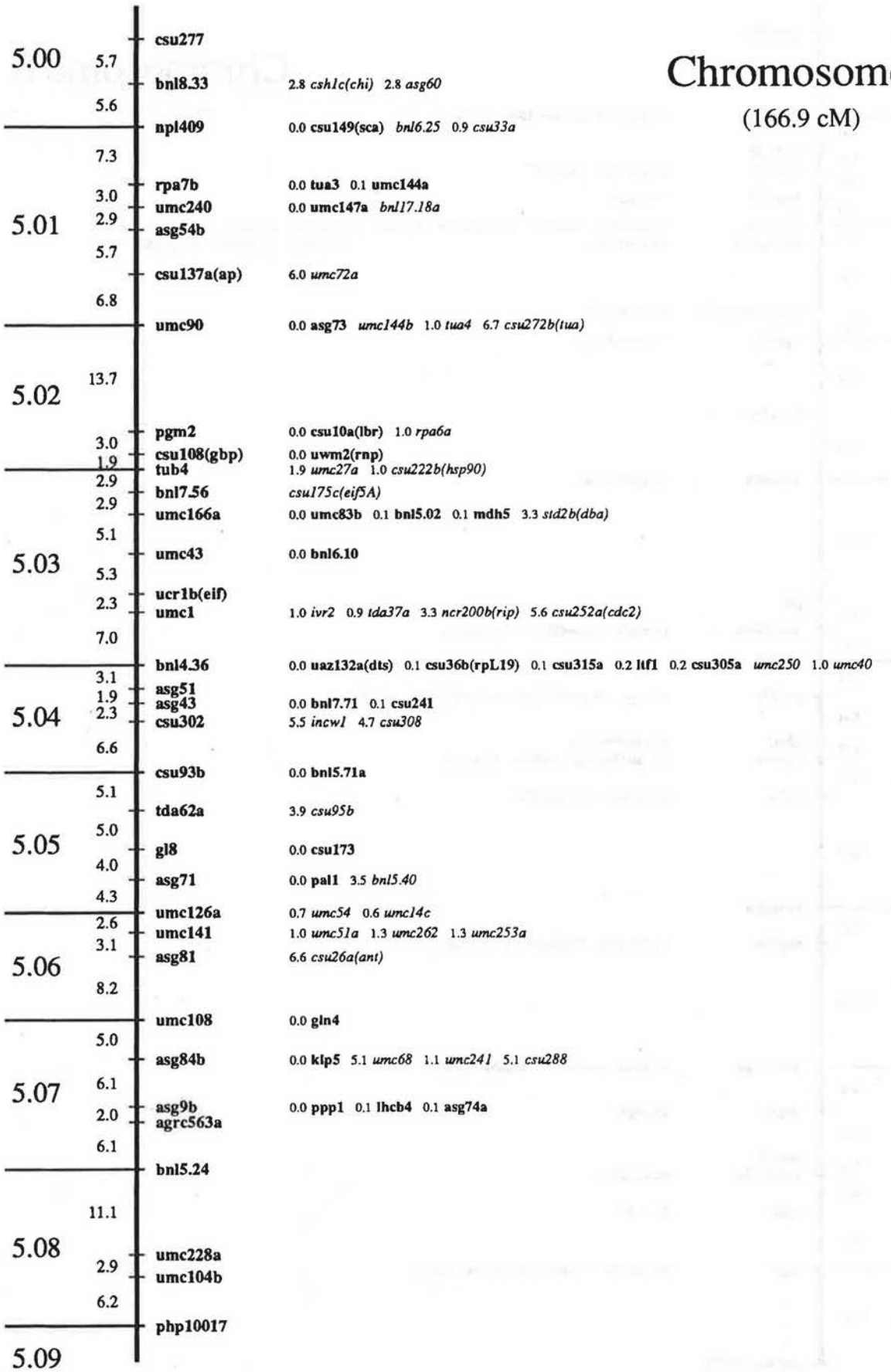


Chromosome 4

(164.7 cM)

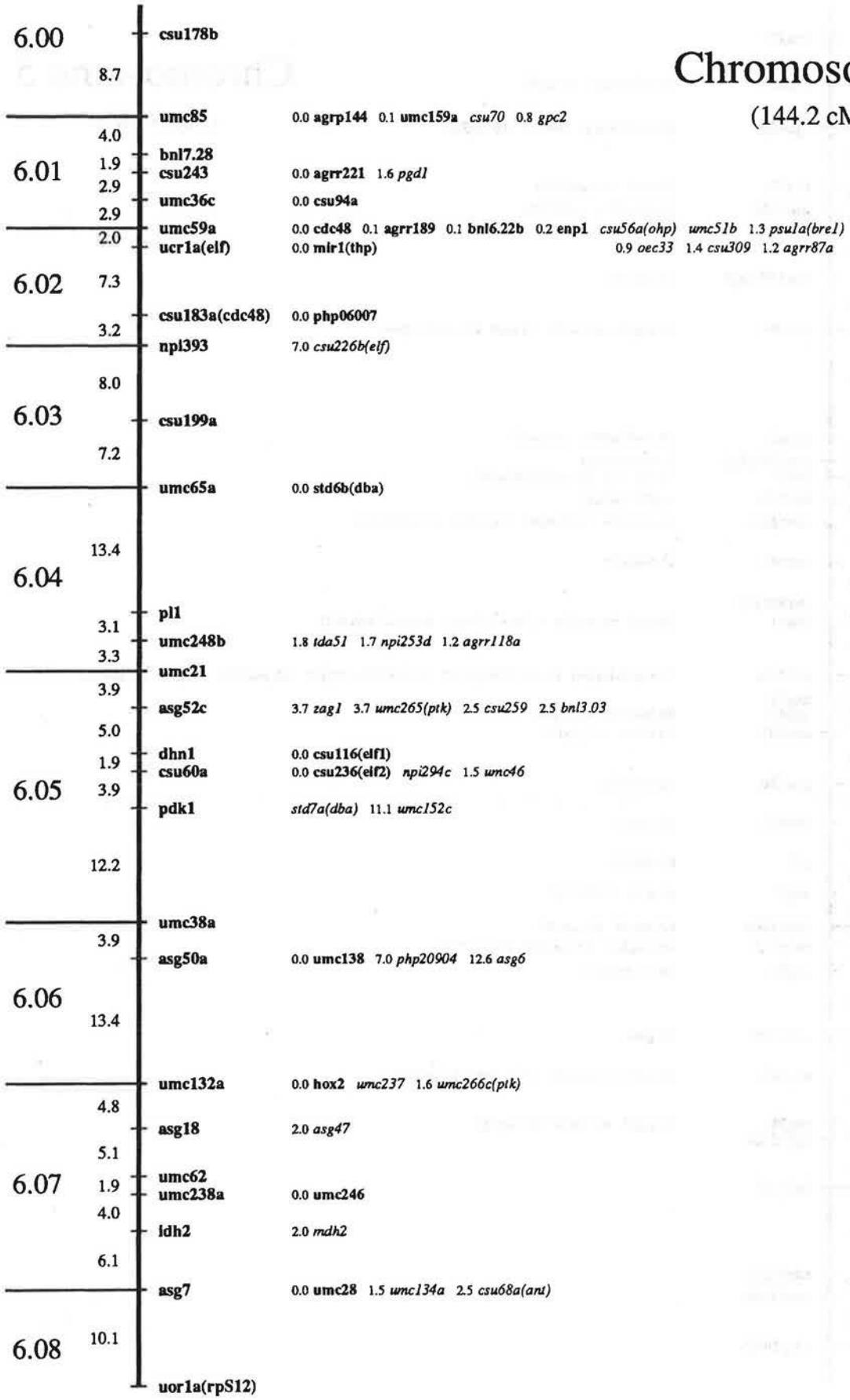
Chromosome 5

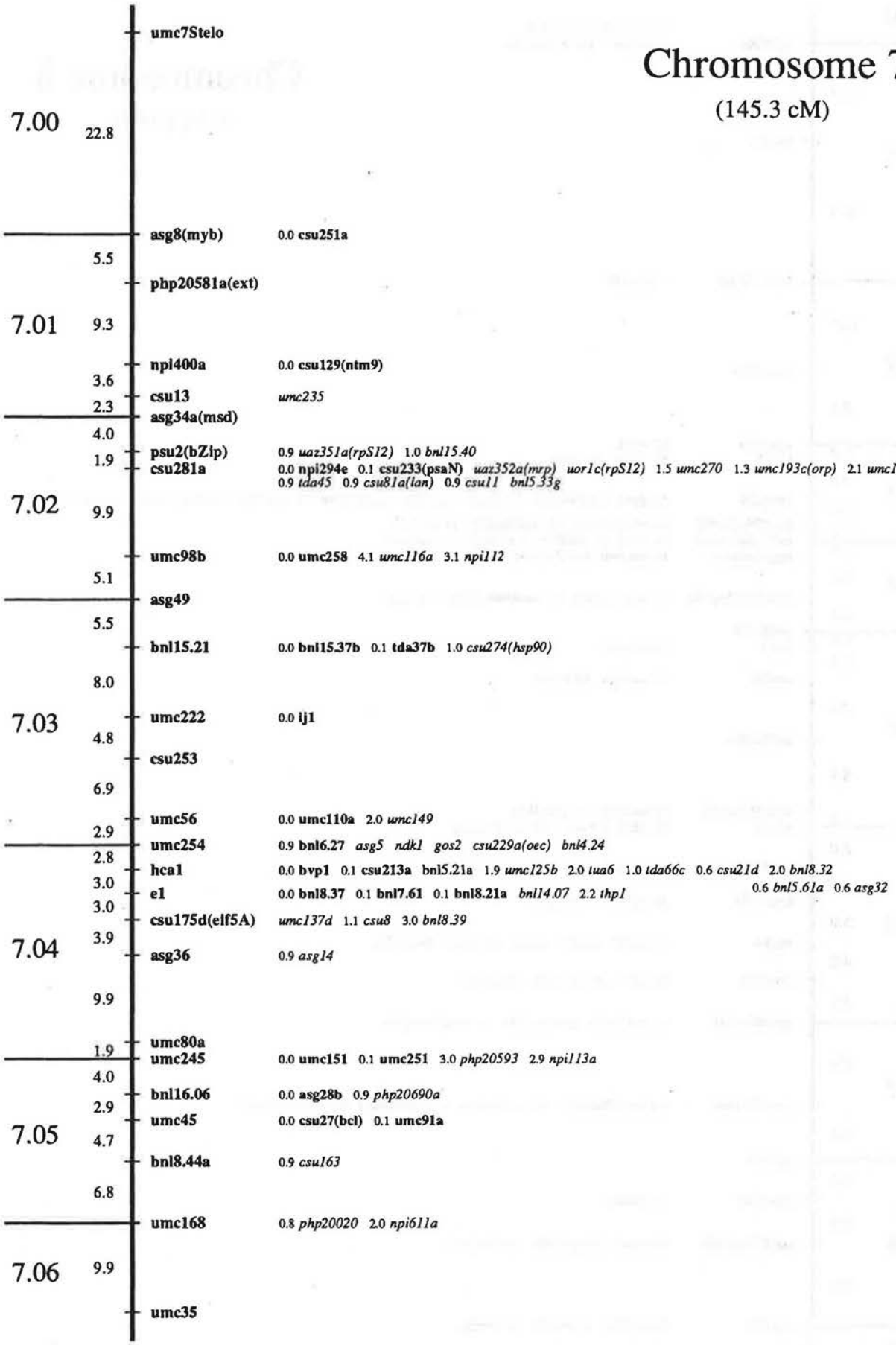
(166.9 cM)



Chromosome 6

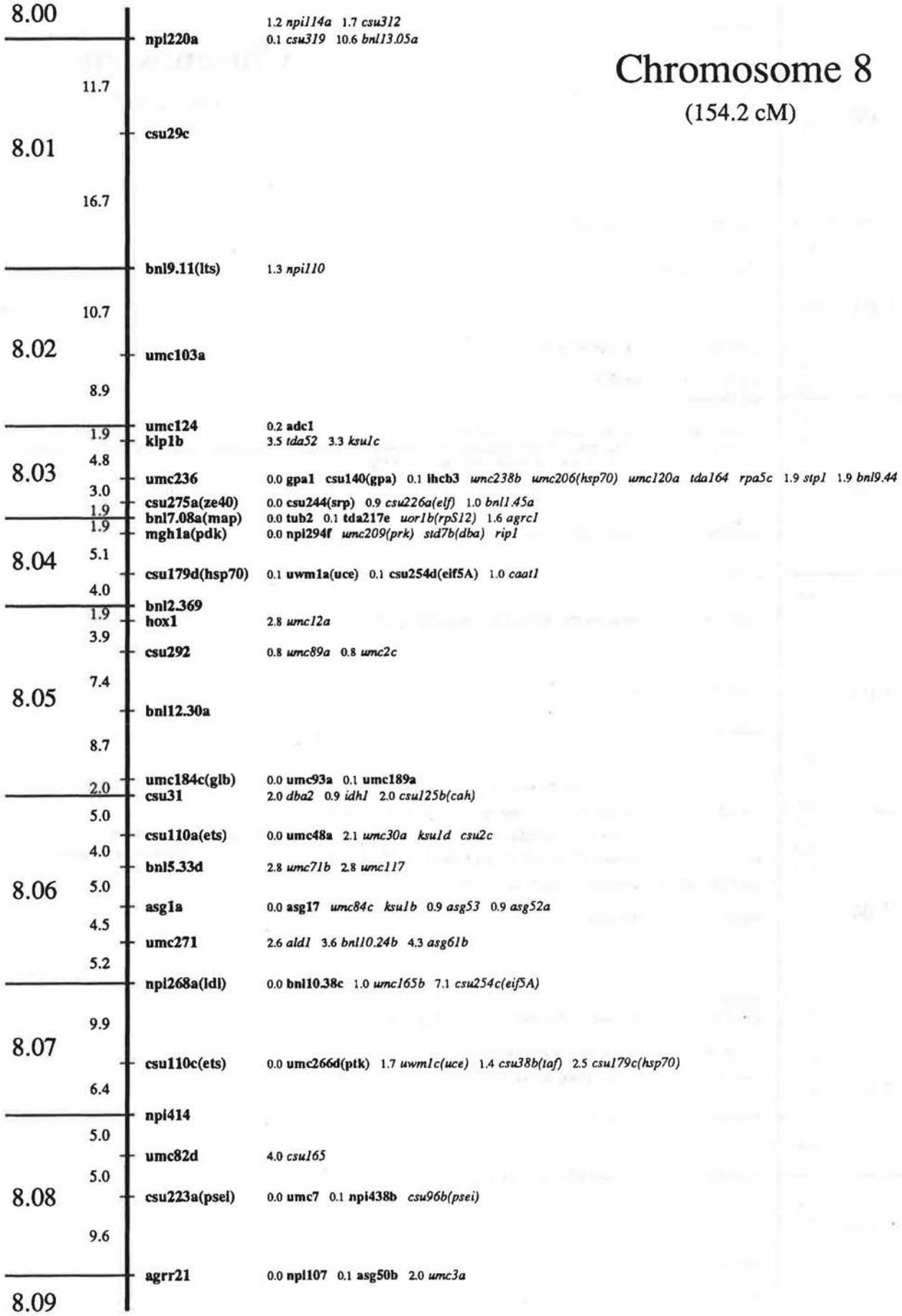
(144.2 cM)




Chromosome 7
(145.3 cM)
7.00
22.8
umc7Stelo
asg8(myb) 0.0 csu251a
5.5
php20581a(ext)
7.01
9.3
npi400a 0.0 csu129(ntm9)
3.6
csu13 umc235
2.3
asg34a(msd)
4.0
psu2(bZip) 0.9 uaz351a(rpS12) 1.0 bnl15.40
1.9
csu281a 0.0 npi294e 0.1 csu233(psaN) uaz352a(mrp) uor1c(rpS12) 1.5 umc270 1.3 umc193c(orp) 2.1 umc112b 0.9 tda45 0.9 csu81a(lan) 0.9 csu11 bnl5.33g
7.02
9.9
umc98b 0.0 umc258 4.1 umc116a 3.1 npi112
5.1
asg49
5.5
bnl15.21 0.0 bnl15.37b 0.1 tda37b 1.0 csu274(hsp90)
8.0
7.03
umc222 0.0 ij1
4.8
csu253
6.9
umc56 0.0 umc110a 2.0 umc149
2.9
umc254 0.9 bnl6.27 asg5 ndk1 gos2 csu229a(oec) bnl4.24
2.8
hca1 0.0 bvp1 0.1 csu213a bnl5.21a 1.9 umc125b 2.0 iua6 1.0 tda66c 0.6 csu21d 2.0 bnl8.32
3.0
e1 0.0 bnl8.37 0.1 bnl7.61 0.1 bnl8.21a bnl14.07 2.2 thp1 0.6 bnl5.61a 0.6 asg32
3.0
csu175d(elf5A) umc137d 1.1 csu8 3.0 bnl8.39
3.9
7.04
asg36 0.9 asg14
9.9
umc80a
1.9
umc245 0.0 umc151 0.1 umc251 3.0 php20593 2.9 npi113a
4.0
bnl16.06 0.0 asg28b 0.9 php20690a
2.9
umc45 0.0 csu27(bcl) 0.1 umc91a
7.05
4.7
bnl8.44a 0.9 csu163
6.8
umc168 0.8 php20020 2.0 npi611a
7.06
9.9
umc35

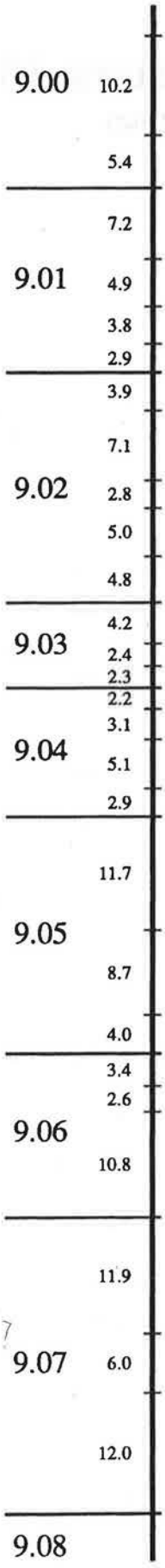
Chromosome 8

(154.2 cM)

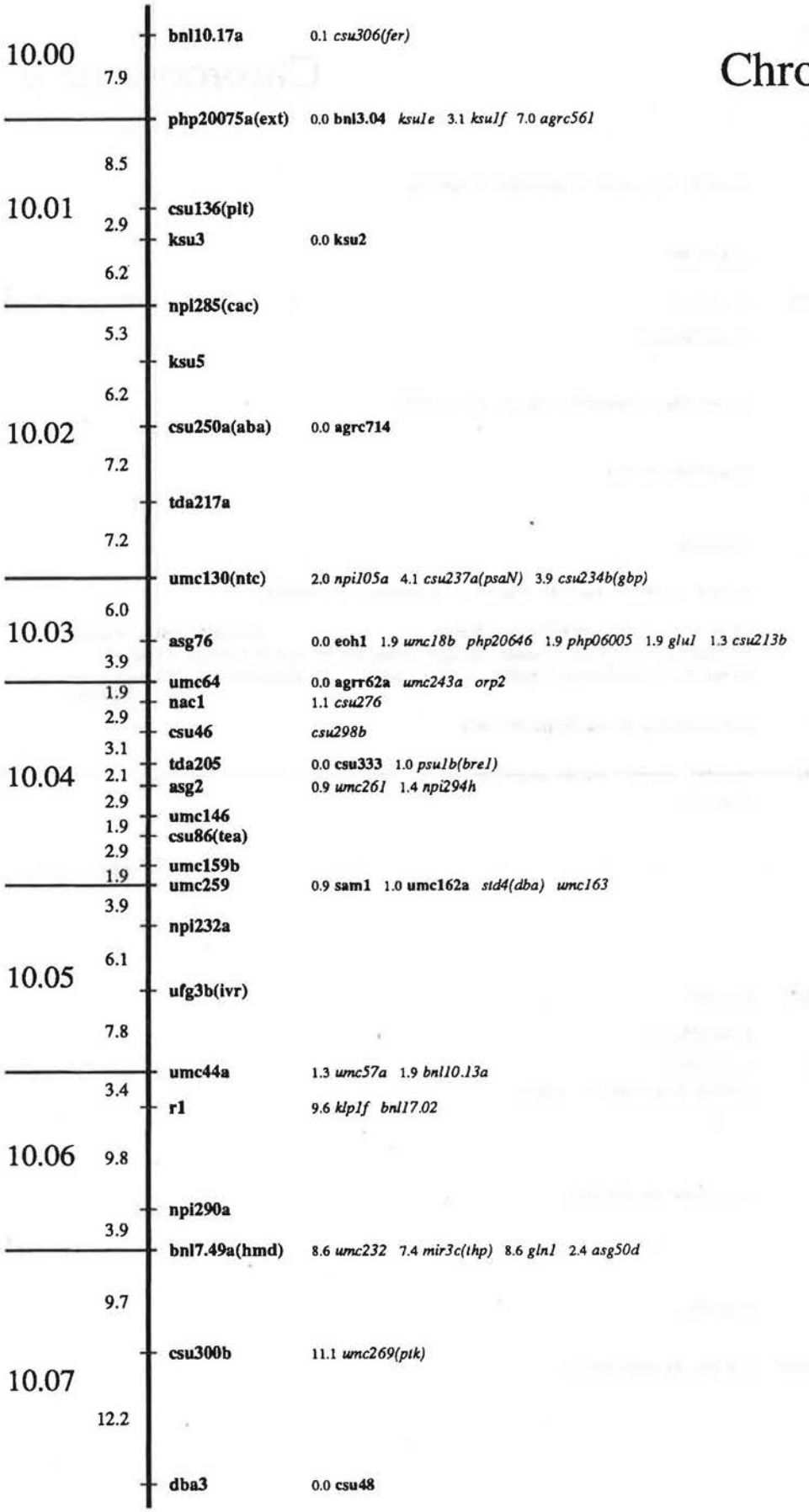


Chromosome 9

(151.1 cM)



		agrr118b	
9.00	10.2		
		bnl9.07a	
	5.4		
		umc109	0.9 *umc70* 1.1 *umc148* 5.1 *php10005* 0.9 *npi253a*
	7.2		
		csu95a	0.0 **umc248a**
9.01	4.9		
		mir3a(thp)	2.8 *umc113a*
	3.8		
		sh1	1.9 *csu250b(aba)*
	2.9		
		bz1	
	3.9		
		asg19	0.0 **umc256a** 0.1 **bnl5.67b** 0.3 *asg82* 3.5 *agrc255b*
	7.1		
		klp1c	0.0 **agrr87b** 0.6 *prc1*
9.02	2.8		
		umc105a	
	5.0		
		csu228	0.0 **csu94b**
	4.8		
		wx1	0.0 **vsp1** 0.1 **tda66d** *umc253b* *umc247* 3.4 *uwm1b(uce)* 0.6 *umc273a*
	4.2		
9.03		**rf2**	1.3 *umc81* 1.2 *csu321* 0.8 *bnl7.24a* *bnl5.33c* 0.4 **asg66** *asg63a* 0.6 *asg68a*
	2.4	**umc153**	0.0 **std6a(dba)** 0.1 **umc20** 0.1 **asg65** 0.2 **asg37** 0.2 **asg67a** 0.2 **bnl5.10** 0.3 **acp1** 0.3 **csu193**
	2.3	**csu147**	0.0 **bnl5.04** 0.1 **csu214a(grp)** *csu254a(eif5A)* 1.0 *umc114* 0.2 *csu252b(cdc2)* *csu181b(maf)*
	2.2	**bnl7.13**	1.0 *csu179b(hsp70)*
	3.1		
9.04		**csu263a**	0.0 **csu56d(ohp)** 0.1 **csu183b(cdc48)** *tub7*
	5.1		
		wsu1(ptk)	0.0 **csu43** 1.0 *sus1* *csu212a* 2.0 *bnl7.50*
	2.9		
		umc95	0.3 *bnl8.17*
	11.7		
9.05		**rpa8**	
	8.7		
		csu219(tgd)	3.9 *csu59*
	4.0		
		csu61	1.1 *csu145a(pck)*
	3.4		
	2.6	**npi425d**	*csu28(rpS22)*
9.06		**asg44**	1.3 *dba4* 8.8 *bnl5.09* 9.8 *bnl14.28a*
	10.8		
		asg12	0.0 **npi209a** 1.8 *std2a(dba)*
	11.9		
		asg59b	4.0 *npi97b*
9.07	6.0		
		umc272(vfa)	10.8 *klp6* 9.1 *csu285(his2B)*
	12.0		
		csu54b	
9.08			



Chromosome 10

(137.8 cM)

UPDATE OF THE PHYSICAL MAPS OF THE MAIZE MITOCHONDRIAL MASTER CHROMOSOMES

--Christiane Fauron, 2100 Eccles Genetics Building, University of Utah, Salt Lake City, Utah 84112 (tel: 801-581-4435; fax: 801-585-717; Email: christiane.fauron@genetics.utah.edu)

References (Review articles):

Fauron,CMR; Casper,M; Gao,Y; Moore,B (1995): The maize mitochondrial genome: dynamic, yet functional. Trends Genet. 11, 228-235.
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Wolstenholme,DR; Fauron,CM-R (1995): Mitochondrial genome organization. In: Advances in cellular and molecular biology of plants. The molecular biology of the plant mitochondria. Vol. 3. (Eds: Levings III,CS; Vasil,IK) Kluwer Academic Publishers, Dordrecht, 1-59.

Figure legend:

The size of each master chromosome is shown in parenthesis. All the known genes are indicated on the outside of each master circle. The repeats are represented by open boxes inside the circles, and the size of each (in kb) is indicated by a number. The integrated forms of plasmids R1 and S2 in maps NA and NB are indicated by black boxes inside the circles, as well as the chloroplast (ct) DNA integrated sequences, the size of which are indicated in kb.

Genes encoded by the maize mtDNA

Ribosomal RNA genes

rrn18 (18S rRNA)	Chao et al. (1984)
rrn26 (26S rRNA)	Dale et al. (1984)
rrn5 (5S rRNA)	Chao et al. (1983)

Transfer RNA genes

trnaC$_{(ct)}$ (GCA)	Wintz et al. (1988)
trnaD (GUC)	Parks et al. (1985)
trnaE (UUC)	Sangaré et al. (1989)
trnaF$_{(ct)}$ (GAA)	Sangaré et al. (1989)
trnaH$_{(ct)}$ (GUG)	Iams et al. (1985)
trnaK (UUU)	Sangaré et al. (1989)
trnafM (CAU)	Parks et al. (1984)
trnaM1(CAU)	Parks et al. (1984)
trnaM2$_{(ct)}$ (CAU)	Sangaré et al. (1989)
trnaN$_{(ct)}$ (GUU)	Sangaré et al. (1989)
trnaP (UGC)	Runeberg-Roos et al. (1987)
trnaQ (UUG)	Sangaré et al. (1990)
trnaS (GCU)	Wintz et al. (1988)
trnaS (UGA)	Sangaré et al. (1989)
trnaW$_{(ct)}$ (CCA)	Maréchal et al. (1985)
trnaY (GUA)	Sangaré et al. (1989)

Ribosomal protein genes

rpl2	Nakazono and Hirai (1993)
rpl5	Fauron (unpublished)
rpl16	Hunt and Newton (1991)
rps1	Gonzales et al. (1993); Fauron (unpublished)
rps3	Hunt and Newton (1991)
rps10	Fauron (unpublished)
rps12	Gualberto et al. (1991)
rps13	Bland et al. (1986)
rps19	Nakazono and Hirai (1993)

Genes for respiration

atpA	Isaac et al. (1985), Braun and Levings (1985)
atp6	Dewey et al. (1985)
atp9	Dewey et al. (1985)
coxI	Isaac et al. (1985)
coxII	Fox and Leaver (1981)
coxIII	McCarty et al. (1988)
cob	Dawson et al. (1984, 1986)
nad1	Wolstenholme et al. (1993)
nad2	Patell et al. (1993)
nad3	Gualberto et al. (1988, 1991)
nad4	Lamattina and Grienenberger(1991); Marienfeld and Newton (1994)
nad5	Pereira de Souza et al. (1991)
nad6	Haouzine et al. (1993)
nad7	Marienfeld and Newton (1994)
nad9	Lamattina et al (1993)
ccl1 (cyt *c* biogeneseis)	Gonzalez et al. (1993)
orf240 (heme transporter)	Bonnard and Grienenberger (1995)

Genes with unknown function

*urf*156	Gualberto et al. (1991)
urf25	Dewey et al. (1986)
urf13 (in cmsT only)	Dewey et al. (1986)

Gene with similarity toRNA maturase in yeast

mat-r	Wahleithner et al (1990); Wolstenholme et al. (1993)

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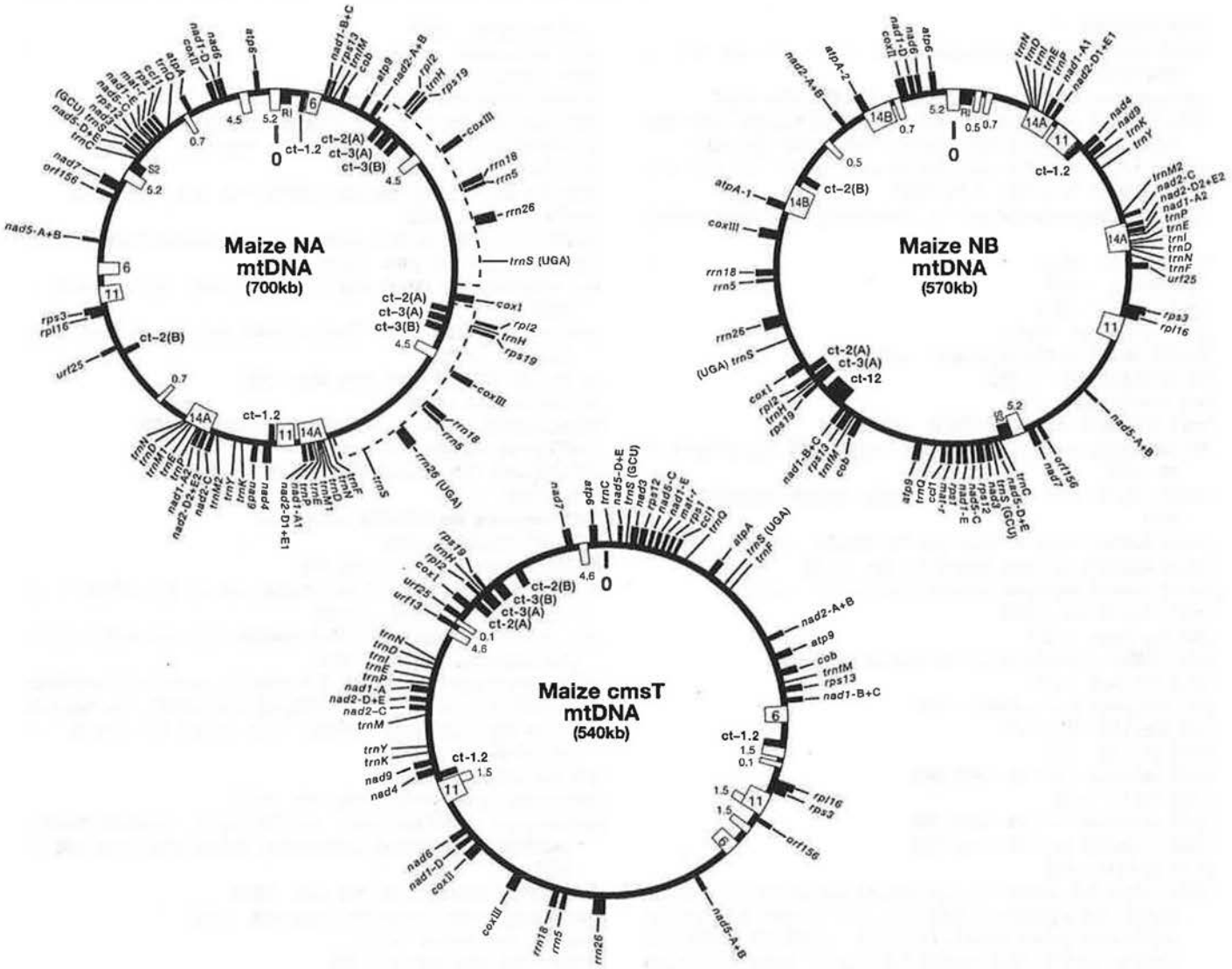
Maize NA
mtDNA
(700kb)
Maize NB
mtDNA
(570kb)
Maize cmsT
mtDNA
(540kb)

IX. ZEALAND 1996

This is a summary of selected genetic research information reported in recent literature and in this News Letter. Numbers preceded by "r" refer to numbered references in the Recent Maize Publications section. New loci ('first report'); mapping; cloning; sequencing; and trait inheritance information that have been added this year to the Maize Genome Database (Maizedb) have been extracted here. The term 'genelist' refers to references with information central to the uniqueness and designation of the gene. Note that the Symbol Index in the back of this issue also accesses journal publications containing studies on gene expression, gene products, developmental control, physiological responses, techniques, etc. Comments or suggestions on these research aids are always welcome.

--assembled by an unrestricted, Prof. Ligate Committee (Ed Coe, Mary Polacco, Pat Byrne, and Georgia Davis)

CHROMOSOME 1

1L3 G-band: *umc58* hybridization in situ; also to 5L5 and 9L6 --MNL70:70

adh1 orthology, phylogenetic analysis --r553 r554 r907 r1000

Adh1-#2, Adh1-1F, Adh1-1S, Adh1-1S, Adh1-3F1124r53, Adh1-54S, Adh1-CO159, Adh1-IL14H, restriction map --r456 r999 r1000

amp1 -11.6- *phi102* -1.2- *umc128(aga)* -2.2- *phi002* -17- *glb1*(aka *phi055*) -8.8- *umc107a* --MNL70:50

an1 sequence:amplification primers; *an1-891339::Mu2,* clone isolation --r72

bz2, promoter --r896

d8, orthology --r907

Ds-1L3 at *bz2* --r633

Ds-1L1 left of *bz2* --r633

Ds-1S1, Ds-1S2, Ds-1S3 left of *dek1* --r633

Ds-1S4 right of *dek1* --r633

hm1, map location --r589

hmp1, first report; before TB-1Sb(1) --MNL70:14

ht4, first report; near T1-9c(1S.48) and T1-9(5622)(1L.10); probably on 1S --r137

isu152 - isu74 - bnl5.59 - isu116 - umc33a - npi236 - umc37a --r513 r684

knox1, genelist, sequence, evolution, map location --r436

knox3, sequence, evolution, *knox3* -1.1- *kn1* --r436

knox8, genelist, sequence, evolution, map location --r436

msv1, map location --r589

olc1, first report --r979

pds-L39266,* sequence; single site maps at *vp5* --r327

pg15, orthology --r907

phi1, sequence, clone isolation --r492

psl6, bins 1.06-1.07 --r125

psl13, bin 1.12 --r125

psl18, sequence, bin 1.06 --r125 r888

psl24, bin 1.1 --r125

psl25, sequence, bin 1.04 --r125 r888

psl33, sequence, bin 1.12 --r125 r888

psl44, bin 1.11 --r125

SSRs: *amp1* -11.6- *phi102* -1.2- *umc128(aga)* -2.2- *phi002* -17- *glb1*(aka *phi055*) -8.8- *umc107a* ; *bnl8.29a* -20.7- *phi064* -3.8- *bnl6.32*; *npi234* -14.3- *p1*(aka *phi095*) -12.8- *isu61; npi236* -7.6- *phi039* -1.4- *umc37a; umc76* -15.6- *npi268* -2.6- *ts2*(aka *phi001*); *tub1*(aka *phi056*) -9.9- *bnl5.62a* -19.5- *umc157(chn)*; *umc76(gne)* -15.6- *npi286* -2.6- *ts2*(aka *phi001*) -4.6- *umc26a* --MNL70:50

tb1: T1-3(5267)(1) - *tb1* - T1-3(5242)(1) --MNL70:3

tb1, map data --r214

ts2: umc76 -15.6- *npi268* -2.6- *ts2*(aka *phi001*) --MNL70:50

tub1(aka *phi056*) -9.9- *bnl5.62a* -19.5- *umc157(chn)* --MNL70:50

uaz151(sar), uaz205b(hsp18), uaz208(mta), uaz228d(his2b), uaz282(pop) located to 1L --r803

uaz248a(his3) located to 1S --r803

uaz249a(ubf9), uaz272(zp19) near 1 centromere --r803

umc89b, umc106a, map location --r714

CHROMOSOME 2

abph1, genelist: *umc6 - b1* -8- (*abph1, umc34*) -13- *umc131* --MNL70:2

agp2, sequence --r293

akh2, map location --r613

ask2, map note --r612

B1-Peru, restriction map --r679

betl1 map note, sequence;*Betl1-Z49203* sequence --r377

ck2::umc36b -9.6- *ck2*; *umc36b* -4.9- *ck2*, map note --MNL70:62

csu6a(sam), map location --r505

dks8 near 2S-36 in BNL RIs; near *npi290b*, map note --MNL70:20

Ds-2S1 before *b1* --r633

Ds-2S2, variegation for *B1-b*, possibly an unstable chromosome --r633

Ds-2S3, *Ds-2S4* at *B1-Peru* --r633

fht1, sequence, first report, *fht1* -11.5- *php20568b* -10.7- *umc53a* --r199

gl14 right of TB-2Sb, left of TB-1Sb-2L4464, linkage with T2-9b *wx1*, map note --r781

gl2 -0- *ias6*; *gl2* -7.8- *umc6*, map data --r781

ht1, map location --r589

knox4, genelist, sequence, evolution, map location --r436

npi271a, map location --r714

ole1 near *umc134b*, bin 2.04-2.05, map note --r510 r511

psl1, bin 2.07 --r125

psl11, sequence, bin 2.04-2.06 --r125 r888

psl31, bin 2.05-2.06 --r125

psl32, sequence, bin 2.07 --r125 r888

rf3: *whp1* -8.9- *rf3* -8.9- *bnl17.14*; *umc49a* -4.8- *rf3* -2.7- *OPE08-1.2kb* -10- *umc36a* --MNL70:24 70:69

se1: *umc49a* -27- *php20581b* -13.4- *umc36a* -12.1- *se1* in 205 F2:F3, fully classified, map data --r860

SSRs: *umc131(pext)* -8- *nc003* -9.1- *umc36b*; *umc34* -6.3- *prp2*(aka *phi083*) -6.4- *phi10012; umc53a(gag)* -2.2- *phi098* -0.6- *npi254a* -11.6- *bnl7.49c(hmd)*; *umc98a* -16.3- *phi127* -31- *umc4a* --MNL70:50

tpi2, map location --r714

uaz124a(rpL7) located on 2, map note --r803

uaz191(rap), uaz194a(ugu), uaz194b(ugu), uaz228a(his2b), uaz232(sci), uaz235(px), uaz269b(kri), located to 2L, map note --r803

uaz236b(ser) located to 2S, map note --r803

uaz265a(sbe) near 2 centromere, map note --r803

umc137a, map location --r714

umc32c(cgn), map location --r505

umc44b, map location --r714

CHROMOSOME 3

a1, promoter --r896

apomixis (APO) segment of *Tripsacum dactyloides* left of *csu32, csu56b(ohp), csu134c, csu58* on 3L, and right of loci on 6L (see), map note --r774

atp1, orthology --r907

bet1 tightly linked to *bnl13.05b*, map note --r986

bnl8.35a, map location --r714

Ds-3L1, *Ds-3L2* left of *a1* --r633

e8, orthology --r907

got1, map location --r714

gst4: umc29d -2.6- *tpi4*(aka *phi029*) -12.9- *umc175* -7.8- [*umc18a* &

gst4(aka *phi073*)] -4.6- *umc26a* --MNL70:50
hox3, evolution --r436
lg3, sequence, evolution --r436
me1, map location --r714
mv1, map location --r589
nl-1517* before TB-3Sb(3), map note --MNL70:15
OPN20-675, map location --MNL70:24
pgd2, orthology --r907
psl4, sequence, bin 3.05 --r125 r888
psl5, sequence, bins 3.01-3.03 --r125 r888
psl10, sequence, bin 3.04 --r125 r888
psl16, sequence, bin 3.06 --r125 r888
psl28, sequence, bin 3.05 --r125 r888
psl47, sequence, bin 3.02-3.04 --r125 r888
rf-nf81-67-9*, association with T3-9c and T3-9(8447), map note --MNL70:65
rp3, orthology --r907
rp3: *lg3* -3- (*rg1*, *rp3*); (*npi114b*, *umc10a*, *umc161b*) -2- (*rp3*, *php20802*) -2- *umc102*; *umc92a* -6- *npi219* -2- (*umc10a*, *php20509*, *php20576*, *lg3*) -2- *npi114b* -2- (*rp3*, *rg1*) -1- *umc102* -1- (*umc18a*, *bnl6.06a*, *php20508*) -2- *umc26a* -8- *bnl5.37a* --r589 r769
SSRs: *umc29d* -2.6- *tpi4*(aka *phi029*) -12.9- *umc175* -7.8- [*umc18a* & *gst4*(aka *phi073*)] -4.6- *umc26a*; *phi036* -14.1- *umc10a* -2.3- *phi053* -1.6- *umc102* --MNL70:50
te1: *umc18* -15- *te1*, QTL -6.3- *bnl8.01* -11.2- *umc60* --r214
Te1-Zpa, evolution --r214
tru1 on 3L, map note --r214
uaz161e(elf), *uaz198a(rpL10)*, *uaz218b(gss)*, *uaz243a(atp)* located to 3L, map note --r803
uaz189(rpL5), *uaz249b(ubf9)* near 3 centromere, map note --r803
uaz210(hsp18) located to 3S, map note --r803
umc50: sucrose content QTL near *umc50*, *OPN20-675* in W6786/IL731a F2:3, map note --r860 MNL70:24
vp1, clone isolation --r950
wsm2, map location --r589

CHROMOSOME 4
adh2:umc31a -4.9- *adh2*(aka *nc004*) -5.1- *bnl5.46* --MNL70:50
akh1, map location --r613
bm3 sequence, *bnl5.46* -21.4- *bm3* -8.3- *umc47*; *bnl5.46* -8.5- *bm3* -2.1- *bnl15.45* in two Pioneer maps, map note --r928
bx1, map location --r589
c2, promoter --r896
cat3: *umc169* -3.1- *cat3*(aka *phi006*) -1- *ncr(b70b)*; *isu77* -17.8- *umc111a* -23.5- *cat3*(aka *phi076*) --MNL70:50
cyp2, *cyp3*, *cyp4*, *cyp5*, sequence *cyp3* -0.1- *cyp2* -1.1- *cyp4* -4.1- *cyp5* --r273
Ds-4S1, variegation for *bt2*
Ds-4L3 at *C2* --r633
Ds-4L1, *Ds-4L4*, *Ds-4L5*, *Ds-4L6*, *Ds-4L7* right of *c2* --r633
dzr1, restriction map; contained by *z1c(zp22)*; *rz329* -6.6- *dzr1* -1.1- *php20725*, map note --r155
gl4, orthology --r907
gpc1: *umc49d* -4.9- *zp19/22(pms2)*(aka *phi096*) -2.5- *gpc1*(aka *nc005*) -24.9- *umc66a* -29.2- *ssu1*(aka *phi093*) --MNL70:50
knox7, sequence, evolution, map location --r436
la1: *sos1* -21.3- *la1* -7.9- *su1*, map data --r215
ms-LI89*: *umc158* - *ms*-LI89* - *umc15a*, map note --MNL70:30
mtl1(aka *phi072*) -6.2- *umc123* -11.3- *php20071* -23.4- *bnl5.46* -11.4- *zp22.1*(aka *phi074*) -11.1- *bnl15.45* --MNL70:50
ncr(b70b): *umc169* -3.1- *cat3*(aka *phi006*) -1- *ncr(b70b)* --MNL70:50
nk1(ck): *bnl5.46* -4.5- *nk1(ck)*, map note --MNL70:62
psl26, bin 4.11 --r125
psl35, sequence, bin 4.03-4.04 --r125 r888
psl45, bin 4.03-4.05 --r125
psl75, bin 4.09-4.1 --r125
rp4, map location --r589
sos1, origin; *sos1* -21.3- *la1* -7.9- *su1*; *php20075* -4.4- *sos1* -9.6- *bnl5.46*, *php20725a* -2.6- *sos1* -3.7- *bnl5.46*, map data --r215
SSRs: *umc31a* -4.9- *adh2*(aka *nc004*) -5.1- *bnl5.46*; *mtl1*(aka *phi072*) -6.2- *umc123* -11.3- *php20071* -23.4- *bnl5.46* -11.4- *zp22.1*(aka *phi074*) -11.1- *bnl15.45*; *umc169* -3.1- *cat3*(aka *phi006*) -1- *ncr(b70b)*; *isu77* -17.8- *umc111a* -23.5- *cat3*(aka *phi076*); *umc49d* -4.9- *zp19/22(pms2)*(aka *phi096*) -2.5- *gpc1*(aka *nc005*) -24.9- *umc66a* -29.2- *ssu1*(aka *phi093*) --MNL70:50
su1, sequence --r389
uaz44a(zp19), *uaz130b(tlk)*, *uaz145(ahh)*, *uaz157(rpL19)*, *uaz161d(elf)*, *uaz171*, *uaz222*, *uaz228c(his2b)*, *uaz247(ubi)*, *uaz252a(ptk)*, located to 4L, map note --r803
uaz44b(zp19), *uaz149(zp19)*, *uaz184(hfi)*, *uaz185(zp22)*, *uaz280a(ppp)* located to 4S, map note --r803
uaz195(ms), *uaz218a(gss)*, *uaz246(vsp)* located near 4 centromere, map note --r803
uwo3, map note --r525
uwo8, map note --r525
zp19/22cluster2, restriction map --r548

CHROMOSOME 5
5L5 G-band, *umc58* hybridization in situ; also to 1L3 (mapped site) and 9L6, map note --MNL70:70
a2, promoter --r896
cat1, promoter --r968
Ds-5S1, *Ds-5S2* right of *a2* --r633
Ds-5L1 left of *bt1* --r633
gl25 left of TB-5Sc, map note --r781
gl8, orthology --r907
gl8 -0- *ias3*, map data --r781
gln4, map location --MNL70:50
gln4: *umc126a* -8.4- *phi101* -13.8- (*umc108*, *phi048*) -2.6- *gln4*(aka *phi085*) -38.7- *php10017* --MNL70:50
got2, orthology --r907
incw1, sequence --r798
knox10, sequence, evolution, map location --r436
knox6, sequence, evolution, map location --r436
ms13, orthology --r907
ms5, orthology --r907
ncr(b70a), map location --MNL70:50
ohp2 (aka *nc007*) -14.3- *umc147a* -19- *umc107b* --MNL70:50
ole2: *bnl6.25* -36.1- *ole2*(aka *phi113*) -20.2- *php20872* --MNL70:50
ole3 near *npi213*, bin 5.03-5.04, map note --r511
pgm2 -9.9- *rab15*(aka *phi008*) -12.8- *bnl7.56* --MNL70:50
psl7, bin 5.03 --r125
psl8, sequence, bin 5.04-5.05 --r125 r888
psl20, bin 5.03 --r125
psl21, sequence, bin 5.05 --r125 r888
psl39, sequence, bin 5.04-5.05 --r125 r888
psl43, bin 5.03 --r125
rab15: *pgm2* -9.9- *rab15*(aka *phi008*) -12.8- *bnl7.56* --MNL70:50
ren1: *bnl5.40* -2- *phi107* -2.3- *umc51a* -2.3- *phi087* -12.5- *ren1*(aka *isu10*) -12.7- *umc68* -2.6- *phi128* --MNL70:50
sh4, orthology --r907
SSRs: *umc126a* -8.4- *phi101* -13.8- (*umc108*, *phi048*) -2.6- *gln4*(aka *phi085*) -38.7- *php10017*; *ohp2* (aka *nc007*) -14.3- *umc147a* -19- *umc107b*; *bnl6.25* -36.1- *ole2*(aka *phi113*) -20.2- *php20872*; *pgm2* -9.9- *rab15*(aka *phi008*) -12.8- *bnl7.56*; *bnl5.40* -2- *phi107* -2.3- *umc51a* -2.3- *phi087* -12.5- *ren1*(aka *isu10*) -12.7- *umc68* -2.6- *phi128* --MNL70:50
uaz130c(tlk), *uaz201(tua)*, *uaz205a(hsp18)*, *uaz215b(odo)*, *uaz219(hsp)*, *uaz226(cat1)*, located to 5S, map note --r803
uaz132a(dts), *uaz186*, *uaz215a(odo)*, *uaz238(ppi)*, *uaz248b(his3)* located to 5L, map note --r803
uaz158(alt), *uaz159* located on 5, map note --r803

uaz190(gpc) located near 5 centromere, map note --r803
umc39c, map location --r714
xet1, sequence --r757

CHROMOSOME 6
6L1 G-band, *umc65* hybridization in situ (map site *umc65a*), map note --MNL70:70
agp1: umc62 -4.4- *phi123* -12.1- *agp1* --MNL70:50
apomixis (APO) segment of *Tripsacum dactyloides* right of *umc71a*, *umc28*, *csu68a* (on 6L), left of markers on 3L (see), map note --r503 r774
bnl5.47a - *php10016* - *npi280* - *umc62*, map --r513 r684
dzs23, sequence --r855
fdx1 (aka *phi075*) -1.2- *phi106* -20.8- *npi235a* -7.7- *phi077* -47.9- *pl1* --MNL70:50
hex2, map location --r714
hox2, evolution --r436
l10: T6-9e(6) - *l10* - T6-9(043-1)(6), map note --r121
l12: T6-9e(6) - *l12* - T6-9(043-1)(6), map note --r121
l12: T4-6(8428)(6) - *l12* - T4-6(6623)(6), map note --r121
l12: T6-9(6019)(6) - *l12* - T6-9(043-1)(6), map note --r121
l15: distal to T6-9(043-1)(6), map note --r121
ln1, oil QTL tightly linked to *umc65a*, *ln1*, map note --r17
maltose content QTL near *umc59a* in W6786/IL731a F2:3, map note --r860 MNL70:24
mdh2, map location --r714
mdm1: umc85 -1.9- *po1* -.03- *csu70(gfu)* -0.2- (*mdm1*, *nor*) -0.7- *bnl6.29a* -0.1- *npi235* -3.2- *y1*; *jc1270* -2.5- *npi245* -1.6- (*umc85*, *po1*) -0.5- (*mdm1*, *nor*) -0.5- *bnl6.29a* -0.5- *npi235* -0.8- *npi101* -4.3- *umc59a* --r813
ms1: T6-9e(6) - ms1 - T6-9(043-1)(6), map note --r121
pdk1, evolution, structure --r579
pdk1: *uaz127a(pdk)* located to 6L; *umc85* -6.8- *phi077* -14.7- *phi126* -58- *umc65a* -4.8- *pl1*(aka *nc009*; *nc010*) -2- *phi124* -5.9- *umc21* -1.6- *phi129* -15- *pdk1*(aka *nc012*) -7.5- *bnl5.47a* -- r803 MNL70:50
pgd1, map location --r714
po1: umc85 -1.9- *po1* -.03- *csu70(gfu)* -0.2- (*mdm1*, *nor*) -0.7- *bnl6.29a* -0.1- *npi235* -3.2- *y1*; *jc1270* -2.5- *npi245* -1.6- (*umc85*, *po1*) -0.5- (*mdm1*, *nor*) -0.5- *bnl6.29a* -0.5- *npi235* -0.8- *npi101* -4.3- *umc59a*, map data --r813
psl15, bins 6.02-6.03 --r125
psl29, sequence, bins 6.04-6.05 --r125 r888
rf-nf79-21-27*, association with T6-9(4505) and T6-9(4778), map note --MNL70:65
rhm1, *rhm2: rhm1* -9.1- *rhm2*; *npi245*, *umc85*, *rhm1* before TB-6Sa; *bnl6.29a*, *umc85* after TB-6Sa, map data --r813
si1: T6-9e(6) - *si1* - T6-9(043-1)(6), map note --r121
SSRs: *umc62* -4.4- *phi123* -12.1- *agp1; fdx1* (aka *phi075*) -1.2- *phi106* -20.8- *npi235a* -7.7- *phi077* -47.9- *pl1*; *umc85* -6.8- *phi077* -14.7- *phi126* -58- *umc65a* -4.8- *pl1*(aka *nc009*; *nc010*) -2- *phi124* -5.9- *umc21* -1.6- *phi129* -15- *pdk1*(aka *nc012*) -7.5- *bnl5.47a; umc132a* -3.6- *tlk1*(aka *phi070*) -23.7- *umc62* --MNL70:50
tlk1, sequence --r951
tlk1: umc132a -3.6- *tlk1*(aka *phi070*) -23.7- *umc62* --MNL70:50
uaz161a(elf), uaz220(elf), uaz243b(atp), uaz244a(prh), uaz265b(sbe), uaz269d(kri) located to 6L, map note --r803
uaz197a(cdpk), uaz227(end), uaz233b(act), uaz237b(prc), located near 6 centromere, map note --r803
uaz197b(cdpk), uaz233d(act), located to 6, map note --r803
uaz80(iron), uaz206(uce), uaz269c(kri), located to 6S, map note --r803
UBC281-900, UBC425-700, map --MNL70:24
w15: cent6 - *w15* - T6-9e(6), map note --r121
wsm1, map location --r589
y1: T6-9e(6) - *y1* - T6-9(043-1)(6), map note --r121
y1: T4-6(8428)(6) - *y1* - T4-6(6623)(6), map note --r121
y1 right of T4-6(055-8)(6) and T6-9(6019)(6), map note --r121

CHROMOSOME 7
bnl8.44a -3.1- *umc35* -1.4- *uaz230c*(aka *phi082*) --MNL70:50
cyp6: php20581a(ext) -15.1- *o2*(aka *phi057*) -9.6- *cyp6*(aka *phi034*) -6.3- *umc5b* --MNL70:50
Ds-7L2 probably left of *o5* --r633
gl1 -12- *umc116a*, map data --r781
gzr1 near *umc35* by bulk segregant analysis, map note --r190 r537
o15 near *umc35* by bulk segregant analysis, map note --r190
o2 (aka *phi057*) -10- *bnl15.40* -10.2- *umc98b* --MNL70:50
o2, sequence, microsatellite, evolution --r337
oec17-Z26824: php15037* -18.4- *oec17**(aka *phi114*) -5.9- *php20746* -21.9- *umc56* --MNL70:50
phi069 -19.4- *phi043* -2.9- *umc168* -2.3- (*umc35 phi051*) --MNL70:50
psl23, sequence, bin 7.03 --r125 r888
psl27, bin 7.03-7.04 --r125
rip2, sequence: *bnl8.32* - *rip2* - *bnl7.61*, map note --r60
rs1, sequence, evolution, map location --r436 r782
SSRs: *bnl8.44a* -3.1- *umc35* -1.4- *uaz230c*(aka *phi082*); *php20581a(ext)* -15.1- *o2*(aka *phi057*) -9.6- *cyp6*(aka *phi034*) -6.3- *umc5b; o2* (aka *phi057*) -10- *bnl15.40* -10.2- *umc98b*; *php15037* -18.4- *oec17**(aka *phi114*) -5.9- *php20746* -21.9- *umc56*; *phi069* -19.4- *phi043* -2.9- *umc168* -2.3- (*umc35 phi051*) --MNL70:50
uaz119b(rpS6), uaz221(his2a), uaz224(eif2), uaz225(lox), uaz233c(act), uaz245(gbp), uaz91(ndk) located to 7L, map note --r803

CHROMOSOME 8
8L7 G-band, *umc65* hybridization in situ (map site *umc65d*), map note --MNL70:70
act1: bnl13.05a -18.9- *php10040* -25.5- *act1*(aka *phi115*) -7.5- *bnl9.08* --MNL70:50
bnl5.62c, map location --r751
bnl9.11(lts), map location --r714
caat1, genelist --r803
gpa1, promoter --r222
gst1: umc7 -14.6- *gst1*(aka *phi015*) -3.9- *npi107* --r751 MNL70:50
gstIIB, map location --r751
hox4, first report --r454
ht2, map location --r589
htn1, map location --r589
knox11, sequence, evolution, map location --r436
knox5, sequence, evolution, map location --r436
psl19, sequence, bin 8.04-8.05 --r125 r888
psl38, bin 8.02 --r125
psl42, bin 8.01 --r125
rf-nf79-23-27* association with T8-9d and T8-9(043-6), map note --MNL70:65
rf4, orthology --r907
rip1: bnl9.08 -4.6- *rip1*(aka *phi014*) -24.2- *umc48; umc92b* -0.6- *phi119* -11.4- *umc124* -4.1- *umc120a* -1.8- *phi125* -12- *phi121* -0.9- *rip1*(aka *phi060* & *phi014*) -14.3- *umc89a* --MNL70:50
SSRs: *bnl13.05a* -18.9- *php10040* -25.5- *act1*(aka *phi115*) -7.5- *bnl9.08; umc7* -14.6- *gst1*(aka *phi015*) -3.9- *npi107*; *bnl9.08* -4.6- *rip1*(aka *phi014*) -24.2- *umc48; umc92b* -0.6- *phi119* -11.4- *umc124* -4.1- *umc120a* -1.8- *phi125* -12- *phi121* -0.9- *rip1*(aka *phi060* & *phi014*) -14.3- *umc89a* --MNL70:50
uaz119a(rpS6), uaz127b(pdk), uaz249d(ubf9), uaz252b(ptk) located to 8L, map note --r803
uaz193(rip), uaz233a(act), uaz244b(prh), uaz249c(ubf9), uaz269a(kri) located near 8 centromere, map note --r803
uaz93a(tpi),uaz243c(atp) located to 8S, map note --r803

CHROMOSOME 9
9L6 G-band, *umc58* hybridization in situ; also to 1L3 (mapped site) and

5L5, map note --MNL70:70
acp1, map location --r714
bnl10.13b, map location --r714
bz1, promoter --r896
bz1, orthology --r907
c1, orthology --r907
c1, regulatory site --r918
c1 -6- *phi122* -1.9- *sh1*(aka *phi044*) -3.8- *isu136b* -0.4- *bz1*(aka *phi017*) -19.6- *isu124* -6.8- *bnl3.06* -0.3- *wx1*(aka *phi061*) -6.2- *pep1*(aka *phi065*) -1.5- *umc153* -15.6- *sus1*(aka *phi032*) -2.9- *isu98a* --MNL70:50
d3, map note --r889
d3, sequence --r973
Ds-9S1 probably right of *c1* --r633
hm2, map location --r589
hsk1: wx1 -2- *d3* -0.5- *hsk1*(aka *uaz144*) -1- *uaz166c*, using *d3* clone and CM37 x T232 RIs, map --r973
knox2, sequence, evolution, map location --r436
koln2b(hox), genelist --r454
ms2, orthology --r907
ms45, clone isolation; located to chr 9, map note --r13
npi209a -2.1- *bnl14.28a* -14- *phi108* --MNL70:50
npi404c, map location --r714
pep1: umc113a -3.7- *sh1*(aka *phi044*) -5- *bz1*(aka *phi017*) -20.5- *umc105a* -12.5- *wx1*(aka *phi061*) -4.7- *pep1*(aka *phi065*) -1- *umc81* -14.8- *sus1*(aka *phi016*) -5.4- *umc95; c1* -6- *phi122* -1.9- *sh1*(aka *phi044*) -3.8- *isu136b* -0.4- *bz1*(aka *phi017*) -19.6- *isu124* -6.8- *bnl3.06* -0.3- *wx1*(aka *phi061*) -6.2- *pep1*(aka *phi065*) -1.5- *umc153* -15.6- *sus1*(aka *phi032*) -2.9- *isu98a* --MNL70:50
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sem1 (was *dek*-Mu1364*) is before TB-9Sd(9); re-tests contradict prior indication of 9L, map note --MNL70:14
SSRs: *c1* -6- *phi122* -1.9- *sh1*(aka *phi044*) -3.8- *isu136b* -0.4- *bz1*(aka *phi017*) -19.6- *isu124* -6.8- *bnl3.06* -0.3- *wx1*(aka *phi061*) -6.2- *pep1*(aka *phi065*) -1.5- *umc153* -15.6- *sus1*(aka *phi032*) -2.9- *isu98a; npi209a* -2.1- *bnl14.28a* -14- *phi108; umc113a* -3.7- *sh1*(aka *phi044*) -5- *bz1*(aka *phi017*) -20.5- *umc105a* -12.5- *wx1*(aka *phi061*) -4.7- *pep1*(aka *phi065*) -1- *umc81* -14.8- *sus1*(aka *phi016*) -5.4- *umc95* --MNL70:50
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Ds-10L4 left of *r1* --r633
gdcp1 -7- *npi285*; *gdcp1* -18- *bnl3.04* (in CM37 x T232); *gdcp1* is included in the terminal def(*bnl3.04-Rp5-Rp1-M*), which is distal to *npi371c* (=*npi422*), map note --MNL70:15
gl21, orthology --r907
glu1, map location --r714
glu1: (*phi041 phi117*) -25.8- *npi285(cac)* -1.5- *phi063* -12.4- *phi059* -1.2- *pZmISU167* -9.8- *umc130(ntc)* -6- *phi054* -2.3- *glu1* -4.8- *phi050* -1.7- *umc64* -2.6- *hsp90**(aka *phi071*) -0.8- *mgs1*(aka *phi062*) -19- *umc44a* -2- *phi035* -30.7- *npi245b* --MNL70:50
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uaz124b(rpL7) located on chr 10, map note --r803
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6L1 70 138
8L7 70 138
9L6 70 136 137 138
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28kb-inversion-break(cp) r561
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a1-mum2 r522 r523
a2 4 137 r436 r633 r896
a3 4
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abph1 2 136
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ask2 136 r612
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B1-I r84 r147
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B1-Peru 136 r147 r679
b1-Pm5 r679
B1-V r679
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Zhang, MD r115
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Zivy, M r888
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Zon, J r300
Zorec, R r874

CLONE INFORMATION SHEET (PLEASE SUPPLY FOR EACH CLONE)

CLONE DESIGNATION: ISOLATING LAB/PERSON:

IS THIS A KNOWN SEQUENCE CLONE (circle one)? Yes No GENE SYMBOL:

WHAT PRODUCT OR FUNCTION?

PRODUCT ACRONYM: EC NO.:

CLONE TYPE (genomic, cDNA, etc.): ISOLATED FROM WHAT ORGANISM:

REFERENCE:

GENBANK, EMBL, EST, SWISSPROT NOS. :

SOUTHERN BLOT INFORMATION

LINE ANALYZED	ENZYME(S) TRIED	# BANDS SEEN	APPROX. MW

NORTHERN BLOT INFORMATION

TISSUE(S)	CONDITION(S)	# BANDS SEEN	APPROX. MW

CHROMOSOME ARM, IF KNOWN:
NEAREST MARKERS, IF KNOWN:

If you already have map information for this clone, please submit mapscores and mapping population information in typed or electronic format with this form for inclusion in the Maize Genome Database.

IT IS OPTIMAL FOR US TO RECEIVE A STAB (ELSE 10μg OF DRIED PLASMID WOULD BE ACCCEPTABLE).

HOST OF SUPPLIED STAB CULTURE: AMT. OF PURIFIED PLASMID:

VECTOR: SELECTIVE AGENT:

ENZYME(S) TO CUT OUT INSERT: INSERT SIZE:

CAN THE INSERT BY PCR'D? Yes No PRIMER SEQUENCE:

SPECIAL CONDITIONS NEEDED FOR PCR:

MAY WE FREELY DISTRIBUTE THIS CLONE NOW? Yes No
AFTER PUBLICATION OR ONE YEAR? Yes No

CONTACT PERSON REGARDING CLONE:

NAME:

ADDRESS:

PHONE: FAX:

E-MAIL:

SEND CLONES AND INFORMATION TO:

MS THERESA MUSKET
302 CURTIS HALL
UNIVERSITY OF MISSOURI
COLUMBIA, MISSOURI 65211

PHONE: 573/882-2033
FAX: 573/884-7850

EMAIL: MUSKET@teosinte.agron.missouri.edu

July, 1996

SUBSCRIPTION AND INFORMATION FORM
MAIZE GENETICS COOPERATION NEWSLETTER and MAIZE GENOME DATABASE

Please complete both sides and return. Your cooperation in providing this information is needed, whether you subscribe to the Maize Newsletter or not, to keep the database and mailing lists current. Phone, FAX, and E-MAIL addresses are particular aids to Cooperation today.

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Payment is required in U.S. funds: By check drawn on a U.S. bank; or by instruments such as postal money orders or Eurochecks made out to Maize Genetics; or by bank transfer to account 0102013147, bank 80-86/815; or by credit card with the following information:

Name of card holder.....Discover or Visa or MasterCard?.....

Address of card holder.....

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Account No.....Exp. Date.....

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ADDRESS:

PHONE:

FAX:

EMAIL:

Please identify (mark) whether you wish:

To receive the annual "Call and Deadline" for notes for Maize Newsletter: yes ..... no .....
To receive the annual Notice for the Maize Genetics Conference: yes ..... no .....
To receive a diskette, annually, of selected parts of MNL issues: yes ..... no .....

(Available only to Lifetime contributors to the Endowment Fund--please see below; specify whether you need a 3" or 5" disk; MS-DOS or Mac; and Microsoft Word, Word Perfect, or ASCII)

Please identify yourself as follows (mark):

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Teacher: yes ..... no .....
Corporate research group: yes ..... no .....
Public library subscriber: yes ..... no .....
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Other subscriber (Please list) yes ..... no ....

Interests (please circle):

Genome/Mapping	Genetic Manipulation	Breeding/Selection	Biochemistry	Development/Biology
genic	cloning/sequencing	field corn	photosynthesis	cell biology
molecular	transposable elements	sweet corn	growth regulators	cell cycle/kinetics
cytogenetics	transposon tagging	industrial	flavonoids	reproductive biol.
molec. cytology	regulation/expression	food corn	carotenoids	meiosis
evolution	transformation	Physiology	storage proteins	life cycle
fine structure		Stress	carbohydrates	
QTLs	Germplasm	Pests/Diseases	oil content	Other .....

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Your Gift to the Maize Genetics Newsletter Endowment (confers Lifetime Subscription ; donors will be acknowledged in the Newsletter):

Kernel Endowment	$ 150.00
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This is an informal newsletter by which working research information on the genetics and cytogenetics of maize is shared. The information and data are shared by Cooperators with the understanding that they will not be used in publications without their specific consent.

Notes for the 1997 Maize Genetics Cooperation Newsletter need to be in the editor's hands by January 1. Be concise, not formal, but include specific data, tables, observations and methods. A double-spaced, letter-quality copy of your text is needed. Please follow the simple style used in this issue (title; authors; use minimal citations in text but list citations of the references). Whenever possible send an electronic version on 3-1/2 or 5-1/4 floppy disk, identifying the operating system (e.g., MS-DOS) and the word processor (e.g., Microsoft Word). Figures, charts and tables should be compact and camera-ready, and provided in electronic form if possible. Please use tabs instead of spaces to separate columns in tables. Send your submissions to E. H. Coe, Jr., 210 Curtis Hall, University of Missouri, Columbia, MO 65211; email: ed@teosinte.agron.Missouri.edu. Submission by email is acceptable, but not preferred.

Subscription information is provided on the form included in this issue, or can be requested from the editor (address and email above).

Author and Name Indexes (and see **MaizeDB**)	
Nos. 3 through 43	Appendix to MNL 44, 1970 (copies available)
Nos. 44 through 50	MNL 50
Nos. 51 to date	Annual in each issue
Symbol Indexes (and see **MaizeDB**)	
Nos. 12 through 35	Appendix to MNL 36, 1962 (copies available)
Nos. 36 through 53	MNL 53
Nos. 54 to date	Annual in each issue
Stock Catalogs	
Marker Stocks	In this issue and **MaizeDB**
Translocations	MNL 55 and **MaizeDB**
Rules of Nomenclature (1995)	MNL69 and **MaizeDB**
Cytogenetic Working Maps	MNL 52:129-145; 59:159; 60:149 and **MaizeDB**
Gene List	MNL69 (supplement in this issue) and **MaizeDB**
Clone List	MNL 65:106; 65:145, this issue and **MaizeDB**
Working Linkage Maps	In this issue and **MaizeDB**
Plastid Genetic Map	MNL 69 and **MaizeDB**
Mitochondrial Genetic Maps	In this issue and **MaizeDB**

Cooperators (that means you) need the Stock Center.
The Stock Center needs Cooperators (this means you) to:

(1) Send stocks of new factors you have reported in this Newsletter or in publications, and stocks of new combinations, to the collection.

(2) Inform the Stock Center on your experience with materials received from the collection.

(3) Acknowledge the source of the stocks for research when you publish, and advice or help you have received in development of your research project.

MaizeDB needs Cooperators (this means you) to:

(1) Look at the entries in **MaizeDB** (see section IX in this Newsletter) for "your favorite genes" and send refinements and updates to maryp@teosinte.agron.missouri.edu.

(2) Compile and provide mapping data in full, including the ordered array of map scores for molecular markers or counts by phenotypic classes; recombination percentage and standard error.

(3) Probe or primer information per the information sheet in the back of this issue; fingerprint data indicating enzyme and fragment sizes and defining mapped as well as unmapped fragments.

Cooperators, Clone Home! Each functionally defined clone enhances the map, and mapping information enhances further exploration of the function. Your clone is wanted; please see Section VIII, p. 118, and the information sheet in the back of this issue.