MAIZE GENETICS COOPERATION

NEWSLETTER

75

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

The Maize Genetics Executive Committee

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Selected Web Sites

Please notify the editors, mnl@chaco.agron.missouri.edu if you know of other sites.

MNL vol 55 (1981) - current.	www.agron.missouri.edu/mnl.html
Arizona Plant Chromatin Project, maize and Arabidopsis; ChromDB	AG.Arizona.Edu/chromatin/chromatin.html
Berkeley Cytogenetics Project.	mcb.berkeley.edu/labs/cande/
BNL Brookhaven National Laboratory. Maps and raw data for BNL map population.	burr.bio.bnl.gov/
CIMMYT International Center for Amelioration of Maize and Wheat	www..cimmyt.mx
CSH Cold Spring Harbor Maize Genome Analysis RFLP STSs pre-submission	clio.cshl.org/maizegenome
CSH MTM Targeted Mutagenesis. Mu induced mutations and sequence insertions	mtm.cshl.org/
CUGI Clemson; BAC clones, libraries, contigs	www.genome.clemson.edu/projects/maize/fpc
Delaware Seed Quality Traits Project Oil QTL and SNP's	genetics.mgh.harvard.edu/goodman/MaizeEST/NSF_abstract.html
EU Map Maize Project	www.lars.bbsrc.ac.uk/cellbiol/devbio/mapmaiz.html
GABI German Plant Genomics - Chilling Tolerance	mips.gsf.de/proj/gabi/projects/maize1.htm
Georgia Centromeres Project.	dogwood.botany.uga.edu/maize/centromeres.html
GRIN Germplasm Resources Information Network	www.ars-grin.gov/npgs
Incyte Genomics - RFLP clones formerly available from UMC	www.incyte.com/reagents/index.html
INRA Maize Genome Database	moulon.moulon.inra.fr/imgd
ISU Maize Genome Project.	maize.math.iastate.edu/isumaize/homepage.html
Long Ashton BBSRC Maize Projects Functional Genomics; Mu knockouts; transgene promoters.	www.cerealsDB.UK.net/index.htm
MaizeDB integrated maize genome database	www.agron.missouri.edu
Minnesota Maize Project Oat x Maize Radiation Hybrids	www.agro.agri.umn.edu/rp/genome/
Maize Gene Discovery Project.	www-sequence.stanford.edu/group/maize/maize2.html (general description) www.zmdb.iastate.edu (database)
Maize Genetics Cooperation Stock Center	w3.aces.uiuc.edu/maize-coop
Maize Mapping Project	www.cafnr.missouri.edu/mmp
NSF funded Plant Genome Projects	plantgenome.sdsc.edu
NSF Plant Genome Program	www.nsf.gov/bio/dbi/dbi_pgr.htm
The Institute for Genome Research TIGR Maize Gene Index	www.tigr.org/tdb/zmgi/
Wisconsin Evolutionary Genomics Project.	www.wisc.edu/genetics/CATG/doebley/index.html brooks.statgen.ncsu.edu/panzea (project site)

The Maize Genetics Executive Committee (MGEC)

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With the advent of the genomics era and the unparalleled opportunities this provides, it has become apparent that maize genetics has suffered both from a lack of visibility within the life sciences community and from the absence of a community-wide vision for the future of our discipline. In March of 1999, Ed Coe assembled an informal group to discuss the future of maize research and how it might be facilitated. Over a several month period in 1999, this committee polled members of the maize genetics community (defined as subscribers to maize.net or to the Maize Genetics Cooperation Newsletter) for their opinions of the current limitations to pursuing maize genetics research. The poll was conducted informally at meetings and in other conversations. The poll results indicated that deficiencies in maize transformation technology stood out as a limitation to the pursuit of the highest quality maize genetics. A subgroup of the informal committee (Jeff Bennetzen, Vicki Chandler and Pat Schnable) traveled to Washington DC on April 13 of 2000 to meet with the senior staff at NSF that deal with proposals related to plant genetics. Comparable staff at the USDA were also invited, but were unable to attend. As an outcome of these discussions, the guidelines for both the NSF Plant Genome and USDA IFAS programs were changed to include wording that indicated a particular interest of these agencies to receive proposals that addressed improving the efficiency and broadening the germplasm amenable to maize transformation. Several such proposals were received and at least one was funded in 2001.

Earlier, Torbert Rocheford had decided to organize a meeting at Allerton Illinois that would bring together a manageably small group of maize researchers to discuss the past, present, and future of maize genetics. At this Allerton meeting (March 10-12, 1999), and at the Maize Genetics Conference held in Lake Geneva directly afterwards, informal discussions yielded the consensus that a permanent committee should be formed. The charge to this group would be to gather information about the needs and interests of the maize genetics community, and then to communicate this information to interested parties within the industrial, academic, charitable and governmental sectors worldwide. Nearly all discussants agreed that this group should center its activities on issues confronting maize geneticists in the public sector, because the private sector already has its own voice amply supported by lobbyists and other communication organs. The Maize Genetics Executive Committee (MGEC) was chosen as the name for this new permanent committee, and it was decided that it should be elected by a vote of the entire maize genetics community

In accordance with these ideas, nominations and an election were held in May of 2000 for ten positions on the MGEC. The first elected members were Jeff Bennetzen, Jim Birchler, Vicki Chandler, Ed Coe, Mike Freeling, Sarah Hake, Ron Phillips, Pat Schnable, Virginia Walbot, and Sue Wessler. Not surprisingly, because so many of the members of the community are based in the US, no overseas nominee received sufficient votes to join the Committee. Hence, the elected MGEC members asked Jane Langdale to join the Committee to provide an international perspective, and she generously accepted. The MGEC elected Jeff Bennetzen as chair for its first year. We also decided that members should have five-year terms. By random draw, this first set of MGEC members were given positions of 1 to 5 years, so that two member would rotate off of the committee each year. Jeff Bennetzen and Ron Phillips were the first two members to have their seats expire, in 2001. In June of 2001, they were both re-elected, and Jeff Bennetzen was also re-elected chair by the MGEC.

An early activity of the elected MGEC was to assist Ed Coe in his efforts to evaluate the performance of MaizeDB. This process has involved numerous communications between MaizeDB staff and members of the MGEC. In addition, the MGEC conducted a brief survey of opinions about MaizeDB at the 2001 Maize Genetics Conference.

A second activity of the MGEC has been to publicize its existence, both by electronic means and by invited presentations of MGEC members at various meetings. We hope that creating awareness of the MGEC (and its functions) will alert the broader life sciences community to the fact that the maize genetics community is becoming more organized and proactive.

A third activity of the MGEC in its first year was to compose a letter in support of increased funding for individual investigator awards at the USDA CSREES NRI program. This letter was discussed and approved in open forum at the 2001 Maize Genetics Conference, and then sent to numerous Senators and Congresspersons that sit on committees that are involved in the funding of the USDA. Although many replies were received, it is not clear whether these letters had any significant effect.

Within the MGEC, numerous email discussions were generated concerning a vision for the Maize Genetics Community and what steps should be taken to validate this vision. Using our own insights and the results of the earlier informal poll, the MGEC came up with two written statements that were meant to describe highlighted and comprehensive visions for the future of maize genetics. These documents were discussed in open forum of all attendees at the 2001 Maize Genetics Conference. The broader community suggested some revisions to these documents, and the revised documents have been sent to appropriate programs within NSF, the USDA and to the National Corn Growers Association.

Beyond the suggested revisions, a significant contribution by the attendees at the 2001 Maize Genetics Conference was their agreement that sequencing the maize genome is now the highest priority for the maize genetics community. Following this recommendation, the MGEC has undertaken several actions to bring about a Maize Genome Sequencing Project. Progress along these lines will be discussed in another contribution to this year's Maize Genetics Cooperation Newsletter.

For the future, the MGEC hopes to continue its mission to identify both the needs and the opportunities for maize genetics, and to communicate this information to the broadest possible life science community. This community includes scientists, funding sources for scientists, and the end users for the accomplishments of maize genetics, from farmers to consumers. In the next year, the MGEC plans to (1) further pursue efforts to support sequencing the maize genome, (2) conduct a second poll, this time in greater depth and breadth, of the needs of the maize community, and (3) develop a Web presence for the MGEC. This internet face of the MGEC should contain information on the goals, membership, organizational processes and contributions of the MGEC. The MGEC, through its members, is open to (and eager for) suggestions from all members of the maize genetics community about future actions. We hope to provide a dependable and adaptable resource to serve the maize genetics community.

Progress Towards Sequencing the Maize Genome

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Starting in June of 2000, the Maize Genetics Executive Committee (MGEC) began discussing possible visions for the future of maize genetics. From these discussions, it became clear that the landscape for plant genetics research had changed tremendously in the preceding year, and that the time was now right to support an effort to sequence the maize genome. A strong majority of the MGEC proposed that this should be the highest current priority for maize genetics research.

The MGEC prepared an executive summary and a more detailed document that included a number of outlined possible priorities for maize genetics over the next few years. These documents were disseminated electronically to the entire maize genetics community and were also discussed by attendees in an open forum at the 2001 Maize Genetics Meeting. From this feedback, the community voiced its opinion that sequencing the maize genome deserved the highest priority.

A subset of the MGEC, Jeff Bennetzen, Vicki Chandler and Pat Schnable, organized a one-day workshop in St. Louis (July 2, 2001) to discuss how the maize genome might best be sequenced. A grant was funded by NSF to support this meeting. To make the meeting manageable, only 28 scientists were invited. These scientists included experts in maize genome analysis, informatics, and full genome sequencing from the public, private and federal sectors, including overseas representatives. Discussion subjects included the techniques that should be pursued, the availability of sufficient sequencing capacity, how the information would be disseminated, predicted costs, and possible timeframes.

The results of this meeting were the concurrence that sequencing the maize genome is completely feasible, and that the whole project could be accomplished in one to two years at a cost of $20 million to $100 million. The great variation in possible costs reflects the diversity of techniques that could be pursued and the degree of sequence redundancy that would be generated. At the moment, there is enthusiasm among animal geneticists for producing "drafts" in many projects to sequence higher eukaryotic genomes. Because a draft sequence is at a relatively low redundancy (3X to 6X, usually), it is impossible to assemble final sequences that are very long, but most gene sequences are identified. The draft costs less and can be produced more rapidly than a complete sequence. The final costs to finish the sequence can dwarf the cost of the draft.

The most controversial subject at the workshop was the sequencing strategy that should be employed. Most participants felt that a gene-enriched sequencing approach should be pursued initially, thus providing the most important targets at an early time and a relatively low cost. The gene-enrichment technologies discussed included various shotgun approaches based on the low methylation level of maize genes, their low repetition frequency, the lack of stop codons in their coding regions, or the proximity of DNA transposons. Two participants felt that the sequencing of BACs from gene-rich regions would be most appropriate. Several of the industrial participants felt that a full genome shotgun sequence should be employed. In all of these cases, there were questions of whether all genes would be found and of how difficult it would be to assemble this sequence information. All participants agreed that, for an acceptable final result, the sequence must be unambiguously and precisely ordered on the physical and genetic maps of maize. How best to do this, and thus how best to undertake the full genome sequencing process, appeared to require additional studies that could be completed within a few months time.

Bennetzen, Chandler and Schnable produced a summary of the outcomes and proposed next steps from this meeting. This report has been disseminated to federal funding agencies, the National Corn Growers Association and the maize genetics community. Representatives of all three of these groups have voiced their interest in sequencing the maize genome. The National Corn Growers Association has placed sequencing of the maize genome at the top of its priority list for 2001 - 2002.

The MGEC will continue to monitor and encourage steps towards sequencing the maize genome by the most appropriate method. We hope that this project will initiate in 2002 and be completed within two years of that start date.

I. FOREWORD

In the fall of 2000, Ed Coe convened us to say that he would step down as Editor of the Maize Genetics Cooperation Newsletter. This action ends a 25 year tenure for him in this position. Much has changed in the interim in the way that scientific information is handled. Most genetic organisms now have internet sites that maintain information useful to investigators. The creation of the site for maize, MaizeDB, was also initiated by Dr. Coe. It is a tribute to his intellect and energy that these tasks were maintained with such thoroughness in addition to his scholarly contributions on gene expression, plant development, genetic mapping, organelle genetics and genomics. The maize community is indebted to Dr. Coe for this selfless service and we urge you to convey your gratitude to him at your convenience.

What has not changed is the cooperation in the maize community. The extensive sharing of ideas, stocks and information has set us apart as a group of scientific investigators. Indeed, now with a fusion of genetics and genomics, cooperation is even more important to solve increasingly complex problems. We hope that the "Newsletter" will continue to foster this cooperation.

We remind the readers that contributions to the Newsletter do not constitute formal publications. Citations to them should be accompanied by permission from the authors if at all possible. Notes can be submitted at any time and are entered into MaizeDB. The deadline for the next print copy, volume 76, is January 1, 2002.

We encourage the community to carry studies of general scientific interest to the formal literature. However, there is a great need to share technical tips, protocols, mutant descriptions, map information, ideas and other isolated information useful in the lab and field.

As in the past, Shirley Kowalewski has been responsible for assembly and correcting of the copy. She has performed this task with precision and with good humor.

Mary Polacco
James A. Birchler
Co-editors

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Univ. California, and the Plant Gene Expression Center

Some observations on the *grassy tillers* (*gt1*) mutant
--Colasanti, J

The meaning of 'vegetatively totipotent': Maize plants that are homozygous for the *grassy tillers* mutation (*gt1*) exhibit a proliferation of small, grass-like shoots from the base of the culm. These tillers seem to form in lieu of normal tillers, although, occasionally, tillers of normal size form as well. I am studying the *gt1* mutation because there is a tentative connection between the *indeterminate1* mutant (*id1*) and the *gt1* mutant. Mutant *id1*/*id1* plants flower extremely late (or not at all) and they often produce tassels and ears that revert to vegetative growth; i.e., plantlets emerge from within the spikelets of the tassels and the ears form as branches. In addition to the late flowering phenotype, descriptions of the *id1* mutant invariably include the following statement: "*id1* is vegetatively totipotent with *gt1* and factors for perennialism to produce a form of perennialism in maize" (Mutants of Maize, pg. 252, 1997). The origins of this statement can be traced back to studies by D. Shaver (J. Heredity 58:270-273, 1967). In this report he describes a double mutant of *id1* and *gt1*, and then introduces a recessive factor for perennialism (*pe1*) from teosinte to create a form of perennial maize. The use of the word 'perennial' in this instance means that the plants do flower eventually, but growth continues from basal branches indefinitely, under favorable environmental conditions. The key to this perennial behavior is the ability of branches to remain in a state of vegetative growth and continue propagating a vegetative meristem that is not consumed by inflorescence formation and, therefore, will make more shoots.

These traits are notable in the *id1gt1* double mutant, which exhibits a sort of synthetic perennialism. Figure 1 shows two nodes (arrows) of an *id1gt1* double mutant plant (with leaves removed). The part of the plant shown here is about 10 nodes from the ground. Whereas in normal plants prop roots form on the first or second nodes closest to the ground, in *id1* mutants prop root formation expands to the upper nodes of the plant, often reaching to just a few nodes below the tassel. In the double mutant shown in Figure 1, the *gt1* phenotype of grassy tillers is observed in every node that forms prop roots, thus the 'tufts of grass' formation at each node. In addition, the number of small tillers increases compared to single *gt1* mutants. If these 'tufts' are allowed to contact the soil, the adventitious prop roots grow out and the small tillers develop into a new, somewhat bushy, plant.

Mapping *gt1*: The *gt1* gene is located on chromosome 1, according to current maps, but its exact location (or even chromosome arm) is unknown. Since *id1* is located on the long arm of chromosome 1, very near to *bz2*, the location of *gt1* relative to *id1* was tested. An F1 plant carrying mutant alleles of *id1* and *gt1* in repulsion was selfed and the resulting progeny scored for *id1* and *gt1* single mutants and *id1gt1* double mutants (see Table). The original *gt1* mutant allele was obtained from Ben Burr (Brookhaven Laboratory) and the *id1* mutant allele, *id1-m1,* mutant was isolated by transposon tagging (Colasanti J. and Sundaresan V., MNL 65:5, 1995).

As shown in the table, the frequency of *id1gt1* double mutants (~ 3%) is somewhat lower than expected for two genes that are not linked (6.25%). This would suggest that *gt1* is on the long arm of chromosome 1, about 30 cM from *id1*. However, the population of plants examined here is too small to make a definite conclusion. Further, it does not tell us whether *gt1* is proximal (which would put it very near the centromere) or distal to *id1*. Experiments are in progress to refine the map position of *gt1*.

TABLE

id1 Gt1*$^+$*/id1*$^+$*gt1 $\otimes \longrightarrow$

Total # plants	Normal	*id1*/*id1*	*gt1*/*gt1*	*id1*/*id1 gt1*/*gt1*
188	**93**	**48**	**41**	**6**
Expected (unlinked)	106	35	35	12
Expected (very closely linked)	94	47	47	0

Preliminary tagging experiment: An initial experiment to isolate the *gt1* gene by *Mu* transposon tagging was attempted. Homozygous *gt1* mutant plants were crossed as pollen parents to *Mu* active plants, and the F1 progeny were screened the next summer in Davis CA. From a total of about 35,000 F1 seeds planted, no plants with a clearly identifiable grassy tiller phenotype were found. The number screened might be too low to guarantee a tagged allele, but this initial experiment did reveal one problem with this screen. Specifically, the F1 plants had a large number of normal large tillers that made it difficult to identify the small tillers of the *gt1* mutants.

To get around this problem, the *gt1* allele was introgressed

into a Mo17 inbred line that shows very little tillering in the field. (The *Mu* lines are already in a low-tillering background). However, and perhaps not surprisingly, the more the *gt1* mutation was introgressed into the Mo17 background (after 5 backcrosses), the more difficult it became to score the grassy tiller phenotype. If nothing else, this finding suggests that the grassy tillers of *gt1* mutants are a variation of normal tillers and are subject to the same developmental controls. It might be possible to proceed with this tagging by using one of the less introgressed lines.

A connection between grassy tillers and silky tassels: By putting *gt1* in an *id1* mutant background, the developmental abnormalities caused by the loss of *gt1* function were amplified and more obvious. That is, in the double mutant it is clear that the grassy tillers emerging from each node are the result of uncontrolled proliferation of meristems at the base of each shoot (Fig. 1). In the *gt1* single mutation, this tiller upon tiller proliferation is present but is not as conspicuous.

One other characteristic that seems to be associated with the *gt1* mutant allele is the presence of a silky tassel phenotype. I have noticed that nearly all *gt1* homozygous plants are associated with silks emerging from the tassels. These silky tassels resemble the tassels of tillers, which often undergo feminization. Of course it is possible that the silky tassel trait is caused by another mutation that is simply linked to *gt1*. However it is interesting to note that, in the Mo17 introgressions described above, the increased difficulty of identifying the grassy tiller phenotype was accompanied by a parallel reduction of silk formation in *gt1* tassels. Only one *gt1* mutant allele has been available so far; therefore, characterization of other *gt1* alleles could clarify the relationship between the formation of grassy tillers and silky tassels.

If both traits are in fact the result of a lesion in the same gene, it might give clues about how the *gt1* gene functions. The profusion of grassy shoots and the growth of silks from the tassel could be traits associated with unrestrained proliferation, as is evident of *gt1* in the *id1* background. Is it possible that the *gt1* mutation is a manifestation of reduced apical dominance? This could explain the excess proliferation of small tillers at the base of the culm. Further, tassel feminization might indicate that the central stalk of the plant is developing characteristics of an axillary tiller.

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Information from Castle-Wright experiment
--Simic, D, Hallauer, AR

Plant breeders have made limited use of the Castle-Wright formula because of the underlying assumptions. Main assumptions of this method are 1) with respect to all relevant loci, one parent is fixed with the alleles increasing the trait of interest and the other parent is fixed with alleles decreasing the trait of interest; 2) additive gene effects; 3) unlinked loci; and 4) equal allelic effects at all loci. When these assumptions are violated the method substantially underestimates the true number of loci (Zeng, Houle, and Cockerham, 1990). Using selected lines and choosing properly examined traits (Hallauer and Miranda, 1988) our experiment does not violate assumptions 1 and 2. Biased estimates, however, occur largely due to linkage and unequal effects at alleles (Zeng, 1992). We estimated the number of effective genes of an F2 population that was not in linkage equilibrium and in the F2 population (Syn 10) after 10 generations of intermating which is an approximate linkage equilibrium. Results are summarized in Table 1.

Table 1. Sample size (N), means ($\hat{\mu}$), variances ($\hat{\sigma}^2_w$ and $\hat{\sigma}^2_s$) and number of genes (N_E) for three traits estimated in F_2 population and F_2 population advanced by 10 generations of random intermating (F_2 Syn. 10), and N, μ, and σ^2_w for F_1, P_1 (B73), and P_2 (Mo17) generations.

Trait	Parameter†				No. of effective loci		
	N	$\hat{\mu}$	$\hat{\sigma}^2_w$	$\hat{\sigma}^2_s$	n_E1	n_E2	n_E3
Silk date (no.)‡							
F_2 Syn. 10	1191	17.1	8.27	1.66	4.82	6.17	2.90
F_2	709	18.5	9.84	3.22	2.48	2.79	3.11
F_1	751	18.0	4.94				
B73	494	23.0	5.70				
Mo17	584	24.0	10.28				
Plant height (cm)							
F_2 Syn. 10	1218	207.3	446.39	332.36	0.02	0.02	33.97
F_2	717	199.7	422.58	308.55	0.02	0.02	35.45
F_1	760	231.4	134.90				
B73	488	183.4	97.37				
Mo17	591	176.5	112.90				
Ear height (cm)							
F_2 Syn. 10	1214	104.6	247.40	145.18	0.51	0.52	20.59
F_2	713	95.6	261.45	159.23	0.46	0.47	18.71
F_1	760	118.4	138.27				
B73	494	101.4	83.84				
Mo17	591	77.0	92.15				

†N and μ refer to the sample size and generation mean, respectively;

$\sigma^2_w = \sigma^2$; $\sigma^2_s = \sigma^2_G$; $n_E1 = (\mu P_1 - \mu P_2)^2 / 8\sigma^2_s$; $n_E2 = \dfrac{(\mu P_1 - \mu P_2)^2}{8(\sigma^2_{F2} - (\sigma^2_{P1} + \sigma^2_{P2} + \sigma^2_{F1})/3}$; and

$n_E3 = \dfrac{\text{Maximum range}}{(\text{Genetic standard deviation})^2} \times 1/8$.

‡Days after July 1.

Three versions of estimates of the effective number of loci are given without their standard errors. n_E1, n_E2, and n_E3 for the silking date are similar for F2 and more different for F2 Syn. 10. While n_E1 and n_E2, for plant height are similar for F2 and F2 Syn. 10, n_E3 (33.97 and 35.45) almost reached a recombination index of about 36 (Darlington, 1937 in Lande, 1981).

According to Zeng (1992) only at ear height were all three favorable conditions met: 1) the two parental populations are "many" (approx. 10) phenotypic standard deviations apart. In this experiment three deviations for silk date, plant height and ear height are 5.66, 4.91, and 17.21, respectively; 2) no linkage; and 3) large sample size (>200). Estimates of the number of genes for ear height, however, seem underestimated. Linkage did not affect the estimates because the number of estimated genes are similar for F2 and F2 Syn. 10 populations. Consequently, unequal effects of alleles seem to be important. There is no reliable procedure for correcting the bias from unequal effects of alleles. Zeng (1992) suggests use of parameter *z*, composite measure of variability of allelic effects and frequencies among loci. There are difficulties, though, in estimating the parameter *z*. Linkage effects, however, summarized by the mean recombination frequency is estimable, and can be corrected (Zeng, 1992). Hence, efforts of intermating are not necessary. Additionally, random intermating plants within F2 populations did not increase the genetic variability. Similar results were reported by Covarrubias-Prieto, Hallauer and Lamkey (1989) and Han and Hallauer (1989). Linkage was, probably, primarily in repulsion phase (Cavalli, 1952). On the basis of the estimates obtained for the F2 and F2 Syn. 5 populations, however, it

does not seem that repulsion phase linkages had a large affect on the estimates of σ^2_A (Han and Hallauer, 1989). We could not obtain estimates of the dominance parameter in our experiment because no backcross data were available.

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A mutant for *sh2* kernel type from high Space induced

--Zeng, M, Yang, T

In our previous paper we described a significant influence of space flight of maize seeds on progeny, including the young plant, ear and kernel (MNL.74:2-3). Five types of traits have been obtained, including a mutant for the *sh2* kernel type from Yi 01—4—1 Sp3,Yiol—4—1 Sp4 and Yi141 Sp4. The frequency of mutation for the mutant was smaller, about 0.5%. The plant, ear and kernel characters of the *sh2* mutant in the Sp4-Sp6 generations were measured; the results obtained are given in Table 1. The *sh2*-like mutant showed many favorable components:

Table 1. Plant and ear traits for space flight induced maize mutant of the *sh2* kernel type.

Plant height (cm)	165
Ear height (cm)	60
Length of the leaf of ear site (cm)	71.5
Width of the leaf of ear site (cm)	7.8
Ear length (cm)	16.2
Ear diameter (cm)	4.3
Tassel length (cm)	24.5
Tassel branch number	16
Leaf number	20~21
Number of kernel row	14~16
Kernel number per row	47~51
Weight of 1000 kernel (g)	153
Day from seedling to kernel maturing	114
Kernel Colour	yellow
Cob Colour	pale-yellow

early maturity - plants should produce all ears between 51-56 days after seedling; more ears per plant - plants should bear at least three ears per plant; under conditions of high density planting, the quality, size and shape of young ears is better; fewer husks for young ears - ear husk numbers show 6-7 per ear; proper ear and plant height - plant height is 165 cm, ear height is 60 cm. It all boils down to this, the *sh2*-like mutant may be optimized breeding material for baby corn.

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Phylogenetic analysis reveals that a maize member of the MSI/RbAp sub-family of WD-repeat proteins clusters in an evolutionary separate group

--Lanzanova, C, Locatelli, S, Hartings, H, Rossi, V

Members of the MSI/RbAp sub-family of WD-repeat proteins are widespread in eukaryotes and are part of a variety of multi-protein complexes involved in different biological pathways, including chromatin assembly, regulation of gene transcription, and cell division (reviewed in Verreault, A, Genes Dev 14: 1430-1438, 2000). Recently, we have identified and characterized a cDNA sequence from *Zea mays* encoding a homologue of the Retinoblastoma associated protein (*ZmRbAp1*). This gene shows structural and functional features common to the MSI/RbAp proteins, including the ability to bind acetylated histones H3 and H4, and to negatively regulate the Ras/cAMP pathway in yeast. During the molecular characterization of *ZmRbAp1* we have identified two additional partial cDNAs (ZmRbAp2 and ZmRbAp3) that exhibit 81% and 96% nucleotide identity with *ZmRbAp1*, respectively. This finding, together with Southern analysis, which revealed a complex hybridization pattern, suggests that maize *RbAp* genes belong to a gene family. Because MSI/RbAp subfamily members have been found in different eukaryotes and because many organisms possess multiple copies of these genes, we performed a phylogenetic analysis to compare the MSI/RbAp amino acid sequences available in databank. We used BLASTP (scores > 70, p values < 0.05 Altschul, SF et al., J Mol Biol 215: 403-410, 1990) to search in the non-redundant peptide sequence database at the National Center for Biotechnology Information for proteins similar to human RbAp48, yeast MSI1 and ZmRbAp1. Eighteen amino acid sequences, among the most representative for different species, were aligned using ClustalW software (Thompson, JD et al., Nucl Acid Res 22: 4673-4680, 1994) and a tree construction was performed (neighbor joining method using MEGA software v.1.0; Kumar, S et al., Pennsylvania State University). Interestingly, two separate groups were identified (see Fig. 1). ZmRbAp1 clustered together with AtMSI4 and SlY1, suggesting a common origin for these proteins. The two additional ZmRbAp clones we have identified also belong to this group. A second major cluster contained MSI/RbAp members of *Homo sapiens*, *Drosophila melanogaster* and *Saccharomyces cerevisiae*; for these proteins a role in chromatin modification, histone assembly and binding to retinoblastoma protein has been reported. Particularly, it has been shown that mammalian MSI/RbAp components possess a partially distinct activity (reviewed in Verreault, A, Genes Dev 14:1430-1438, 2000).

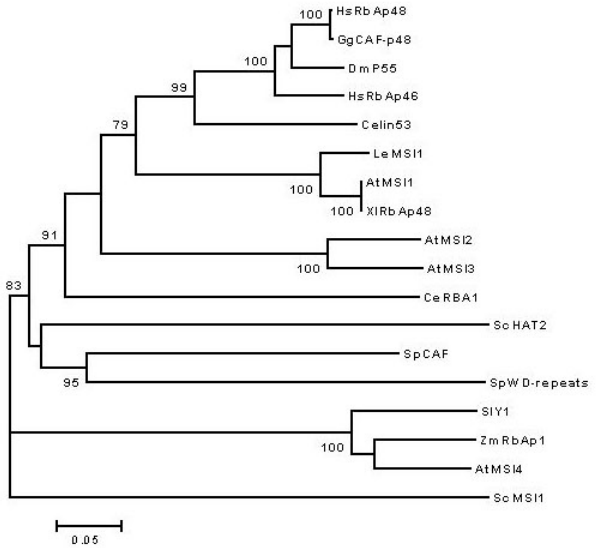

Figure 1. Phylogenetic tree based on the alignment of 18 members of the MSI/RbAp sub-family of WD-repeat proteins. ZmRbAp1 from *Z. mays* was aligned with 17 MSI/RbAp-like proteins from *H. sapiens* (HsRbAp46 and HsRbAp48), *G. gallus* (GgCAF-p48), *X. laevis* (XlRbAp48), *D. melanogaster* (Dmp55), *C. elegans* (Celin53; CeRBA1), *L. esculentum* (LeMSI1), *A. thaliana* (AtMSI1; AtMSI2; AtMSI3 and AtMSI4), *S. latifolia* (SlY1), *S. pombe* (SpCAF and SpWD-repeats), *S. cerevisiae* (ScMSI1 and ScHAT2). The lengths of the tree branches are proportional to the genetic distance. Bootstrap values based on 500 replicates supporting the branches at 75% cut-off value are indicated.

Our analysis indicates that at least three copies of functionally related *MSI*/*RbAp* genes exist in maize and that these genes have evolved differently with respect to the best characterized members of the MSI/RbAp sub-family of WD-repeat proteins. Peptide microsequencing of a recently described acetyltransferase HATB-associated RbAp protein (Lusser, A et al., Nucl Acid Res 27: 4427-4435, 1999) revealed a low degree of similarity with ZmRbAp1. Altogether these findings suggest the presence in the maize genome of different MSI/RbAp members performing specific tasks, while maintaining other functions common to all members of this sub-family.

Maize Rpd3-type histone deacetylase interacts with maize retinoblastoma-related protein

--Locatelli, S, Lanzanova, C, Motto, M, Rossi, V

Several bodies of evidence indicate that the dynamic alteration of the chromatin structure due to acetylation and deacetylation of histones is strongly related to the control of gene transcription (reviewed in Cress, WD and Seto, E, J Cell Physiol 184:1-16, 2000). Regulators involved in many important biological processes can recruit multiprotein complexes containing histone acetyltransferases (HATs) and deacetylases (HDACs) to regulate transcription at specific promoter levels. Recently, it was reported that the retinoblastoma (pRb)/E2F pathway alters the chromatin structure using HDACs to control G1/S progression in the mammalian cell cycle (reviewed in Harbour, JW and Dean, DC, Genes Dev 14:2393-2409, 2000).

We have previously identified and characterized a maize Rpd3-type histone deacetylase (ZmRpd3I; Rossi, V, et al., Mol Gen Genet 258:288-296, 1998). In addition, the identification of components of the pRb/E2F pathway in plants suggests that the basic molecular control of cell cycle has been conserved from animals to plants (reviewed in Huntley, RP and Murray, JAH, Curr Opin Plant Biol 2:440-446, 1999). Analysis of the protein interactions between ZmRpd3I, maize retinoblastoma-related (ZmRBR1) and retinoblastoma associated (ZmRbAp1) proteins was performed by means of in vitro GST-pull down assays. The results indicate that ZmRBR1 interacts with ZmRpd3I and that ZmRbAp1 can bind both ZmRBR1 and ZmRpd3I. Deletions and site-specific mutants were used to analyze the regions of ZmRBR1 and ZmRpd3I involved in the protein interaction. We observed that the integrity of both A/B pocket and C-terminal domains of ZmRBR1 are required for the binding to ZmRpd3I. The same domains are also responsible for the association with ZmRbAp1, although mutations affecting the structure of the A/B pocket did not reduce the binding. It is noteworthy that the A/B pocket of pRb is highly conserved in higher eukaryotes. Particularly, it is believed that the LXCXE binding site, located within the pocket, is required in mediating the interaction with several pRb-associated proteins containing the LXCXE domain, including two of the three mammalian Rpd3-type HDACs identified so far (Harbour, JW and Dean, DC, Genes Dev 14:2393-2409, 2000). Because ZmRpd3I does not contain the LXCXE domain, we carried out GST-pull downs in which a synthetic LXCXE peptide was added to the reaction mix to detect its effect on binding. Our results suggest that the ZmRBR1 LXCXE binding site is not involved in the interaction with ZmRpd3I and ZmRbAp1. Hence, different domains in the A/B pocket and C-terminal region of ZmRBR1 are likely to be required to mediate these protein interactions.

Deletions in the ZmRpd3I sequence showed that the simultaneous removal of both C- and N- termini abolished the interaction with ZmRBR1 and ZmRbAp1, indicating that there are multiple contacts between these proteins. The two ZmRpd3I regions required for association with ZmRBR1 are partially overlapping with those involved in the interaction with ZmRbAp1. This finding suggests that ZmRbAp1 may mediate, at least in part, the contacts between ZmRpd3I and ZmRBR1. Accordingly with this scenario, we observed that addition of recombinant ZmRbAp1 protein in the reaction mix in GST-pull downs increased the amount of in vitro translated ZmRBR1 specifically retained by the GST-ZmRpd3I fusion protein. Similar results were obtained in reciprocal experiments. Conversely, addition of ZmRpd3I recombinant protein did not alter the association between ZmRbAp1 and ZmRBR1.

These results provide the first, although still preliminary, evidence of plant multiprotein complexes containing Rpd3-type HDACs and regulators that play a pivotal role in controlling cell cycle progression.

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Gene action for knob number in corn

--Mandal, SS, Akhtar, SA

The combining ability analysis revealed that significant differences existed for general (gca) and specific (sca) combining ability for number of knobs. The fixed effect model (Model 1 and Method 1 of Griffing 1956a) in the present study does not provide estimates of variance components and thus it was not possible to know precisely the relative importance of additive and dominance components in the control of knob number. However, the relative importance of gca and sca in determining progeny performance can be obtained by calculating general predictability ratio (GPR), on the basis of gca and sca variance components of mean squares. The value of GPR for knob number was 0.13 (Table 1).

Table 1. Analysis of variance for combining ability

Character	gca (df=3)	sca (df=6)	reciprocal (df=6)	error (df=30)	GPR
Knob number	1.48**	2.315**	1.74**	0.01	0.13

The estimates of this ratio indicated that progeny performance was based on both gca and sca for genetic variability. Moll et al. (1972) suggested additive and dominance, and dominance and dominance gene action for knob number in maize.

Knob in relation to altitude

--Mandal, SS, Akhtar, SA, Sinha, NK, Srivastava, M

Low land tropical parents, namely CML47 and CML49, exhibited comparatively higher knob number, 7.0 and 6.0 respectively. Three hybrids, namely CML47 x CML49 (6.33), CML47 x CML107 (6.00) and CML49 x CML47 (5), have comparatively higher number of knobs with significantly higher yield. It is remarkable that the Gangetic plain of Bihar (Maize Research Centre Dholi) lies in lower altitudes of 52.2 MSL. Furthermore, Ganga Safed-2, a stable variety doing well for the last 3 decades in the Gangetic plains of India, has a comparatively higher number of knobs (6.0). The present finding was in agreement with the findings of Longley (1938), Mangelsdorf and Cameron (1942), Brown (1945), Wellhausen et al. (1951), Wellhausen and Prywer (1954), McClintock (1960) and Pandey et al. (1988). However, one higher

yield cross, CML107 x CML47, possesses only 4.0 knobs. Remarkably, one parent (CML47) involved in the cross possesses a relatively higher number of knobs (7.0). Keeping in view this fact, there is a growing need to consider knob heterochromatin in a controlled, reproducible and predictable manner to derive hybrids and selection of inbreds.

Membrane permeability as a marker of low temperature resistance in maize

--Sinha, NK, Mandal, SS, Handoo, JK, Srivastava, AK

A laboratory experiment was conducted for the determination of decrease in seed permeability of maize in terms of release of exudates, by determining the electrical conductivity. The value of electrical conductivity of the exudates were higher under low temperature stress (8±1 C) than for the seeds germinated in 25±1 C. Minimum leakage determines membrane permeability of the germinating seeds of resistant maize varieties.

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Allelism of chromosome 2 endosperm mutants

--Whalen, RH

Graham, Suresh and Phillips (MNL 67: 102, 1993) mapped the recessive mutation *opaque8* (*o8*) to the vicinity of *umc134* on chromosome 2. Since the Maize DB map indicates this is near *floury1* (*fl1*), we crossed the two mutants to test for allelism. Since *fl1* shows a dosage effect (i.e., *fl/fl/Fl* is floury) but *o8* does not, the *fl1/fl1* plants were used as pollen parents on to +/*o8* plants. The resulting ears segregated floury, indicating allelism.

Stierwalt and Crane (MNL 47: 166, 1973) reported a mutation *opaque4* (*o4*) which, unlike *fl1*, is recessive and does not exhibit dosage effects. As they found it to be allelic to *fl1*, it is now designated as *fl1-o4*. Crosses of this mutant with *fl1-Ref* males gave ears with only floury seeds, confirming Stierwalt and Crane's findings of allelism. Crosses of +/*o8* plants as males onto +/*fl1-o4* plants gave ears that segregated for normal and floury kernels, again confirming allelism of *o8* and *fl1*.

Since *o8* is allelic to both *fl1-Ref* and *fl1-o4*, the *o8* mutant should be renamed *fl1-o8*.

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3D visualization of stem by MRI technology

--Cheng, P-c, Chen, J-H, Lin, C-P, Sun, C-K, Walden, DB, Cheng, WY

Recent development in confocal and multi-photon fluorescence microscopy allows 3D imaging of plant tissue in high resolution. However, other than physical sectioning, macroscopical study of plant organs in 3D remains a difficult task. Among various available technologies for macroscopical imaging (e.g., X-ray macrotomography, optical coherent tomography and MRI), MRI is an ideal choice for its contrasting modality in volumetric imaging of soft tissues. In this study, a 3T Biospect MRI system (Brucker, Germany) equipped with a 6cm inner diameter micro-quadrature coil for RF transmission and reception of MRI signals was used. Spin echo based RARE sequence was used to obtain T2 weighted images with TR/TE = 3160.5/58.5ms and field-of-view of 1.67cm x 1.67cm (256 x 256 pixels) at a slice thickness of 0.8mm. This corresponds to a pixel size of 65 x 65 x 800μm. Data were obtained over 0.5 hour with number-of-excitations (nex) set at 16.

Figures (1)-(12) (following page) show a series of MRI cross-sections through a node (the node below the main ear insertion) from field-grown maize stem (Odyssey sweet corn). The stem was fixed in 1:3 EtOH/acetic acid, and washed thoroughly in water prior to imaging. Air bubbles trapped in the leaf sheath were removed by vacuuming to avoid imaging artifact due to low magnetic susceptibility of air. Note the branching pattern of vascular bundles in the node. The image set shown in this article is suitable for computer 3D reconstruction and visualization. Tracing and reconstruction of vascular bundles in the node region is possible.

This project was supported by the National Science Council, Republic of China under grant number NSC-88-2811-B-001-0023 (PCC), NSC-89-2811-E-002-0058 (PCC), NSC-89-2215-E-002-064 (CKS). The Biospec MRI facility is a national user facility funded by the National Science Council, Republic of China and operated by the Precision Instrument Center, National Taiwan University.

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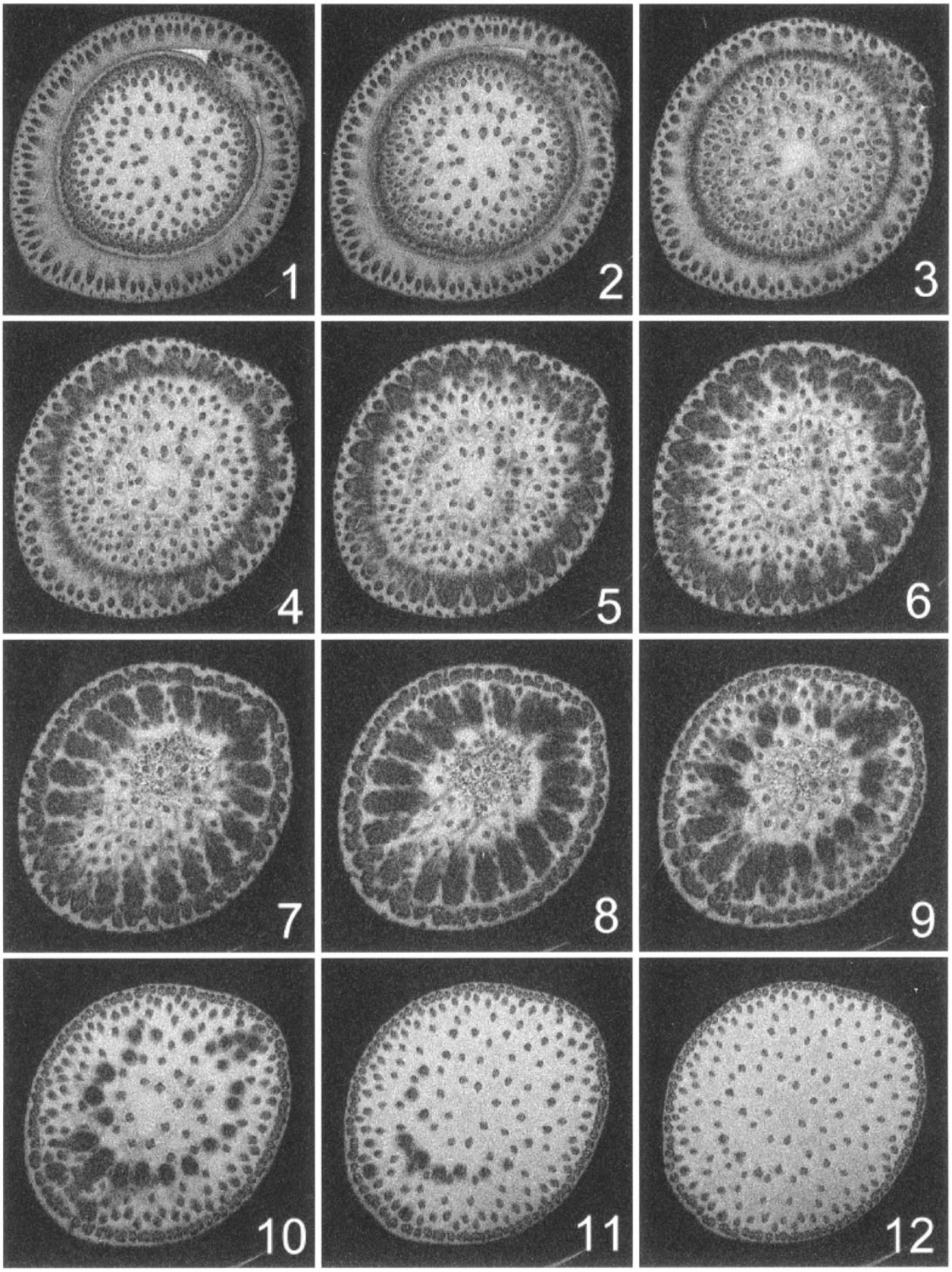
Stem development in *na1/na1* and *na2/na2*

--Cheng, WY, Cheng, P-c, Gu, M, Gan, X, Chung, H-W, Walden, DB

In contrast to the parallel arranged longitudinal vascular bundles commonly found in the internodes of wild type (a, e), *na1/na1* appears poorly organized (b). However, cross-sectional views reveal that the vascular arrangements of the entire *na1/na1* stem (f, g and h) resemble those found in the nodal region of a normal plant (d). Therefore, one may consider the entire *na1/na1* stem comprises a single node (b). Similar to the main stem, the ear branch of *na1/na1* also lacks a well-defined internode structure. It is important to point out that the elongation and vascular arrangement in the internodes of *na1/na1* tassel are "normal". The branching of a vertically arranged vascular bundle (v) is evident in the series of optical sections (k, i, m and n) obtained by multi-photon fluorescence microscopy.

In contrast, *na2/na2* stem has a "normal" stem appearance but the internode length is significantly shorter (c). The cross-sectional views of *na2/na2* stem (i and j) reveal similar nodal and in-



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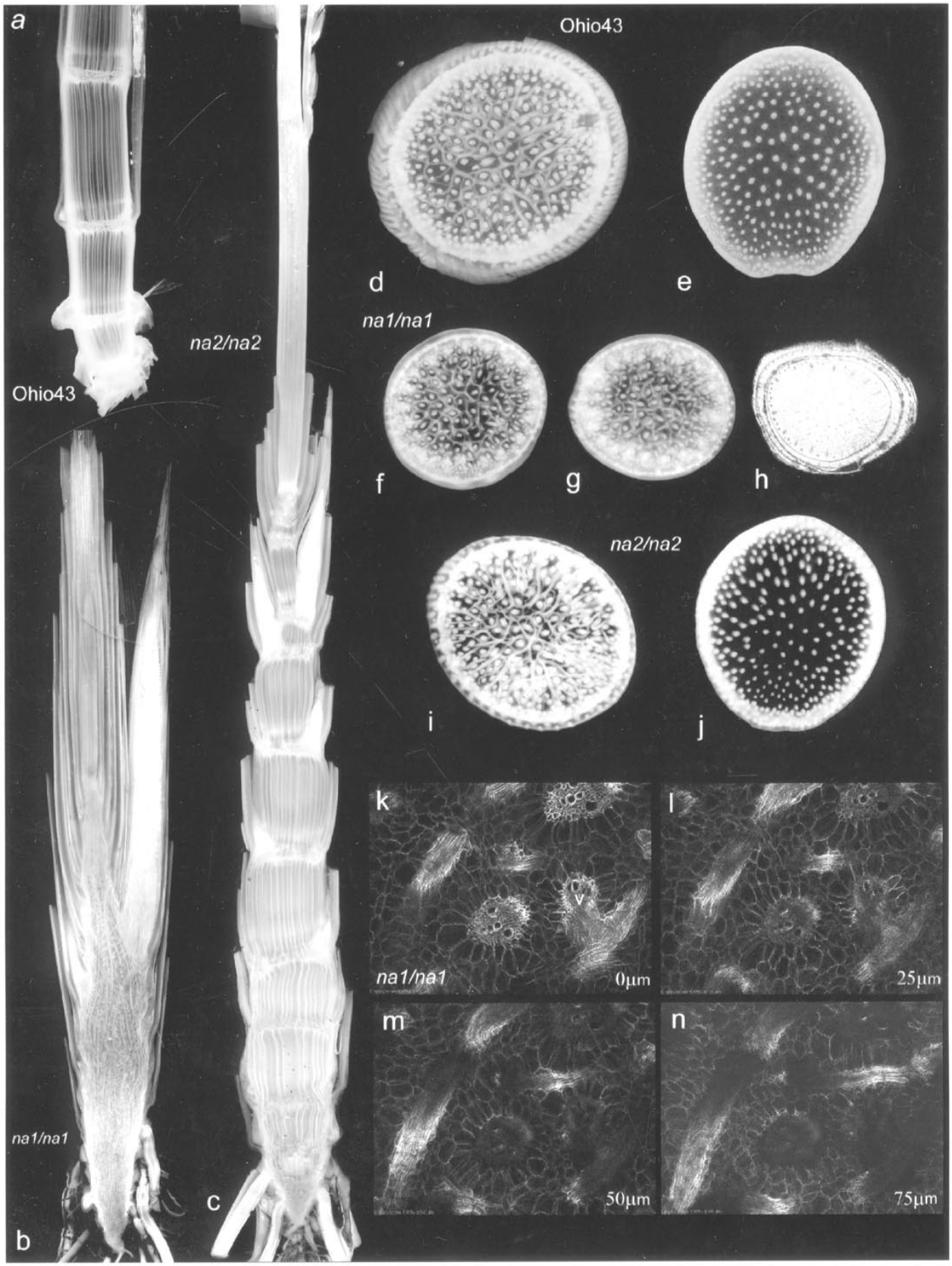

Cheng et al. Stem development in *na1/na1* and *na2/na2*

ter-nodal vascular arrangement, as found in the wild type (d and e). The elongation of tassel internodes occurs in *na2/na2* (c).

Figures (previous page): (a) longitudinal section of a wild-type maize stem (Ohio43 inbred). (b) *na1/na1* stem; (c) *na2/na2* stem; (d and e) cross-sections at node (d) and internodes (e) from wild-type plant; (f, g and h) cross-sections at various levels of *na1/na1* stem; (f) and (g) are physical sections while (h) is an MRI section; (i and j) cross-section of *na2/na2* stem at node (i) and internodes (j). All the plants used in this study were grown at the field station of the University of Western Ontario, London, Canada in the summer of 2000. The specimens were fixed in methanol, serial sectioned with a razor blade using a specially made jig. The image was obtained by using a modified Acer 600CU flat-bed scanner (600dpi optical resolution, equipped with back-lighting) in liquid. (k-n) show a set of optical sections (cross-sections) from *na1/na1* stem. The optical sections were obtained at various depths (0μm – 75μm) by two-photon florescence microscopy using 870nm near IR illumination. An Olympus Fluorview FL300 confocal microscope equipped with a Spectra-Physics Mai-Tai tunable Ti-sapphire laser was used for this study.

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Transposable element in maize anther culture-derived microspore-plants and their progenies

--Ting, YC, Tran, L

In the last few years, selection of stable inbred maize from anther culture-derived progeny plants was made (MNL74:73). This inbred line was descended from a single self-fertilized PO (first generation of microspore-plant) plant of KH-13. Every summer, more than 100 progeny plants were grown in the field for observation. Among them, five to 10 percent were classified as dwarf-yellow-green. These potential mutants were weak, had barren stalks and had sterile male inflorescences. It was almost impossible to make any further genetic evaluation on them. However, in each summer, three to five of the normal sib plants were selected and self-pollinated. In the next year, those self-fertilized kernels were employed for further testing. More than 100 plants were grown again for study. The dwarf-yellow-green plants reappeared in the new progeny . When a X^2-test was made, the frequency of the appearance of these mutant plants did not fit the expected ratio of either monohybrids or dihybrids. The above experiments were repeated for more than five years. Last summer, the same procedures were followed. It was surprising to find that no dwarf-yellow-green variants were observed. In other words, the selected progeny plants had become a stable line. Its immediate offspring were close to 100 percent fertile and uniform in morphology. It is concluded that the previous segregations of dwarf-yellow-green vs. normal plants were an indication of the presence of a transposable element in the parental plant. This element was originally silent and activated through anther culture. It is conceivable that after being through more than five generations of self-fertilization, the transposable element was thrown out by irregular meiotic division. Furthermore, it is tenable to say that anther culture of maize may lead to the production of useful inbreds. These inbreds can be employed to facilitate the improvement of food supplies.

Conditional expression of maize vegetative cloning gene

--Ting, YC, Tran, L

The effect of day length on the expression of the maize vegetative cloning gene was reported in last year's Maize Genetics Cooperation Newsletter. Since then, studies of this gene were carried out further. In the later part of last March, 21 kernels of a self-fertilized plant were employed for experiment. This plant had a simplex genotype of *Clg clg clg clg*. The kernels were sown in pots in the greenhouse. At that time, the daily illumination was a little more than 12 hours in the Boston area. The kernels germinated readily. The plants were generally healthy. Three months later, or in the middle of June, transplantation of these plants into the field plot was made. All of the plants survived well. However, in August and September, it was found that none of the plants expressed the cloning gene by regenerating plantlets on the tassels, even though three quarters of them were expected to do so. Therefore, it is postulated that in order to have the cloning gene expressed, the plants need to be grown under short day, particularly in the first three months of growth. As stated above, the seeds for this study were sown in the second half of March. Throughout their whole life period, the plants grew and developed under long day conditions. More than 12 hours of daily illumination might inhibit plantlet regeneration.

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Maize productivity: an example of non-allelic interaction

--Chernov, AA, Mihailov, ME

The question of heterosis may be reduced to a question of factors causing advantage for heterozygous organisms. The great role of allelic interaction (dominance and overdominance) has been demonstrated theoretically and experimentally, but non-allelic interactions remain less investigated, especially these, in which effects of different loci can't be summarized.

Here we show an example of such an interaction between the loci *wx1* and *R1*. Maize productivity was measured in F2 hybrids Ku123 x 2-9m and Uit757 x 2-9m (see Table).

Table. The productivity of F2 plants (gm/plant) in the combinative classes *wx1-R1*

	Hybrid and year		
Genotype	UIT-757 x 2-9m 1993	Ku123 x 2-9m 1993	UIT-757 x 2-9m 1995
wx1+/+ R1+/+	111+8 (15)*	132+12 (16)	159+13 (6)
R1+/-	132+8 (27)	134+7 (31)	159+15 (13)
R1-/-	147+12 (11)	133+11 (13)	172+19 (10)
wx1+/- R1+/+	149+13 (13)	161+11 (20)**	170+15 (15)*
R1+/-	155+8 (37)	152+6 (57)	173+10 (31)
R1-/-	146+11 (19)	143+10 (22)	130+12 (16)
Total	142+4 (122)	145+4 (159)	162+6 (91)

Comment 1. The number of plants is given in brackets.
Comment 2. The asterisks relate to whole cell and show significance of effect of the *R1* locus.

It is seen in the table that details of this interaction depend on genetical environment and year conditions. Nevertheless, here is a common feature. The *R1* locus regulates productivity, and the *wx1* locus regulates the *R1* locus. One allelic state of *wx1* (+/+ for UIT-757 x 2-9m and +/- for Ku123 x 2-9m) allows *R1* to be regulator, another allelic state blocks this regulative function.

The productivity of the heterozygous genotypic class *wx1*+/-

R1+/- in all cases is higher than the mean value. Therefore, gene interactions of such a type can provide a role in heterosis.

Male gametophyte viability of waxy maize in conditions of low temperature

--Kravchenko, OA, Kravchenko, AN

The purpose of this study was to reveal the effect of low temperature on male gametophyte viability at the pollen germination stage and pollen tube growth stage. Inbred lines 346 and 502, and their waxy counterparts as well as their MR4 progeny (obtained from irradiated immature embryos in vitro), were taken as experimental material. Freshly collected pollen from each genotype was planted on the nutrient medium (developed by Cook, F.S., Walden, D.B., Can. J. Bot. 43:779-786) and subjected to low (+12 C) temperature treatment for 6 hours. At the same time pollen of control variants was cultivated in normal (+24 C) temperature conditions. On average, 500-700 pollen grains from each genotype were analyzed to determine pollen viability.

Generally, low temperature treatment resulted in decreasing of maize pollen viability. The reliable effect of genotype and temperature was revealed by two factor analysis of variance (Table 1). The results obtained indicated that pollen viability of MR4 progeny of inbred lines 346 and 502 was less genotype-dependent than that of their waxy counterparts. It should be noted that pollen viability of MR4 progeny of inbred line 502 was more temperature-dependent in comparison with MR4 progeny of other inbred lines. Thus, a significant variability of male gametophyte viability among plants of the MR4 generation was found.

Table 1. Genotype and temperature effect (%) on male gametophyte viability

MR4 progeny of inbred lines:	Factors: genotype	temperature	their interaction
346+/+	74.61***	13.32***	11.53***
346wx1wx1	83.71***	9.5***	6.28***
502+/+	51.49***	39.72***	8.21***
502wx1wx1	75.47***	19.07***	5.91***

***- P<0.001

Studying some features of maize genetics and developmental biology using electrophysiological techniques

--Lysikov, VN

In the Republic of Moldova, the possibility of employing electrophysiological techniques was first studied on maize plants. The experimental evidence suggests that precisely these techniques provide new insights into extremely involved processes of maize genetics and developmental biology.

Modern breeding programs are aimed at producing heterotic maize hybrids. This involves identification in parental lines of valuable traits and features associated with their combining ability. All experimental evidence from parental lines of hybrids can be classified into two groups: static parameters recorded as dots on the plotting paper, and dynamic parameters representing temporal variation of the developmental process which are recorded as lines on the plotting paper.

Dynamic indices are known to generally provide more complete and adequate information about the occurring processes and are especially good indicators of the effect of environmental factors on an individual cell, tissue, organ, or a whole organism (plant). Electrophysiological techniques allow, without disturbing the plant's vital activity, the dynamics of the processes occurring in the plant to be demonstrated and the results recorded as plots, curves and diagrammes.

That is why electrophysiological techniques were used in obtaining numerous unambiguous electrophysiological data for generative and vegetative organs of maize lines, mutants and hybrids. The essential feature required of the measurement procedure was that the effect of the recording instruments on the pattern of life activity be minimum, because this is the only way to ensure that the data obtained are as highly informative as possible.

Based on these specific requirements, all the electrophysiological techniques employed can be classed into two groups: (1) intracellular recording of bioelectrical potentials (biopotentials), and (2) extracellular measurement of biopotentials. In our study, the second group was represented by two independent types of experiments: (1) measurements performed in artificial conditions - greenhouse, hothouse, climate chamber, laboratory, etc.; (2) extracellular biopotential measurements on plants in the field.

In addition to these two major methods of studying electrophysiological properties of maize, work has been done on recording dielectric properties of maize plants, measuring the electric resistance of stem and pistil, and the electric charge of pollen grains, as well as some other work which is touched upon in passing in the present study.

The intracellular recording of biopotentials was performed by Dr. A. I. Doukhovny. Not only did he carefully study maize pollination and fertilization processes, but he also developed a number of methods and approaches, being one of the first to carry out investigations like these.

For measuring the bioelectrical potential of an individual plant cell, conditions ensuring minimum alteration of the cell should be observed. This is only possible where the cell wall size is an order of 2 to 3 larger than the area of perforation resulting from the microelectrode introduction into the cell. To this end, glass microelectrodes were made in the form of micropipettes whose tip diameter was no more than one micron. Thin Pirex glass tubes were used to produce micropipettes.

Using a device called microforge, the tubes were fixed at both ends and split in half in the middle. The resulting two microelectrodes were filled, under vacuum, with 2.5 M solution of KCl. A filled microcapillary is a microelectrode. This was connected to a mercurous chloride or silver chloride macroelectrode.

A microelectrode produced in the above manner was introduced, using a micromanipulator under constant visual control in a binocular microscope, into the plant cell. The biopotential recording itself was carried out on DC electrometric amplifiers of the UI-2 type at whose outlet quick - response self-balancing EPP potentiometers were connected which recorded the signals on the diagram paper. In addition, connected to the same electrometric amplifiers were electron oscillographs, enabling visual observation of the rapid processes occurring in the cell.

It should be noted that maize proved to be a very convenient experimental plant for intracellular biopotential measurements. This is due to the fact that the female reproductive organ of maize, the ovary in particular, has the style with an elongated stigma often called the pistil filament.

When expanding in cross section, the maize pistil filament is very similar to an asymmetric eight figure with a slight depression at the centre. Through the centre of each half of the figure of eight run vascular bundles normally composed of 3 to 6 strands

extending from the stigma to the ovary.

The maize pollen grains and elongating pollen tubes act on pistil tissues as an effective combined mechanical stimulus. Preliminary experiments showed that it is the vascular strand cells that are capable of receiving the stimulus signals and transforming them into electrical signals, and transmitting the latter over particular distances. In vascular strand cells, the resting potential (i.e. the transmembrane difference of potentials of a nonexcited cell) is several dozen millivolts higher than that in the surrounding stigmatic cells, and is normally in excess of 80 mV. Electrophysiological specificity like this allowed reliable identification of the cells under study.

Another important finding of the preliminary experiments is the one-way conductance (transmission) of action potentials in the direction of the ovary, which is probably due to physiological and biochemical polarity of the pistil.

The initial bioelectrical response of the maize pistil prior to pollen germination is manifested in the generation of a single impulse of the action potential, with an amplitude of more than 20 mV and pulse duration of 2.5 to 34 sec in the pistil filament and 1.3 to 2.0 sec in the ovary. Generated 3 to 18 min after pollen application, the first impulse travels in a nondecreasing manner at a rate of 12 mm/sec, such that in 20 to 30 sec, depending on the pistil length, it reaches the ovary. It has been found that prior to generation of action potentials, the resting potential of the excited cells increases by 16 to 27 mV.

As a result of further pollen growth, another two impulses are generated whose characteristics are very similar to the first one. One of these arises in the pistil filament 64 to 83 min and the other 49 to 67 min following the first single impulse. These two impulses differ from the first one in that they show a higher travel speed. What we deal with here is probably the "duration" effect. This process takes about 1.5 h to complete after the start of pollen germination. It is worth noting that the essential difference of these impulses from the first one is that they produce (elicit) in the ovary only a local response of resting potential fluctuation, with an amplitude of several millivolts.

It has been shown that the incoming action potentials are transformed at the pistil base. With the start of more intensive elongation of pollen tubes and of their active penetration into the pistil tissues, the stage of higher electrical activity commences, characterized by the generation of a large number of impulses of action potentials which alternate with the local electrical response.

Impulses with an amplitude of 15 to 39 mV travel, almost nondamped, towards the ovary for nearly 1.5 h. The transformation of the incoming action potentials is most pronounced during the subsequent time interval, which starts 97 to 130 min after pollen application, and lasts for about 70 to 80 min. Generation and transmission of a large number of single impulses of action potentials occurs presumably due to higher metabolic rates. It is these impulses, travelling in a nondecreasing manner, that control rhythmic generation of potentials in the ovary.

The rhythmic electrical activity of the ovary manifested as rhythmic generation of resting potentials is a two-stage process. The duration of the first stage is about 35 min and of the second stage about 20 min, such that the second stage starts, on average, 38 to 41 min after the completion of the first one.

A distinctive feature of the first stage is a lower frequency of action potentials, longer pulse and between-pulse duration with the advance of the stage (i.e. towards its end).

Seven pulse trains have been identified and characterized, each with its particular constant or smoothly varying frequency of potential generation. In transition from one pulse train to another caused by single pulses arriving at the ovary from the pistil filament, the frequency of pulse generation varies in a saltatory manner. Furthermore, the transition between some pulse trains is due to an additional increase in the resting potential.

The second stage of rhythmic activity comes about 40 min after the first one and consists of three pulse trains differing in the potential shape and frequency. Characteristic features of the second stage are an increase in frequency action potentials and a decrease in frequency of resting potentials towards the end of the stage, respectively up and down to the values corresponding to those of a nonexcited cell.

The period of multiple pulse generation in the pistil filament, like that of rhythmic pulse generation in the ovary, appears to be the most functionally loaded one. The subsequent bioelectrical response of maize pistils is characterized by generation of widely separated single action potentials which reach the ovary without being transformed at the style base. The type (pattern) of response remains unchanged throughout the pollen tube elongation period.

By the time of pollen tube penetration into the embryo sac and subsequent fertilization, the generation of single action potentials is terminated, and the resting potentials begin to exhibit wave-like variation characterized by rhythmic fluctuations distorting the smooth shape of the wave. Two wave-like variations are the most characteristic ones: the first, in order of appearance, and the fourth or fifth. The distinctive feature of these patterns of variation is a brief (12 to 45 sec) increase in the potential with an amplitude of 2 to 9 mV.

The first characteristic wave-like variation gives rise to a wave of excitation, which is recorded in maize stems during extracellular measurement of biopotentials. This wave originates at the base of the pollinated ear and spreads up and down the stem at a rate of 40 to 61 cm/min. The amplitude is not the same at different points in the stem: a maximum amplitude of up to 18 mV was recorded at the base of the stem, and up to 17 mV at the point of ear attachment. The duration of the process in maize lines and hybrids varied between 20 and 50 min.

Thus, the results from the above experiments suggest that the bioelectrical potentials traveling through maize generative organs and detectable during intracellular measurements, and the ones traveling through maize stems and detectable during extracellular measurements, offer a tool for analyzing complex concurrent, but spatially isolated, physical and biochemical reactions in a living body.

It has been suggested that recording ten thoroughly studied pulse trains on a magnetic tape and their subsequent application (presentation), through specially implanted microelectrodes, using electronic instruments and observing the timing, the pattern, the specificity and sequence of pulses may be of interest in studying some issues such as apomixis or other involved processes associated with fertilization.

Based on the method of multichannel measurement of bioelectrical potentials with the aid of macroelectrodes, A. I. Doukhovny designed, using a DC electrometric amplifier and a self-balancing twelve-point potentiometer, a special switch enabling simultaneous measurement of potentials at different points in the plant. He demonstrated that normally stabilized, more or less invariable,

frequently straight, and parallel bioelectrical potential lines appearing on the plotting paper prior to pollination start, upon landing of pollen on the stigma, to change their direction such that, not infrequently, they "tremble", occasionally become nonparallel to one another, and even intersect.

Pollination and fertilization have been shown to result in higher electrical activity at various points in the stem. An increase in the number of "intersections" in the stem always occurs more smoothly than does the variation of bioelectrical potentials in the pistil, although in the stem they persist, at a particular level, for 2 to 3 days.

In other words, the maize plant "trembles" in terms of electrophysiological parameters, resulting in a higher number of intersections and nonparallel biopotential lines on the plotting paper.

Application of extracellular biopotential measurement techniques deserves to be considered in greater detail. The largest number of experiments employing the techniques have been carried out by S.N. Maslobrod in the laboratory and by F.G. Oloer in the field.

Based on the topography of maize leaf and plant surface biopotentials, S.N. Maslobrod established the existence of more than one type of bioelectrical polarity (right and left), and outlined the bioelectrical stereopolarity and the dynamics of polarity from the seed stage up to the mature plant stage. Subsequently he studied the spatiotemporal organization of maize surface biopotentials in terms of electrophysiological polarity, oscillation, and signal generation and transmission.

Based on the assumption of endogenous rhythmicity of plant biopotentials being genetically preprogrammed, S.N. Maslobrod suggested that the function of genes responsible for a particular trait be regarded in terms of operation of an electrophysiological oscillator with a given frequency range, and that the structural gene be represented as a "wave gene" sui generis, which is in good agreement with the "wave" function of gene activity proposed by Chirkov (Chirkov, 1994).

S. N. Maslobrod made an electrophysiological evaluation of plant genotypes differing in phenotype, including marker lines, lines with high general combining ability, thermotolerant genotypes, samples showing general (nonspecific) ecological stability, cold-hardy forms, ancestral forms, as well as specimens exhibiting high competitiveness under overcrowding. The results of his studies can be presented briefly as follows:

1. Phenotypic characters of the genotypes: It has been established that maize seedlings with marker pigmentation traits differ in the amplitude of response to light and temperature treatment.

2. Ancestral forms of maize are characterized in terms of general ecological stability of genotypes. They exhibit higher ecological stability as compared with cultivated forms. Their ranges (amplitudes) of electrical response are narrower whereas the electrical response values of the cultivated forms are 2 to 3 orders of magnitude higher.

3. General combining ability of lines: Positive correlation has been established between the level of general combining ability of maize lines (topcross) and positive biopotential values, in particular for coleoptile and leaf biopotentials.

4. Heat tolerance of maize lines: Heat-tolerant maize lines have been shown to differ from heat-sensitive ones in that they exhibit smaller amplitudes of electrical response to alternate light / darkness exposure at 40 C and to variation in temperature between 20 C and 40 C.

5. Cold tolerance of maize lines: It has been demonstrated that maize lines whose cold tolerance is due to the genotype or environmental factors exhibit smaller amplitudes of electrical response to a sharp drop in temperature (5 C and more) and retention of amplitude during repeated exposure.

6. Competitiveness of genotypes: Viewing competitiveness as tolerance of maize lines and hybrids to overcrowding, the author distinguishes competitive and less competitive lines by: 1) lower electrical resistances of root contacts of seedlings within the group, and 2) better synchronization, i.e. by the uniformity of morphological, physiological and electrical variables; normally, higher absolute values of these variables are observed in plants belonging to the group.

Based on the above theoretical points, S.N. Maslobrod devised a number of express methods of practical importance for which he obtained author's certificates. Among these, the following should be mentioned first of all:

1. Express methods for estimating stimulative doses of gamma and laser irradiation in presowing treatment of maize seeds.

2. Express methods for producing bioisomeres (right and left) in maize plants.

3. Electrophysiological express methods for evaluating economic traits in maize such as heat tolerance, cold tolerance and competitiveness.

4. Electrophysiological methods for evaluating genotypes of evolutionarily different plant forms (wild, cultivated and segregating).

5. Electrophysiological methods for estimating the effects of physical factors: rhythmic light, weak current, etc.

Studies by S.N. Maslobrod yielded numerous data characterized by a high degree of novelty. Among these, the following should be mentioned.

A. Maize plants have been found to possess two induced electrophysiological stereopolarities of the mirror type, the so-called "flat structure" and "hollow structure". They depend on the environmental factors and on the pattern of maize plant architectonics. Structural and functional elements of stereopolarity have been identified.

B. The existence of an intimate relationship between maize plant electrophysiological stereopolarity and disymmetry (left and right symmetry) has been established, and the morphological role of the former with respect to the latter demonstrated.

C. It has been shown that plants, as well as plant communities (phytocenoses), represent ensembles of electrical and physiological oscillators whose degree of adjustment to one another determines competitiveness of the components of a unified oscillatory system.

D. Using maize as an experimental object, the ability of action potentials to propagate from one plant to another through the mechanism of electromagnetic induction has been demonstrated.

E. Maize plants have been found to be capable of responding electrically to unconventional stimulants (gamma and laser irradiation) and of assuming the state of total electrical excitation via the mechanism of spatial synchronization of action potentials.

F. Action potentials of maize plants have been shown to be able to transmit information about stereoscopic structure of the object and to coordinate functions of the underground and above ground plant parts upon exposure to light.

In light of the above, the use of stationary (time-independent)potentials to test maize growing capacity and productivity,

as well as ecological stability, is justifiable.

It is also logically justifiable to employ the method of electrical control of adaptive potential of maize plants by simulation of their electrophysiological parameter adjustment and optimization.

Summarizing S. N. Maslobrod's studies, we can say that the formation and maintenance of spatiotemporal organization of maize plant surface biopotentials is ensured by electrophysiological control systems, performing in a plant body the functions of nutrient and energy transfer, and transmission of information, including that of plant body stereoscopic structure.

An extensive and interesting study of electrophysiological methods directly in the field has been carried out by F.G. Oloer. To this end, nine mutant lines derived by maize experimental mutagenesis from a single VIR-44 line, and one single-cross hybrid synthesized from lines derived from mutants, were examined. The above mutant lines differed considerably from their original line in morphological and agronomic traits.

For experiments in the field, a special experimental plot consisting of 100 test strips whose area totaled 700 sq.m, was established. Each strip was sown to 12 plants including 9 mutant lines, 1 hybrid and 2 control plants (VIR-44 line). For randomization, each strip had its own, differing from the others, order of positioning of mutants and controls.

Measurement of electrical parameters of maize mutants was performed using a specially re-equipped unit MTL-62(magneto-telluric laboratory) mounted on a bus. The additional equipment included: (a) DC electrometric amplifiers A1-2, EPP-09 potentiometers, a PSR-1 potentiometer, an S1-1 oscillograph, a set of meteo instruments, a transportable electric power station with power generating capacity of 1 kWt and a knockdown screening box 200x150x150 cm in size.

A biopotential measurement procedure suitable for field studies was developed. Thus, measurements were carried out simultaneously on 6 plants, 5 of which were mutants and 1 control. Measurements were performed using nonpolarizing silver chloride electrodes of the 5268-AgCl-180 type. A total of 36 electrodes with agar-agar adapters were used. Biopotentials were measured on the lower leaf surface of maize plants at points located 3/4 of the leaf length from the stem. Reference electrodes were placed at the base of the plant.

The biopotentials measured were transmitted by wires to 6 specially designed arithmetic units, automatically calculating arithmetic means of biopotentials for each particular mutant. While still measuring biopotentials, each arithmetic unit was, one by one, connected in a certain order to the amplifier general input via a specially designed automatic switch. Connected to the amplifier output via a compatible voltage divider was a self-balancing potentiometer of the EPP-09 type, on which recorder chart averaged values of biopotentials were recorded for each mutant.

To control the magnitude and pattern of electromagnetic disturbance, connected to the A1-1 amplifier output was an S1-1 oscillograph offering visualization of the disturbances on the screen.

In order to overcome the adverse effects of electromagnetic disturbance in measuring biopotentials, a combination of measures was taken including: (a) balancing of electric parameters of input measuring circuits with respect to earth, (b) use of braided (shielded) wires, (c) employment of high-frequency filters, and (d) compensation of variable and constant disturbances. The above combination of measures allowed measurements of biopotentials in the field without shielding boxes. However, in a few isolated instances, a knockdown shielding box was used.

Another peculiarity of measuring biopotentials on plants in the field is the need for simultaneous recording of environmental quantitative indices such as light intensity, soil and air temperature, soil moisture and air humidity, *etc.*

To examine the sensitivity of mutants to environmental factors, abrupt alternate switches from light to darkness were performed by obscuring the box or using a light-proof screen, or by employing a red or blue light filter. The results from studies of bioelectrical indices of mutant sensitivity were processed on the BSM-4 computer by solving a multiple regression equation by the least squares method.

In addition to general regularities in the topography of distribution of biopotentials on the plant vegetative organs (leaf, stem), F.G. Oloer proposed an ingenious technique for characterization of mutants by: (a) bioelectrical light sensitivity, (b) bioelectrical moisture sensitivity, and (c) bioelectrical thermosensitivity.

It was demonstrated that when the degree of exposure to one or another meteorological factor is varied, mutants tend to adjust (adapt) to new environmental conditions by changing their bioelectrical sensitivity to a particular environmental factor. Differences among mutants in bioelectrical sensitivity are readily detectable under low light intensity. Thus, mutants with dark-green leaf color (No 61 and No 67) exhibited high values of bioelectrical light sensitivity whereas low values were observed in mutants with light-green leaf color (No 35 and No 149).

With varying air humidity, mutants change their bioelectrical moisture sensitivity. Thus, with relative air humidity ranging from 70 to 90%, bioelectrical moisture sensitivity of both mutants and the control is insignificant or even negative in sign. Outside this range, bioelectrical moisture sensitivity changes abruptly and reverses its sign.

Of particular interest here is mutant No154, whose absolute value of moisture sensitivity is relatively small over a wide range of air humidities. Morphological features of this mutant are its long and narrow leaves which do not twist or wilt even under drought conditions. The opposite is observed in the control: its leaves exhibit severe wilting and twisting under drought.

Of considerable interest is also mutant No56. It has very high bioelectrical moisture sensitivity of negative sign. During the morning dew, it folds its leaves in a peculiar way, like a closed book, thus probably retaining moisture for a longer period of time, resulting in that its leaves do not wilt or twist during drought periods.

Under temperatures ranging from 20 to 30 C, bioelectrical thermosensitivity is relatively low in both mutants and the control. With temperature decrease below 20 C, bioelectrical sensitivity rises sharply. Thus, in mutant No149, bioelectrical thermosensitivity exhibits a sharp increase in the direction of positive sign.

A peculiar feature of this mutation (No149) is that on exposure to lower temperatures (15-19 C) its biopotentials decrease, such that its leaves begin to show anthocyan in coloration. In another mutant (No56),under lower temperatures (15-19 C), bioelectrical thermosensitivity continues to be high, but is of negative sign. Biopotentials in this mutant are, nevertheless, higher than in the control.

Analysis of biopotential variation during ontogenesis revealed

that maize plants (both mutants and the control) are capable, in the course of their development, of increasing their biopotentials from 5-30 mV to 50-70 mV at the stages of 3-4 leaves through flowering. Following the flowering stage, biopotentials start to decrease, being reduced to zero at full maturity.

Most significant differences in the magnitude of biopotentials between the control and mutants are readily observable in the wax stage. Admittedly, some mutants (tall, polyphyllous and multi-ear) compare favorably with the control in that their biopotentials are higher throughout the growth season.

Interestingly, while analyzing coefficients of correlation between bioelectrical parameters and some breeding characteristics, F. G. Oloer established correlation between biopotentials of mutants during grain filling and their general combining ability (r=0.75+0.13) determined by the topcross method.

It proved possible to make early prediction of general combining ability of mutant lines at early stages of ontogenesis. Thus, correlation was established between bioelectrical thermosensitivity at the stage of 5-7 leaves and general combining ability (r=0.44+0.29).

Direct correlation was also established between biopotentials of mutants at the grain filling stage and their yielding capacity at full maturity (r=0.51$\pm$0.26).

Very interesting data were obtained while examining bioelectrical characteristics of maize mutants following artificial stimulation. Thus, sharp changes in light intensity, temperature or air humidity result in plant biopotential variations. Sunlight is the most powerful stimulant for maize mutants. As short as 10 min shading of maize mutants with an opaque screen against the sunlight induces biopotential oscillations which are not damped until 10 to 15 min later.

It was found that at the beginning of exposure to light (following shading), biopotentials are shifted towards positive values. Most commonly, the first positive amplitude of biopotential oscillations is reached as soon as the first minute of exposure to light. It is at minutes 2 to 7 of light exposure that the biopotential reaches a maximum negative value. It was established that at this point in time the stomata show intensive opening, the biopotential is shifted towards positive values and exhibits a few damped oscillations, equivalent to the original ("shaded") level.

It should be noted that in some mutants biopotential oscillations may last for as long as a few hours. Interestingly, in cases like this, the frequency of biopotential oscillations coincides with the frequency of stomatal pore oscillations.

It must be emphasized that the most important parameter of mutant biopotential variation in the shade-light transition is the first amplitude, which is an indicator of the magnitude and sign of electrical charges formed on leaves in the first minute of light exposure, and the slope of the curve which represents biopotential variation precisely at the initial moment of light exposure.

With increasing light intensity, the first positive amplitude increases, but its growth stops under very high light intensity, and there sets in, as it were, the saturation effect. The rate of biopotential variation is also increased, but without saturation.

It is in the above two parameters that nearly all mutants differ among themselves. They can be classed, as it were, into two groups: (1) mutants superior to the control in these two parameters and exhibiting high intensity of photosynthesis (No61 and No122), and (2) mutants inferior to the control in the above two parameters (No149, No700, and No67).

Of particular interest here is that the curves representing decreasing biopotentials under shading and those representing increasing biopotentials after removal of shading may be regarded as mutant specific.

Ingenious studies with a view to developing techniques for identifying the characteristics of maize mutant lines by kernels were carried out by M.E. Volinsky using the method of extracellular biopotential measurement. He succeeded in demonstrating the possibility of identifying maize mutant lines by sprouting kernels, such that particularly clear-cut results were obtained on exposure of the sprouted kernels to extreme factors, such as temperature (hot water). Curves representing the damping of biopotentials due to mortality of plants from exposure to superhigh doses of extreme factors also proved to be mutant specific.

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Influence of selection of haploid sporophyte on reaction of diploid maize population exposed to γ–irradiation

--Rotarenco, VA, Chalyk, ST

In our work, maternal haploid plants are used in recurrent selection for improvement of two synthetic populations of maize, SA and SP (Chalyk S. T. and Rotarenco V.A., 1999). Selection of favorable genotypes is carried out at the haploid sporophyte level.

There are no inter-allelic interactions at the haploid sporophyte level, i.e. effects of both dominant and recessive genes are displayed. Thus, an effective natural selection is provoked at the haploid level in a population, which clears up unfavorable mutations. The purification of the population from semilethal and lethal recessive genes has a positive effect on its viability and productivity, as well as significantly enhances its combining ability (Strunikov V.A. 1983; Strunikov V.A., Stepanova N.L., 1983; Seryi A.P., Golovin V.P., 1987).

Our work was aimed at the investigation of the reactions of diploid populations derived through haploid recurrent selection to γ–irradiation. To accomplish this, dry seeds of the initial SAC0 population and the results of two selection cycles, SAC1 and SAC2, were irradiated before planting with four doses, 150 Gr, 200Gr, 250Gr and 300Gr. Control and irradiated variants were planted in the field on two-row plots (10m^2). Four plant traits were measured after flowering: plant height, ear height, leaf length, and leaf width. Ear traits were measured after harvesting and after drying to normal moisture: seed weight per ear (productivity), ear length, ear diameter, number of seed rows, number of seeds per row, number of seeds per ear, weight of 1,000 seeds, and percentage of seed set. Estimation of the population reaction to irradiation was presented as a ratio to the control. Differences in means between irradiated variants and the control and statistical significance of the differences are presented in the Tables.

Table 1 summarizes the results of the estimation for plant traits and shows that all control for these traits exceeded significantly the means of the irradiation variants, excluding leaf width in the 150 Gr. irradiation variant in the SAC1 population. Reaction of different cycles of haploid selection on γ–irradiation was different. A tendency of the reduction of the difference between control and irradiated variants, was observed for three plant traits: plant height, ear height and leaf length in the SAC1 and SAC2 populations in comparison with the SAC0. The SAC2

Table 1. Excess (%) of the control over the means of the irradiated treatments for plant traits.

Traits	Populations	Irradiation doses			
		150Gr.	200Gr.	250Gr.	300Gr.
Plant Height	SAC0	7.1***	10.7***	15.4***	32.7***
	SAC1	8.8***	16***	31***	17.4***
	SAC2	2.5***	7.4***	13.7***	24.6***
Ear Height	SAC0	16.1***	41.9***	117.6***	131.6***
	SAC1	6.5***	14.8***	84.8***	52.7***
	SAC2	3**	9.5***	29.4***	77.2***
Leaf Length	SAC0	12.5***	18.5***	19***	35.8***
	SAC1	20.9***	17.5***	30.9***	12.9***
	SAC2	4.4***	14.9***	27.6***	24.7***
Leaf Width	SAC0	7.3***	12.1***	16.8***	25.1***
	SAC1	-3.2***	12***	31.3***	12.8***
	SAC2	5.3***	28.6***	24.8***	25.3***

,* Different from the control at 1% and 0.1% significance level, respectively

population should be mentioned specially, as the differences among the controls for almost all the variants of these traits are significantly lower than in the initial SAC0 population.

Table 2 presents the assessment of the populations for ear traits. As opposed to the plant traits of the populations, the ear traits, to a larger extent, demonstrate the difference in the population reaction to irradiation. Based on productivity as a trait in which all the ear traits are expressed, it can be noted that the differences in relation to the control were significant in all three populations, but in the SAC1 population these differences were negative for three of the four irradiation treatments, i.e. the productivity of the control was lower than in the irradiated treatments. The difference of the productivity of the irradiated variants and the control in SAC2 population were significantly lower than for the SAC0 population. An interesting result was found for the weight of 1,000 seeds in the experimental treatments under study. The mean of this trait increased in all the populations, but in the SAC1 and SAC2 populations this increase was several times higher than in the SAC0 population. We speculated that this is associated with the increase of seed set in the irradiated variants, as compared to the control, but inspection showed that seed set was at the same level for these populations.

Table 2. Excess (%) of the control over the means of the irradiated treatments for ear traits

Traits	Populations	Irradiation doses			
		150Gr.	200Gr.	250Gr.	300Gr.
Productivity	SAC0	52.7***	49.3***	250.1***	254.4***
	SAC1	-36.5***	-11.9***	24.4***	-18.9***
	SAC2	20.6***	39.9***	52.1***	88.7***
Ear length	SAC0	8.5***	9.3***	18.2***	29.1***
	SAC1	-6.6***	-4***	2.2	-16.6***
	SAC2	1.3***	1.2***	0.8	9.8***
Ear diameter	SAC0	6.5***	8.9***	18.8***	27.7***
	SAC1	-7.2***	-1.8**	2.7**	1.2
	SAC2	4.9***	5.5***	10.4***	12.5***
Number of seed rows	SAC0	5.4***	12.8***	9.3***	14.3***
	SAC1	0.6	0.08	0.3	1.2
	SAC2	6***	8***	12.7***	14.1***
Number of seeds per row	SAC0	19.3***	23.5***	36.1***	46.5***
	SAC1	-3.5**	4.3**	17.9***	-4
	SAC2	7***	11.3***	7.3***	22***
Number of seeds per ear	SAC0	39***	57.3***	198.7***	227.6***
	SAC1	5.5**	30.5***	73.4***	27.5***
	SAC2	28.5***	63.2***	83.6***	136.7***
Weight of 1,000 seeds	SAC0	5.7***	-9.5***	-6*	-8.1*
	SAC1	-48***	-43.4***	-49.5***	-59.8***
	SAC2	-9.9***	-19.7***	-24.4***	-29.3***
Seed set	SAC0	-248.6	-311.5	-1964	-1619
	SAC1	-137.3	-208.8	-698.3	-1431
	SAC2	-319.2	-574.2	-1076	-1846

*,**,*** Differences from the control at 5%, 1% and 0.1% significance level, respectively

This research allows us to conclude that a combination of artificial and natural selection at the haploid sporophyte level significantly improved a population for plant and ear traits, and enhanced the population's resistance to effects of γ-irradiation.

The influence of post-radiation treatments on genetic processes and mutation frequency

--Ikhim, YG

The series of post-radiation factors of a chemical and physical nature were used to study the variability of viability of M1 of maize. These factors were certain biological and synthetic regulators of growth, biologically active substances, electromagnetic irradiation of different frequency, etc. A significant increase was observed for the viability of mutants of the first regeneration under the influence of sublethal doses of irradiation for some variants. The frequency and spectrum of variability of genetic processes induced by γ-irradiation for the same variants was maintained.

In the field experiments for the study of the variability of genetic processes on dependence of a post-radiation factors, the following methods were used. For the revealing of recessive lethal and vital mutations the process of induction of haploid forms was made. As a female form, line 19-3-3 was used and treated with the method mentioned above. As a male form haploid inductor, MHI was used. At the first step the variability of the induction was studied. By the marker system of the inductor, hybrid seeds were chosen with pigmentation of the aleurone and an embryo because haploid seeds have unpigmented embryos.

For determination of the frequency of mutations at a locus, a hybrid between the line MK-01 (female form) and the multimarker line 2-9M was used, marked with seven genes: *ws3* (2-0), *lg1* (2-11), *gl2* (2-30), *y1* (6-17), *c1* (9-26), *sh1* (9-29), *wx* (9-59). The staining of the aleurone of F1 seeds was estimated and the percentage of mosaic forms was counted.

Table 1 shows the variation of the genetic processes induced by the combined action. We have counted lethal mutations in the M2 by calculating the percentage of the plants grown from the number of the seeds sown. We agree that these findings are conditional as there are many factors causing the decreased plant emergence and death under the conditions of a field experiment. However, these figures are of a certain interest. A maximal number, 9%, of viable M2 genotypes was in the treatment Radiation+Crossing, while in the irradiated control the number of organisms carrying lethal damage was 100%. The second line shows the variation of the haploid induction in the 19-3-3 line using the MHI inducer. The findings suggest that this treatment technique may significantly modify the process of haploidy induction. Thus, the treatment Radiation+Phytostim and Radiation+SHF, influencing the plant physiology, changes significantly the percent of haploid seeds. This experiment was set with the aim of determining the number of recessive mutations capable of being displayed only at the haploid level of the organism organization. An experiment using a multimarker line 2-9M was set with the aim of estimating the mutation frequency per locus or 100,000 gametes which may change in relation to the treatment type. The

line is marked for seven genes and particularly for the *C1* locus (chromosome 9). MK-01 treated according to the techniques under study was used as a maternal form. A marker line was used as paternal form. While studying the F1 seeds, mosaicum was detected for the aleurone coloration. The high percentage of mosaics in the control suggests the presence of mobile elements in the genotype, but the exact kind of elements will be determined in the future. However, it is interesting to know to what extent this combined effect may influence the display of mosaicism. It is enough to compare the number of mosaics in the radiated control and Radiation+SHF treatment.

Table 1. Induction of variability of genetic processes by combined treatments.

	Control	Radiated control	γ + Crossing	γ + Phytostim	γ + EF	γ + SHF
Lethal mutations in M2, %	0	100	91.19	98.45	94.90	95.73
Induction of haploidy in M2,%	5.38	5.37	5.32	6.58	5.92	4.19
Mosaic of aleurone coloration in F1,%	2.63	0.59	1.19	2.69	3.32	6.35

Table 2 shows the results of the investigation of the lethal recessive mutations and the mutations of the *C1* locus of the MK-01 X 2-9M hybrid. The utilization of the haploid level allows the discovery of recessive mutations, particularly, lethal events. The percentage of surviving plants is expressed in relation to the number of seeds sown. The results show that the post-radiation treatments with the "Crossing" growth regulator do not reduce the number of mutations in comparison with the irradiated control, which has confirmed our cytological investigation (Ikhim, YG, MNL 74, 2000). This confirms that this growth regulator has an effect at the physiological level, without having a direct impact on genes. The post-irradiation treatment with SHF decreases significantly the level of lethal events. A similar pattern is observed in the research of the mutation number at the *C1* locus. However, the frequency level has increased by 2-3 orders in all treatments.

Table 2. Mutation percentage at the utilization of combined treatments

Variants	Lethal recessive	C1
Control	86.59	0.0000
Radiated control	96.78	0.0658
γ + Crossing	96.97	0.0988
γ + Phytostim	100	0.0625
γ + EF	95.24	0.0922
γ + SHF	85.72	0.0453

The results presented show that it is reasonable to use post-irradiation treatments to modify viability of the first generation mutations and, notably, of the factors under study.

Digenic control of lemon colour of aleurone in maize grains

--Mihailov, ME, Chernov, AA

In the previous letter (MNL, 73) it was reported that the *Lm1* gene causes lemon coloration of the maize aleurone.

The *Lm1* line carrying genotype *Lm1* +/+ y1-/- (lemon aleurone and white endosperm) was crossed with a 2-9m line (genotype *Lm1* -/- y1-/-). The self-pollinated F3 ears were produced on 149 F2 plants. On 14 F3 ears all the grains were violet due to the genotype of the mother plant (C1+/+ R1+/+). The remaining 135 ears were divided into 4 classes: 1) 9 ears: all the grains are lemon; 2) 18 ears: the grains are lemon and white in a 3:1 proportion; 3) 50 ears: the grains are lemon and white, the proportion of lemon grains is 0.20-0.50; 4) 58 ears: all the grains are white. These numbers of classes correspond to a 1:2:6:7 ratio, and suggest digenic inheritance. So, we propose a second gene for lemon color (named *Lm2*). A positive allele originates from the *Lm1* line, a negative one from the 2-9m line. The genotype of the mother F2 plant would be: *Lm1* +/+ *Lm2* +/+ for class 1; *Lm1* +/- *Lm2* +/+ for class 2; *Lm1* +/+ *Lm2* +/- and *Lm1* +/- *Lm2* +/- for class 3; *Lm1* -/- Lm2~ and Lm1~ *Lm2* -/- for class 4.

In class 3 the color intensity is highly variable, and classification is essentially more difficult than in class 2. Usually a relatively homogenous group of grains of maximal intensity (0.05-0.30 of total family volume) exists in class 3. This suggests that the action of the *Lm2* gene essentially depends on gene dose: 1 dose provides no coloration, 2 doses provide slight coloration and only 3 doses provide maximal coloration.

The *Lm2* locus remains unlocated. Linkage with the loci of chromosomes 9 (*sh1*, *wx1*) and 10 (*R1*) was not detected.

COLUMBIA, MISSOURI
University of Missouri

Fast, simple, inexpensive, safe and reliable method to prepare maize samples for PCR

--Carson, CB, Coe, EH, Jr.[1]
[1]USDA-ARS

The Missouri Maize Project at the University of Missouri includes a component that seeks to map as many as possible from a large set of relatively uncharacterized mutants. The following method has been used routinely to obtain SSR marker map data, using PCR and 4.5% SFR-agarose gel electrophoresis, from large numbers of small, individual samples. We have chosen a DNA preparation method that does not involve organic extraction or alcohol precipitations, but instead uses a crude, preserved preparation. The method is fast, simple, inexpensive and safe. Samples prepared in this manner are as effective as purified DNA samples. The original method was presented in Steiner et al. (Nucl. Acids Res. 23:2569-70, 1995).

This method provides samples for PCR using 96-well titer plates and 12-channel pipettes, but it can also be used for samples in individual tubes. Our routine method for grinding tissue for DNA extraction involves freeze-drying followed by pulverizing with glass beads. While freeze-drying is preferred, this method has been used successfully without freeze-drying, see below. Specified equipment includes a Mini-Bead-Beater-8 to agitate tubes and plates, and a tool for loading glass beads into 96-well plates.

Tissues that are successfully and routinely processed for SSR-PCR mapping: developing endosperms and embryos; seedling leaf tissues; immature lateral branch buds and ear shoots; leaves from maturing and adult plants; punches from mature freeze-dried leaves.

Sample size: 0.1 grams fresh weight samples into 1.5ml tubes or 1ml deep 96-well plates. This is generally equivalent to 10-20mg dry weight. Mature maize leaves that were previously freeze-dried have also been used by collecting 20mg samples with

a paper punch. When using 96-well plates, care to prevent cross-contamination of samples is necessary at this stage.

Freeze-dry: Samples in 96-well plates or tubes are first completely frozen (liquid nitrogen or ultracold freezer), and are then freeze-dried. The dried samples are stable and easy to store before processing and provide a more concentrated (DNA) sample than fresh tissue.

Grinding: Next, three 3mm glass beads per tube/well are added. To save time and headache a tool was built on campus to add beads to all 96-wells at one time (see below). The dried samples are pulverized by the beads. We use a Mini Bead-Beater-8 that has been modified by the company to hold 1 ml deep 96-well microtiter plates. Grinding takes only a few minutes for most tissues.

Extraction and preservation: The pulverized samples are then treated with ROSE solution at 90 C. The ROSE solution has SDS for lysis, a high concentration of EDTA to preserve the sample, and insoluble PVPP to bind and exclude inhibitory phenolic compounds. Before each use ROSE must be mixed to distribute the insoluble PVPP equally.

Rapid-One-Step-Extraction Solution (ROSE): 312.5mM EDTA; 10mM Tris, pH 8; 1% SDS; 1% insoluble polyvinyl-polypyrrolidone (PVPP) (w/v). Add 200uL ROSE solution to each sample and mix well to wet the powdered tissue samples. Then the samples are heated to 90 C in a water bath for 20 minutes with additional regular mixing. The samples may then be cooled rapidly at 4 C for 5 minutes to use immediately. The cooled samples can be stored cold or frozen, but we find that they are stable at laboratory temperature indefinitely.

Dilution: Dilution reduces the concentration of EDTA and SDS. Using wide bore pipette tips, we remove 3uL from the liquid portion of recently mixed samples, and dilute 200-fold into 600uL sterile water containing 1% PVPP. The diluted samples are thoroughly mixed and the PVPP is allowed to settle. PVPP can inhibit the PCR reaction. Diluted samples are less stable than the original crude concentrated ones.

PCR, agarose gel detection of SSR alleles: The method for PCR is described in detail at the MaizeDB website: ftp://ftp.agron.missouri.edu/pub/methods/ssr_methods.html. From the diluted sample, we use 2uL in a 15uL PCR reaction. Because primer sets do not always have exactly the same optimum annealing temperatures, we typically use 10 cycles with 1 C decremental annealing temperatures, from 65 C to 55 C, followed by 30 cycles at 55 C. ROSE treated samples diluted 200-fold have 0.2mM EDTA, which reduces the effective Mg2+ concentration, but does not interfere. To resolve PCR products we use 4.5% SFR-agarose (Amresco) gels made with 1X TBE and 0.27ug ethidium bromide per 150mL gel.

Additional Considerations: Samples are relatively insoluble. We always mix the samples thoroughly and allow a minute or longer for the bulk of tissue debris to settle. Routine mixing provides equivalent, uniform samples, especially when using 12-channel pipettes. When pipetting from crude samples in ROSE solution, we use pipette tips with a slightly larger diameter tip; or, cut the tip ends from standard (1-200ul) tips with scissors. Because the samples can sometimes clog the tips of standard narrow-bore pipette tips, this helps to reduce differences between samples. In addition, crude samples should not be centrifuged, because the bulk of the DNA is probably still associated with insoluble cellular debris.

Alternative method to freeze-drying: We have explored using cellulase treatment of fresh tissue as an alternative to freeze-drying and have had good results. For each sample, add (~50ul) 1% cellulase in pH 6.5 buffered solution to thoroughly wet 0.05-0.1g tissue, incubate at 37 C for 1-2 hours, then freeze. The ROSE solution is added directly to these samples. A higher concentration ROSE solution (391mM EDTA, 0.012mM Tris, 1.25% SDS, and 1.25 % PVPP) may be used. The samples can then be treated as described above, if briefly homogenized by hand with a small pestle.

Equipment sources: DynaBlock1000 96-wells, 1ml deep with cap-mat lids: Research Products International Corp., Mt. Prospect, IL 60056-2190, www.rpicorp.com

Lyophilizers: Labconco, Kansas City, Missouri 64132-2696, www.labconco.com

Mini-BeadBeater-8™ modified for 96-well plates (<$2000): BioSpec Products, Inc., Bartlesville, Oklahoma 74005-0788, www.biospec.com

3mm glass beads: Jaygo, Inc. Union, NJ 07083, www.jaygoinc.com

Bead counter to add beads to 96-well plates ($550): University of Missouri, Science Instrument Machine Shop, Columbia, MO 65211, www.research.missouri.edu/web_research/internal_funding/res_facil/machines.html

Mapping the *leaf burn1* mutant

--Carson, CB, Robertson, J, Bennett, J, Melia-Hancock, S, Coe, EH, Jr.[1]
[1]USDA-ARS

The *bu1* (*leaf burn1*) mutant has a phenotype where leaves show burning, sometimes in horizontal bands, that is accentuated by high temperature. *bu1* was first identified by Galinat et al. (Galinat, WC, Chandravadana, P, Starbuck, J, MNL 52:58-59, 1978), but had not been mapped. Using an informative set of SSR markers and a bulk segregant analysis technique to examine pools of mutants compared to pools of normal sibling samples, we found that *bu1* is located on chromosome 7, bin 2. Further, one marker, *phi034*, shows no crossovers with the *bu1* locus when individual homozygous mutants are examined (see below). The *phi034* SSR is found in *cyp6*, a cytochrome P450 gene on chromosome 7. Given the phenotype of *bu1* and no crossovers, *cyp6* becomes a strong candidate for the *leaf burned1* gene.

F1: A619 x *bu1*: no crossovers detected between *phi034* and *bu1*, in 24 F2 *bu1*/*bu1* individuals

F1: Mo17 x *bu1*: no crossovers detected between *phi034* and *bu1*, in 16 F2 *bu1*/*bu1* individuals

COLUMBIA, MISSOURI
University of Missouri
URBANA, ILLINOIS
University of Illinois and USDA/ARS

Genetic mapping of *zebra3*

--Rugen, M., Stinard, PS, Cone, KC

The recessive *zebra3* (*zb3*) phenotype is apparent as a distinct light-green crossbanding on seedling and adult leaves of the maize plant. In an earlier study (MNL 73:23), we showed that pre-

vious reports that *zb3* maps on 5L were incorrect. To determine the correct map location, *zb3* was crossed by a series of TB stocks; the results indicated that *zb3* is on the short arm of chromosome 1. For more specific localization, we used molecular segregation analysis. We generated a segregating population by crossing *zb3* (Coop stock 519G) to a W23/L317 hybrid and then self-pollinating the F1 to generate an F2. F2 seed were planted and the phenotypes scored; 27 of 100 plants had the *zb3* phenotype. DNA was isolated from the *zb3* plants, digested with restriction enzymes, blotted and probed with markers from chromosome 1S. The following data were obtained:

probe	# chromosomes tested	# crossovers	recombination frequency (%)
tub1	54	0	0
asg31	54	3	5.6
umc157	54	2	3.7
asg45	54	8	14.8

We conclude that *zb3* is tightly linked to *tub1*.

COLUMBUS, OHIO
Ohio State University

The C-terminal domain of the maize *P1* gene has a putative activation domain

--Smialek, JL, Hernandez, JM, Grotewold, E

In maize, the flavonoid biosynthetic pathway has two main branches, which result in the accumulation of the phlobaphene or anthocyanin pigments. The *P1* gene regulates the phlobaphene biosynthetic pathway, and *C1/Pl*, in conjunction with *R1/B1*, regulate anthocyanin biosynthesis. *P1* and *C1* encode Myb-domain transcription factors, whereas *R1* encodes a bHLH protein (reviewed in Mol et al., Trends Plant Sci. 3:212-217, 1998). Both Myb-domain proteins are capable of binding to the promoter of the *A1* genes and activating transcription. However, unlike *C1*, no co-activator has yet been identified for *P1*.

Previous research indicated that the Myb domain is responsible for the DNA-binding activity (Grotewold et al., Cell 76: 543-553, 1994) and DNA-binding specificity (Grotewold et al., PNAS 97: 13579-13584, 2000) of *P1*. The *P1*-encoded protein contains an acidic region in the non-Myb C-terminal portion, between amino acids 207 and 242, suspected to serve as an activation domain (Grotewold et al., Proc. Natl. Acad. Sci. USA 88: 4587-4591, 1991). Chopra and co-workers (Plant Cell 8: 1149-1158, 1998) found that other alleles of *P1* retain this region, providing further evidence of its significance for the *P1*-regulatory function. Although the *P1-wr* and *P1-rr* alleles differ in their C-terminal ends, the proteins that they encode contain identical Myb DNA-binding domains as well as identical acidic regions.

To more precisely define the regions in *P1* important for its regulatory activity, truncations of the protein were generated. These truncations were cloned under a CaMV 35S promoter, and each truncation was then tested for its ability to activate a construct containing the *A1* promoter driving the expression of the luciferase gene in transient expression assays as described (Grotewold et al. PNAS 97: 13579-13584, 2000). Figure 1A illustrates the position of the termination points of each construct. *P1* provides the full-length protein, serving as a positive control. P^{1-152} excludes the putative activation domain, P^{1-231} contains

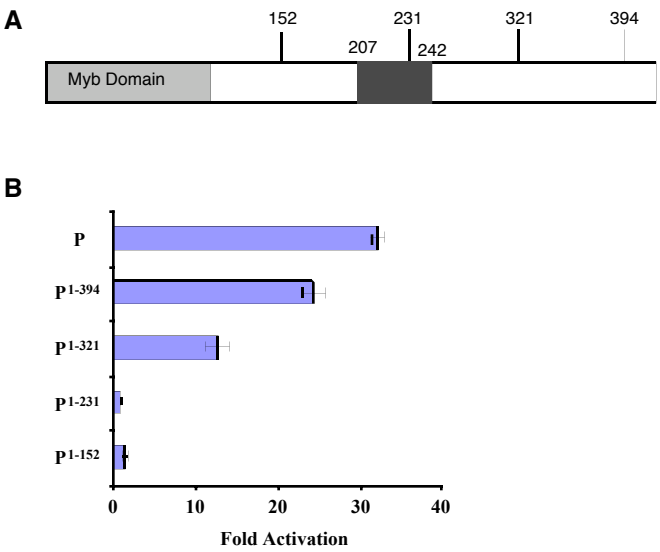

Figure 1. (A) Various truncations made of the *P1* gene, outside of the Myb domain in the C-terminal region. Numbers indicate amino acid termination points of each truncation. The putative activation domain spans from amino acid 207 to 242 and it is represented as a black box. **(B)** Levels of activation of the luciferase gene driven from the *A1* promoter by *P1* and the truncation constructs in transient expression experiments carried out in BMS cells.

approximately two thirds of it, and P^{1-321} and P^{1-394} contain the entire putative activation domain. As shown in Figure 1B, only those constructs which include the entire putative activation domain were able to activate transcription from the *A1* promoter. P^{1-231} was not able to activate in spite of the fact that it contains about two thirds of the acidic region. These results suggest that residues in the region between amino acids 231 and 321 are essential for *P1* activity, and that residues C-terminal to 321 can be deleted without a significant loss in *P1* activity. Interestingly, this C-terminal part of *P1* is the region that is different between the *P1-rr* and *P1-wr* alleles, which show distinct pigmentation patterns in the pericarp and cob tissues. Currently, experiments are underway to show whether the acidic region (207-242) is responsible for the essential nature of the 231-321 region.

CORVALLIS, OREGON
Oregon State University

Evolution of new targeting specificity in duplicate genes for tetrapyrrole biosynthesis

--Williams, P, Hardeman, K, Rivin, CJ

Duplication of a gene provides an opportunity for genetic change without sacrificing essential gene function. We have examined duplicate genes in maize that encode coproporphyrinogen III oxidase (CPX), which catalyzes an essential step in the synthesis of tetrapyrroles. We looked at the sequence and expression patterns of the two genes, which we are calling *Cpx1* and *Cpx2*, and we are characterizing the phenotypes of mutations in these loci to learn whether their products and/or biological roles have become divergent. Although the predicted amino acid sequences of the mature enzymes are almost identical, we found that the targeting information for each is unique and is likely to result in localization to different organelles. The expression patterns and the mutant phenotypes of the two genes are also distinctive. From all our

data, we hypothesize that the *Cpx1* product plays the major role in the production of porphyrins in the chloroplast, while the product of *Cpx2* has an uncharacterized role in the mitochondrion.

Coproporphyrinogen III oxidase is the eighth enzyme in the biosynthesis of tetrapyrroles in plants, catalyzing the oxidative decarboxylation of coproporphyrinogen III to protoporphyrinogen IX (Reinbothe, S. and Reinbothe, C. Plant Physiol 111:1-7, 1996). In plants, this and the earlier porphyrin biosynthetic steps are reported to take place exclusively in the plastid, where protoporphyrinogen IX can be converted to the first intermediate specific to chlorophyll biosynthesis or be processed towards the production of heme. Heme in the chloroplast serves as the precursor to the phytochrome chromophore, as well as providing for the synthesis of photosynthetic cytochromes. Protoporphyrinogen IX can also be exported from the plastid to the mitochondria where it is also converted into heme.

We cloned two genes encoding coproporphyrinogen III oxidase from maize. Using RFLP with recombinant inbreds, the genes were mapped to syntenous regions of chromosome 2S and 10L (Hardeman, K. et al., MNL 70:20-21. 1996). We have the entire genomic and cDNA sequence for *Cpx1*, which consists of 8 exons. For *Cpx2*, we are still missing the sequence for the last 3 exons. Sequence comparisons between the mature enzyme-encoding regions of the genes indicate a very strong preservation of identity, so that no portion of the proteins are less than 97% identical, including three highly invariant domains believed to be enzymatically critical. However, the N-terminal extension carrying the targeting information for each protein is unique and predicts targeting of the enzymes to different organelles.

The *Cpx1* gene encodes an N-terminal extension to the mature enzyme sequence that has the features of a chloroplast target peptide, as expected from studies in other plants (Madsen, O. et al., Plant Mol Biol 23:35-43, 1993; Kruse, E. et al., Planta 196:796-803, 1995). In *Cpx2*, however, 150 base pairs of this sequence are deleted, cleanly eliminating the transit peptide. Just 5' of this deletion, there is very substantial homology between the genes, but a series of small deletions/additions distinguish them. As shown in the figure, 5' UTR sequences of *Cpx1* are homologous to an open-reading frame, headed by a methionine codon in *Cpx2*. This ORF is contiguous with the first exon, forming an N-terminal extension.

To test whether the N-terminal extension of CPX2 has potential targeting information, we applied a series of algorithms designed to look for and distinguish N-terminal peptides for chloroplast, mitochondrial and exported proteins. Using the PSORT, ChloroP, TargetP, and Predotar programs (Nakai, K. and Kanehisa, M. Genomics 14:897-911, 1992; Emanuelsson, O, et al., Protein Science 8:978-984, 1999; Emanuelsson, O. et al., JMB 300:1005-1016, 2000; Peeters et al., 1999, submitted), the CPX2 protein was strongly rejected as a chloroplast protein, and strongly predicted to be mitochondrial in location. To experimentally test this idea, we fused the putative *Cpx2* N-terminal extension sequence to GFP to make a reporter gene driven by the 35S promoter, and introduced the construct into leaf epidermis biolistically. The GFP was found in small, dispersed spots, of a size and distribution that matched that seen when GFP was fused with a bona fide mitochondrial targeting peptide from CoxIV. We hypothesize, therefore, that a series of mutations has changed the targeting information and thereby the location of the coproporphyrinogen III oxidase encoded by *Cpx2*, but we have not yet demonstrated CPX activity in maize mitochondria.

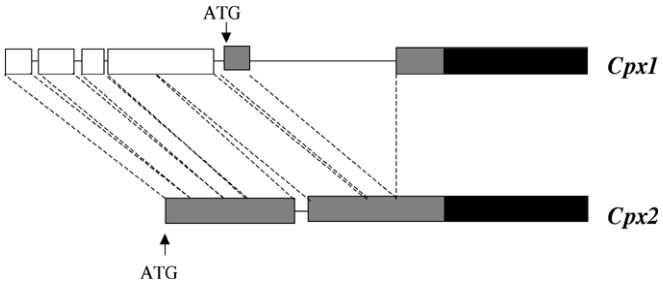

Figure: Alignment of 5' UTR and exon 1 DNA sequences of the *Cpx1* and *Cpx2* genes. The boxes show homologous DNA sequences and lines represent non-homologous sequences. Dashed lines indicate the alignment of homologous DNA. Putative 5' UTR (white), translation starts (ATG), code for the organellar targeting peptides (grey), code for the N end of the mature enzyme (black).

In order to distinguish roles for *Cpx1* and *Cpx2*, we looked at their expression patterns and we have begun to characterize the phenotypes of mutants in each gene. Using a semi-quantitative RT-PCR for detection, both *Cpx* mRNAs could be found in root, shoot, vegetative and reproductive tissue. The quantity of *Cpx2* message did not vary much from tissue to tissue, and was at a similar level to *Cpx1* in non-green tissue. However, *Cpx1* mRNA was found at a level approximately three-fold higher than *Cpx2* in leaf tissue. A *Mu8*-induced mutant in the *Cpx1* gene was initially characterized in tandem with a very closely linked *dek* mutation (Hardeman, K. et al., MNL 1996). The *dek* seeds germinated into yellow seedlings whose leaves became necrotic, leading to plant death within about 2 weeks. This yellow phenotype is consistent with the function of CPX1 in the production of chlorophyll, and the necrotic phenotype is expected when blockage of the porphyrin pathway produces phototoxic tetrapyrrole intermediates. These phenotypes have also been reported for the *Necrotic-4* locus (Hoisington, DA and Neuffer, MG, MNL 57: 159-160, 1983) which maps to the same small interval of chromosome 2. In a complementation test, one quarter of the cross progeny had a yellow, necrotic phenotype, indicating that *Nec4* is probably the locus encoding coproporphyrinogen oxidase. In other plants examined, there is a single gene for coproporphyrinogen oxidase, and the enzyme activity is exclusively in the chloroplast. From the putative transit peptide, expression pattern, and mutant phenotype, we hypothesize that this is the role of the *Cpx1* gene product.

Using the TUSC system in collaboration with Pioneer HiBred Inc., a line was found carrying a *Mu* insertion in the first exon of *Cpx2* (*cpx2-578*). This mutant is viable and fertile as a homozygote, although we have not detected any normal mRNA produced from the *cpx2-578* allele. The biological role associated with CPX2 is mysterious, but the strong conservation of the presumed active site sequences indicates that it encodes a working coproporphyrinogen oxidase, but of unknown function. It cannot compensate for a mutation in *Cpx*1. Perhaps earlier steps of tetrapyrrole biosynthesis occur in the maize mitochondrion than have been seen in other plants. Or, perhaps the *Cpx2* coproporphyrinogen oxidase serves to detoxify superfluous tetrapyrroles in the mitochondrion. We are still crossing the extraneous *Mu* elements out of the *cpx2* mutant line, so we are not yet sure whether there are milder phenotypes associated with it.

FORT COLLINS, COLORADO
Colorado State University

Recombination frequency for maize inbred line KYS using recombination nodules

--Anderson, LK, Stack, SM

Recombination nodules (RNs) have been demonstrated to faithfully reflect crossovers in a wide range of organisms. In order to examine the distribution of crossing over at the highest possible cytological resolution (using electron microscopy), we are preparing a map of RNs on synaptonemal complexes (SCs) from the inbred line KYS. To date, we have identified more than 1000 SCs (approximately 100 of each of the 10 SCs) that we are using to map RNs. While the mapping effort is still underway, there is sufficient data to present a summary of the results (Table 1).

Table 1. Average number of RNs for each SC of maize and a comparison of the map lengths predicted from the RN frequency with the map lengths determined by genetic methods (Maize DB).

SC	Relative length	Average Number of RNs	Predicted map length - RNs	Map length -genetic map
1	14.9	2.54	127.0	258
2	11.9	2.39	119.5	224
3	11.0	2.20	110.0	216
4	10.7	2.09	104.5	172
5	10.9	2.20	110.0	185
6	8.9	1.75	87.5	144
7	8.6	1.77	88.5	128
8	8.6	1.81	90.5	177
9	7.7	1.83	91.5	178
10	6.7	1.62	81.0	174
Total	99.9	20.2	1010	1856

The average number of RNs per SC set is 20.2. This compares well with estimates of 18-27 chiasmata per cell (Beadle, G.W. 1933, Cytologia 4:269-287; Darlington, C.D. 1934, Z. Indukt. Abstammungs Vererbungsl. 67:96-114). In addition, SC length is a good predictor of average RN number ($y = 0.12x + 0.78$; $r^2 = 0.92$), an observation that is consistent with prior observations made in a number of different organisms. In general, regardless of SC length, if there is only one RN on an SC, it is more often in the long arm than in the short arm. If there are two RNs on an SC, usually there is one RN in the long arm and one RN in the short arm. If there are three RNs on an SC, the most common pattern is for one RN to be in the short arm and two in the long arm. If there are four RNs on an SC, two RNs in each arm or three in the long arm and one in the short arm occur at about the same frequency. SCs with more than four RNs are rare. Overall, most RNs occur in the distal third of each SC arm. The predicted map length for maize KYS based on RN frequency is (# RNs X 50 map units =) 1010 map units. In comparison, the genetic map for maize is almost twice as long at 1856 map units (Maize DB). This difference may be due to genetic versus cytological techniques and/or differences in the crossover rate in an inbred (KYS) compared to hybrids. To determine the basis of this difference, we will examine the number and distribution of RNs on SCs from B73, Mo17, and B73 X Mo17. This work was supported by NSF grant MCB-9728673.

Synaptonemal complex karyotype for maize

--Anderson, LK, Stack, SM

We are mapping the distribution of recombination nodules (RNs) on spreads of maize (KYS) synaptonemal complexes (SCs = pachytene chromosomes) using electron microscopy. Since RNs occur at sites of crossing over, an RN map will show the frequency and distribution of crossing over on each chromosome. This will be useful for integrating molecular, genetic and cytogenetic maps for maize. As a necessary prerequisite for mapping RNs, it is necessary to identify each of the ten maize SCs. While several different characteristics can be used to identify squashed maize pachytene chromosomes (including relative length, arm ratio, chromomeres, knobs, nucleolar association), only relative lengths and arm ratios can be used to identify maize SCs because the other features are usually lost during the spreading procedure. Nevertheless, we have observed a good correspondence between the SC karyotype and the pachytene karyotype that is based on squashed chromosomes (Freeling, M. and Walbot, V., Eds., The Maize Handbook, 1994; Table 1). The most noticeable difference

Table 1. Karyotype from pachytene chromosome squashes compared to karyotype from SC spreads.

Chromosome or SC rank	Pachytene Chromosome squashes		SC spreads	
	Arm Ratio	Relative Length (%)	Arm ratio	Relative Length (%)
1	1.23	14.5	1.25	14.9
2	1.14	12.4	1.08	11.9
3	2.0	11.3	1.97	11.0
4	1.63	11.1	1.54	10.7
5	1.07	11.1	1.10	10.9
6	3.1	7.7	2.57	8.9
7	2.6	8.9	2.73	8.6
8	3.0	8.9	3.05	8.6
9	2.0	7.7	1.93	7.7
10	2.6	6.3	2.45	6.7

between the two karyotypes is for chromosome/SC 6. It is possible that the large nucleolus that is present in squashes (but dispersed in SC spreads) may obscure part of the short arm of chromosome 6 and result in a shorter relative length and larger arm ratio for squashes compared to spread SCs. This work was supported by grant MCB-9728673 from the National Science Foundation.

HAMBURG, GERMANY
University of Hamburg

Identification of genes induced during early kernel development in *Zea mays* (L.)

– Lorbiecke, R, Kukula, J, Paul, C, Wienand, U

The identification of seed specific genes from maize endosperm is currently of growing interest to provide more efficient approaches for plant improvement. To get more insight into the regulation of endosperm and kernel development we performed a PCR-based subtractive hybridization based on the method described by Buchanan-Wollaston and Ainsworth (Plant Mol. Biol. 33:821-834, 1997). cDNAs for driver and target populations were synthesized using mRNAs from kernels 0 and 8 days after pollination. The enriched cDNA fragments were cloned and further screened for differentially regulated genes by dot blot hybridization using driver and target cDNAs as probes. Based on this screening we estimated that about 30-40% of the subtraction-enriched cDNAs represent differentially regulated genes. So far, all cDNA fragments cloned are different in sequence.

Northern analysis confirmed an induced, transient expression

pattern of the genes analyzed, showing the efficiency of the subtraction and screening procedure. In addition, most of the isolated genes showed strongest expression in developing kernels and weak or no expression in other tissues analyzed, i.e. tassels, silks, leaves or young plants. Database searching led to the identification of new genes involved in lipid metabolism and pathogen response as well as genes already known to be endosperm specific, i.e. BETL2 Hueros et. al (1999).

Small transposable elements isolated from transcripts of the *intensifier* alleles *in* and *In-D*

--Pusch, I, Herrmann, M, Hoogvliet, O, Prause, A, Scheffler, B*, Lorbiecke, R, Wienand, U
*USDA, ARS, Natural Products Utilization Research Unit

Sequence analysis of clones of the recessive *intensifier* allele *in* and the dominant allele *Intensifier-Dilute* (*In-D*) revealed the presence of small transposable elements in the genomic and cDNAs of both alleles. In allele *In-D,* a 122 bp transposable element called *BEB* is present in exon 6 of this allele. *BEB* is also found in transcripts of *In-D* and leads to non-functional proteins. The *BEB* element has also been found in a seedling cDNA isolated from a W22 color converted line (Line C). The insert is absent in an EST clone isolated from a tassel cDNA library of line Oh43. A 315 bp transposable element called *ROH* was found in the misspliced transcripts of the recessive allele *in*. The ROH element is integrated at the 3´ end of the second intron of *in* and was also found in truncated transcripts of *in*. The termination of *in* mRNAs in the second intron might be due to a poly-adenylation site in the *ROH* element. So far no other sequence homologies to the *ROH* and *BEB* elements have been found in the reported maize genome.

Characterisation of *ZmKCS-1* and *ZmKCS-2*, two β-ketoacyl-CoA-synthases from maize, possibly involved in seedling wax biosynthesis

--Frenzel, K, Janke, SA[1], Brettschneider, R, da Costa e Silva, O[2], Wienand, U
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The epicuticular wax layer on plant leaves is a heterogeneous mixture of polymers synthesized in different biosynthetic pathways. Some components are derived from the fatty acid elongation pathway (Bianchi et al., Maydica 30:179-198, 1985). Fatty acids are elongated by a complex of four enzymes which successively add two carbon units to fatty acids. The ß-ketoacyl-CoA-synthase (ß-KCS) is a condensing enzyme that plays a key role in the fatty acid elongation complex (Millar et al., Plant J. 12:121-131, 1997).

Two different cDNAs *ZmKCS-1* and *ZmKCS-2* from maize, with high homology to the *Cut 1* gene from *A. thaliana* (Millar et al., Plant Cell 11:825-838, 1999) and various other plant ß-KCSs, were isolated from a cDNA-library of germinating kernels and a cDNA-library of young seedlings. The two cDNAs show a high sequence similarity in the coding region but are differently expressed in the endosperm of germinating kernels, in young seedlings and in tassels. There is no expression in adult leaves and developing kernels.

Overexpression of *ZmKCS-1* in yeast did not lead to a change in long chain fatty acid. This observation and the particularly high homology to the wax biosynthesis related ß-KCS *Cut 1* from *A. thaliana* as well as the high expression of both genes during germination indicates an involvement of *ZmKCS-1* and *ZmKCS–2* in the biosynthesis of seedling wax precursors.

Antisense experiments in maize were carried out within a partial clone of *ZmKCS-1*. Young transgenic seedlings showed small changes in leaf wax composition. The precise gene function, however, remains unclear and has to be further examined.

The *Etched1* gene product of *Zea mays* contains a zinc ribbon-like domain and is homologous to the eucaryotic transcription elongation factor *TFIIS*

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Etched1 (*et1*) is a pleiotropic mutation in maize affecting endosperm and seedling development. *et1* kernels are fissured and cracked and *et1* seedlings appear virescent until approximately two weeks after germination. The *etched 1* gene was identified from a *Mutator*-induced mutant allele using the *AIMS* (amplification of insertion mutagenized sites; Frey et al., Plant J. 13:717-721, 1998) technique. Several mutant alleles as well as the wild-type allele were cloned and analyzed molecularly. The *etched 1* gene is about 3 kb in size and contains 4 exons. Expression analysis revealed transcripts, approximately 800 bp in size, in wild-type endosperm and leaves. The putatively encoded protein is 163 amino acids in length. It contains a zinc ribbon-like domain and shows homology to the eucaryotic transcription elongation factor *TFIIS*. The mRNA has been localized by in situ experiments in the outer cell layers of the endosperm. Organelle localization experiments revealed that the ETCHED1 protein is transported into the stroma of chloroplasts. From the analyses of the *etched 1* gene we conclude that the ETCHED1 protein may be part of a transcription complex involved in plastid development.

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The study of cold shock protein CSP 310 function in maize mitochondria

--Grabelnych, OI, Pobezhimova, TP, Kolesnichenko, AV, Voinikov, VK

Previously the presence of cold shock protein CSP 310 and CSP 310-like proteins in maize mitochondria was established (Kolesnichenko et al., J. Therm. Biol., 25:203-209, 2000). It was found that cytoplasmatic CSP 310 caused uncoupling of oxidation and phosphorylation (Voinikov et al., J. of Thermal Biology. 23:1-4, 1998) because of its association with mitochondria (Kolesnichenko et al., J. Plant Physiol., 156:805-807, 2000). CSP 310 was found in maize mitochondrial proteins in lower amounts than in cold-resistant winter rye and winter wheat. The aim of the present work was to study an influence of cold shock, stress protein CSP 310 and anti-CSP 310 serum on the energetic activity of maize mitochondria.

Mitochondria were extracted from winter wheat shoots by differential centrifugation as described previously (Pobezhimova et al., J. Therm. Biol. 21:283-288, 1996). The activity of mitochondria was recorded polarographically at 27 C using a platinum electrode of a closed type in a 1.4 ml volume cell. The study of an influence of cold shock (0 C, 1 h) on the energetic activity of maize mitochondria showed that cold shock caused slight uncoupling in mitochondria. If the rate of non-phosphorylative (state 4) respiration was 27.8±1.5 nMol O_2/mg of mitochondrial protein and respiratory control coefficient (RC) was 3.76±0.12 in non-stressed mitochondria, then in mitochondria isolated from stressed shoots these values were 33.5±1.6 nMol O_2/mg of mitochondrial protein and 3.35±0.02, accordingly.

The study of an influence of CSP 310 on the energetic activity of isolated maize mitochondria showed that an addition of 0.5 mg CSP 310 per 1 mg of mitochondrial protein after 60 min incubation caused a significant increase of state 4 respiration (from 27.8±1.5 to 45.1±1.1 nMol O_2/mg of mitochondrial protein) and a decrease of RC value from 3.76±0.12 to 2.32±0.11. So, we can suppose that uncoupling observed during cold stress can be caused by CSP 310 association with mitochondria in vivo.

To verify this presumption we studied an influence of anti-CSP 310 serum on energetic activity of maize mitochondria. The results obtained showed that if non-immune serum failed to result in any changes in mitochondrial energetic activity, anti-CSP 310 serum caused significant coupling of oxidation and phosphorylation in maize mitochondria. RC coefficient after this treatment increased up to 7.0±1.5.

Based on the data obtained we can conclude that the maize defense mechanism against cold stress is associated with uncoupling in mitochondria caused by cold stress protein CSP 310.

An influence of cold stress on temperature of maize shoots

--Kolesnichenko, AV, Pobezhimova, TP, Grabelnych, OI, Tourchaninova, VV, Voinikov, VK

It was earlier considered that, because of the particularities of the organism, plants are not able to adjust their temperature. However, in the 60's it was found that during the blossoming of *Aroide*, strong activation of alternative cyanide-resistant respiration causes thermogenesis to occur (Wilson, Smith, Z. Pflanzenphysiol. 65:124-129, 1971). This fact allowed some researchers to suggest that cyanide-resistant alternative oxidase can also participate in processes of plant thermoregulation during low-temperature stress (Vanlerberghe, McIntosh, Plant Physiol., 100:115-119, 1992). Recently it was found that uncoupling proteins, which are homologues of mammalian mitochondrial uncoupling proteins (UCPs), exist in plants (Vercesi et al., Nature, 375:24, 1995). Researchers who found these proteins supposed that they participate in plant protection from low-temperature stress (Laloi et al., Nature, 389:135-136, 1997). Some years ago cytoplasmatic protein CSP 310 was discovered, that also uncouple oxidation and phosphorylation in winter cereals' mitochondria during low-temperature stress (Kolesnichenko et al., Russ. J. Plant Physiol., 43:771-776, 1996). The mechanism of CSP 310 uncoupling action is still unknown but there are some data that show that CSP 310 is present in maize mitochondria (Kolesnichenko et al., J. Therm. Biol., 25:203-209, 2000). Previously it was shown that under cold shock (-4 C, 1 h), living winter wheat shoots can generate heat and their temperature was above 0 C for the initial 25-30 min (Voinikov et al., Biochem. Physiol. Pflanzen., 179:327-330, 1984). We supposed that other cereals also could produce heat during cold stress. So, the present work was aimed at the investigation of an influence of cold stress on temperature of maize seedling shoots.

The temperature of chilled seedlings was recorded by a copper-constantan thermocouple with sensitivity of about 0.025 C (wire diameter 0.1 mm) connected to the input of a high-sensitive microvoltmeter. For the measurement, seedling shoots (3 g) were tightly packed in a small container at 20 C and then transferred to a thermostat with an experimental temperature (0 or -4 C). Temperature changes were recorded for 1 h. The shoot sample then was placed in hot water (95 C) to stop all metabolic processes, and then the temperature changes were recorded in killed samples cooled from 20 C to the experimental temperature. Thus, we obtained temperature curves following chilling with one tissue sample for living and for dead tissue and calculated the temperature difference (ΔT^0) between "killed" and "alive" seedling shoot tissue.

The study of an influence of cold shock on temperature of maize shoots showed that maize seedlings, like winter wheat seedlings, are able to generate heat during cold stress (Fig. 1).

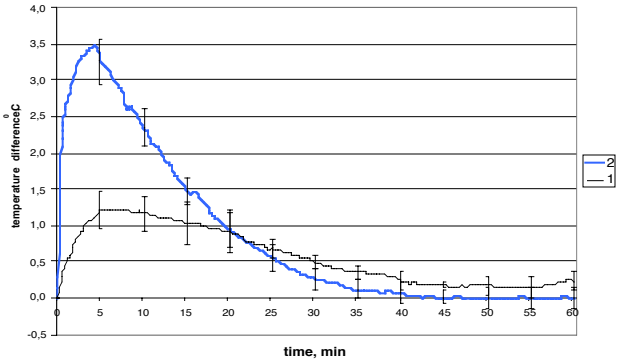

Figure 1. Temperature difference between alive and killed shoots of maize at 0 C (1) and –4 C (2).

When maize seedlings were exposed to cold shock at 0 C, the temperature difference between "alive" and "killed" seedling shoots was up to 1.25 – 1.5 C during the 20 min of cold shock. Subsequent chilling of maize shoots caused the reduction of temperature difference between "alive" and "killed" seedling shoots to 0.5 C. At the same time, the results show that increasing the cold stress intensity caused an increase of heat production by maize shoots at the first moment of cold shock: if the maximum temperature difference between "alive" and "killed' shoots at 0 C was about 1-1.5 C, then at –4 C it was about 3-3.5 C (Fig. 1). At the same time, at –4 C after 35 min of cold shock temperature difference between "alive" and "killed' shoots was not detected – seedlings were killed by low temperature. Therefore, based on the data obtained we can conclude that in maize a low-temperature stress defense mechanism exists that involves heat generation by seedling shoots.

The study of an influence of cold stress on lipid peroxidation at different mitochondrial respiratory chain complexes function in maize mitochondria

--Kolesnichenko, AV, Zykova, VV, Grabelnych, OI, Tourchaninova, VV, Voinikov, VK

It is known that in plants the development of chilling injury symptoms is frequently coincident with peroxidation of fatty acids (Parkin et al., Food Biochem. 13:127-153, 1989). The source of activated oxygen during freezing stress is not established exactly, but there is experimental evidence to indicate that mitochondria are a major source of superoxide in chilling-sensitive plant tissues at low temperatures (Purvis et al., Physiol. Plant 94:743-749, 1995). It was shown that about 1-2% of oxygen reduced in mitochondria by iron-sulfur centers in complex I and partially by reduced ubiquinone and cytochromes *b* in complex III is constitutively converted to superoxide, which is a powerful oxidant radical, but, these data were mainly obtained by use of mammalian mitochondria (Chakraborti et al., Cell. Signal 11:77-85, 1999). It is necessary to note that most of the studies of lipid peroxidation during cold stress are concerned with freezing temperatures. Some data on lipid peroxidation at chilling temperatures show that lipoxygenase activity and lipid peroxidation were increased in leaves of maize crops during low temperatures. This suggested that lipoxygenase-mediated peroxidation of membrane lipids contributes to the oxidative damage occurring in chill-stressed leaves (Fryer et al., Plant Physiol. 116:571-580, 1998). Therefore, the present work was aimed at the investigation of an influence of cold stress on lipid peroxidation in maize mitochondria and as a function of different respiratory chain complexes.

The rate of lipid peroxidation was determined by measuring the primary products of lipid peroxidation – conjugated diene formation. Mitochondria were incubated in a medium containing 175 mM KCl and 25 mM Tris-HCl (pH 7.4). To determine the lipid peroxidation as a function of different mitochondrial respiratory chain complexes, different substrates were used. Malate was used to study complex I, succinate to study complex II, NADH to study complex III, and ascorbate+TMPD to study complex IV.

The data obtained showed that if electron transfer occurred through complexes I, II or III in mitochondria isolated from non-stressed maize shoots, the rate of lipid peroxidation was equal and rather low (Fig. 1). At complex IV function, the rate of lipid peroxidation was about 50% higher (Fig. 1). These results can be caused by the fact, that at the first two complexes electrons are transferring through the ubiquinone complex, which in plants can function as an effective antioxidant system (Pobezhimova, Voinikov, Membr. Cell Biol., 13:1–8, 2000).

The study of an influence of low-temperature stress on the rate of lipid peroxidation at different respiratory chain complexes function in mitochondria isolated from stressed (4 C, 1 h) maize shoots showed that low-temperature stress increased dienic conjugates formation associated with function of all respiratory chain complexes. The most pronounced increase (about 75%) was detected for complex IV (Fig. 1).

Thus, based on the data obtained, one can conclude that in maize mitochondria, unlike mammals, the highest lipid peroxidation was associated with complex IV function. Cold stress caused a detectible increase of lipid peroxidation at complexes I, III and especially IV function.

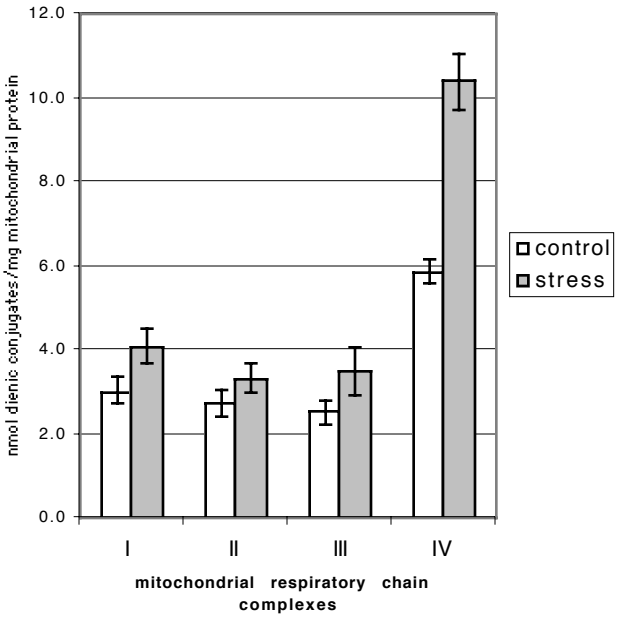

Figure 1. An influence of cold stress (4 C for 1 h) on lipid peroxidation in mitochondria isolated from maize shoots.

The effect of redox conditions on transcriptional activity in isolated mitochondria

--Konstantinov, YM, Subota, IY, Tarasenko, VI, Arziev, AS

We hypothesize that expression of mitochondrial genes is under redox control and involves glutathione. We have shown that the oxidized form of glutathione (GSSG) causes the activation of translation, while the addition of the reduced form of glutathione (GSH) induces substantial repression of mitochondrial protein synthesis in organello (MNL 72:33, 1998).

The aim of the present work was to verify our hypothesis about the possible involvement of the glutathione system in the redox regulation of transcriptional activity in mitochondria.

Mitochondria were prepared from 3-day-old etiolated maize seedlings of hybrid VIR42 MV. The isolation of mitochondria and assay of RNA synthesis in organello are described in our accompanying note.

The effects of the reduced forms of glutathione and sodium dithionite on the kinetics of RNA synthesis in maize seedling mitochondria are shown in Figure 1. The mitochondrial transcriptional activity is seen to decrease in the presence of the reduced glutathione. The effects of reduced glutathione and sodium dithionite on the activity of mitochondrial RNA synthesis were similar to those observed for the protein synthesis in mitochondria in the presence of these reduced agents (MNL 72:33, 1998).

We reported previously (MNL 69:63-64, 1995; MNL 70:29-30, 1996) that under oxidizing conditions mitochondrial transcription and translation were activated, while under reducing conditions they were strongly repressed. Experimental study of redox conditions impact on the activity of mitochondrial DNA topoisomerase I in maize showed that under oxidizing conditions in the presence of GSSG a significant decrease of topoisomerase activity was observed, whereas under reducing conditions in the presence of GSH enzyme activation was observed (MNL 73:39-

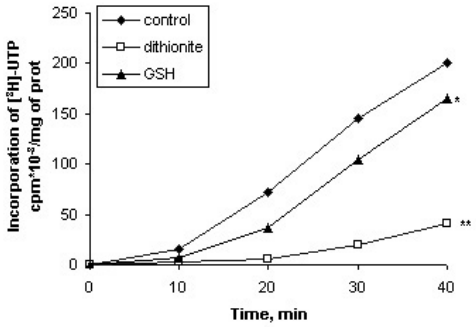

Figure 1. The effects of reducing agents (sodium dithionite and GSH) on the kinetics of in organello RNA synthesis in mitochondria. *P< 0.05; **P<0.001.

40, 1999). This raises the question of whether there is a functional relation of the changes in the mitochondrial DNA topoisomerase I activity in oxidizing and reducing conditions with the phenomenon of changes in the transcriptional activity of the mitochondrial genome in the same conditions.

It was demonstrated previously with the use of a reconstituted system that human topoisomerase I can serve as a repressor of basal transcription (Chen and Xu, Biochem. Mol. Biol. Intern. 39:941-948, 1996). This repression can be overcome by transcriptional activators or TFIIA. It was also reported that a repressing effect of human topoisomerase I was observed only in TATA-box-containing promoters and was mediated by the TATA-binding protein (Chen and Xu, Biochem. Mol. Biol. Intern. 39:941-948, 1996). By analogy with the case described, we presume that the plant mitochondrial topoisomerase I is able to repress the transcription of all or a part of mitochondrial genes. In this case the repression of its activity by oxidizing conditions result in an enhancement of mitochondrial transcription. The likelihood of such a situation is supported by an earlier observation of enhanced transcription by isolated maize mitochondria under oxidizing conditions (MNL 69:63-64, 1995). Under reducing conditions the mitochondrial DNA topoisomerase I is activated and represses the transcriptional activity of mitochondria. We suggest that DNA topoisomerase I can be a regulator of the expression of all or a part of the genes in mitochondria and that it fulfills the function of the "redox response regulator" proposed by Allen (J. Theor. Biol. 165:609-631, 1993; Photosynth. Res. 36:95-102, 1993).

As a whole, the data obtained suggest that the oxidation state of glutathione is involved in the in vivo regulation of mitochondrial genome transcription in plants.

Financial support from the INTAS (Project Number 97-0522) is acknowledged.

Appearance of HSPs immunochemically related to α-crystallin at the temperature close to optimum in the absence of dehydration in crops

--Korotaeva, NE, Borovskii, GB, Voinikov, VK

Plants are able to survive hyperthermia. Heat shock protein (HSPs) synthesis during the heat shock period is one of the grounds of this ability. The α-crystallin-related, small heat shock proteins are ubiquitous in nature, but are unusually abundant and diverse in higher plants as opposed to other eukaryotes. The LMW HSPs range in size from approximately 17 to 30 kDa and share a conserved C-terminal domain common to all eukaryotic LMW HSPs and to the α-crystallin proteins of the vertebrate eye lens (Waters, E.R. et al., J. Exp. Bot. 47:325-338, 1996). Unlike other shock proteins only stress factors such as heat shock can lead to LMW HSP expression. Accumulation of LMW HSPs in plants correlates with thermotolerance emergence (Vierling, E., Annu. Rev. Plant Physiol. Plant. Mol. Biol. 42:579-620, 1991).

However, there are data that LMW HSPs imunochemically related to α-crystallin appear in plants at normal temperature, for example during embryogenesis (Carranco, R. et al., 272:27470-27475, 1997). Here the expression of LMW HSPs plays a general protective role in desiccation tolerance (Wehmeyer, N. et al., Plant Phys. 122:1099-1108, 2000). Thus LMW HSPs are the part of the underlying mechanisms of cell protection against dehydration damage. The aim of our work is testing whether the expression of LMW HSPs occurs in the absence of dehydration at normal temperature conditions. For comparison, we chose maize as a thermotolerant species, and wheat and rye as less not tolerant species.

We used three-day-old etiolated seedlings of maize, wheat, and rye, which were grown at 23 C (wheat and rye) and 27 C (maize). The cut seedlings were placed in water for 3 hours at 42 C, thus being subjected to heat shock. Total proteins were extracted from control and shocked seedlings as described elsewhere (Borovskii, G.B. et al., J. Plant Physiol. 156:797-800 2000). Proteins were subjected to SDS-PAGE (14 % of acrylamide) using a mini-Protean II cell (Bio-Rad, USA) according to the manufacturer's instructions. Western blot and immunodetecton were carried out as was described previously (Timmons, T.M. and Dunbar, B.S., Methods Enzymol. 182:679-688, 1991). Antibodies to α–crystallin sequence, kindly provided by Dr. Craig A. Downs, were used for detection of LMW HSPs (Heckathorn, S.A. et al., Plant Physiol. 116:439-444, 1998).

Electrophoresis of total proteins did not demonstrate a distinct quantitative or qualitative difference between "control" and "shock" in LMW HSPs of all the species (data not shown). Immunoblotting showed that protein samples from all three species contained LMW HSPs as were shown immunologically (Fig. 1). Maize samples included the group of HSPs 22-18 kD, and wheat and rye included one HSP 20 kD. Percentage of the maize LMW HSPs related to α–crystallin is higher than in the wheat and rye. This may be due to higher thermotolerance of maize.

LMW HSPs are clearly apparent in the "control" samples (Fig. 1). It is best expressed in wheat, slightly less in maize, and weak in

Figure 1. Immunodetection of the proteins immunochemically related to α-crystallin. The proteins were extracted from three-day-old seedlings of maize (1, 2), wheat (3, 4) and rye (5, 6), grown at 27 C (maize) or at 23 C (wheat and rye). Before the extraction of the proteins, seedlings were shocked at 42 C for 3h. (2, 4, 6) or left for 3 h. at the growing temperature (1, 3, 5). Molecular weight markers are indicated on the right.

rye. This suggests that either LMW HSPs, as well as high-molecular HSPs, may be synthesized constitutively, or alternatively seedling germination temperature (23 C for wheat and rye and 27 C for maize) may lead to their expression. To check this we chose the temperature of 20 C for germination of the seeds of all the species. Immunoreaction demonstrated a practically complete absence of LMW HSPs in "controls" of maize, wheat and rye grown at 20 C, which is in agreement with our supposition (Fig. 2). Appearance of LMW HSPs in all the species at the temperature close to optimum (23 C) supports the possibility of constitutive synthesis of these proteins in the seedlings. On the other hand, appearance of the LMW HSPs within the frameworks of optimal temperature may prove a high level of thermosensitivity of the LMW HSPs synthesis reaction for all three species.

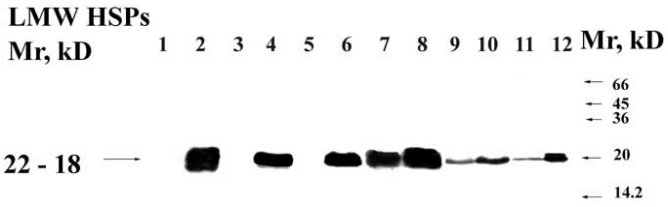

Figure 2. Immunodetection of the proteins, immunochemically related to α-crystallin. The proteins were extracted from three-day-old seedlings of maize (1, 2, 7, 8), wheat (3, 4, 9, 10) and rye (5, 6, 11, 12), grown at 20 C (lines 1 - 6), at 27 C (lines 7, 8) and at 23 C (lines 9-12). Before the extraction of the proteins, seedlings were shocked at 42 C for 3h. (2, 4, 6, 8, 10, 12) or left for 3 h. at the growing temperature (1, 3, 5, 7, 9, 11). Molecular weight markers are indicated on the right.

This work was supported by the Russian Fund of Basic Research (project 99-04-48121).

Mitochondrial low-molecular-weight heat shock proteins and tolerance of crop plant's mitochondria to hyperthermia

--Korotaeva, NE, Antipina, AI, Grabelnych, OI, Varakina, NN, Borovskii, GB, Voinikov, VK

Plants are known to synthesize, under heat shock, a large diversity of low-molecular-weight heat shock proteins (LMW HSPs) that function as protectors on the biochemical level. The α-crystallin-related, low-molecular-weight heat shock proteins range in size from approx 17 to 30 kDa and share a conserved C-terminal domain common to all eukaryotic LMW HSPs and to the α-crystallin proteins of the vertebrate eye lens. LMW HSPs act in vivo as molecular chaperones to bind partially denatured proteins, preventing irreversible protein inactivation and aggregation (Waters, E.R. et al., J. Exp. Bot. 47:325-338 1996).

It is known that LMW HSPs play an important role in protection of the organelles from hyperthermia damage. Chaperone activity of organelle LMW HSPs contributes to the development of thermotolerance. For example, appearance of LMW HSPs in wheat mitochondria correlates with thermotolerance emergence, according to investigation of thermotolerant and non-tolerant varieties of wheat (Joshi, C.P. et al., TAG 95:834-841 1997). We suppose that there may be a correlation between thermostability of the species and expression of LMW HSPs. The aim of our investigation was to determine whether a correlation exists between thermotolerance among species and mitochondria LMW HSPs (mit LMW HSPs) accumulation, including their number and polymorphism. We chose for our investigation maize as a thermotolerant species, and wheat and rye as less tolerant species.

Three-day-old etiolated seedlings of maize, wheat, and rye were grown at 23 C (wheat and rye) and 27 C (maize). Some of the cut seedlings were placed in water for 3 hours at 42 C, thus being subjected to heat shock. Untreated seedlings were "control". Mitochondria were extracted from the control and shocked seedlings by the method of differential centrifugation with further purification by discontinuous Percoll gradient as described elsewhere (Borovskii, G.B. et al., J. Plant Physiol. 156:797-800 2000). Isolated mitochondria were used for the extraction of the proteins and the measuring of the energetic activity. Proteins were subjected to SDS-PAGE (14% of acrylamide) using a mini-Protean II cell (Bio-Rad, USA) according to the manufacturer's instruction. Western blotting and immunodetection were carried out, as described previously (Timmons, T.M. and Dunbar, B.S., Meth. Enzymol. 182:679-688, 1990) using anti-α-crystallin primary antibodies, kindly provided by Dr. Craig A. Downs (Heckathorn, S.A. et al., Plant Physiol. 116:439-444 1998).

Western blot showed the appearance of LMW HSPs immunochemically related to α-crystallin in all three species after heat shock (Fig. 1). Five mit LMW HSPs, 28, 23, 22, 20 and 19 kD, were found in maize, and only one mit LMW HSP 20 kD was found in wheat and rye. It should be noted that LMW HSPs were detected only for "shock" samples. Perhaps the differences in number of LMW HSPs in maize on the one hand, and in wheat and rye on the other hand, are related to differences in stability of the species to heat shock.

Other authors have discovered LMW HSPs 22 and 30 kD in maize mitochondria under heat shock (42 C, 3 h.) (Lund, A.A. et al., Plant Physiol. 116:1097-1110 1998). Based on the similarity of molecular weights, the LMW HSPs 23 and 29 kD which we detected, are likely the proteins 22 and 30 kD mentioned above. However, other mit LMW HSPs were not detected by these authors, while we identified an additional three LMW HSPs 21, 20 and 19 kD (Fig. 1). According to our account, this does not contradict the results of Lund A. et. al., inasmuch as they used maize grown at 29 C, when LMW HSPs immunochemically related to α-crystallin appear in total maize protein fraction at 27 C (see the article "Appearance of HSPs immunochemically related to alpha-crystallin at the temperature close to optimum in the absence of dehydration in crops" in this MNL). In this case only

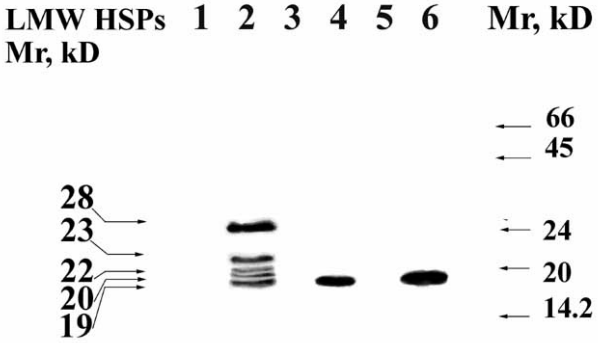

Figure 1. Immunodetection of LMW HSPs, related to α-crystallin, among the mitochondrial proteins of maize (1, 2), wheat (3, 4) and rye (5, 6). Three-day-old seedlings were shocked at 42 C for 3 h. (2, 4, 6) or left for 3 h. at the growing temperature (1, 3, 5) before the isolation of mitochondria. Extracted mitochondrial proteins were divided by SDS-PAGE. Molecular weight standards are on the right.

part of the proteins seem newly synthesized, i.e. HSPs, when comparing "control" and "shock" samples.

In relation to wheat mit LMW HSPs our results were in accordance with the data of other authors (Joshi, C.P. et al., TAG 95:834-841 1997). As far as we know, our data about rye mit LMW HSP is the first such reported.

For determining the thermotolerance of the mitochondria, the activity of the mitochondria respiration after heat shock was measured. The respiration of the mitochondria was recorded polarographically at 27 C using a platinum electrode of a close type in a 1.4 ml volume cell. 10mM malate in the presence of 10 mM glutamate was used as an oxidation substrate. Polarograms were used to calculate the rates of the oxygen uptake in state 3 (phosphorylate respiration) and in state 4 (nonphosphorylate respiration) (Estabrook, R.W., Methods Enzymology 10:41-47, 1967).

The rate of the oxidative activity declined after heat shock (42 C, 3 h.) to a great extent in all three species (Table 1). However, in maize the decrease of the oxidative activity of the mitochondria after stress was less than in wheat and rye. Indeed the rate of phosphorylative and nonphosphorylative respiration in maize mitochondria after heat shock decreased 38.3 % and 30.4 %, while in the wheat and rye mitochondria that were 63% and 59.5 % (wheat), and 65% and 60.6 % (rye) accordingly. Thus, although the mitochondria of all species were damaged under heat shock, the thermotolerance of maize mitochondria was superior to that of mitochondria of wheat and rye.

Table 1. The influence of heat shock (42 C. 3 h.) on the oxidative activity of the mitochondria of maize, wheat and rye. All experiments were made in three biological replications. The data obtained were analysed statistically, means and S.D. (P≥0.95) are presented.

Variants		The rate of oxygen uptake (nmol O_2 / min mg protein)	
		State 3	**State 4**
maize	control	86.6±3.9	29.3±1.4
	shock	53.5±1.5	20.4±1.2
wheat	control	81.1±2.3	35.4±1.8
	shock	29.9±2.0	14.3±0.8
rye	control	82.9±1.1	37.8±1.1
	shock	29.2±3.2	14.9±1.1

The thermotolerance of the maize mitochondria concurs with the accumulation of a number of LMW HSPs immunochemically related to α-crystallin. Our data permit us to suppose that the diversity of LMW HSPs plays an important role in the protection of respiration processes of mitochondria from heat shock damage. It is known that the majority of LMW HSPs are chaperones, i.e. they stabilize protein structure and prevent damage and resultant turnover. For example mit LMW HSP of tomato is a chaperone (Liu, J.A. et al., Plant Cell Physiol. 40:1297-1304 1999). The mit LMW HSP protects NADH:ubiquinone oxidoreductase of the electron transport chain during heat stress in mitochondria of apples (Downs, C.A. et al., FEBS Letters. 430:246-250 1998). Based on information from the literature and our research we expect that various LMW HSPs influence different proteins or recognize various transitional states of partly denatured proteins. In this case maize mitochondria have a more abundant composition of chaperones than wheat and rye, and enhanced capabilities for preventing damage to the enzymes of the electron transport chain.

The activity of maize mitochondria is more thermotolerant than that of organelles of wheat and rye. The number of LMW HSPs, immunochemically related to α-crystallin, appearing under heat stress in mitochondria correlates with thermotolerance of the organelles, and correspondingly with thermotolerance of the species.

This work was supported by the Russian Fund of Basic Research (project 99-04-48121).

Localization of low-molecular-weight heat shock proteins in cell compartments of maize, wheat and rye

--Korotaeva, NE, Antipina, AI, Borovskii, GB, Voinikov, VK

Stress protein synthesis, as a response to adverse environment factor is known to be a protection reaction. LMW HSPs are the most numerous group of HSPs in plants.

The LMW HSPs range in size from approximately 17 to 30 kD and share a conserved C-terminal domain common to all eukaryotic LMW HSPs and to the α-crystallin proteins of the vertebrate eye lens. LMW HSPs function as chaperones preventing polypeptide damage. LMW HSPs form granular structures in cells, at the increased temperature associating with cell endoplasmic reticulum and plastid membranes, preventing their damage. In higher plants six nuclear gene families encoding LMW HSPs have been defined. Each gene family encodes proteins found in a distinct cellular compartment, including the cytosol, chloroplast, ER, and mitochondrion (Waters, E.R. et al., J. Exp. Bot. 47:325-338, 1996). Mitochondrial LMW HSPs (mit LMW HSPs) are nuclear-encoded stress-regulated HSPs, which play an important role in the protection of mitochondria and processes of oxidative phosphorylation. But the location of these LMW HSPs in mitochondria is still unclear. Methods of SDS-PAGE-electrophoresis and Western blot with antibodies to α-crystallin sequence were used to study localization of total and mitochondrial LMW HSPs in maize, wheat and rye cells. For comparison, we chose maize as a thermotolerant species, and wheat and rye as less tolerant species.

Three-day-old etiolated seedlings, grown at 27 C (maize) and at 23 C (wheat and rye) were subjected to heat shock (42 C, 3 h.) and used for the mitochondria isolation as described elsewhere (Borovskii, G.B. et al., J. Plant Physiol. 156:797-800, 2000). Isolated mitochondria were treated with pronase E (1 mg/ml) for one hour. Then mitochondrial proteins were extracted as previously described (Borovskii, G.B. et al., J. Plant Physiol. 156:797-800, 2000). Mitochondria without protease treatment were used for the extraction of the proteins of the "control".

Western blotting demonstrated that LMW HSPs immunochemically related to α-crystallin appear among mitochondrial proteins of all the species under heat shock (Fig. 1). Five proteins were found in maize mitochondria and one protein was found in mitochondria of wheat and rye. Pronase treatment of mitochondria showed that maize mit LMW HSPs 22, 20 and 19 kD are located outside, but maize mit LMW HSPs 24 and 28 kD are located inside of the organelles. Apparently maize mit LMW HSPs 24 and 28 kD are matrix proteins. The absence of 29 and 23 kD in cytoplasm fraction supports this manner of location of LMW HSPs in maize mitochondria (Fig. 2). The location of maize mit LMW HSPs concurs with data of other authors, who identified LMW HSPs in soybean mitochondria by radiolabelling (Chou, M. et al., Plant Phys. 89:617-621, 1989). It was shown that shift of the seedlings to 28 C after heat shock leads to the appearance of organelle-associated LMW HSPs in cytosol. While the group of LMW HSPs 15-18 kD migrates from mitochondria, the 22 and 24

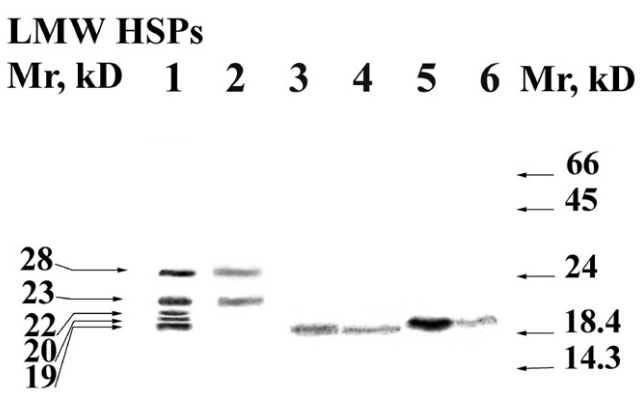

Figure 1. Mitochondrial proteins extracted from shocked seedlings (42 C, 3 h.) of maize (1, 2), wheat (3, 4) and rye (5, 6). Mitochondria were isolated from three-day-old etiolated seedlings and divided into two groups. One group of mitochondria was incubated with pronase E (2, 4, 6), the other one was used for reference (1, 3, 5). LMW HSPs immunochemically related to α-crystallin were identified. Molecular weight standards are indicated on the right. The relative molecular weights of LMW HSPs are given on the right.

kD are always present in the mitochondrial fraction, which allows to submit their location inside of the organelles.

The treatment by pronase of mitochondria of wheat and rye with further protein extraction showed that HSP 20 kD are located outside and inside of organelles. In rye mitochondria the part of the 20 kD is localized inside that was stated by the decline of the coloration depth of the according spots. Other researchers confirm our results concerning wheat mit LMW HSP 20 kD (Basha, E.M. et al., Plant Sci. 141:93-103, 1999).

To determine the location of these LMW HSPs in other cell compartments, we extracted total and cytoplasm proteins as described above. Cytoplasm proteins were extracted from supernatant remaining after isolation of mitochondria and crude cell particles. It contained soluble cell proteins and proteins of membrane structures, nuclei and cell wall. The data showed that maize LMW HSPs 28 and 24 kD were specific for mitochondria, LMW HSP 20 kD of wheat and rye turned out to be not only mitochondrial but common cell protein (Fig. 2). The group of LMW HSPs 22-18 kD was found in the total, mitochondrial and cytoplasm protein fractions of maize.

The absence of two maize LMW HSPs 29 and 23 kD in the cytoplasm confirms the importance of these proteins for the mitochondria. Perhaps α–crystallin-related LMW HSPs attached to the mitochondria outside are able to migrate from the organelles to the cytosol after returning the cells to the normal conditions.

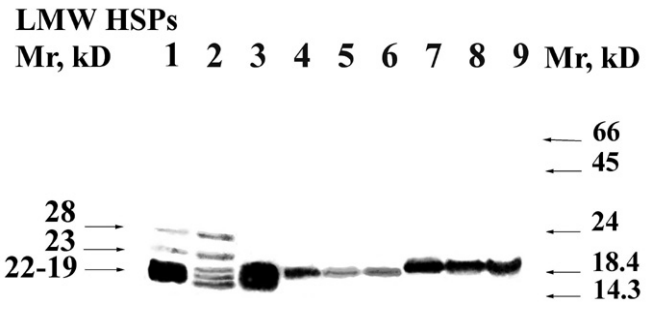

Figure 2. Western blotting of total (1, 4, 7), mitochondrial (2, 5, 8) and cytoplasmic (3, 6, 9) proteins extracted from shocked seedlings (42 C, 3 h.) of maize (1, 2, 3), wheat (4, 5, 6) and rye (7, 8, 9). Molecular weight standards are indicated on the right. The relative molecular weights of LMW HSPs are given on the right.

Cognate process was discovered in soybean mitochondria (Chou et al., Plant Physiol. 89:617-621, 1989). Perhaps external LMW HSPs 20 and 22-18 kD are related to the class I LMW HSPs that originally localized in the cytoplasm. Material speaks well for this supposition about presence of extensive similarities between mit LMW HSPs and class VI LMW HSPs (Goping, I.S. et al., Plant Mol. Biol. 16:699-711 1991). The analysis of the primary polypeptide sequence for determination specific sectors for the VI class of LMW HSPs is required for verification of this supposition.

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The COR-polypeptides of maize, characteristic of cold hardy state, in comparison with those of other cereals

--Stupnikova, IV, Borovskii, GB, Voinikov, VK

Maize (*Zea mays* L.), a plant from warm-temperature habitat, is an example of a chilling-sensitive crop injured by low, non-freezing temperatures. For several chilling- and freezing-tolerant species of temperate origin, cold acclimation, which increases freezing tolerance, has been extensively exploited in order to understand tolerance mechanisms at the cellular and molecular levels. Among the biochemical changes associated with acclimation, increasing interest during recent years has focused on the modifications of protein synthesis and genome expression. Many *COR*-genes have been isolated and characterized from a variety of plant species. Their products fall into a number of families based on amino acid sequence similarities. It was found that many of these COR-proteins are heat stable and have an unusually hydrophilic nature.

In this connection, it was interesting to analyze heat stable COR-proteins of maize; to demonstrate similarity of maize COR-polypeptides to those of freezing-tolerant cereals; to correlate heat stable polypeptide composition of studied cereals with their cryotolerance.

Three-day-old seedlings of maize grown at 28 C were transferred to 10 C for three days to induce acclimation. For comparison, three-day-old seedlings of wheat and rye grown at 22 C were used. They were acclimated at 4 C for three days. Unhardened seedlings were used for reference. The tolerance assessment of control and hardened cereals was conducted by electrolyte leakage techniques (Palta, Plant Physiol., 60:393-397, 1977). In order to study changes in synthesis of heat-stable proteins characteristic of cold acclimation state, thermostable proteins were extracted from seedlings and separated by SDS gel electrophoresis (Stupnikova, Russian J. Plant Physiol., 45:744-748, 1998).

The data show that the amount of leaked electrolytes from control and hardened seedlings of all crops do not differ considerably (Fig. 1).

Freezing at -6 C resulted in increased ion leakage. It reflects perturbation of membrane semipermeability by freeze-thaw stress and is indicative of cell viability. As expected, the maize plants showed higher electrolyte leakage (that is, more freezing injury) in comparison with more tolerant cereals. However, all hardened plants were more tolerant than control, and were characterized by lower amounts of leaked electrolytes (Fig. 1). Thus, chilling-sensitive maize, like chilling- and freezing-tolerant cereals, also developed cryotolerance during hardening.

In this connection it was interesting to study proteins related to cold acclimation state of maize and to compare them with other

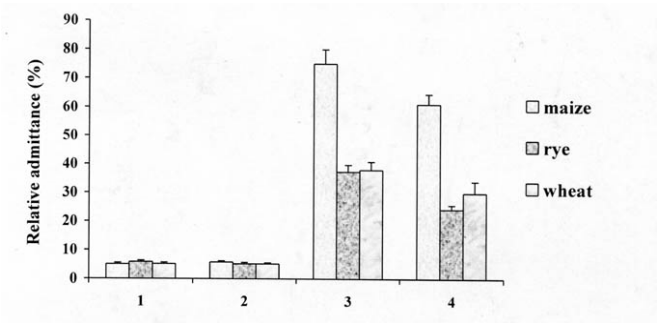

Figure 1. Relative freezing tolerance of maize and other cereals (measured by electrolyte leakage techniques). Relative admittance (% to admittance of killed tissue electrolyte) was assessed in control (1), hardened (2), control and freezing at -6 C (3), hardened and freezing at -6 C seedlings (4). Means and standard errors of the means are shown.

cereals. The total and heat-stable polypeptides were analyzed. It was found that total protein composition of control and hardened seedlings did not differ from each other (data are not presented). At the same time, the difference in heat stable proteins was strong (Fig. 2). The acclimated maize seedlings accumulated thermostable polypeptides with mol. weights 50, 46, 35, 31, 27, 24, 22 kD, from which those with mol. weights 50, 35, 27, 22 kD apparently were synthesized de novo. Conversely, the more tolerant plants accumulated high- and medium molecular proteins.

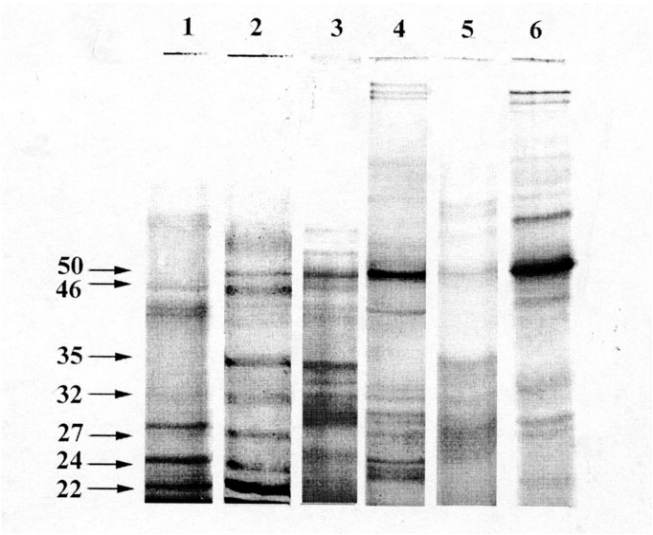

Figure 2. Heat stable proteins from control (1, 3, 5) and hardened (2, 4, 6) seedlings of maize (1, 2) and other cereals (rye – 3, 4; wheat - 5, 6). Mol. wts of maize proteins are indicated on the left. Electrophoresis was run in 13 % SDS-PAGE.

Thus, the medium- and low molecular COR-proteins were characteristic of hardened state of maize and differed from those of tolerant cereals. The accumulation of medium- and low molecular polypeptides during cold treatment was revealed also in such chilling-sensitive plants as soybean (Boudet, 1993, NATO ASI Series, 116, 725-739). Possibly this trait differentiates the maize (and other chilling-sensitive plants) adaptation mechanism from that of chilling- and freezing tolerant cereals.

The research was funded by the Russian Foundation of Basic Research (project 99-04-48121).

Dehydrin-like-proteins in maize mitochondria after cold adaptation, freezing, drought and ABA treatment

--Borovskii, GB, Stupnikova, IV, Antipina, AI, Vladimirova, SV, Voinikov, VK

Plants respond to stress temperatures via physiological, morphological, and metabolic processes. Near-freezing and freezing temperatures like drought stress can also induce cellular dehydration, by which water from within the cell migrates to outside the cell. At the cellular level, this activates different structural and biochemical changes including induction of a number of cold-induced proteins. Among them is the dehydrin family of proteins.

These proteins are induced by both cold and drought stress. Dehydrins (dlps), also referred to as Group II late embryogenesis abundant (LEA) proteins, are glycine-rich, hydrophilic, and thermostable. They have been hypothesized to function by stabilizing large-scale hydrophobic interactions such as membrane structures or hydrophobic patches of proteins (Close, Physiol Plant, 97:795-803, 1996). Dehydrins accumulate in response to cold in the nucleus or cytoplasm, but it is unknown if they can accrue in mitochondria or chloroplasts. In the previous study we have found the accumulation of two dehydrin-like proteins in the plant mitochondria after low temperature treatment (Borovskii et al., J. Plant Physiol., 156:797-800, 2000).

In this connection, the objective of this study was to determine whether dlps localize to maize mitochondria in response to stimuli other than cold adaptation treatment (10 C for maize).

Three-day-old etiolated seedlings of *Zea mays* (L.) (maize) were grown at 27 C. Unstressed plants were maintained under growth conditions for one day. Mild cold treatment (acclimation) was carried out by subjecting seedlings to a temperature of 10 C for 7 days. Freezing stress was performed at –10 C for 20-30 min until ice crystallized on the surface of seedlings. Transfer of two-day-old seedlings onto dry filter paper for 1 day at growth conditions served as a model of drought stress. ABA treatments were made at the control temperature by spraying 1mM ABA (Sigma) solution with 0.1% of Tween-20 (Sigma). ABA treated seedlings were harvested the day after treatment. Control and treated seedlings were compared at similar growth stages. Mitochondria were isolated according to the technique described by Borovskii et al. (2000).

Sonicated (Fig. 1) and unsonicated (Fig. 2) mitochondria were used further for extraction of total and thermostable proteins. Mitochondrial proteins of maize were fractionated by 10% SDS-PAGE (25 μg of protein per lane) using a mini-Protean PAGE cell (Bio-Rad) according to manufacturer's instruction. Western blotting and immunodetection were carried out as described by Timmons and Dunbar (1990). Antibodies against dehydrins were kindly provided by Dr. T. J. Close. All experiments were replicated three to four times.

Five dlps were found in maize mitochondria (Fig. 1). Bands corresponding to all these proteins were very weak or absent when antibodies were blocked by dehydrin peptides (data not shown). Two of these polypeptides were thermostable, but the other three proteins seem not to be thermostable. Finding proteins immunologically related to dehydrins but constitutive and unstable to high temperature is unusual, but sometimes occurred.

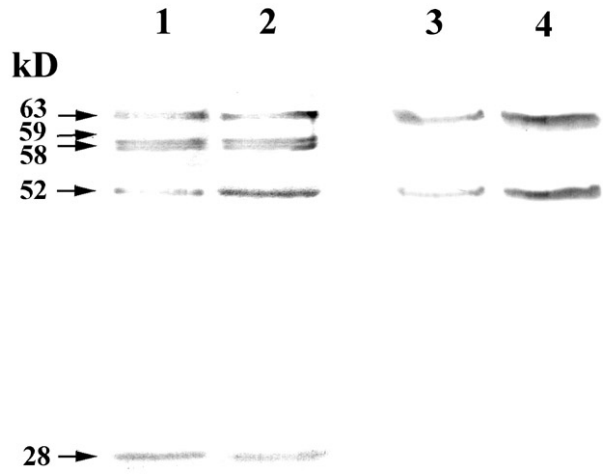

Figure 1. Dehydrin-like proteins (dlps) of maize mitochondria after cold adaptation. Mitochondria from control (1,3) and cold-treated (2, 4) seedlings were disrupted by sonication. Total (1, 2) and thermostable (3,4) mitochondrial proteins were fractionated by 10% SDS-PAGE, electroblotted onto nitrocellulose membrane, and probed with antibody against dehydrin (1:1000). Molecular masses of dlps are indicated on the left.

The dlps with mol. masses 63, 52, 28 kD were found in the previous study (Borovskii et al., J. Plant Physiol., 156:797-800, 2000) in wheat and rye and apparently are "common" mitochondria proteins. Low temperature adaptation of maize resulted in the strong accumulation of "common" thermostable polypeptides with mol. masses 63 and 52 kD (Fig. 1) that was more pronounced in the thermostable fraction. Conversely, the unthermostable proteins did not accumulate. Apart from this, unthermostable dlps were not or very slightly induced by all the treatments used (Fig. 2). Based on this observation we concluded that these proteins were not involved in the stress reaction and adaptation.

The freezing and drought stresses had no effect on the accumulation of dlp 63 kD in mitochondria of maize (Fig. 2, ln. 2). The dlp52 was not observed under any treatment (Fig. 2). The differences in control samples of sonicated (Fig. 1) and unsonicated mitochondria (Fig. 2) illustrated to our minds that some groups of dlps had a strong association with large, slightly disruptive fragments of mitochondria. Such groups of proteins were discarded with undisrupted mitochondria. Because of that, dlp63 was stronger in Fig. 2 and weaker in Fig. 1 in the control samples.

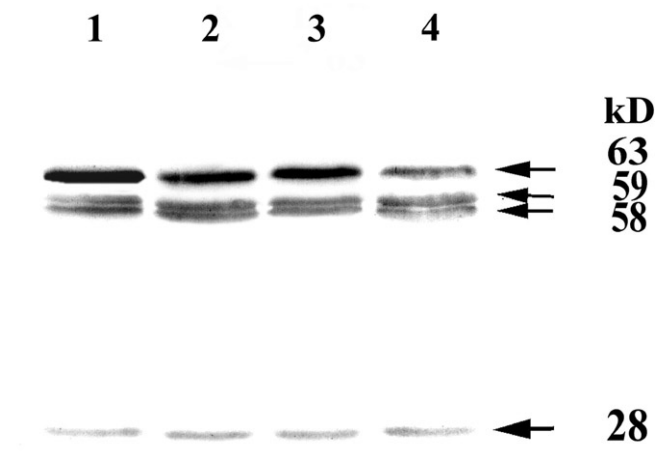

Figure 2. Mitochondrial dehydrin-like proteins from the control (1), freezing (2) and drought stressed (3) and ABA treated (4) maize seedlings. Protein from unsonicated mitochondria was subjected to separation and Western blotting (the same as in Fig. 1). Molecular masses of dlps are indicated.

Both proteins (dlp52 and dlp63) were not induced by ABA treatment in the maize mitochondria (Fig. 2, ln. 4). Moreover, ABA treatment resulted in decrease of dlp63. Apparently, augmentation of dlps concentration during cold adaptation is not associated with ABA accumulation, but dependent on low unfreezing temperature, as they slowly accrue during cold adaptation.

Thus, mitochondria of maize, a plant from a warm-temperature habitat, apparently slowly adapt to cold conditions and are unable to react quickly in severe stress conditions. It is likely to partially account for the chilling-sensitive nature of maize.

The research was funded by the Russian Foundation of Basic Research (project 99-04-48121). We sincerely thank Dr. T. J. Close for the gift of the dehydrin antibody and dehydrin-specific peptide.

ABA-induction of cold hardy state and heat stable COR-proteins in maize seedlings and other cereals

--Stupnikova, IV, Borovskii, GB, Voinikov, VK

There are many studies dealing with acquisition of maize cryotolerance during cold acclimation. At the same time, there has been considerable interest in the role of abscisic acid (ABA) in mediating the tolerance. Exogenous application of ABA has been shown to confer cold hardiness to plant and cell-suspension cultures of different species including maize. It accounts for the fact that this hormone participates in ABA-dependent signaling process and activates cold-responsive genes (*COR*-genes) related to cold hardening (Shinozaki, Yamaguchi-Shinozaki, Plant Physiol., 115:327-334, 1997). In this connection, it was interesting to analyze the pattern of heat stable protein synthesis of maize and other cereals, to compare it with COR-polypeptides and collated results obtained with cryotolerance of the species studied.

With this objective, seedlings of maize were germinated at 27 C, seedlings of wheat and rye at 22 C for 3d in darkness. To determine whether exogenous application ABA affected cryotolerance, seedlings were exposed to 1000 μM ABA with the addition of Tween-20 (0.1% solution) for one day. The tolerance assessment of control and ABA treated cereals was conducted by electrolyte leakage technique (Palta, Plant Physiol., 60:393-397, 1977). In order to study changes in heat-stable protein synthesis during ABA exposure, proteins were labeled *in vivo* with ^{14}C-leucine separated by SDS gel electrophoresis and the derived fluorograms were studied.

The study of response to freezing by electrolyte leakage techniques revealed that freezing at -6 C resulted in an increase of ion leakage from tissues of all cereals (Fig. 1). This points to perturbation of membrane integrity that usually results in decreased survival. Exogenous application of ABA enhanced plant cryotolerance based on the ion leakage levels. As expected the maize plants showed higher electrolyte leakage during freezing (that is more freezing injury) in comparison with more cold-tolerant cereals. It should be noted that the amount of leaked electrolytes from unexposed control and ABA treatment seedlings of all crops are essentially identical (Fig. 1).

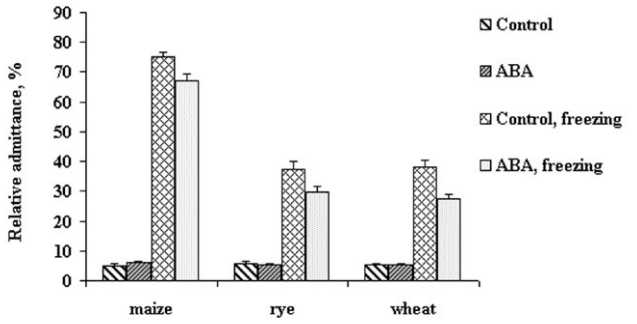

Figure 1. Relative freezing tolerance of maize and other cereals (measured by electrolyte leakage techniques). Relative admittance (% admittance of killed tissue electrolyte) was assessed in control, ABA treatment, control and freezing at -6 C (control, freezing), ABA treatment and freezing at -6 C seedlings (ABA, freezing). Means and standard errors of the means are shown.

The ABA augmentation of maize cryotolerance (as is the case with tolerant cereals) was accompanied by alteration of heat stable protein synthesis (Fig. 2). It is interesting that ABA treatment produced more proteins than low temperature acclimation (Stupnikova et al., in the same issue). ABA treated seedlings of maize synthesized a number of new polypeptides with mol. weights 219, 214, 178, 66, 37, 30, 28 and 26 kD; and accumulated proteins with mol. weights 54, 46, 42, 41 and 32 kD. The concentration of all polypeptides detected was greatly increased during hormone application (Fig. 2). Thus, whereas ABA treated seedlings accumulated 13 ABA-inducible proteins, cold adapted plants accumulated only seven. This also applies to more tolerant cereals (for wheat and rye). Moreover, hormone exposed seedlings of maize, unlike cold acclimated ones, synthesized high molecular weight polypeptides, different from those of wheat and rye.

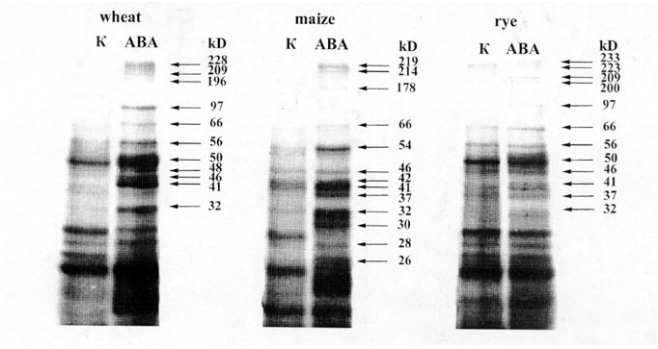

Figure 2. Heat stable ABA-inducible proteins from control (K) and ABA-treatment (ABA) seedlings of maize and other cereals (rye and wheat). Mol. wts of maize proteins are indicated on the right. Electrophoresis was run using 13 % SDS-PAGE.

It appears that increase of maize cryotolerance through exogenous ABA (as is the case with wheat and rye) is associated with both increasing the amount of protein (not only cold-regulated polypeptides) and accumulation of high molecular weight protein.

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Mitochondrial DNA topoisomerase I is involved in in organello RNA synthesis

--Konstantinov, YM, Subota, IY, Tarasenko, VI, Grokhovsky, SL, Zhuze, AL

We have previously described (MNL 71:39-40,1997; MNL 73:39-41, 1999; MNL 74:33, 2000) some properties of nuclear and mitochondrial DNA topoisomerases I, including their sensitivity to different type inhibitors and redox conditions. We showed that mitochondrial DNA topoisomerase I was distinguished from a nuclear topoisomerase by a number of characteristics. The aim of the present work was to investigate the role of mitochondrial DNA topoisomerase I in RNA synthesis in maize mitochondria using an in organello system. For that purpose we studied the kinetics of RNA synthesis in isolated mitochondria in the presence of specific inhibitors of DNA topoisomerase I: camptothecin and bisbenzimidazoles Hoechst 33258 and Hoechst 33342 (Figure 1).

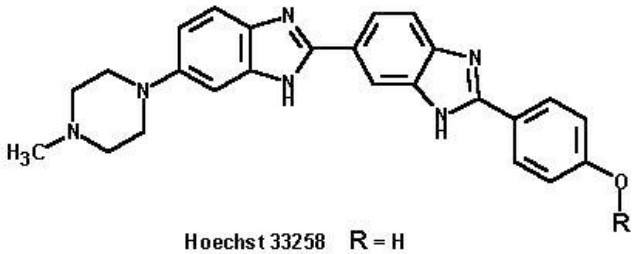

Figure 1. Chemical structure of Hoechst 33258 and Hoechst 33342 used in this study

Mitochondria were prepared from 3–day–old etiolated seedlings of maize (*Zea mays L.* hybrid VIR 46 MV) by the standard method of differential centrifugation. RNA synthesis was measured in mitochondria according to the method of Wilson et al. (Eur. J. Biochem. 242, 81-85, 1996) with the use of [^{3}H]-UTP (specific radioactivity was 1332 TBq mol^{-1}). Reactions were started by the addition of mitochondria and performed at 30 C. Protein was determined by the Lowry method. All kinetic data were obtained from at least 3 independent experiments. Statistical analysis was performed using Students paired t-test.

Figure 2 shows that the specific inhibitor of DNA topoisomerases I, camptothecin, caused substantial repression of RNA synthesis in isolated mitochondria in a dose-dependent manner. Bisbenzimidazoles Hoechst 33258 and Hoechst 33342 belong to the minor groove-binding compounds which are known to bind to the minor groove of DNA with A+T specificity and to cause widening of the minor grooves (Neidle et al., 1987, Biochem. J. 243:1-13). Hoechst 33342 has enhanced membrane permeability in comparison with Hoechst 33258 (Chen et al., 1993, Proc. Natl. Acad. Sci. USA 90:8131-8135). Figure 3 shows the influence of

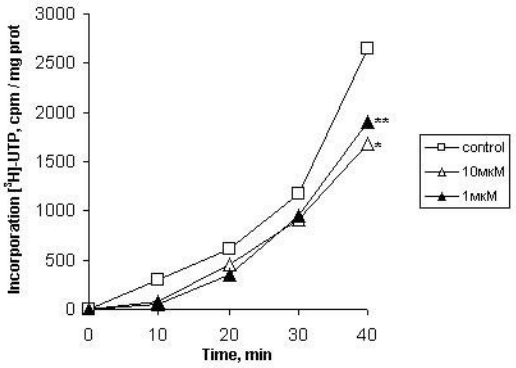

Figure 2. The effect of camptothecin on the kinetics of RNA synthesis in maize mitochondria. * P<0.05; ** P<0.01

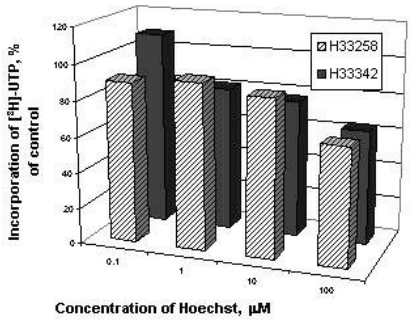

Figure 3. The effects of Hoechst 33258 and Hoechst 33342 on the RNA synthesis in maize mitochondria. The time of exposition of mitochondria with [^{3}H]-UTP was 40 min.

the bisbenzimidazoles at various concentrations on the transcriptional activity of mitochondria. It can be seen that both inhibitors of topoisomerase I repressed the activity of mitochondrial RNA synthesis in a dose-dependent manner, while Hoechst 33342 under, concentrations of 1 and 10 µM was more efficient as repressor of mitochondrial transcriptional activity in comparison with Hoechst 33258.

It is well known that DNA topoisomerases are important, often essential, cellular enzymes involved in nearly all aspects of DNA structure and metabolism (Berger, 1998, Biochim. Biophys. Acta 1400:3-18). The data obtained show clearly that DNA topoisomerase I is involved in transcription of mitochondrial genome under *in vitro* conditions. We suggest that an in organello RNA synthesis system of isolated maize mitochondria may serve as an additional model system for probing and studying anti-DNA topoisomerase I activities.

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Pioneer Hi-Bred Int., Inc.

New male-sterile mutant allele of *Ms22*

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

A new male-sterile allele of *Ms22* has been identified. The new allele was among male-sterile mutants received from the late Dr. Earl Patterson. Earl had designated it as *ms*-6036* (see MNL 69:126-128).

We planted an F2 segregating line of *ms*-6036* in our 1998 Hawaii nursery to determine the chromosome arm map location of the mutant as part of our standard procedure in working with previously unlocated male steriles. We first determine the chromosome arm location, then we conduct the appropriate allelism crosses. Leaf punches were taken from 24 male-sterile plants and from 24 male-fertile plants for DNA isolation. SSR markers were used to genotype these samples. Out of 72 randomly dispersed SSR markers, only one, *phi034*, showed linkage to the male sterility trait. This marker maps to bin 7.02 on chromosome 7, and segregates with *ms*-6036* as follows:

	Homozygous (A)	Heterozygous (AC)	Homozygous (C)	Failed Rxn's
Fertile	9	10	2	3
Sterile	0	6	16	2

Although only one marker showed linkage, we proceeded to test-cross *ms*-6036* with the recessive male-sterile mutants that are located on chromosome 7 (*ms7*, *ms22*, *ms34*), as well as with an unmapped recessive male-sterile mutant (*ms27*). The resultant progeny were grown in our 2000 Johnston, Iowa, nursery. At least 40 plants were observed for each of the test-crosses. The reciprocal test-crosses with *ms27*, *ms7* and *ms34* produced all fertile progeny, indicating *ms*-6036* was not allelic to them. The reciprocal test-crosses of *ms*-6036* with *ms22* gave the following results, indicating allelism:

Female	Male	Progeny		X2
ms-6036* Heterozygote	*ms22* Het	34 Fertiles	8 Steriles	0.79 (3:1)
ms22 Homozygote	*ms*-6036* Het	26 Fertiles	22 Steriles	0.33 (1:1)

Our new designation for this *Ms22* male-sterile allele is *ms22-6036*.

A set of microsatellite markers of general utility in maize

--Register, JC, III*, Sullivan, HR, Yun, Y, Cook, D, Vaske, DA
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Over the past several years microsatellites (often referred to as simple sequence repeats [SSRs] or short tandem repeats [STRs]) have become the most commonly used class of molecular marker for high-throughput genotyping of many higher eukaryotes including maize. During this time we (and others at Pioneer Hi-Bred Int'l Inc.) have, in collaboration with public researchers, made well over 100 SSR markers available for public use (Chin ECL, Senior ML, Shu H, Smith JSC [1996] Genome 39, 866-873; Senior ML, Chin ECL, Lee M, Smith JSC, Stuber CW [1996] Crop Sci 36, 1676-1683; Smith JSC, Chin ECL, Shu H, Smith OS, Wall SJ, Senior ML, Mitchell SE, Kresovich S, Ziegle J [1997] Theor Appl Genet 95, 163-173; also see Maize Genome Database - http://www.agron.missouri.edu). As is always the case for this kind of resource, broad application of these markers has demonstrated that, for various reasons, some are more useful (*i.e.* robust, informative, easily scorable, etc.) than are others. We report here on the subset of those markers that we have found to be most useful for our applications.

All PCR primers were designed to work under a single set of conditions in 10 µl reactions. Genomic DNA (10 ng) was amplified in 1.5 mM $MgCl_2$, 50 mM KCl, 10 mM Tris-Cl (pH 8.3) using 0.3U AmpliTaq Gold DNA polymerase (PE Corporation), oligonucleotide primer pairs at 0.17 µM and 0.2 mM dNTPs. This mixture

MARKER	CHROM	DISTANCE	BIN	REPEAT	PRIMER SEQUENCE (F / R)	MIN/MAX ALLELE*	PIC	NEARBY LOCI**
phi109275	1	0	1.00	AGCT	6FAMCGGTTCATGCTAGCTCTGC	122 / 140	0.77	*umc274, umc275*
					GTTGTGGCTGTGGTGGTG			
phi056	1	9	1.01	CCG	NEDACTTGCTTGCCTGCCGTTAC	239 / 259	0.67	*rgpc654, bnlg149*
					CGCACACCACTTCCCAGAA			
phi427913	1	26.71	1.01	ACG	NEDCAAAAGCTAGTCGGGGTCA	123 / 131	0.23	*bnlg1112, bnlg1458*
					ATTGTTCGATGACACACTACGC			
phi339017	1	72	1.01	AGG	HEXACTGCTGTTGGGGTAGGG	147 / 157	0.34	*csu745d, bnlg2180*
					GCAGCTTGAGCAGGAAGC			
phi002	1	173.9	1.08	AACG	HEXCATGCAATCAATAACGATGGCGAGT	71 / 80	0.51	*csu580a, bnl17.06*
					TTAGCGTAACCCTTCTCCAGTCAGC			
phi423298	1	174	1.08	CCG	NEDGGGCTGCTACTTTGACAAGGAC	128 / 135	0.43	*bnl17.06, umc83a*
					CCTCCATCATCCGCTGGTA			
phi323065	1	179	1.08	AGC	HEXGATCGATCGACGACCAGC	327 / 334	0.53	*csu531, cdo680a*
					CTTCTGCGTGGGCAAAGA			
phi335539	1	181.37	1.08	CCG	HEXGAGTCCGCTGAAATTTTGGT	90 / 93	0.17	*csu1174, csu745e*
					TAGAAGCCGCCGTGCCTAT			
phi011	1	209	1.09	AGC	HEXTGTTGCTCGGTCACCATACC	212 / 232	0.44	*npi282b, uat4a*
					GCACACACACAGGACGACAGT			
phi308707	1	220	1.09	AGC	HEXGCAACAAGATCCAGCCGAT	118 / 125	0.39	*umc161a, csu63a*
					GTCGCCCTCATATGACCTTC			
phi265454	1	224.63	1.10	AGG	6FAMCAAGCACCTCAACCTCTTCG	220 / 238	0.61	*npi238, csu868*
					TCCACGCTGCTCACCTTC			
phi064	1	231	1.11	ATCC	6FAMCCGAATTGAAATAGCTGCGAGAACCT	73 / 110	0.83	*csu33b, csu755*
					ACAATGAACGGTGGTTATCAACACGC			
phi227562	1	266	1.11	ACC	6FAMTGATAAAGCTCAGCCACAAGG	309 / 325	0.78	*csu1114, csu1193*
					ATCTCGGCTACGGCCAGA			
phi109642	2	0	2.00	ACGG	6FAMCTCTCTTTCCTTCCGACTTTCC	133 / 145	0.58	*csu1192, dup1383*
					GAGCGAGCGAGAGAGATCG			
phi402893	2	0	2.00	AGC	HEXGCCAAGCTCAGGGTCAAG	209 / 237	0.73	*csu1192, dup1383*
					CACGAGCGTTATTCGCTGT			
phi96100	2	6.04	2.00	ACCT	6FAMAGGAGGACCCCAACTCCTG	268 / 297	0.76	*rz569b, csu29b*
					TTGCACGAGCCATCGTAT			
phi083	2	86	2.04	AGCT	NEDCAAACATCAGCCAGAGACAAGGAC	125 / 139	0.76	*bnlg1831, umc184b*
					ATTCATCGACGCGTCACAGTCTACT			
phi328189	2	145	2.08	CCG	HEXACGCTCGAAGCAAATCCT	118 / 125	0.64	*csu1103, uaz241b*
					TCGCGCTTGGTAGACGTA			
phi251315	2	147.34	2.08	CCG	6FAMCCAGTCCAATGGAGAGGG	126 / 132	0.47	*umc88(P450), umc36b*
					GAGATTCCCCTGCAGGACT			
phi127	2	149.79	2.08	AGAC	NEDATATGCATTGCCTGGAACTGGAAGGA	110 / 129	0.7	*umc4a, bcd808c*
					AATTCAAACACGCCTCCCGAGTGT			
phi435417	2	161	2.08	ACC	NEDCTGACGCCACTGTTGCTTG	215 / 220	0.6	*uaz239b, bnl8.44b*
					AAAAGTAGCCAATCTGCCACG			
phi090	2	174	2.09	ATATC	6FAMCTACCTATCCAAGCGATGGGGA	139 / 150	0.44	*bnlg1520, csu304a*
					CGTGCAAATAATTCCCCGTGGGA			
phi427434	2	186.05	2.08	ACC	NEDCAACTGACGCTGATGGATG	123 / 139	0.7	*csu200a, csu109a*
					TTGCGGTGTTAAGCAATTCTCC			
phi101049	2	194	2.08	AGAT	6FAMCCGGGAACTTGTTCATCG	229 / 249	0.8	*csu665a, csu810a*
					CCACGTCCATGATCACACC			
phi453121	3	0	3.00	ACC	NEDACCTTGCCTGTCCTTCTTTCT	213 / 225	0.74	*bnl(tas4l), umc32a*
					CAAGCAAGACTTTTGATCAGCC			
phi104127	3	6.88	3.00	ACCG	6FAMCTTTGCTGCTGCTTCCTACG	156 / 166	0.58	*php20905, csu628*
					AACCAGTGACGTACACAAAGCA			
phi243966	3	46.8	3.02	AGC	6FAMCGACCGAAACGAATCAAAA	210 / 228	0.63	*bnlg1647, umc154*
					TACTAGGCTGACACGCACG			
phi374118	3	52	3.02	ACC	HEXTACCCGGACATGGTTGAGC	216 / 230	0.72	*umc92a, bnlg2136*
					TGAAGGGTGTCCTTCCGAT			
phi193225	3	55	3.02	AAC	6FAMGCTCTTGGCGTGCTTCTT	133 / 141	0.72	*umc92a, bnlg2136*
					GCGGGGAGGTGAAGAGCTA			
phi053	3	67.9	3.05	ATAC	6FAMCTGCCTCTCAGATTCAGAGATTGAC	168 / 195	0.71	*cdo459, cdo419a*
					AACCCAACGTACTCCGGCAG			
phi029	3	91	3.04	AG/AGCG***	NEDTTGTCTTTCTTCCTCCACAAGCAGCGAA	142 / 161	0.71	*bnlg1796, npi201a*
					ATTTCCAGTTGCCACCGACGAAGAACTT			
phi102228	3	97.05	3.04	AAGC	6FAMATTCCGACGCAATCAACA	122 / 131	0.67	*npi328b, bnlg1022*
					TTCATCTCCTCCAGGAGCCTT			
phi073	3	120	3.05	AGC	6FAMGTGCGAGAGGCTTGACCAA	176 / 195	0.65	*bnlg1108, umc226a*
					AAGGGTTGAGGGCGAGGAA			
phi072	4	12	4.00	AAAC	HEXACCGTGCATGATTAATTTCTCCAGCCTT	141 / 164	0.63	*bnlg1241, uaz60*
					GACAGCGCGCAAATGGATTGAACT			

phi295450	4	17.3	4.01	AGG/AAG***	6FAMCCTTTTCATGTTGCTTTCCC	187 / 199	0.77	*cyp5, zp11a*
					GCCCAATCCTTCCTTCCT			
phi213984	4	24.1	4.01	ACC	6FAMGTGACCTAAACTTGGCAGACCC	286 / 304	0.52	*umc277, uaz67*
					CAAGAGGTACCTGCATGGC			
phi308090	4	53.03	4.04	AGC	6FAMCAGTCTGCCACGAAGCAA	210 / 223	0.49	*csu855, bnlg292b*
					CTGTCGGTTTCGGTCTTCTT			
phi096	4		4.04	AGGTG	NEDTCCACCATTTGACACTTAGGCA	232 / 241	0.48	*fl2*
					GCGTAGGACGACCGTTGAA			
phi079	4	64	4.05	AGATG	6FAMTGGTGCTCGTTGCCAAATCTACGA	179 / 196	0.73	*uaz69b, bnlg1621a*
					GCAGTGGTGGTTTCGAACAGACAA			
phi438301	4	102	4.05	ACC	NEDCCTTCATTGTTCGGCTGG	210 / 215	0.68	*umc66a, rz446a*
					ACGAAGCTGATGATCTAACGCT			
phi093	4	141	4.08	AGCT	HEXAGTGCGTCAGCTTCATCGCCTACAAG	283 / 295	0.62	*npi449b, rz476a*
					AGGCCATGCATGCTTGCAACAATGGATACA			
phi076	4	178	4.11	AGCGGG	HEXTTCTTCCGCGGCTTCAATTTGACC	160 / 174	0.65	*csu315b*
					GCATCAGGACCCGCAGAGTC			
phi109188	5	0	5.00	AAAG	6FAMAAGCTCAGAAGCCGGAGC	162 / 170	0.61	*cdo484, csh13*
					GGTCATCAAGCTCTCTGATCG			
phi396160	5	73	5.02	AGGCG	NEDGGAGCCTCCTCAACCCTT	300 / 304	0.6	*ucr1b, umc1*
					GCTCGAGGTCCATGAGCA			
phi331888	5	88	5.02	AAG	HEXTTGCGCAAGTTTGTAGCTG	129 / 136	0.67	*php06012, bnlg653*
					ACTGAACCGCATGCCAAC			
phi330507	5	91.32	5.02	CCG	HEXGTAAAGTACGATGCGCCTCCC	134 / 143	0.21	*tum3, bnlg386*
					CGGGGTAGAGGAGAGTTGTG			
phi333597	5	93.55	5.02	AAG	HEXAGCTCGAGTACCTGCCGAG	213 / 259	0.71	*cent5, rz476b*
					TGCATCTCTGAGACCATCACC			
phi085	5	130	5.07	AACGC	HEXAGCAGAACGGCAAGGGCTACT	236 / 266	0.79	*bnlg1885, csu1164*
					TTTGGCACACCACGACGA			
phi423796	6	31	6.01	AGATG	NEDCACTACTCGATCTGAACCACCA	131 / 139	0.45	*csu1196, uaz23a*
					CGCTCTGTGAATTTGCTAGCTC			
phi389203	6	81.33	6.03	AGC	NEDGACGAAAAGGTGGCTCGT	301 / 310	0.23	*tug6, tda51*
					TGCAGTCCTAGATCAGTTCCAA			
phi452693	6	95	6.04	AGCC	NEDCAAGTGCTCCGAGATCTTCCA	124 / 142	0.61	*bcd221a, npi330*
					CGCGAACATATTCAGAAGTTTG			
phi445613	6	106.7	6.05	ACG	NEDTGACCACACACGAGCGAG	99 / 103	0.6	*npi608, php10016*
					GCTCACAATATGTGGCAGAGG			
phi070	6	114	6.07	AGCTG	NEDGCTGAGCGATCAGTTCATCCAG	76 / 90	0.76	*cdo89, bnl8.08c*
					CCATGGCAGGGTCTCTCAAG			
phi364545	6	125.4	6.07	AGC	HEXTAAGCAAAGCAAGGCAACC	127 / 138	0.64	*php20904, npi280*
					TCGCCTCACTCTCACACTCC			
phi299852	6	129	6.07	AGC	6FAMGATGTGGGTGCTACGAGCC	99 / 132	0.76	*uaz251d, umc266c*
					AGATCTCGGAGCTCGGCTA			
phi034	7	33	7.02	CCT	6FAMTAGCGACAGGATGGCCTCTTCT	118 / 145	0.57	*bnlg2160, uaz20b*
					GGGGAGCACGCCTTCGTTCT			
phi328175	7	102.12	7.04	AGG	HEXGGGAAGTGCTCCTTGCAG	101 / 130	0.71	*bnlg1161, bnl8.39*
					CGGTAGGTGAACGCGGTA			
phi069	7	120.3	7.05	GAC	NEDAGACACCGCCGTGGTCGTC	187 / 207	0.66	*bnl16.06, csu920b*
					AGTCCGGCTCCACCTCCTTC			
phi260485	7	134	7.05	AGC	6FAMTCATTCGACAGAGGCAAAAG	288 / 321	0.75	*csu814a, phi051*
					CATGGGAACTAACACTGGATGC			
phi116	7	145.82	7.06	ACTG/ACG***	6FAMGCATACGGCCATGGATGGGA	151 / 174	0.68	*php20728, umc35a*
					TCCCTGCCGGGACTCCTG			
phi420701	8	18	8.00	CCG	NEDGATGTTTCAAAACCACCCAGA	291 / 300	0.73	*rnp2, bnlg2235*
					ATGGCACGAATAGCAACAGG			
phi233376	8	56.32	8.03	CCG	6FAMCCGGCAGTCGATTACTCC	138 / 155	0.69	*cdo1160a, php20727*
					CGAGACCAAGAGAACCCTCA			
phi121	8	77.13	8.04	CCG	HEXAGGAAAATGGAGCCGGTGAACCA	96 / 102	0.59	*cdo1395e, csu254d*
					TTGGTCTGGACCAAGCACATACAC			
phi115	8	84.71	8.03	AT/ATAC***	HEXGCTCCGTGTTTCGCCTGAA	291 / 312	0.56	*rz206c, umc12a*
					ACCATCACCTGAATCCATCACA			
phi100175	8	116.8	8.04	AAGC	6FAMTATCTGACGAATCCCATTCCC	132 / 142	0.81	*bcd134c, umc117*
					GTACGTAACGGACGGACGG			
phi015	8	159	8.08	AAAC	6FAMGCAACGTACCGTACCTTTCCGA	80 / 106	0.7	*csu223a, rz444a*
					ACGCTGCATTCAATTACCGGGAAG			
phi033	9	41	9.01	AAG	NEDATCGAAATGCAGGCGATGGTTCTC	236 / 264	0.24	*bz1, csu665b*
					ATCGAGATGTTCTACGCCCTGAAGT			
phi032	9	90	9.04	AAAG	NEDCTCCAGCAAGTGATGCGTGAC	223 / 243	0.52	*uaz119c, cdo938b*
					GACACCCGGATCAATGATGGAAC			
phi448880	9	108.73	9.04	AAG	NEDCGATCCGGAGGAGTTCCTTA	178 / 188	0.72	*npi425d, bnlg1270*
					CCATGAACATGCCAATGC			
phi236654	9	124	9.05	CCG	6FAMGCTTGTTTCCCTTGGTCG	120 / 127	0.59	*std2a, csu870*
					GGACTCGCGAATAAGGTCTGG			

phi108411	9	126.15	9.05	AGCT	6FAMCGTCCCTTGGATTTCGAC	116 / 123	0.66	*bnlg1191, bnlg1156*
					CGTACGGGACCTGTCAACAA			
phi041	10	7	10.00	AGCC	NEDTTGGCTCCCAGCGCCGCAAA	196 / 218	0.67	*php20626, bnl3.04*
					GATCCAGAGCGATTTGACGGCA			
phi059	10	52	10.02	ACC	6FAMAAGCTAATTAAGGCCGGTCATCCC	146 / 146	0.39	*csu625, npi417b*
					TCCGTGTACTCGGCGGACTC			
phi96342	10	53.16	10.02	ATCC	6FAMGTAATCCCACGTCCTATCAGCC	240 / 250	0.59	*csu625, npi417b*
					TCCAACTTGAACGAACTCCTC			
phi050	10	63	10.03	AAGC	NEDTAACATGCCAGACACATACGGACAG	76 / 87	0.57	*umc155, bnlg1526*
					ATGGCTCTAGCGAAGCGTAGAG			
phi301654	10	85.8	10.04	CCG	6FAMGAATGCATGCTTTTCAAGGAC	132 / 138	0.31	*npi563, npi269b*
					CGCACAGAGAGCAGAACG			
phi062	10	96	10.04	ACG	NEDCCAACCCGCTAGGCTACTTCAA	159 / 165	0.63	*bcd386b, umc44a*
					ATGCCATGCGTTCGCTCTGTATC			
phi323152	10	119.2	10.07	CCG	HEXTCAGGGAGCTCACCTACTACGG	137 / 147	0.68	*bnlg1450, npi254b*
					CACGACTGCACCGATTAGC			
* Min and max allele values were obtained by rounding the former down and the latter up to the next integer								
** Nearby public loci/markers in Maizedb; not obtained directly from mapping data. NM = not mapped with sufficient resolution								
*** Compound repeat motifs								

was incubated at 95 C for 10 min (hot start), then amplified by 45 cycles of: denaturation, 95 C for 50 sec; annealing, 60 C for 50 sec; extension, 72 C for 85 sec, followed by a final 10 min 72 C incubation. A water bath thermocycler manufactured at Pioneer Hi-Bred Int'l Inc. was used. PCR products were prepared for analysis using ABI377 Automated DNA Sequencers (PE Corporation) by diluting 3 μl of each product to a total of 27 μl using a combination of other PCR products (multiplexing) and/or dH_2O. 1.5 μl of this mixture was then diluted to 5 μl with gel loading dye and analyzed using ABI hardware and software according to manufacturer's specifications.

The Table on the preceding pages lists approximately 80 markers and relevant associated information. For some markers, PCR primers have been redesigned since their initial publication for optimal performance under the conditions described above. The Table also notes the fluorescent dyes with which each marker is labeled. Minimum and maximum allele sizes were obtained by rounding down or up to the nearest basepair respectively. These sizes and PIC values (Smith JSC, Chin ECL, Shu H, Smith OS, Wall SJ, Senior ML, Mitchell SE, Kresovich S, Ziegle J [1997] Theor Appl Genet 95, 163-173) were obtained from an analysis of over 500 Pioneer Hi-Bred Int'l Inc. proprietary maize genotypes. Even though the PIC and allele range values were obtained working with proprietary Pioneer Hi-Bred Int'l Inc. germplasm, we do know that the values presented here are largely representative of North American dent germplasm in general.

The shredded leaf mutation, *shr1,* maps near the centromere on chromosome 5

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

An F2 line segregating for the shredded leaf phenotype (*shr1*) was grown for the purpose of mapping the mutation (Trimnell, MR et al. 2000. MNL 74:36). DNA was extracted from 20 wild-type and 24 mutant plants. These samples were subjected to SSR analysis using approximately 96 markers dispersed throughout the genome (Register, JC et al. 2001. MNL 75). From this initial screen, three markers on chromosome 5 showed some linkage with the mutation. Other SSR markers on chromosome 5 were selected for additional mapping. An estimate of linkage was based on a percent recombination value, calculated by dividing the number of wild-type class alleles by the total number of alleles represented in the mutant plant samples. Failed PCR reactions were not included in the total allele calculation. As shown in the table below, five markers on chromosome 5 showed linkage with the

Allele segregations in F2 mapping population

Probe	C5 bin	Wild-type plants	Mutant plants	% Recombination
phi330507	5.04	9AC; 3C	1AC; 23A	2.1
phi386223	5.04	2A; 13AB; 5B	22A; 2AB	4.2
phi196387	5.06	13AB; 5B	19A; 5AB	10.4
phi085	5.07	4A; 14AD	8AD; 15D	17.4
bnlg118	5.07	3D; 4DE; 9E	12D; 4DE; 2E	22.2

mutation., with the two markers in bin 5.04 (*phi330507* and *phi386223*) mapping nearest to the trait. Markers distal to bin 5.04 were not as tightly linked to *shr1*. No linkage was found for markers on the short arm of chromosome 5, suggesting that *shr1* maps near the centromere on the long arm of chromosome 5, most likely in bin 5.04.

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Relationship between chromosome breaks and knob heterochromatin in maize meristematic cells resulting from irradiated pollen

--Viccini, LF, de Carvalho, CR

Relationships between chromosome breaks and heterochromatin regions have been discussed in the literature. While some authors have reported the occurrence of random breaks, others suggest that chromosome breaks occur, mainly, in heterochromatic regions. With the objective of verifying the relationship between chromosomic breaks induced by gamma irradiation and heterochromatic regions, maize line L-869 (of the Federal University of Viçosa) pollen grains were exposed to 36 and 72 Gy of gamma radiation and soon after used for pollination. Seeds that originated from irradiated pollen were germinated in Petri dishes with a film of distilled water in the dark at 29 C. Root tips ranging from 0.5 to 1.0 cm in length were fixed in fresh cold methanol-acetic acid (3:1). Slides were prepared by the air drying technique with enzymatic maceration. The slides were submitted to C-banding technique to identify the heterochromatic regions. After

drying on a hot plate, the slides were stained with Giemsa solution. The percentage of abnormal anaphase cells carrying chromosomal bridges was evaluated. It was observed that the occurrence of bridges was not directly related to the presence of heterochromatic regions (Figure 1). In the case of lower radiation dosages, about 66% of the anaphases showed evidence of heterochromatin on the bridges, while for the higher dosage, only 42% of them presented heterochromatin (Figure 2). Fifty-two percent of the

Figure 1. Mitotic anaphases of a maize line L-869, which was derived from irradiated pollen, lacking evidence of heterochromatin on the bridge. Note the regions deeply stained (heterochromatin) on the chromosomes already separated (bar = 10 μm)

Figure 2. Mitotic anaphases of a maize line L-869, which was derived from irradiated pollen, with evidence of heterochromatin on the bridge (bar = 10 μm)

analysed anaphases presented bridges with strongly stained regions, indicating heterochromatic regions. Considering that maize C-banding technique identifies heterochromatic regions present in the knobs, it is possible that, for the anaphases without strongly stained regions on the bridges, the involved chromosomes do not have knobs. This fact hinders the establishment of a straight relationship between the occurrence of bridges and the presence of heterochromatin. These observations suggest that other mechanisms could be involved in the origin of chromosomal structural rearrangements and that the presence of the heterochromatin should not be considered as necessary for the occurrence of bridges.

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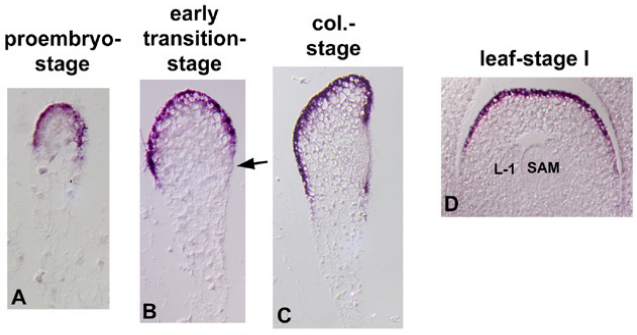
The expression pattern of *Lipid Transfer Protein 2 (LTP2)* gene indicates regionalisation in the proembryo and confirms the coleoptile to be in lineage with the scutellum

--Bommert P, Werr W

In a pattern formation process during early plant embryogenesis at least two patterns are superimposed. Firstly, an apical-basal axis is established, and, secondly a radial pattern defining the inside and the outside of the embryo is superimposed. In maize as in most angiosperms, the apical and basal poles of the embryo are fixed by the first asymmetric division of the zygote oriented perpendicular to the chalazal/micropylar axis of the embryo sac. The upper, chalazal daughter cell gives rise to the embryo proper while the lower, micropylar cell develops to the suspensor. In contrast to Arabidopsis or other dicots, successive divisions of the zygote do not follow a predictable pattern in maize, but result in an undifferentiated club-shaped cell mass, the proembryo. The first evidence of morphological differentiation becomes visible in the early-transition stage with the appearance of a distinct outer cell layer, the embryonic protoderm (Randolph, J. Agric. Res. 53:881-916, 1936). Slightly later in the midtransition stage the anlage of the shoot apical meristem (SAM) is histologically detectable as a group of small, densely packed cells at the adaxial surface of the embryo. The SAM itself has a tunica/corpus organization composed of at least two clonally distinct cell layers the outer L1 Layer and subtending L2 and L3 Layers, but it is still unclear whether maize organizes a distinct L2 layer. Here we report on the expression pattern of the *LTP2* gene (Sossountzov et al., Plant Cell 3:923-933, 1991) during the early stages of embryogenesis.

LTP2 transcripts can be detected in the proembryo-stage in all cells of the outer cell layer of the embryo proper, but are absent in the subtending suspensor (Fig. A). Both hemispheres of the proembryo therefore specify different peripheral cells, and the *LTP2* molecular marker allows us to distinguish between the suspensor and the embryo proper early in maize embryogenesis. The difference between the suspensor and the embryo proper observed in outer cell layers presumably reflects functional differ-



B: Arrow indicates adaxial face and position of the prospective meristem

ences, which may reside in nutrient uptake by the suspensor versus separation of the embryo proper from surrounding endosperm development.

A series of longitudinal sections through late proembryo/early transition-stage embryos showed that distribution of the *LTP2* transcript in the protoderm is not completely radial symmetrical. At the adaxial side of the embryo proper, the *LTP2* transcript is absent in a few protodermal cells above the suspensor (Fig. B). This position coincides with the prospective SAM anlage, which at this developmental stage is neither detectable histologically nor by analyzing *Knotted1 (Kn1)* expression pattern. The absence of *LTP2* transcripts in the embryonic protodermal region, which is specified to form the L1 layer of the prospective SAM, indicates that the embryo proper is regionalized before the meristem marker *Kn1* is activated.

During further stages of development *LTP2* expression remains confined to the outer cell layer of embryonic organs like the scutellum and the coleoptile (Fig. C). In the epidermis of true leaves, as in the L1 layer of the SAM, *LTP2* expression is generally absent (Fig. D) This observation provides molecular evidence that the coleoptile is in lineage with the scutellum but is not a derivative of the SAM. Absence of the *LTP2* transcript in the L1 layer of the SAM and leaves also shows that epidermal cell fate is different from the identity of cells comprising the outer cell layer in the maize proembryo. In the late proembryo/early transition stage lack of *LTP2* expression above the prospective SAM anlage indicates that epidermal cell fate may be realized prior to activation of the *Kn1* meristem marker. The *LTP2* radial asymmetry in the proembryo can be taken as first evidence that despite the irregular cell division pattern, positional information is imposed very early in maize embryogenesis.

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Relationships between *Zea mays* ssp. *mays* and *Zea mays* ssp. *parviglumis* by genomic in situ hybridization (GISH)

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Fluorescent in situ hybridization (FISH) is a tool which, when combined with genomic in situ hybridization (GISH), reveals homologies in DNA, mainly in regard to repetitive sequences. These techniques are also very useful in detecting amplifications and divergences of DNA sequences. Moreover, they can be used to discriminate genomes having sequences of allopolyploid origin as well as to detect chromosomes or chromosomal segments derived from introgression. This technique allows us to understand the cryptic polyploid nature of the genus Zea, and the genomic constitution of meiotic configurations in those hybrids where chromosomes from different parents have been distinguished using as a probe total genomic DNA or a repetitive sequence present in one of them (Poggio et al., Cytogenet. Cell Genet. 81:134, 1998; Poggio et al., Genome 42:993-1000, 1999; Poggio et al., Bol. Soc. Argent. Bot. 35:297-304, 2000; and Poggio et al., in press).

Maize and related wild species are of polyploid origin, but which species should be considered the ancestral ones is still unresolved. GISH studies conducted by our group and other research workers using DNA of co-generic species and even related genera as probes, failed to reveal genomic differences. In the present work, we have applied GISH with washing at very high stringency after the hybridization reaction and using unlabeled total genomic DNA as blocking agent in order to reveal cryptic genomic differences.

The species analysed here were *Zea mays* ssp. *parviglumis* (Balsas, cult. 6836, IFSC) and *Zea mays* ssp. *mays* (knobless line cultivated in IFSC). Chromosome preparations and GISH were carried out according to Poggio et al. (1999). The blocking procedure (Anamthawat-Jonsson et al., Theor. Appl. Genet. 79:721-728, 1990) was applied by adding unlabeled DNA from *Zea mays* ssp *mays* and labeled DNA from *Zea mays* ssp. *parviglumis* in a 10:1 proportion respectively, on chromosome preparations of *Zea mays* ssp. *parviglumis*. This procedure allowed us to discriminate three regions of differential hybridisation: unlabeled, labeled and highly labeled. The first region contains shared DNA sequences of high homology between both taxa and is located in all the telomeric regions of *Zea mays* ssp. *parviglumis*; the second region contains free unblocked DNA sequences that could hybridize with DNA from the same species. This region probably corresponds to repetitive DNA inherent to *Zea mays* ssp. *parviglumis*. The last chromosome region, with strong hybridization signals, corresponds to the heterochromatic knobs of *Zea mays* ssp. *parviglumis* which were not blocked by heterologous DNA from maize because the line used for blocking does not have "knob sequences". These "knob" hybridized regions were taken into account as positive controls of the whole blocking experiment. The experiment reported here demonstrates that there are divergent chromosome regions between these two taxa that are considered subspecies of *Zea mays* by Doebley and Iltis (Amer. J. Bot. 67:982-993, 1980) and Iltis and Doebley (Amer. J. Bot. 67:994-1004, 1980).

The meiotic analysis of the hybrid *Zea mays* ssp. *mays* x *Zea mays* ssp. *parviglumis* (2n=20) reveals that 10 bivalents (II) are observed in 80% of the analysed cells in Metaphase I, the remaining 20% showed 9 II + 1 I or 8 II + 2 I. Besides, the mean of closed bivalents was 7.2 with terminal chiasmata. These data suggest that *Zea mays* ssp. *mays* and *Zea mays* ssp. *parviglumis* have genomes homologous enough for normal pairing to occur.

It is interesting to point out that in situ hybridization used under conditions of high stringency and with blocking agents, can provide valuable information about the type and localization of repetitive sequences in *Zea mays* and related species, being an adequate complement to the data obtained by classical cytogenetic analysis.

Postharvest mycoflora associated with kernels of flint maize native Argentinian populations

--Astiz Gassó, MM, Aulicino, MB, Lori, G

The flint maize grains have been shown to be more resistant than the dent ones to either pre- or postharvest attack by fungi and insects. However, there might be flint genotypes with differential resistance to fungal colonization. The objectives of our study were: a- identify postharvest mycoflora associated with kernels of some flint grain native population; b- relate the fungal

occurrence on kernels with maize population passport and characterization data.

From 1998 to 1999, 15 early maturity and flint populations (belonging to INTA germplasm bank, Argentina) were planted in a completely random block design with four replications at the IFSC (Instituto Fitotécnico de Santa Catalina, Llavallol in Buenos Aires) experimental farm. Each plot consisted of 15 plants in a single row (3,5 m long), with 25 cm between plants and 80 cm between rows. Five corn ears randomly sampled from each row were harvested and their kernels were shelled and pooled. A subsample of 100 kernels per plot was taken to determine fungal contamination. Twenty-five kernels per Petri dish (9 cm diameter) were placed on filter paper watered with sterile distilled water. The Petri dishes were incubated at 24 C ± 2 C for 7 days under 12/12 h photoperiod and cold white and black fluorescent lamps (1). One hundred seeds per replication were evaluated by the blotter test, according to ISTA rules.

The fungi developed in those kernels were subcultured in PDA and then identified. The percentage of contaminated seeds by each genera of fungus in the different replicates was recorded. Data (arcsin transformed) were analyzed by ANOVA, through a mixed model of two factors in which genotypes were used as the fixed factor. Means were compared by LSD test at 0.05 probability level. Simple correlation between % of each fungus vs. passport data (origin, latitude, longitude, altitude) and characterization data (racial form, endosperm colour, heat units from planting to silking) were calculated. The coefficient of product-moment correlation, formulated by Pearson, was used. Furthermore, a "t" test for significance of this coefficient with n-2 degree of freedom was done (Sokal and Rohlf, 1995).

The external mycoflora identified included: 3 species of *Fusarium (F)* Genera of the Section *Liseola: F. moniliforme, F. proliferatum* and *F. subglutinans*; two species of *Aspergillus* Genera: *A. flavus* (Af), *A. niger* (An) and *Penicilium* spp. (P).

The maize populations didn't show dissimilar behaviours for the presence of Af, An and P contaminants. However, genotypes (populations) had a differential response to *Fusarium.* This could indicate some sort of coadaptation between host-pathogen related with the collection sites of accessions (longitudinal position) and with some characters (highly heritable) such as heat units from planting to silking and endosperm colour. Earlier maturity populations with white or yellow endosperm showed a higher level of *Fusarium*. Genotype-environment interaction was the most important source of variation for *A. flavus, A. niger* and *Penicilium* spp. This possibly prevented the differences among genotypes from showing. It would also indicate that the populations of fungi would change their behaviour according to the environment. Possibly, environmental factors related to grain storage were responsible for some changes, but they were not controlled during this experiment.

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Stability analysis for yield and expansion volume in popcorn hybrids

--Burak, R, Broccoli, AM

Popcorn culture is actually in expansion in Argentina, and native open-pollinated varieties have been replaced by simple hybrids introduced from the USA. Our work is focused on the study of adaptability for grain yield and popping expansion of these hybrids in a non-traditional region in the milk belt of Buenos Aires (Cuenca del Salado) at 34º 38'LS and 58º 48' Long. 14 popcorn hybrids of current commercialization (H1-H14) were evaluated conducting 10 trials in 5 locations during 1998 and 1999, using standard experimental units. The variables analyzed were yield, grain yield per experimental unit (kg) and popping expansion or expansion volume (exvol), expanded volume of a 100 popcorn grain randomized sample within each experimental unit. Analysis of variance was made in a randomized complete block design , with a simple factorial including 14 treatments x 3 replications x 10 environments under the model:

$$y_{ijk} = \mu + b(E)_{jk} + G_i + E_j + (G^*E)_{ij} + \varepsilon_{ijk}$$

Here y_{ijk} is the observation of the *k*th replication of the *i*th genotype of the *j*th environment, m is the population overall mean, G_i is the fixed effect of *i*th treatment, E_j is the randomized effect of *jth* environment, $(g^*a)_{ij}$ is the genotype x environment interaction effect, $b(E)_{jk}$ is the replications nested in environments effect and ε_{ijk} is the experimental error randomized variable.

Stability analysis was made using bilinear regression models (Verma et al., 1978, Silva et al., 1985, Cruz et al, 1989). Each genotype is described by three parameters: two regression coefficients (b_1 and b_2) and the variance of regression deviation $S^2_{di.}$ Coefficient b_1 indicates genotype response in unfavorable environments and $b_1 + b_2$ measures response in the favorable ones. Environmental indexes are the independent variables of this multiple regression method and the zero value is the intercept of each one. The advantage of using this method is the ability to evaluate genotypes also under unfavorable environmental conditions. The model is:

$$E(Y_{ij}) = B_0 + B_1 I_j + B_2 J_j$$

Expected observation of the *i*th genotype in the *j*th environment, B_0 is the mean for each genotype, B_1 is the unfavorable environments regression coefficient, $B_1 + B_2$ is the favorable environments regression coefficient for each genotype, I_j = the environmental index (Eberhart and Russell, 1966), $J_j = I_{j(+)} - \hat{I}_{j(+)}$ the environment index of favorable ones minus their average.

The following matricial equation represents Y_{ij} values:

$$X\beta + E = Y$$

The X matrix has three columns, the unity, the environmental effects, and thirdly, the favorable environmental effects minus its average. Unfavorable effects have zero value. β is the vector of the unknown regression coefficients and E is the vector of the experimental error for each genotype. Y is the vector of the observations. Applying the minimum square method we obtain the following system:

$$X'X\beta = X'Y$$

(X' is the trans X matrix and β the regression coefficients estimations vector)

Table 1 shows genetic x environment significant effect results; effects for genotypes and environments also were significant.

Table 1. Analysis of variance for (YIELD) and (EXVOL) .(**p<0.01, *p<0.05).

S V / G L Variables	Environments 9	Rep(Env.) 20	Treatments 13	Treat x Env 117	Error 260	VC(%)
(YIELD)	93.43**	0.631	0.822**	0.188**	0.097	12.34
(EXVOL)	22052**	1923.4	5707.4**	1461.6**	1154.2	9.09

Tables 2a and 2b show the environment average for each

hybrid in two conditions: unfavorable ($E_{(-)}$) and favorable ($E_{(+)}$). B_0 is the overall mean including both environment conditions. The slopes (B) feature responses for genotypes on each environment (B_1 y $B_1 + B_2$). R^2 is the determination coefficient, which measures fitness for the model and S_{di} is the regression device mean squares, measuring stability response of the hybrids. For each genotype, yield shows high R^2 values; expansion volume (exvol) shows high R^2 values except for H3, H9, H11 genotypes.

For yield, all genotype slopes are 1 despite the environment (Table 2a) However, for H1, H6 , H9, H10, H14, S_{di} was significant. The hybrids differ not in their responses but in their stability. For the mentioned hybrids, behavior is not predictable on the environment range of this experiment.

Table 2a. Stability parameters for (YIELD).

Test t student for B_1=1 y B_1+B_2 =1 .(*p<0.05). Test F.(*p<0.05).

HYBB	$E_{(-)}$	$E_{(+)}$	B_0	B_1	B_2	B_1+B_2	R^2	S_{di}
1	0.993	3.796	2.675	1.056	0.213	1.269	96.37	0.383*
2	1.006	3.757	2.657	1.035	-0.06	0.972	98.61	0.126
3	1.094	3.752	2.689	1.000	0.177	1.177	99.45	0.049
4	0.877	3.488	2.442	0.981	0.034	1.015	98.25	0.148
5	0.748	3.260	2.255	0.935	-0.275	0.660	97.67	0.166
6	0.981	3.491	2.487	0.947	0.021	0.968	94.51	0.450*
7	0.999	3.898	2.739	1.089	-0.664	1.023	99.16	0.084
8	0.732	3.583	2.442	1.066	-0.192	0.874	98.86	0.107
9	0.861	3.715	2.574	1.063	-0.117	0.945	97.58	0.233*
10	1.254	3.792	2.777	0.949	0.214	1.163	97.51	0.211*
11	0.901	3.506	2.464	0.979	0.175	1.154	98.74	0.11
12	0.850	3.200	2.260	0.885	0.078	0.963	98.95	0.073
13	0.893	3.659	2.553	1.040	-0.151	0.890	99.33	0.059
14	0.849	3.435	2.407	0.972	-0.048	0.924	97.34	0.218

Table 2b. Stability parameters for the variable (EXVOL).

Test t student for B_1=1 y B_1+B_2 =1 .(*p<0.05). Test F.(*p<0.05).

HYB	$E_{(-)}$	$E_{(+)}$	B_0	B_1	B_2	B_1+B_2	R^2	S_{di}
1	351.87	389.14	366.78	1.034	-0.482	0.552	68.02	917.4
2	379.76	427.11	398.70	1.162	-0.448	0.713	53.18	2198*
3	351.39	370.47	359.02	0.455*	-0.812	-0.357*	28.11	1013
4	325.11	386.80	349.79	1.397	-1.365	0.032	69.18	1517
5	362.61	405.17	379.63	1.021	0.042	1.062	58.18	1533
6	340.24	394.30	361.87	1.306	-0.018	1.288	57.27	2566*
7	347.59	394.94	366.53	1.261	-0.608	0.653	72.06	1122
8	352.17	395.50	369.50	1.036	0.051	1.087	72.63	830
9	388.16	397.56	391.92	0.221*	0.929	1.151	27.21	1229
10	372.86	425.49	393.91	1.354	1.101	2.455*	96.24	191
11	371.93	385.39	377.31	0.435*	0.263	0.697	24.94	1404
12	347.76	411.81	373.38	1.730*	0.710	2.440*	82.37	1476
13	361.87	390.29	373.24	0.651	0.201	0.852	45.98	1109
14	356.25	390.79	370.07	0.935-	0.435	1.370	66.25	1046

H10 and H7 had yield upper values in both environments, but H10 was unstable while H7 was stable and predictable in this evaluation (Fig 1). For exvol, genotype responses differ under unfavorable environments. For H3, H9 and H11 B1 <1 and for H2 B1>1. In favorable environments, for H3, B_1+B_2 < 1 while for H10 and H12 >1. Sdi was significant only for H2 and H6. Even when H2 showed the best popping expansion, H9 retained its capability in both environment situations, becoming better for this character (Fig. 2).

Table 3 shows means and the environment index for both variables. For yield, environments 1, 4, 5, 6, 3 and 2 were profitable, for exvol environments 7, 8, 1, 3 were. Instead of profitability of environment 1 for both characters, we found that a favorable environment for one is unfavorable for the other. This agrees with other classical studies describing a negative correlation between

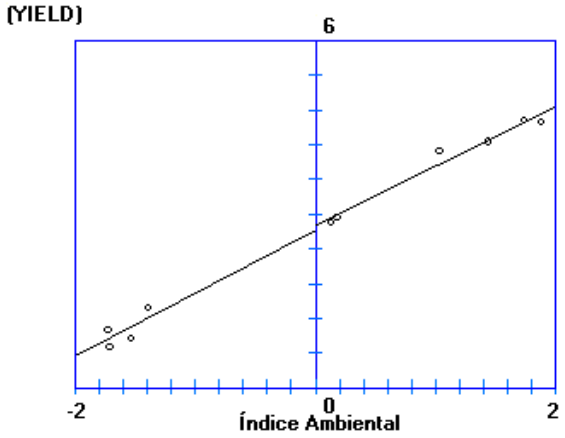

Figure 1. Genotype H7

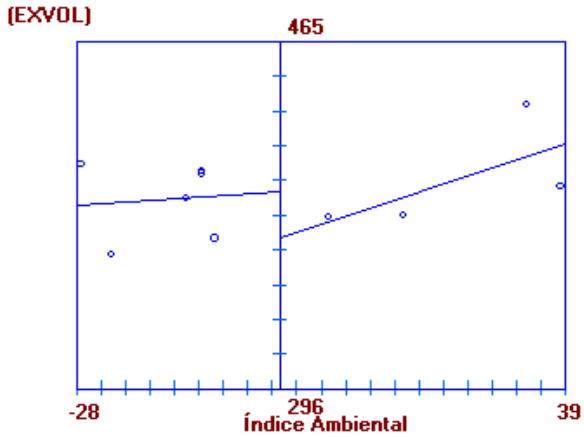

Figure 2. Genotype H9

Table 3. Means and environments. (+) favorable. (-) unfavorable.

Env	(YIELD)			(EXVOL)		
	Mean	I_j	$I_{j(+)}$	Mean	I_j	$I_{j(+)}$
1	4.41 (+)	1.88	0.81	390.4 (+)	16.71	-7.08
2	3.56 (+)	1.03	-0.032	364.5 (-)	-9.19	-
3	2.66 (+)	0.13	-0.94	380.2 (+)	6.50	-17.29
4	4.26 (+)	1.73	0.67	362.7 (-)	-10.99	-
5	3.97 (+)	1.44	0.37	360.5 (-)	-13.21	-
6	2.71 (+)	0.18	-0.89	362.8 (-)	-10.88	-
7	1.13 (-)	-1.41	-	412.0 (+)	38.31	14.51
8	0.79 (-)	-1.73	-	407.3 (+)	33.65	9.85
9	0.81 (-)	-1.72	-	346.1 (-)	-27.56	-
10	0.98 (-)	-1.54	-	350.4 (-)	-23.34	-

yield and expansion volume. These results contribute to aiding farmers in selecting better genotypes with yield stability, quality properties and adaptation for this no traditional zone.

Genetic and environmental correlations between yield components and popping expansion in popcorn hybrids

--Burak, R, Broccoli, AM

Six field trials under a three replication complete randomized block design were conducted; 14 simple popcorn hybrids were evaluated for: sowing date (early and late) and three plant densities (62.500, 74.000 and 85.000 plants per hectare), with stan-

dard experimental units. Triple factorial design was used for estimating sowing date, genotype and plant density effects, according with the following model:

$y_{ijqk} = m + B_{k(iq)} + G_i + D_j + F_q + (G*D)_{ij} + (G*F)_{iq} + (D*F)_{jq} + (G*D*A)_{ijq} + \varepsilon_{ijqk}$

where:

y_{ijqk} = *l*th treatment of *g*th plant density of the *q*th sowing date of the *k*th replication; μ = overall mean; G_i = randomized effect of genotype *i* th; PD_j = fixed effect of plant density *j*th; SD_q = fixed effect of sowing date *q*th ; $(G*F)_{ij}$ =.G X SD interaction effect; $(G*D)_{ij}$ =.G x PD interaction effect; $(PD*SD)_{ij}$ =.PD x SD interaction effect; $(G*PD*SD)_{ijq}$ = triple interaction; $Rk_{(jq)}$ = replications nested in PD and SD effect; ε_{ijqk} = experimental error randomized variable.

Genetic and environmental variances for each variable were estimated from expected mean square (Table 1) and covariances were calculated following the Kempthorne procedure.

$$MP_{xy} = 1/2 (MS_{x+y} - MS_x - MS_y)$$

where:

MP_{xy} = X e Y variables mean product; MS_x y MS_y = mean squares of X and Y variables; MS_{x+y} = mean squares of the sum between X and Y variables.

Table 1. Expected means squares for factorial design, considering simple hybrids a randomized sample of the commercially available ones.

S. V.	D. F.	M.S	Expected M.S
(R/PD)/SD	(r-1) f d	MS_1	$\sigma^2_E + g\sigma^2_r$
G	(g-1)	MS_2	$\sigma^2_E + r d f \sigma^2_G$
SD	(f-1)	MS_3	$\sigma^2_E + g\sigma^2_r + (f / f-1)\, r d \sigma^2_{GF} + r d g \phi_F$
PD	(d-1)	MS_4	$\sigma^2_E + g\sigma^2_r + (d/d-1)\, r f \sigma^2_{GD} + r f g \phi_D$
G*SD	(g-1) (f-1)	MS_5	$\sigma^2_E + (f / f-1)\, r d \sigma^2_{GF}$
G*PD	(g-1) (d-1)	MS_6	$\sigma^2_E + (d/d-1)\, r f \sigma^2_{GD}$
SD*PD	(f-1) (d-1)	MS_7	$\sigma^2_E + g\sigma^2_r + (f / f-1)\,(d/d-1)\, r \sigma^2_{GDF} + r g \phi_{FD}$
G*SD*PD	(g-1)(f-1)(d-1)	MS_8	$\sigma^2_E + (f / f-1)\,(d/d-1)\, r \sigma^2_{GDF}$
Error	(b-1)(g-1) d f	MS_9	σ^2_E

Variables analyzed were: Grain yield (kg/ experimental unit) (YIELD); Expansion volume (cc/gr) (EXVOL); Grain roundness index (GRI); Harvest index (HI); % of cob (COB); Kernel density not expanded (gr/cc) (KNED); Kernel density expanded (gr/cc) (KED).

Higher expansion volumes usually obtained from samples with medium to small kernels, rounder than the average was reported in classic papers, and indicates the roundness index RI (relation between thickness, width and length of the seed) is an adequate parameter to measure this phenotypic correlation.

(RI) = KTH / (KW + KL)

Harvest index was calculated as no. of ears/no. of plants by experimental unit. % of cob (COB), by the rate weight of the kernels/weight of the ears

Table 2 shows significant interaction for (G*PD*SD) and (G*SD) for the variables (YIELD) and (KED), therefore it is necessary to make the analysis within sowing date, for both variables. For the other variables, interactions were not significant and therefore the mean analysis was done for the factors genotype, sowing date and plant density. (EXVOL), (RI) and (COB) were affected by the three factors and (HI) by sowing date and genotype, while (KNE) was only affected by sowing date. Based upon this results, for this no traditional region under study the correct management of these three factors is priority for ensure the popcorn quality measure as expansion volume. For yield stability of the genotypes is a very important factor.

Table 2. Mean squares from the combining ANOVA for all the variables. (**p<0.01, *p<0.05).

S. V.	D. F.	YIELD	EXVOL	R I	H I	COB	KNED	KED
(r/PD)/SD	12	0.975	4.43	$7.4x10^{-4}$	0.096	3.52	$8x10^{-4}$	$1.6x10^{-5}$
G	13	0.782 **	16.02 **	$1.7x10^{-3}$ **	0.064 **	39.87 **	$1.3x10^{-3}$	$5.8x10^{-5}$ **
SD	1	0.699	49.16 **	$6.1x10^{-3}$ *	0.93 **	67.20 **	$8.3x10^{-3}$ **	$2.1x10^{-4}$ **
PD	2	59.18 **	19.12 *	$9.5x10^{-3}$ **	0.112	22.55 *	$2.2x10^{-3}$	$5.7x10^{-5}$
G*SD	13	0.295 **	8.18	$4.4x10^{-4}$	0.013	4.02	$6x10^{-4}$	$3.3x10^{-5}$ *
G*PD	26	0.158	5.96	$2.4x10^{-4}$	0.017	4.87	$9x10^{-4}$	$1.9x10^{-5}$
SD*PD	2	1.665	5.35	$7.6x10^{-4}$	0.22	12.83	$1.1x10^{-3}$	$1.9x10^{-5}$
G*SD*PD	26	0.277 **	6.97	$5.5x10^{-4}$	0.024	3.45	$7x10^{-4}$	$2.5x10^{-5}$ *
Error	156	0.128	4.57	$3.2x10^{-4}$	0.012	6.00	$9x10^{-4}$	$1.5x10^{-5}$
V.C. (%)		9.98	9.09	6.13	9.79	12.48	3.89	8.99

Table 3 shows the values of genetic and enviromental correlations between the seven variables under study. These will be useful for selection and development of specific genotypes within this region. Similar negative genetic and environmental correlations (r_G = -0.1876**; r_E = -0.1641**), with (YIELD) and (EXVOL) agree with many papers reporting this negative association. (YIELD) has positive correlations with (HI), r_G = 0.307**; r_E = 0.241**, in agreement with classic maize bibliography, and is relevant to indirect selection. Positive genetic correlation also was registered with (KNED), r_G = 0.415**. Negative correlations between (YIELD) and (COB) are obvious (r_G = - 0.452**; r_E = -0.164**) Genetic correlation (which influences kernel length) is higher than environmental, affected by deficient grain filling Strong association exists between (COB) and (RI), r_G = 0.928** and r_E = 0.169**, being the genetic component more important than the environmental because the filling of grain influences kernel shape. (EXVOL), a measure of popcorn quality, has strong genetic correlation also with kernel shape (RI), r_G = 0.613** and with (KNED), r_G = 0.691**, without environmental influence. Opposite relationships were verified between (EXVOL) y (KNED), r_G =

Table 3. Genetic and environmental correlations (**p<0.01, *p<0.05).

Genetic correlations							
-	YIELD	EXVOL	R I	H I	COB	KNED	KED
YIELD	-	** -0.1876	** -0.359	** 0.307	** -0.452	** 0.415	* -0.128
EXVOL	** -0,1641	-	** 0.613	0.048	0.095	** 0.691	** -0.981
RI	-0.0102	0.045	-	** -0.246	** 0.928	** -0.519	** -0.592
HI	** 0.241	-0.104	0.064	-	** -0.411	-0.118	-0.082
COB	** -0.164	-0.055	** 0.169	0.078	-	** -0.226	-0.111
KNED	0.104	-0.111	0.105	0.007	-0.028	-	** -0.712
KED	** 0.152	** -0.921	-0.051	0.102	0.054	** 0.187	-
Environmental correlations							

-0.981** ; r_E = -0.921**, because both variables (DECA Y DCEX) were inverse. The same criteria is applicable for the correlations between (KNED) and (RI) with (KED) r_G = -0.712** and r_G = -0.592**, where even the environmental correlation between (KNED) and (KED) is positive r_E = 0.187**.

Prolificacy influences kernel shape, based on the negative correlation between (HI) and (RI)), r_G = -0.246**. COB proportion influences (KNED) with a negative genetic correlation r_G = -0.226**. Kernel shape is modified by (COB) and affects the kernel density measurement procedure, where smaller grains have more density than the bigger ones; there is a high negative genetic correlation between (KNED) and (RI) r_G = -0.519**.

These results indicate that kernel shape is an important trait associated with quality. Genetic correlations are higher than environmental, therefore this would be a relevant trait for a popcorn expansion volume breeding program. Breeding strategy for simultaneous quality (popping) and yield improvement could be grounded in selection for the component (HI), strongly associated with yield but without negatively influencing popping expansion.

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A modified set of *Rp* differential lines

--Hulbert, SH, Webb, CA, Smith, SM

Rp genes confer resistance to *Puccinia sorghi*, the causal agent of maize common rust. Individual *Rp* genes can be differentiated by their map position and the combinations of rust biotypes that they confer resistance to. Different *Rp* genes are more or less effective in controlling common rust in a given area or growing season, depending on the rust biotypes that are prevalent. The effectiveness of *Rp* genes is monitored by growing lines carrying the different *Rp* genes (*Rp* differentials) in various locations every season (e.g. Pataky and Tracy, Plant Dis. 83:1177, 1999).

Most of the known *Rp* genes map to the *Rp1 complex* (Hulbert, Ann. Rev. Phytopathol. 35:293-310, 1997) near the end of the short arm of chromosome 10. Different maize lines carry different numbers of *rp1* genes in their *rp1* haplotypes (generally between 4 and 20) but most do not confer resistance to any known rust biotypes. For example, the *Rp1-D* haplotype carries the *Rp1-D* gene and eight others with no detectable phenotypes (Collins et al., Plant Cell 11:1365-1376, 1999). Genetic recombination experiments have generated recombinant haplotypes with two or more *Rp1* genes with characterized resistances. Some of these recombinant haplotypes confer resistance to a very broad spectrum of rust biotypes and have been incorporated into breeding programs (e.g. Hulbert and Drake, Hortsci. 35:145-146, 2000). The *Rp5* and *RpG* loci map approximately two map units distal to the *Rp1* locus. Recombinants with *Rp5* and/or *RpG* combined with one or more *Rp1* genes have also been constructed and allow multiple *Rp* genes to be manipulated as a single locus in breeding programs.

Resistance conferred by most *Rp* genes is dominant or incompletely dominant. *Rp8* is unique in that only *Rp8-A*/*Rp8-B* heterozygotes confer resistance (Delaney et al., MPMI 11:242-245, 1998). Most maize lines carry the *Rp8-B* allele and some carry *Rp8-C*, which confers no known resistance in homozygotes or heterozygotes. To determine if *Rp8* provides effective resistance against a specific rust population, an F1 hybrid between H95 and the *Rp8-A* line can be examined.

An extensive *Rp* differential series in the R168 genetic background was developed by Art Hooker and coworkers in the 1960s. A number of problems exist with this series in its current state (Hulbert et al., Plant Dis. 75:1130-1133, 1991). Due to their propagation for many years without routine testing with a set of characterized rust biotypes, different investigators stocks are missing the resistance genes they are thought to carry, or carry the wrong gene. The series is also redundant in the genes they carry. The *Rp1-C*, *Rp1-L* and *Rp1-N* lines all carry the same *Rp1* haplotype as determined by gel blot analysis with an *rp1* probe and by phenotype. The same is true for the *Rp1-E*, *Rp1-I* and *Rp1-K* lines, and the *Rp1-A* and *Rp1-F* lines. The *Rp1-H* and *Rp1-J* lines do not carry identical *rp1* haplotypes but probably carry a functionally identical gene, since they confer resistance to the same rust biotypes. Six lines carrying *Rp3* genes (designated *Rp3-A* to *Rp3-F*), originally identified from different sources (Wilkinson and Hooker, Phytopathology 58:605-608, 1968) also appear identical when tested with many rust isolates indicating they also carry a functionally identical gene. Some stocks of the *Rp3-C* line are resistant to a broader spectrum of rust isolates than the other *Rp3* lines but we have found these stocks to be contaminated with an *Rp1* gene. Another problem with the current series is that the R168 background makes the lines difficult to propagate in many environments.

We have recently constructed a new differential series in the H95 genetic background (Table 1). The H95 inbred line is susceptible to all known rust biotypes. The H95 *Rp* series was constructed by crossing lines carrying the resistance genes (often the R168 *Rp* lines) to the H95 line, and backcrossing progeny carrying the *Rp* genes to H95. Most lines have four or more backcrosses to H95 in their pedigrees, but some lines do not; therefore

Table 1. *Rp* differential lines in the H95 background.

Rp Line	*Rp* genes present	Chromosome
Rp1-A	*Rp1-A*	10
Rp1-B	*Rp1-B*	10
Rp1-C	*Rp1-C*	10
Rp1-D	*Rp1-D*	10
Rp1-J	*Rp1-J*	10
Rp1-K	*Rp1-K*	10
Rp1-M	*Rp1-M*	10
Rp1-Kr1	*Rp1-Kr1*	10
Rp1-Kr3	*Rp1-Kr3*	10
Rp1-Kr4	*Rp1-Kr4*	10
Rp1-Kr1J92	*Rp1-Kr1J92*	10
Rp1-Kr1J6	*Rp1-Kr1J6*	10
RpG	*RpG*	10
Rp5	*Rp5*	10
Rp1-DJ4	*Rp1-D, Rp1-J*	10
Rp1-JC13a	*Rp1-J, Rp1-C*	10
Rp1-FJ69	*Rp1-F, Rp1-J*	10
Rp1-FJC1	*Rp1-F, Rp1-J, Rp1-C*	10
Rp-GI5c	*RpG, Rp1-I*	10
Rp-GFJ	*RpG, Rp1-F, Rp1-J*	10
Rp-GDJ1	*RpG, Rp1-D, Rp1-J*	10
Rp-5D	*Rp5, Rp1-D*	10
Rp-G5	*RpG, Rp5*	10
Rp-G5JCa	*RpG, Rp5, Rp1-J, Rp1-C*	10
Rp3-A	*Rp3*	3
Rp4-A	*Rp4-A*	4
Rp4-B	*Rp4-B*	4
Rp7	*Rp7*	?
Rp8-A	*Rp8-A*	6
H95	*rp1, rp3, rp4, rp5, rp7, Rp8-B*	

they should not be considered to be nearly-isogenic. After back crossing, lines carrying the *Rp* genes were self-fertilized and homozygous lines were selected by progeny testing with appropriate rust biotypes. The H95 series does not include each of the 14 original *Rp1* genes (*Rp1-A* to *Rp1-N*), but includes a representative line for each different resistance specificity. For example, it does not include *Rp1-F* because this has the same *rp1* haplotype and confers resistance to the same rust biotypes as the *Rp1-A* line. Similarly, the series includes only one of the six *Rp3* genes because these are indistinguishable with our collection of rust biotypes. The series includes novel *Rp1* genes and haplotypes that have been generated by recombination or spontaneous mutation and confer resistance to novel combinations of rust biotypes. Some of these carry different combinations of *Rp1*-area genes while others are thought to represent recombinant genes (Richter et al., Genetics 141:373-381, 1995). In cases where several recombinant *rp1* genes or haplotypes were isolated that appeared phenotypically identical after challenging with multiple rust isolates, only one was included in the H95 series. The lines were designated for the specific haplotype they carry. For example, several different recombinant *Rp1* haplotypes have been identified that carry both *Rp1-J* and *Rp1-F*, but we prefer to distribute only the *Rp1-JF69* haplotype to prevent future confusion if phenotypic differences between these haplotypes are revealed by challenge with rust biotypes.

The new differential series does not include a line with the *Rp6* gene. This is because we have not found a rust isolate that can be used to detect this gene. Those isolates used by Wilkinson and Hooker (Phytopathology 58:605-608, 1968) to identify the gene are no longer viable. It is possible the *Rp6*-R168 line may no longer carry the *Rp6* gene, although we have tested seed samples from several different sources and all appear susceptible to our current collection of rust isolates. It is also possible that rust isolates carrying the avirulence gene corresponding to *Rp6* have become very rare in North America.

A well-characterized differential series will be useful for determining the effectiveness of the *Rp* genes or gene combinations in different areas and for monitoring changes in *P. sorghi* populations. It will also be useful in characterizing specific rust biotypes that can then be used to estimate which *Rp* genes are carried in various maize lines and breeding material. The lines may be obtained from the Maize Genetics Cooperation Stock Center or by contacting the authors.

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Fine structure mapping of *wsm2* in maize

--Webb, CA, Jones, MW, Hulbert, SH, Louie, R

Wheat streak mosaic virus (WSMV) is a major pathogen of wheat. Unfortunately, commercial wheat cultivars with high levels of resistance are lacking. Attempts to incorporate high levels of WSMV resistance from *Agropyron* spp. sources via traditional breeding methods have proved frustrating and resulting lines are seldom free of undesirable agronomic or bread-making-quality defects (Seifers, DL et al., Plant Dis. 79:1104-1106, 1995). Maize can also play host to this serious ryemovirus. Infection commences when WSMV is transmitted from maturing wheat to adjacent late-planted corn by the wheat curl mite, *Eriophyes tulipae*. Systemic symptoms begin as small chlorotic rings, spots, or streaks on leaves. As the leaf matures, longitudinal streaks, delimited by large veins in the leaf, coalesce to form mosaics and mottled patterns that are quite diagnostic (Louie, R. Pages 49-55 in: *Compendium of corn diseases. Third edition*, APS Press, 1999).

Unlike wheat, many maize inbred lines show significant levels of resistance to WSMV. There are three known genes in maize for resistance to WSMV located on three different chromosomes (McMullen, MD et al., Mol. Plant-Microbe Interact. 7:708-712, 1994). The *wsm1* gene was found to map to chromosome 6S between the maize restriction fragment length polymorphism (RFLP) loci *umc85* and *npi235*, near the nuclear organizer region (NOR). Another viral resistance gene, *mdm1*, conferring resistance to maize dwarf mosaic virus (MDMV) was closely linked on chromosome 6. The long arm of maize chromosome 10 harbored the *wsm3* locus. Mapping experiments placed *wsm3* between markers *umc163* and *umc44*. *Wsm2* was positioned on the maize genetic map near the centromere of chromosome 3 between *umc102* and *umc18*. This map position is near the *rp3* locus, a dominant gene for resistance to *Puccinia sorghi*, the causal agent of maize common rust. Genes conferring resistance to maize mosaic virus (MMV) and sugarcane mosaic virus (SCMV) and QTLs for resistance to other pests also map to this general area (McMullen and Simcox, Mol. Plant-Microbe Interact. 8:811-815, 1995; Ming et al., Theor. Appl. Genet. 95:271-275, 1997; Xu et al., Mol. Gen. Genet. 261:574-581,1999)

A recent attempt to identify candidate sequences for resistance genes identified the *PIC13* probe which hybridizes to a family of resistance gene-like sequences at the *Rp3* locus (Collins et al., Mol. Plant-Microbe Interact. 11:968-978, 1998). Recently we examined the relative position of the *rp3* and *wsm2* loci to determine if the PIC13 gene family might also include the *Wsm2* gene. A line carrying the *Rp3-A* allele in an H95 genetic background (*Rp3-A*/*Rp3-A*, *Wsm2*/*Wsm2*), resistant to the rust (*Puccinia sorghi*) biotype IN1 and the Wooster WSMV strain was developed. This line was crossed to the rust and WSMV susceptible inbred OH28 (*rp3*/*rp3*, *wms2*/*wsm2*). The F1 was backcrossed to the susceptible OH28 parent and BC1 progenies self-fertilized. Individual seedlings of the resulting BC1F1 families were scored in the greenhouse after inoculation with talc-diluted rust spores and rub inoculation with the Wooster WSMV strain (Louie, R, Phytopathology 76:769-773, 1986). Plants with resistance to WSMV are symptomless. However, a 'virus resistant' recombinant class would be the most likely class in which escapes could occur and would be the most difficult to score. To reduce the number of escapes, a minimum of three independent virus inoculations were made, each spaced 2-3 days apart, on the two/three leaf-stage seedlings. Furthermore, efforts were made to maintain a high virus titer in our inoculum and to introduce an equal amount of inoculum load to each seedling.

Resistance or susceptibility to rust infection was very definitive and was observed as either hypersensitive flecking or sporulation, respectively. We observed no latent symptoms. One application of fresh rust urediniospores was made to the seedling

leaves, typically after the second virus inoculation. The scoring of rust and WSMV symptoms commenced seven days post-inoculation. Recombinants were identified as being either rust resistant/virus susceptible (RRVS) or rust susceptible/virus resistant (RSVR). Table 1 summarizes these scoring data. The recombinant heterozygous seedlings were transplanted from flats to five-gallon pots and then self-fertilized. Self-fertilized families from most of the putative recombinants were progeny tested. Progeny testing indicated that all but three individuals assigned to the RRVS class had been scored correctly. However, individuals in the RSVR class were more often mis-scored. Even after progeny testing, a disproportional number of what appeared to be RSVR-recombinant types resulted. Relatively equal proportions of the two recombinant classes are expected from such an experiment. There are two explanations that could account for these observations. First, there remains the possibility that poorly challenged plants or latent viral symptoms led to mis-classification of virus resistant plants even during progeny testing. Alternatively, it is possible that there is a second, unidentified gene segregating in this population. The presence of a second gene may make a *wsm2*/*wsm2* plant appear to be resistant to WSMV, and lead to the inflated numbers we observed in the virus resistant class.

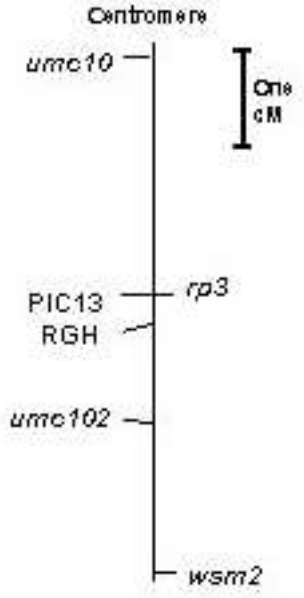
Table 1. *wsm2* mapping population: greenhouse data

Non-recombinant phenotypes	Originally identified
RSVS	403
RRVR	1,348
Recombinant phenotypes	
RRVS	29
RSVR	69
Population total	**1,849**

Because we were much more confident in accurately scoring them with few escapes or mis-scores, we chose to use the frequency of the RRVS-class seedlings to calculate map distance. This gave an estimate of roughly 3 cM between the *rp3* and *wsm2* loci.

The recombinant individuals were also used to order DNA markers in the *rp3-wsm2* interval. DNAs were analyzed from 29 progeny-tested, homozygous individuals and 20 other recombinants that were not homozygous. The *PIC13* probe detected a single polymorphic *Hpa*II restriction fragment and two polymorphic *EcoR1* restriction fragments. All three polymorphisms cosegregated perfectly with each other and with *rp3*. This indicates that at least most of the *PIC13* family members cluster tightly to the *rp3* locus and that it is unlikely that any members of this family account for the *Wsm2* gene. A second resistance gene analog clone, designated *RGH*, was obtained from M. Chen and J. Bennetzen. *RGH* was placed between *PIC13* and *wsm2* on this population, more tightly linked to *PIC13* than to *wsm2*. The core markers *umc10* and *umc102* were also mapped with this population and their positions are in agreement with the UMC 1988 molecular marker map of maize chromosome 3 (Davis, G et al., MNL 72:118-128, 1998). Figure 1 shows the position of molecular markers for this chromosomal region in relation to *rp3* and *wsm2*. The *Mv1* gene for resistance to MMV was placed 4 cM below *umc102* (Ming et al., Theor. Appl. Genet. 95:271-275, 1997) and may be close to the *Wsm2* locus. The *Scm2* gene, conferring resistance to SCMV, was mapped approximately 4 cM above

Figure 1: Chromosome 3 markers relative to *rp3* and *wsm2*



umc102 (Xu et al., Mol. Gen. Genet. 261:574-581,1999), and may be close to *Rp3*. The *PIC13* and *RGH* probes should be mapped with respect to *Scm2* to scrutinize these resistance gene-like sequences as candidates for this gene.

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The plastid chromosome of maize (*Zea mays*): Update of the complete sequence and transcript editing sites

--Tillich, M, Schmitz-Linneweber, C, Herrmann, RG, Maier, RM

The nucleotide sequence of the plastid chromosome from maize as well as the number and positions of transcript editing sites (Maier et al., J. Mol. Biol. 251:614-628, 1995) has been updated.

An insertion of three adenosine residues at position 116 of the *psa*A coding region (position 43,488 of the complete plastid chromosome sequence) which has been found not to be conserved in homologous sequences of other plant species turned out to be incorrect. The revised maize plastid chromosome sequence now consists of 140,384 base-pairs. It contains a pair of inverted repeat regions (IRA and IRB) with 22,748 base pairs each, which are separated by a small and a large single copy region (SSC and LSC) of 12,536 and 82,352 base-pairs respectively (Figure 1). With the recent identification of conserved reading frames as functional genes, the gene content of the maize plastid genome in total is 108, with 74 polypeptide-encoding genes, 30 tRNA genes and four rRNA genes (Table 1).

In addition to the 25 editing positions identified in 13 different plastid-encoded transcripts (Maier et al., see above) three new editing sites have been determined. In contrast to the C-to-U editing of *ycf*14 (*mat*K)-mRNA (position 1957 of the maize plastid chromosome) which restores a highly conserved amino acid residue already found at the gene level in the liverwort *Marchantia*

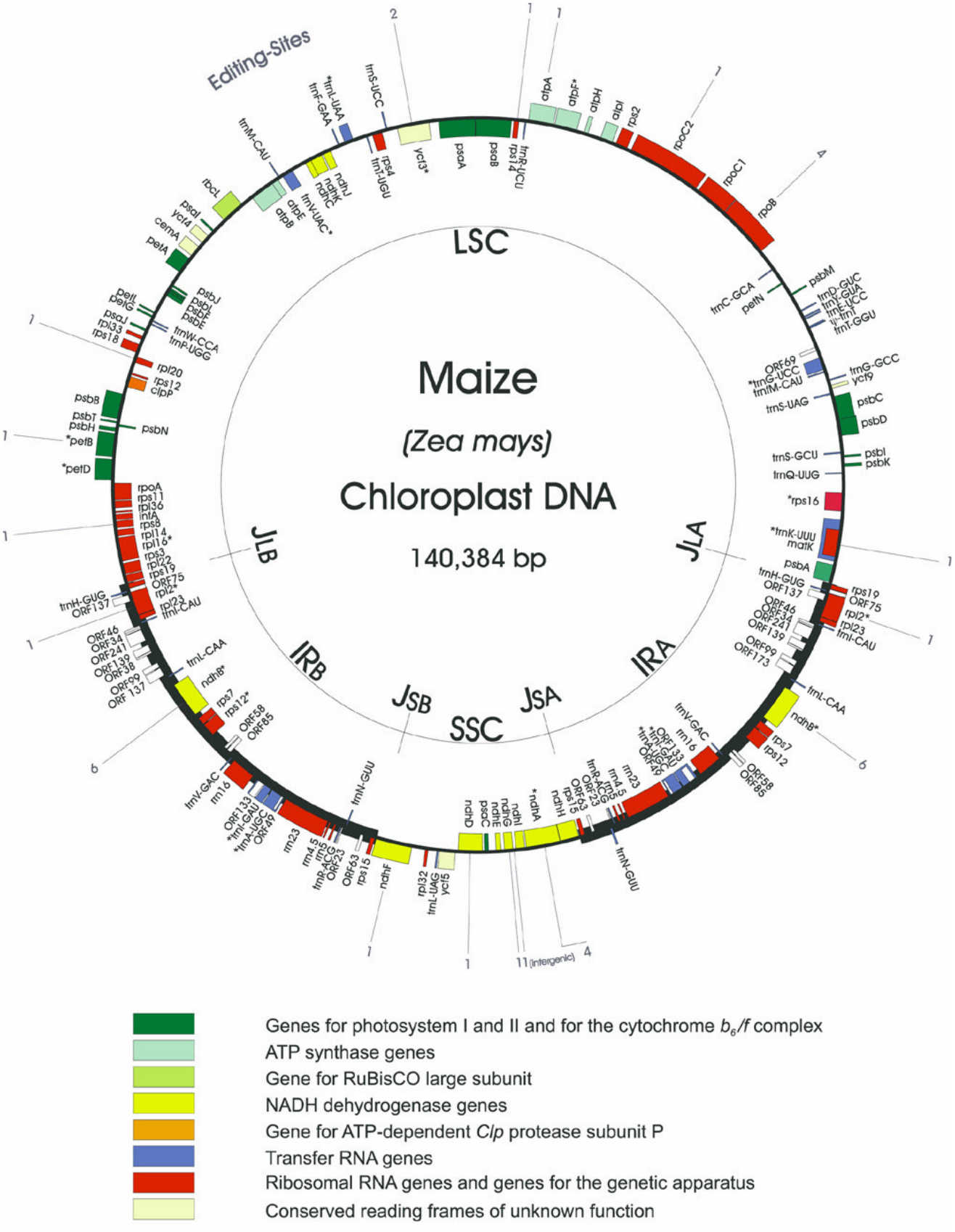

Figure 1. Gene organization of the *Zea mays* plastid chromosome. The inverted repeat regions IRA and IRB, respectively, divide the rest of the circular chromosome into large (LSC) and small (SSC) single copy regions. Genes drawn outside the circle are transcribed clockwise. Intron-containing genes are marked by asterisks. The numbers around the circle indicate the numbers of editing sites observed in the respective genes.

Table 1. Classification of the encoded genes within the plastid DNA of *Zea mays*

RNA genes

Ribosomal RNA genes

*rrn*23[#], *rrn*16[#], *rrn*5[#], *rrn*4.5[#]

Transfer RNA genes

*trn*A(UGC)*[#], *trn*C(GCA), *trn*D(GUC), *trn*E(UUC), *trn*F(GAA), *trn*G(GCC), *trn*G(UCC)*, *trn*H(GUG), *trn*I(CAU)[#], *trn*I(GAU)*[#], *trn*K(UUU)*, *trn*L(CAA)[#], *trn*L(UAA)*, *trn*L(UAG), *trn*fM(CAU), *trn*M(CAU), *trn*N(GUU)[#], *trn*P(UGG), *trn*Q(UUG), *trn*R(ACG)[#], *trn*R(UCU), *trn*S(GCU), *trn*S(GGA), *trn*S(UGA), *trn*T(GGU), *trn*T(UGU), *trn*V(GAC)[#], *trn*V(UAC), *trn*W(CCA), *trn*Y(GUA)

Polypeptide genes

Ribosomal protein genes

*rps*2, *rps*3, *rps*4, *rps*7[#], *rps*8, *rps*11, *rps*12[§†], *rps*14, *rps*15, *rps*16*, *rps*18, *rps*19

*rpl*2[#], *rpl*14, *rpl*16*, *rpl*20, *rpl*22, *rpl*32, *rpl*33, *rpl*36

Transcription/ translation apparatus genes

*rpo*A, *rpo*B, *rpo*C1, *rpo*C2, *inf*A

Photosynthetic apparatus genes

*rbc*L

*psa*A, *psa*B, *psa*C, *psa*I, *psa*J

*psb*A, *psb*B, *psb*C, *psb*D, *psb*E, *psb*F, *psb*H, *psb*I, *psb*J, *psb*K, *psb*L, *psb*M, *psb*N, *psb*T

*pet*A, *pet*B*, *pet*D*, *pet*G, *pet*L, *pet*N (*ycf*6)

*atp*A, *atp*B, *atp*E, *atp*F*, *atp*H, *atp*I

*ycf*3[§], *ycf*4, *cem*A *(ycf*10*)*, *ycf*9

NADH dehydrogenase genes

*ndh*A*, *ndh*B*[#], *ndh*C, *ndh*D, *ndh*E, *ndh*F, *ndh*G, *ndh*H, *ndh*I, *ndh*J, *ndh*K

Other protein genes

*clp*P, *ccs*A (*ycf*5)

Conserved reading frames

*ycf*14 (*mat*K; partially homologous to intron maturases)

Notes:

* Intron-containing gene

§ Gene containing two introns

† Divided gene

Two gene copies due to the inverted repeat

polymorpha, editing of *ndh*G-mRNA (position 113,177 of the maize plastid chromosome) alters coding from proline to leucine, whereas in this case a phenylalanine residue is encoded at the corresponding position in the liverwort gene. A further editing site has been detected in the non-coding 5´-untranslated region of maize *ndh*G transcripts (position 113,533 of the plastid chromosome).

The updated maize plastid chromosome sequence has been deposited in the EMBL data base (accession no. X86563).

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Analysis of genetic diversity in selected Indian maize inbreds using microsatellite markers

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A preliminary analysis of genetic relationships among thirty-two public domain Indian maize inbred lines, most of which are currently being utilized as parental lines in hybrid breeding programs across the country, was carried out using a set of microsatellite or Simple Sequence Repeat (SSR) markers. The inbred lines included 18 CM lines (from the All India Coordinated Maize Improvement Project), two LM lines (from Punjab Agricultural University, Ludhiana), four NAI lines (from Nagenahalli, Karnataka) and eight inbreds used as parental lines for some promising single-cross hybrids (designated as BIO lines). The inbred lines selected also included CM111 and CM202, often used as heterotic testers in the Indian maize breeding programs.

SSR polymorphism among the inbred lines was analyzed using Super Fine Resolution agarose gel electrophoresis, following the procedure suggested by Senior and Heun (1996). Data obtained from 22 polymorphic loci, distributed over all 10 chromosomes, was used for analysis of genetic diversity. Except for chromosome 4, where only one polymorphic SSR marker could be identified in the present study, the rest of the chromosomes were represented by at least 2-3 SSR loci distributed at different map locations. A total of 58 alleles were detected for the 22 polymorphic SSR markers, giving an average of 2.64 alleles per locus. Although a large number of SSR loci used in the present study revealed only 2-3 alleles using the agarose system, a few loci such as *bnlg105*, *bnlg125*, *bnlg389* and *phi116* showed 4-5 alleles per locus in various inbred lines.

Polymorphism Information Content (PIC), a measure of allelic diversity at a locus, was estimated for various SSR loci used during the study. The values ranged from 0.06 (*phi042*) to 0.72 (*bnlg105*). The mean PIC value estimated across all SSR loci was 0.43. The PIC values of 10 primers were greater than this mean value. A comparison of the PIC values for SSR loci with different repeats shows that the mean PIC value for 10 SSR loci with di-repeats was 0.47, two loci with tri-repeats was 0.62, five loci with tetra-repeats was 0.32, one locus with penta-repeat was 0.6, two loci with hexa-repeat was 0.32, and one locus with a complex repeat was 0.56. These values do not show any clear association of PIC values with the nature of repeat.

The SSR marker data could facilitate discrimination of various inbred lines on the basis of occurrence of 'rare alleles' (with frequencies less than 0.25) for different SSR loci. The allelic frequencies indicated for various inbreds in Table 1 reveal the occurrence of many alleles with frequencies less than 0.10; this means that these alleles occur in no more than 2 out of the 22 inbreds. Such alleles could be effectively employed as possible diagnostic alleles for discrimination of specific inbred lines either alone or in combination. Rare alleles could not be detected in seven (BIO-1, BIO-4, BIO-5, BIO-6, CM202, CM137 and CM138) of the 22 inbreds analyzed. The present analysis also indicated instances where the SSR profiles for some inbreds showed deviations from the expected patterns. Inbreds are assumed to be highly homozygous, revealing one band per SSR locus. However, double bands could be consistently detected in some of the inbreds for specific SSR loci. An analysis of the frequency of heterozygous SSR loci revealed that eleven inbreds, including CM119, CM123, CM135, CM136, CM137, CM138, CM140, CM111, CM202 and BIO-1 have considerably high frequencies (>10%) of double bands.

The SSR data matrix was utilized to estimate the genetic relationships among the various selected inbreds. The genetic simi-

Table 1. PIC of SSR loci across various inbreds analyzed

SSR locus	Bin location	No. of alleles	PIC	SSR locus	Bin location	No. of alleles	PIC
bnlg439	1.03	2	0.43	*phi112*	7.01	2	0.16
phi002	1.08	3	0.26	*phi034*	7.02	3	0.60
phi098	2.02	2	0.49	*bnlg572*	7.03	3	0.68
bnlg125	2.02	4	0.43	*phi116*	7.06	4	0.56
phi099	3.02	2	0.43	*phi119*	8.02	2	0.14
phi029	3.04	2	0.22	*phi125*	8.03	1**	0.12
phi093	4.08	2	-*	*phi033*	9.01	4	0.63
bnlg105	5.02	5	0.72	*phi042*	9.04	1**	0.06
bnlg389	5.09	4	0.70	*phi041*	10.00	2	0.63
phi077	6.01	3	0.57	*phi050*	10.03	2	0.23
phi070	6.07	3	0.60				

*PIC value for *phi093* was not estimated due to high frequency of occurrence of double bands

**Consistent occurrence of a 'null allele' in 2 inbreds (*phi125*) and one inbred (*phi042*)

larity matrix between various inbreds was computed in a pair-wise comparison using Jaccard's coefficient and the resulting similarity matrix was subjected to the UPGMA clustering algorithm; computations were carried out using NTSYS-pc 2.02. The cophenetic correlation coefficient (r) was 0.664, showing a moderate fit of the dendrogram with the similarity matrix generated using SSR data. This indicates the need for further analysis using a greater number of markers to ascertain the genetic relationships among various Indian maize inbreds. The dendrogram obtained in this study (Fig. 1) provides preliminary information about the genetic similarities among the inbreds. On the basis of canonical discriminant analysis, the inbreds could be grouped into five distinct clusters (Fig. 2). It could be observed that CM111 and CM202

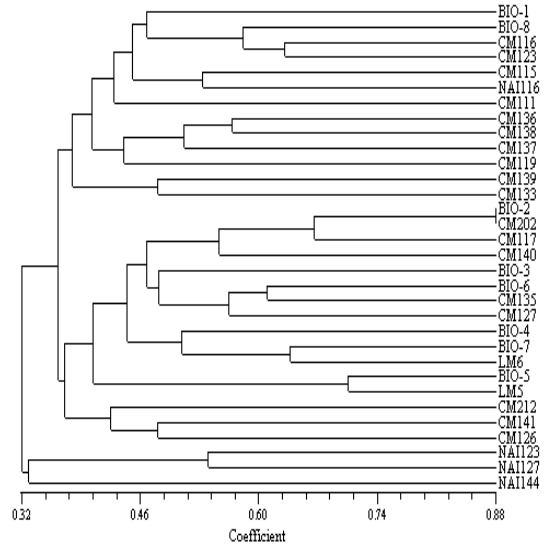
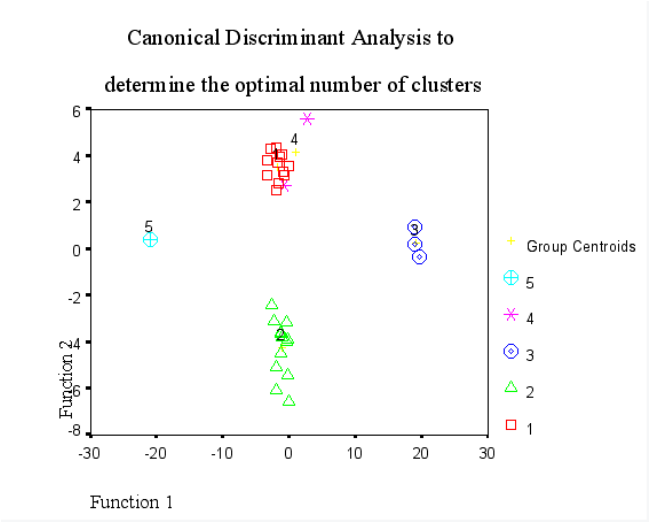


Figure 1. Dendrogram depicting genetic relationships among the Indian maize germplasm based on SSR analysis.



Group 1 - BIO-1, BIO-8, CM116, CM123, CM115, NAI116, CM111, CM136, CM138, CM137, CM119, CM139 and CM133
Group 2 - BIO-2, CM202, CM117, CM140, BIO-3, BIO-6, CM135, CM127, BIO-4, BIO-7, LM6, BIO-5 and LM5
Group 3 - CM212, CM141 and CM126
Group 4 - NAI-123 and NAI127
Group 5 - NAI144

Figure 2. Canonical discriminant analysis for determining acceptable number of clusters

(heterotic testers for Indian maize germplasm), CM139 and CM140 (parents of a single-cross hybrid 'Parkash'), BIO-7 and BIO-8 (parental lines of a promising experimental hybrid BH1183) fall into distinct groups. Interestingly, both CM212 and CM141 (parents of single cross hybrid 'Vivek-4') were found to be genetically similar as also LM5 and LM6 (parental lines of the hybrid 'Paras'), for the SSR markers used for analysis. Close genetic relationships could be observed between some of the BIO lines (from Hyderabad) and the LM lines (from Ludhiana). The study also clearly distinguished the NAI lines, NAI123, NAI127 and NAI144, from the other inbreds. This could be because these inbreds were essentially derived from foliar disease resistant maize materials obtained from Thailand and the Philippines (although the exact pedigree is not known), while most other inbreds used in this study were developed either from indigenous maize populations or from materials obtained from the USA or to some extent, CIMMYT, Mexico. Further analysis using a greater number of polymorphic SSR markers with adequate coverage of the entire genome, and methodologies with better resolving power (such as PAGE), will lead to a more comprehensive understanding of the genetic diversity in the Indian maize germplasm.

Analysis of genetic polymorphism among downy mildew resistant and susceptible maize inbred lines using Simple Sequence Repeat (SSR) markers

--Yen, TTO, Prasanna, BM

Thirteen inbred lines with distinct responses to maize downy mildew in India were selected for analysis of genetic polymorphism using a set of SSR markers. The genotypes included four inbreds provided by CIMMYT-Asian Regional Maize Program [AMB109 (AMATLCOHS115-1-2-3-3-1-2-B-B), AMB115 (AMATLCOHS 245-1-1-1-2-1-1-BB), AMB112 (P345C3S3B-46) and AMB119 (IPB9204-1-3-1-2-4-B) from CIMMYT-ARMP], which were highly resistant to both sorghum downy mildew (SDM) and Rajasthan downy mildew (RDM) in India. Four inbred lines from Mandya (Karnataka, India), designated as MAI lines, were included for this study: MAI101, MAI105 and MAI110 were susceptible to SDM at Mandya and resistant to RDM infection at Udaipur, while MAI114 was moderately susceptible to SDM and resistant to RDM. Three elite Indian maize inbreds, CM105, CM119 and CM139, with high susceptibility to both SDM and RDM infection, and CML51 and CML292 (CIMMYT inbred lines) which were also highly susceptible to SDM infection in India, were included in this study.

Out of 52 SSR markers analyzed, including 18 'bnlg', 29 'phi', one 'nc', two 'dupssr', and two 'umc' primers, polymorphic profiles could be observed for 45 SSR loci in the selected inbreds. Except for chromosome 10, where only two polymorphic SSR markers were identified each chromosome was represented by at least three polymorphic SSR loci. A total of 137 alleles could be detected for 45 polymorphic SSR loci, giving an average of 3.04 alleles per locus. The number of alleles detected per locus was relatively higher in the case of 14 'bnlg' primers in comparison with the 26 'phi' primers. SSR loci with considerably high polymorphism include *bnlg105* and *bnlg490*, with six alleles each within the thirteen inbred lines analyzed, and *bnlg1828* with five alleles.

Polymorphism Information Content (PIC), a measure of the allelic diversity at a locus, was estimated for each of the polymorphic SSR loci detected in the present study (Table 1). The PIC values ranged from 0.02 (*phi002*) to 0.73 (*bnlg490*). Loci

Table 1. Polymorphic SSR loci and mean PIC values identified among the DM resistant and susceptible maize inbreds

SSR locus	bin location	No. of alleles detected	PIC
bnlg149	1.00	3	0.39
bnlg147	1.02	2	0.31
phi002	1.08	3	0.02
phi037	1.08	2	0.50
bnlg1347	1.10	2	0.16
bnlg504	1.11	4	0.42
phi098	2.02	3	0.64
phi083	2.04	3	0.48
dupssr21	2.05	3	0.45
phi127	2.07	4	0.30
bnlg198	2.08	3	0.57
phi090	2.08	2	0.16
phi099	3.02	3	0.47
phi029	3.04	3	0.47
phi073	3.05	3	0.43
phi088	3.07	1	0.31
phi046	3.08	3	0.66
phi072	4.00	2	0.32
nc004	4.03	3	0.14
bnlg490	4.05	6	0.73
dupssr34	4.07	3	0.45
phi093	4.08	2	0.26
phi024	5.00	3	0.46
bnlg105	5.03	6	0.69
bnlg1346	5.07	3	0.66
umc1225	5.08	4	0.65
bnlg389	5.09	4	0.59
phi075	6.00	3	0.45
phi077	6.01	3	0.54
phi102	6.05	2	0.15
phi070	6.07	3	0.64
phi089	6.08	3	0.57
umc1066	7.01	3	0.44
phi114	7.02	3	0.64
phi051	7.06	3	0.36
bnlg162	8.05	3	0.44
bnlg1828	8.07	5	0.63
phi080	8.08	3	0.49
bnlg1272	9.00	3	0.43
phi033	9.01	2	0.43
phi032	9.04	2	0.47
bnlg619	9.07	4	0.58
phi063	10.02	4	0.49
bnlg2336	10.04	3	0.46

bnlg490 and *bnlg105* showed the best PIC values (0.73 and 0.69, respectively). The mean PIC value estimated across all the polymorphic SSR loci was 0.45. A comparison of the PIC values did not show any clear association of higher PIC values with the nature of repeat: PIC value of 0.48 for 21 SSR loci with di-repeats; 0.41 for 6 loci with tri-repeats; 0.42 for 10 loci with tetra-repeats; 0.43 for 3 loci with penta-repeats; 0.46 for 2 loci with hexa-repeats; and 0.56 for 2 loci with complex repeats. However, among the nine SSR loci showing more than 0.60 PIC value, five loci (*phi098*, *bnlg105*, *bnlg1346*, *umc1225* and *bnlg1828*) have di-repeats, two loci (*phi046* and *phi114*) have tetra-repeats, one locus (*phi070*) has a penta-repeat and one locus (*bnlg490*) has a complex repeat, indicating that SSR loci with di-repeats may provide higher PIC values than loci with other kinds of repeats.

The SSR allelic profiles of SDM resistant inbreds, AMB109, AMB112 and AMB119, were compared with the allelic profiles of SDM susceptible inbreds, CM139, CM105, CM119, CML51 and CML292, for each of the 45 SSR loci. Four SSR markers, *phi083*, *phi029*, *phi070*, and *phi114* showed a common allelic pattern in the DM resistant lines with distinct polymorphism in the DM susceptible inbreds. These primers could be promising in molecular marker mapping for SDM resistance and consequently, marker-assisted selection.

The data matrix obtained using SSR data was utilized in estimating genetic similarities among various inbreds under study. Similarity coefficients between various inbreds, in a pair-wise comparison, were computed using Jaccard's coefficient and the resulting similarity matrix was further analyzed using UPGMA clustering algorithm; the computations were carried out using NTSYS-pc 2.02. Canonical discriminant analysis was carried out to aid in determining optimal number of clusters from the dendrogram (Figures 1 and 2). The grouping provided an indication about the close genetic similarities among the DM resistant inbreds (AMB109, AMB112 and AMB119), and their genetic divergence from CM139 (DM susceptible elite Indian maize inbred; female parent of 'Parkash', a single-cross hybrid released recently in India) and the two CML lines. The information generated in this study will aid molecular marker mapping for downy mildew resistance in maize.

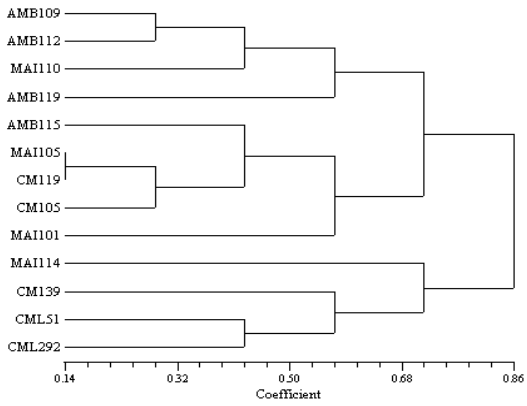
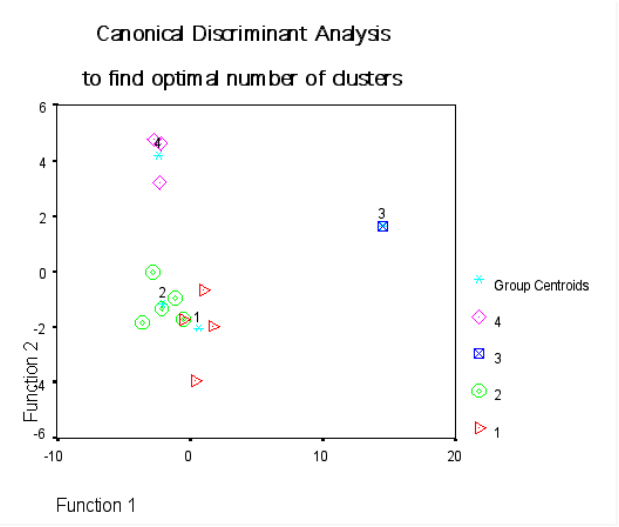


Figure 1. Dendrogram depicting genetic relationships among selected downy mildew resistant and susceptible inbreds based on SSR analysis



Group 1 - AMB109; AMB112; MAI110 and AMB119
Group 2 - AMB115; MAI105; CM119; CM105 and MAI101
Group 3 - MAI114
Group 4 - CM139; CML51 and CML292

Figure 2. Optimal number of clusters of genotypes identified based on canonical discriminant analysis

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Towards molecular marker mapping of genes conferring resistance to sorghum downy mildew (*Peronosclerospora sorghi*) in maize

--Nair, SK, Setty, TA, Rathore, RS, Kumar, R, Singh, NN, Prasanna, BM

One of the major factors limiting the productivity of maize in the tropical Asian region is the increased incidence of insect pests and diseases. Among the various maize diseases in south and southeast Asia, downy mildews (DM) are considered to be major diseases. Sorghum downy mildew (SDM) in maize, caused by *Peronosclerospora sorghi*, is one of the most important among the DM diseases prevalent in India. Another severe form of DM disease found in the state of Rajasthan in India is Rajasthan downy mildew (RDM), caused by *Peronosclerospora heteropogoni*, which does not infect sorghum, but is capable of infecting maize and a wild grass, *Heteropogon contortus*. There is no published information so far about resistance/susceptibility of Indian maize inbreds in the public domain to these two important DM diseases. A research program was initiated under the Asian Maize Biotechnology Network (AMBIONET) with the following objectives: (i) to analyze the responses of all the important maize inbred lines released under the All India Coordinated Maize Improvement Project (AICMIP) to SDM and RDM infection; (ii) to study the genetic basis of resistance to SDM and RDM diseases; and (iii) to map the genes conferring resistance to sorghum downy mildew in maize using microsatellite or Simple Sequence Repeat (SSR) markers, and carry out marker-assisted selection for SDM resistance. The present investigation is a component in this effort.

Responses of Indian maize inbred lines to SDM and RDM infection: A set of 47 Indian maize inbred lines were evaluated in a Randomized Block Design with two replications under artificial infection at the two DM 'hot spots' in India, Mandya in Karnataka for sorghum downy mildew and Udaipur in Rajasthan for Rajasthan downy mildew, during the monsoon (*Kharif*) seasons of 1999 and 2000. The 47 Indian maize genotypes included 37 elite inbreds and 10 inbred lines developed at the Agricultural Research Station (of the University of Agricultural Sciences, Bangalore), Nagenahalli, Karnataka, designated as 'NAI' lines. The NAI lines were derived from the DM resistant maize germplasm obtained from Thailand and the Philippines in the 1970s. Disease scoring was carried out on the basis of percent DM incidence in each genotype: 0 to 10% - Resistant; >10 to 30% - Moderately resistant; >30 to 50% - Moderately susceptible; and >50% - Susceptible. The following are the salient findings from the experiments carried out in Mandya and Udaipur during 1999 and 2000:

- Only one inbred line, NAI116, showed a strong resistance response to both sorghum downy mildew and Rajasthan downy mildew among the Indian maize lines. Almost all the elite Indian maize inbreds, including those used in hybrid seed production in the public sector, are highly vulnerable to SDM infection.
- Genotypes found to be resistant to RDM infection at Udaipur showed a differential response to SDM infection at Mandya. Therefore, there appear to be distinct differences in host-pathogen interaction at Mandya and Udaipur; the DM pathogen at Udaipur probably has lower virulence in comparison with the one in Mandya. This conclusion is also reinforced by the observation that all the inbreds found to be highly susceptible to SDM at Mandya showed varying responses to RDM infection at Udaipur.

This study emphasizes the urgent need to transfer DM resistance to the elite maize lines which are parents of important single cross, double cross and three way cross hybrids in India. A systematic analysis to understand the nature of inheritance of resistance to the disease is highly important for this effort. As a step towards this direction, various crosses were carried out in 6 x 6 diallel and 9 x 5 line x tester mating designs involving resistant, moderately resistant, moderately susceptible, and susceptible inbred lines identified through the present study. These cross combinations were evaluated in randomized complete block design during Monsoon season of 2000 under artificial inoculation at both Mandya and Udaipur. Statistical analysis of the results obtained from both locations is currently in progress and is expected to provide better understanding of the modes of inheritance of resistance to SDM and RDM infection in India.

Analysis of SSR polymorphism among SDM resistant and susceptible lines: A set of seven elite, SDM susceptible inbred lines (CM115, CM116, CM117, CM119, CM123, CM133 and CM139) along with the resistant line, NAI116, were screened using 108 SSR markers at the AMBIONET-India Lab at the Maize Genetics Unit, Indian Agricultural Research Institute, New Delhi. Super Fine Resolution agarose gel electrophoresis was used to detect SSR polymorphism, following the protocol suggested by Senior and Heun (1998). Two genotypes, CM139 and CM117 showed higher polymorphism with NAI116 than other inbred lines. Since CM117 revealed a high frequency of 'double bands', CM139, an elite inbred line which is also being used in the Indian hybrid maize programme as the female parent of a popular single-cross hybrid 'Parkash', has been selected as one of the parents for generating the mapping population. A total of 44 polymorphic SSR markers have been identified so far between NAI116 and CM139 (Table 1). Fifty-two SSR markers, found to be monomorphic during this study shall be reconfirmed using PAGE + silver staining protocol standardized under the AMBIONET programme. The team is presently analyzing an additional set of 150 SSR markers for detection of additional polymorphic SSR loci. A backcross mapping population has been generated using CM139 as the female parent and NAI116 as male parent. Genotyping of the mapping population using polymorphic SSR markers and phenotyping under SDM artificial infection at Mandya (during monsoon season, 2001)

Table 1. Preliminary information on SSR loci found to be polymorphic between SDM resistant (NAI116) and susceptible (CM139) Indian maize inbreds.

Chromosome	Polymorphic SSR loci
1	*phi097, bnlg615, bnlg400, bnlg504, umc1331*
2	*dupssr21, magE.05, bnlg371, bnlg198*
3	*phi099, 1452, phi073, phi053, bnlg420, bnlg1182*
4	*bnlg1729, phi079, bnlg490, dupssr34*
5	*phi113, bnlg105, bnlg653, bnlg278*
6	*phi078, phi102, phi070*
7	*phi057, bnlg339, bnlg572, bnlg469, phi116*
8	*phi115, phi014, bnlg1065, bnlg240, bnlg1056, phi015*
9	*bnlg1272, phi033, phi022, bnlg127, bnlg619*
10	*phi050, bnlg210*

shall be carried out for molecular marker mapping and consequently, marker-assisted selection for SDM resistance in maize.

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Inheritance of resistance to sorghum downy mildew (*Peronosclerospora sorghi*) and Rajasthan downy mildew (*P. heteropogoni*) in maize in India

--Yen, TTO, Rathore, RS, Setty, TA, Kumar, R, Singh, NN, Vasal, SK, Prasanna, BM

Among various diseases affecting production and productivity of maize in tropical Asia, Downy Mildew (*Peronosclerospora* sp.) is considered as one of the most destructive diseases. In India, important species causing downy mildew (DM) disease in maize are sorghum DM [*Peronosclerospora sorghi* (Weston & Uppal) Shaw], Philippine DM [*P. philippinensis* (Weston) Shaw] and Brown Stripe DM (*Sclerophthora rayssiae* var. zeae Payak & Renfro). Sorghum DM (SDM) causes considerable yield losses in several maize growing states, particularly Karnataka, Tamil Nadu and Rajasthan. A survey conducted in Karnataka revealed that the incidence of disease ranged from 10 to 90% and yield loss from 30-40% (Krishnappa et al., 1995).

In Rajasthan, the disease cycle of *P. sorghi* remained unknown until 1973 when *Heteropogon contortus* (speargrass), a wild grass growing in the vicinity of maize fields, was found to be a collateral host of this pathogen. Although the fungus resides on this perennial grass in the form of oospores, the conidial stage is the sole cause of primary infection of maize in that region. While some workers considered that the DM caused primarily through *Heteropogon contortus* should be redesignated as *P. heteropogoni*, others considered this a different isolate of *P. sorghi,* in view of the striking similarities in disease symptoms and very minor differences in pathogen morphology (Payak, 1975; Frederiksen and Renfro, 1977). The DM disease, caused by *P. heteropogoni*, has been recently designated as Rajasthan downy mildew (RDM) (White, 1999).

A detailed study was carried out to analyze the genetic variability and inheritance of resistance to two important DM diseases of maize in India - sorghum downy mildew (SDM) caused by *P. sorghi* and Rajasthan downy mildew (RDM) caused by *P. heteropogoni*. Experiments carried out under artificial infection during *Kharif* (Monsoon) season in 1999 and 2000 at two different DM 'hot spot' locations in India - Mandya in Karnataka and Udaipur in Rajasthan - aided in characterization of the responses of a set of public sector maize inbreds to the SDM and RDM pathogens, respectively.

Responses of maize inbred lines to SDM and RDM infection in India: A total of 41 inbred lines were evaluated after artificial infection by SDM and RDM at Mandya and Udaipur, respectively. Since a specific set of maize inbred lines was evaluated by both SDM and RDM infection at two different locations, the study provides an insight into the possible differences in the interaction of the genotypes with SDM and RDM. Analysis of the results obtained in two seasons (1999 and 2000) revealed five inbreds - AMB103 (Nei9008), AMB109 (AMATLCOHS115-1-2-3-3-1-2-B-B), AMB110 (AMATLCOHS233-1-1-1-1-2-2-BBB), AMB112 (P345C3S3B-46) and AMB119 (IPB9204-1-3-1-2-4-B) that are highly resistant to both SDM and RDM infection. The 'AMB' lines were those provided by the CIMMYT-Asian Regional Maize Program, Thailand. Among these lines, AMB103 and AMB112 were resistant to SDM (*P. sorghi*) in Thailand and Philippine DM (*P. philippinensis*) in the Philippines, and are currently being utilized for molecular marker mapping and marker-assisted selection under the Asian Maize Biotechnology Network (AMBIONET) program in these countries (Des Hautea, personal communication; Apichart Vanvichit, personal communication). Such inbred lines with broad-spectrum resistance to DM infection in tropical Asian countries would be highly useful for a variety of basic and applied research on downy mildew resistance breeding.

Significantly, among the 41 inbreds analyzed in the present investigation, no inbred could be found that was resistant to SDM disease at Mandya, and susceptible to RDM infection at Udaipur. A large number of inbreds resistant to RDM infection showed differential responses to SDM infection. Elite Indian maize inbreds such as CM119 and CM133 were highly susceptible to both SDM and RDM, highlighting the necessity of utilizing DM resistant germplasm for deriving elite Indian inbred lines, particularly for hybrid maize breeding. The CIMMYT inbred lines (CML20 and CML281) also showed severe susceptibility to both the SDM and RDM pathogens.

Inheritance of resistance/susceptibility to downy mildew infection in maize: Two sets of data were used to analyze the inheritance of resistance/susceptibility to SDM at Mandya and RDM at Udaipur: (a) responses of various experimental crosses generated among the materials under study; and (b) F2 and BC progenies of selected experimental crosses. Several cross combinations were generated using resistant (R), moderately resistant (MR), moderately susceptible (MS) and susceptible (S) inbreds identified in this study. F1 plants from three cross combinations - NAI116 x CM105; MAI110 x NAI139; and MAI113 x MAI110 - were selfed to generate the F2 population. Also, NAI116 x CM105 (a cross between resistant and susceptible lines) was backcrossed to both parents to generate backcross (BC) progenies. F1, F2 and BC progenies were evaluated for their responses to DM infection at both Mandya and Udaipur during *Kharif* 2000.

Inheritance of SDM resistance in maize: A total of 38 experimental crosses were evaluated for SDM resistance/susceptibility. Progeny of the R x R crosses showed only a resistant response, while the R x S crosses revealed only a moderately resistant response. The S x R crosses, in contrast, showed susceptibility in general (62.91%), with one cross combination recording moderate resistance and another recording moderate susceptibility. Both S x MR and MR x S crosses showed moderate susceptibility. Analysis of various categories of crosses indicated the complex and polygenic nature of inheritance of SDM resistance in maize. Orthogonal contrast also revealed distinct results depending on whether the resistant line was the male or female parent; DM incidence was greater in the second group than the first, highlighting the significance of the cytoplasmic constitution of the female parent in determining the inheritance of SDM resistance.

F2 progenies from the cross NAI116 x CM105 (R x S) showed

a large number of resistant plants (190 out of 291 plants), while F2 progeny from the S x S crosses behaved differently. In the F2 progeny of MAI110 x NAI139 (S x S), only 16 plants were resistant among a total of 194 plants. In contrast, the F2 progeny of MAI113 x MAI110 recorded a significantly higher frequency of resistant plants (120 out of 245 plants). Recovery of resistant plants in F2 of S x S crosses suggests the possibility that resistance/susceptibility might be under the control of both dominant and recessive genes and susceptible lines might also contribute alleles contributing to resistance of the F1. While the F1 progeny of the cross NAI116 x CM105 had a moderately resistant phenotype, the BC1 progenies, designated as BC(P1) and BC(P2), revealed distinctly different responses. The BC(P1) progeny (backcross with highly resistant parent) showed a very high frequency of resistant plants, with only 8 SDM infected plants out of a total of 142. In contrast, the BC(P2) progeny (backcross with highly susceptible parent) revealed a very high frequency of DM susceptible plants. These observations not only suggest that resistance to SDM disease is under polygenic control, but also a 'threshold effect': accumulation of alleles governing resistance to SDM in BC(P1) led to distinctly different response in comparison with F1, while accumulation of alleles responsible for susceptibility in BC(P2) tilted the response towards high susceptibility. Also, susceptibility for SDM appears to be partially dominant over resistance, and both dominant and recessive alleles might be contributing to the susceptible/resistant responses.

Inheritance of RDM resistance in maize: A total of 32 experimental crosses, generated using various inbreds characterized for their RDM resistance/susceptibility during *Kharif* (Monsoon) 1999, were evaluated at Udaipur under artificial infection during *Kharif* 2000. Almost all of the R x R progeny showed a highly resistant response, except CM124 x MAI105 which showed moderate resistance. Both R x MR as well as MR x MR progeny revealed only resistant responses. The R x S progeny displayed resistance in all cases, except for MAI101 x CM119, which had moderate resistance. In contrast, the progeny of S x R crosses showed a different pattern, with two crosses resulting in resistance, two in moderate resistance, and two in moderate susceptibility. All three S x MR crosses resulted in a moderately susceptible phenotype. Similarly, progeny of the S x S crosses were always susceptible. It is interesting again to note that both R x S and S x R crosses of the inbred lines did not show either completely resistant or susceptible phenotypes in F1, suggesting a polygenic nature of inheritance of RDM resistance. Orthogonal contrast also revealed that the effect of the second group where the resistant line was used as the male parent is greater than the first where the resistant line was used as the female parent, indicating that DM incidence was greater in the second group than the first. This observation highlights the possible role of the cytoplasmic constitution, in combination with the nuclear genes, in determining the magnitude of RDM resistance. F2 progenies of R x S crosses clearly revealed the distinct differences in the number of infected plants. While the F2 progeny from the NAI116 x CM105 cross showed an extremely low incidence of susceptible plants, MAI110 x NAI139 included a relatively higher frequency of susceptible plants. The F2 progeny from the MR x R cross was largely resistant, similar to those for R x S crosses. The backcross of NAI116 x CM105 to the highly resistant parent (NAI116) had no susceptible plants in the progeny. A comparison of this response with that of the parent NAI116 x CM105 indicated an increase in the resistance capacity of the BC progeny (0% DM incidence in BC progeny vs. 3% in F1).

This study highlights the distinct modes of inherited resistance to SDM and RDM diseases in India. While susceptibility to SDM infection was found to be partially dominant over resistance, resistance to RDM infection appeared to be partially dominant over susceptibility. Analysis of F1, F2, BC(P1) and BC(P2) progenies clearly revealed the differences in modes of inheritance of SDM and RDM resistance. The data also suggested that both dominant and recessive alleles contribute to the response to SDM and RDM infection. Inheritance of resistance to RDM infection was found to be less complex than that of SDM resistance. Further studies are being carried out to clearly discern the significance of additive, dominance, epistatic effects and their interactions in the inheritance of resistance to SDM infection in India.

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Effect of recurrent selection for increased oil content in maize (*Zea mays* L.)

--Bocanski, J, Petrovic, Z

Apart from continuous, long-range work on increasing maize yield, improving disease resistance, lodging and many other desirable traits, maize breeding has also been employed to change the usual chemical kernel content, i.e., to enhance total oil content in the kernel.

Owing to its favorable chemical content, the maize kernel has multiple applications and it is used as feed, food and raw material in the food processing industry. Besides developing high yielding hybrids of standard kernel quality, there are also hybrids developed with increased content of oil, protein and starch.

Oil hybrids have not only increased oil content, but also enhanced content of essential amino acids, which increases the biological value of the kernel. Therefore, oil hybrids are used for the needs of the oil industry for production of edible oil of high quality, and owing to their increased biological value in relation to ordinary maize, they are used for feeding of domestic animals, especially poultry.

In order to produce lines for increased oil content, recurrent selection for phenotype has been used. The work on production of lines by the means of recurrent selection started in 1967 by establishing the original population. The original population was made of simple hybrids produced by cross breeding eight domestic and four foreign lines originating from the USA. Domestic lines, produced in Institute for Field and Vegetable Crops, were: NSL 637, 1006, 1083, 763, 816, 789, 897 and 796. Foreign lines were: R 30, 38-11, C 103 and HOI11.

The original population of the first selection cycle had 5.72% oil. Oil content in analyzed S1 ears ranged from 5.17 - 6.91%, and their average was 6.19% oil. Average oil content in kernel of selected S1 ears amounted to 6.41%. The population of the second cycle produced from the hybrid combinations of the first cycle had 6.50% oil. Oil content in the population of the third cycle was 7.79%, and the population of the fourth cycle had an average oil content of 8.71%. From the 4th population 19 ears with the highest oil content were selected. In order to expand genetic variability, oil synthetic Syn. D.O., with an oil content of 9.59% was in-

cluded for further selection. Oil content in the population from the 5th cycle was 9.44% oil. Average oil content in the population from the 6th cycle was 9.50%. The population of the 7th cycle had an average oil content of 10.25%. Oil content in an average population sample of the 8th cycle was 10.48%. The population of the 9th cycle had an average oil content of 11.13%. Oil content in an average population sample of the 10th cycle was 10.71%. The 11th cycle population had an average oil content of 9.86%. Oil content in an average population sample of the 12th cycle was 11.43%. The 13th cycle population had an average oil content of 12.74%. The 14th cycle population had an average oil content of 13.56%.

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The effect of pollinator on kernel weight in pseudogamous apomictic corn-gamagrass hybrids

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We have previously reported the suppression of imprinting effect in hybrids of corn with gamagrass (Sokolov, VA et al., MNL 73:74-75, 1999; Sokolov, VA, ANL 11:16-20, 1999) and development of kernels with an abnormally high ratio of maternal and paternal maize genomes in the endosperm. In the present report we attempted to analyze the influence of pollen parent genotype and ploidy on kernel size in two apomictic hybrids differing in number of corn genomes and set of gamagrass chromosomes.

The line with 18 chromosomes of gamagrass was a trisomic for chromosome 4 or 5 of corn; its genome was 2n=21Zm + 18Td. The line with 49 chromosomes had the genotype 2n=40Zm + 9Td, where a set of 9 small chromosomes of gamagrass was added to 40 chromosomes of corn - minimally necessary to maintain apomictic development.

As pollinators, diploid forms were used: 1) Montana White; 2) commercial F1 hybrid Wilson (Seeds Inc.); 3) line with a T6-9 translocation (wx 18A); and 4) tetraploid N 102 A (Maize Genetic Cooperation Stock Center).

The results obtained by us are presented in Tables 1 and 2.

Table 1. Effects of gamagrass chromosome number and pollinators on hybrids 2n = 21Zm +18Td kernel weight.

Male	n	x	± m	δ	V,%	min	max	% Montana White
Montana White	19	0.038 a	0.0062	0.0270	71.4	0.010	0.128	100
T6-9	67	0.021 b	0.0020	0.0167	78.8	0.002	0.077	55
Wilson	39	0.083 c	0.0071	0.0446	53.9	0.010	0.154	218
Tetraploid N 102 A	90	0.069 c*	0.0028	0.0269	38.7	0.007	0.131	182

Table 2. Effects of gamagrass chromosome number and pollinators on hybrids 2n = 40Zm + 9Td kernel weight.

Male	n	x	± m	δ	V,%	min	max	% Montana White
Wilson	91	0.106 d	0.0027	0.0258	24.4	0.010	0.153	279
Tetraploid N 102 A	305	0.105 d	0.0016	0.0283	27.0	0.024	0.160	276

The results marked by the letters a, b, c, d reliably differ with P = 0.05. The values c and c* differ with P = 0.1. For comparison, the mean kernel weight of T. dactyloides = 0.03 ± 0.001 g and of the maternal tetraploid corn = 0.215 ± 0.003 g.

As is seen from Table 1, the diploid pollinators differ largely in the quantitative effect of imprinting. It is notable that the F1 hybrid (Wilson) is superior to even the tetraploid in this parameter though in the latter's offspring the ratio of genomes in endosperm will be 2 : 1, compared with 4 : 1 in the former.

The results adduced in Table 2 suggest that the hybrid is not inferior to the tetraploid in the "efficiency" of imprinting, though the difference in the ratio of maternal and paternal genomes is still more radical (8 : 1 in the former and 8 : 2 in the latter). It is remarkable that the mean kernel weight from pollination by the F1 hybrid of the 49-chromosome form increased by 84 %, the maximum weight remained as it was (Table 2) whereas both the mean and maximum weight increased from pollination by the tetraploid.

In this connection it may be supposed that one of the elements of the combining ability of lines producing heterosis is epigenetic modification specific to them, leading to an increase in kernel weight in the F1.

The analogous results from dependence of endosperm formation on pollen source and its ploidy are obtained on aposporous *Paspalum notatum* (Quarin, CL, Sex. Plant Reprod. 11:331-335, 1999). The suppression of imprinting is likely to be characteristic of all pseudogamous apomicts irrespective of their type as well as the value of endosperm development depends on pollinator.

Completing this section of our report we can conclude:
1) the size of kernels in the hybrids of corn with gamagrass shows dependence on both their ratio of corn male and female genomes and the type of pollinator;
2) the kernel weight trait in the corn - gamagrass hybrids has high genetic variability and can be increased by genetic and "selection" methods.

The authors express appreciation to Dr. E. Coe for fruitful discussions. The research was supported by the Netherlands Organization for Scientific Research Grant No. 047.007.019 and Russian Foundation of Basic Research Grant No. 00-04-49542.

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Transposable genetic elements as factors establishing novel regulatory links: models explaining experimental data

--Koterniak VV

We have reported about closely related lines derived from disruptive selection for frequency of reversion of a mutable allele at the *opaque2* (*o2*) locus, that is controlled by the *Bg-rbg* system of transposable elements. Sharp differences exist among these lines with respect to properties of the components of the *Bg-rbg* system of transposable elements and the expression of quantitative traits (Maydica 44:195-203, 1999; MNL 73:76-79; 74:57-58; this issue), suggesting a connection between the action of transposable elements and the expressivity of quantitative traits. Possible mechanisms explaining such a connection are discussed below.

Model 1. Taking into account that *o2* is an important regulatory gene in zein accumulation, we propose that *o2* regulates the quantitative traits under consideration (especially the ones related to kernel weight and volume). For these traits, changes in *o2* activity (conditioned for example by changes in state of a mutable allele) would modify their expressivity (Fig. 1).

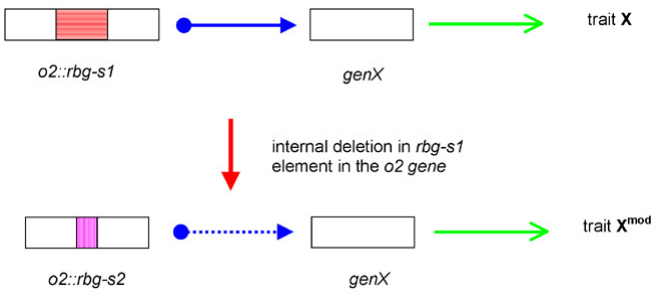

Figure 1. Interaction between (1) the regulatory gene *o2*, carrying insertion of a *rbg* element (designated as *rbg-s1* (state 1), represented by a horizontally hatched box on the figure) and (2) a quantitative trait gene, designated as *genX*, which determines trait X. Expression of *genX* is regulated by *o2*. A change in state in the *rbg-s1* element (e.g. due to internal deletion in this element) leads to the appearance of the *rbg-s2* element (represented by vertically hatched box). This change alters activity of *o2*, which in turn leads to modified expression of trait X (the modified trait is designated as X^{mod}).

Model 2. Changes (e. g. internal deletions) in the receptor elements contained in the mutable *o2* alleles can affect expression of other genes through transposition of the receptor elements into these genes (Fig. 2). Taking into account differences between the receptor elements contained in the *o2-lf* and *o2-hf* alleles of lines studied (Maydica 44:195-203, 1999; MNL, this issue), we can expect that transpositions of the receptor elements in the same genes will lead to different levels of expression of these genes.

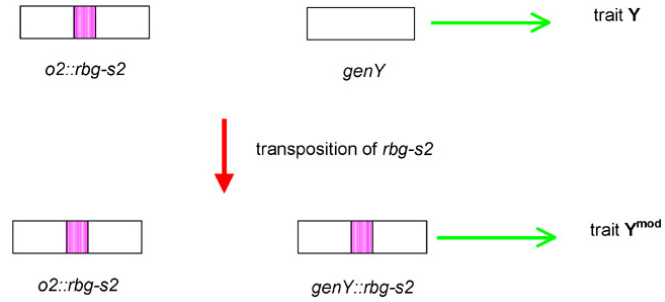

Figure 2. Receptor element *rbg-s2* (derived from an internal deletion in *rbg-s1* on *o2*) can transpose to a certain gene, *genY*, which is not regulated by *o2*. *genY* participates in determination of trait Y. Transposition of the *rbg-s2* element changes activity of the *genY* gene and modifies trait Y (designated as Y^{mod}).

Other Models. Other schemes for regulatory action of transposable elements invoke gene products of transposable elements. In Cuypers et al. (EMBO J. 7:2953-2960, 1988) it was reported that a defective *En-I102* element reduced the excision frequency of both the autonomous *En-1* element and the inhibitor element *Spm-I5719A*. The authors suggested that the changed product of a defective *En-I102* element acted as a competitive inhibitor and was responsible for reduced excisions.

Because differences in quantitative traits between lines studied did not depend on the activity of the regulatory (autonomous) element (MNL, 74:57-58; this issue), we can assume that the interactions between receptor elements play a predominant role. If the receptor element inserted into *o2* encodes the a competitive inhibitor of the products encoded by the *rbg* element inserted into quantitative trait genes, can expect changes in expressivity of quantitative traits (Fig. 3). In this model insertion of the receptor element into *o2* would show pleiotropic action regarding quantitative trait loci (which could be observed as pleiotropic action of the *o2* gene). In addition, in this model we could observe the appearance of new regulatory links between previously independent genes.

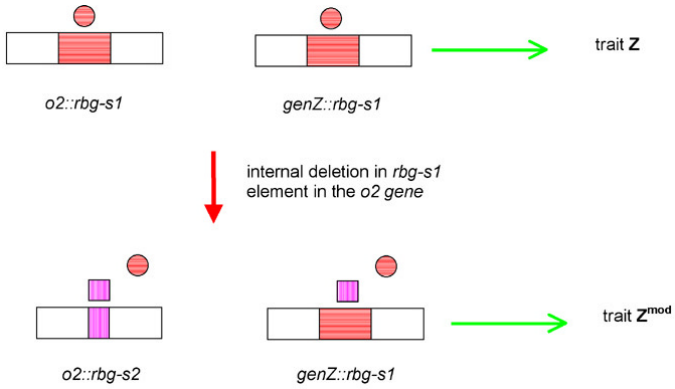

Figure 3. The interaction with *rbg* products. The *rbg-s2* (vertically hatched square) and the *rbg-s1* product are competitive inhibitors (horizontally hatched circle). The *rbg-s2* arose by internal deletion, from *rbg-s1* contained in the *o2* gene. *genZ* expression is conditioned by interactions between the *rbg-s1* insert and the *rbg-s2* product. Though *o2* does not normally regulate, the expression of *genZ* is now affected by the product of the *rbg-s2* element contained within *o2*. Thus changes in state of *o2* can lead to changes of expression not only of the *o2* gene, but also the *genZ*.

Furthermore, it is possible that regulatory activities of *o2* may be subject to a "feedback" type of regulation , based on the competitive interaction of different products of *rbg* (Fig. 4).

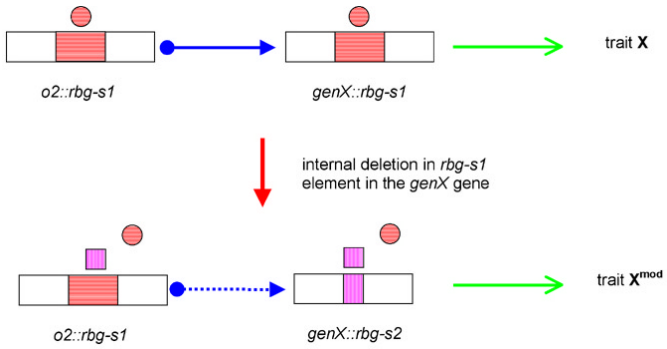

Figure 4. The "feedback" type of interaction based on *rbg* products. The product of the *rbg-s2* (vertically hatched square) acts as competitive inhibitor of the *rbg-s1* product (horizontally hatched circle). The *rbg-s2* insert arose by an internal deletion of the *rbg-s1* present in *genX*. Activity of *o2* is conditioned by the interaction between the *rbg-s1* insert present in this gene and the product of the *rbg-s2* element. Expression of the *genX* gene remains regulated by *o2*, but now the product of the *rbg-s2* insert into *genX* modifies the activity of *o2*.

Earlier we reported the possibility of rapid, inheritable changes in traits under transposable element control (Maydica 44:195-203, 1999; MNL 73:76-79). Study of the expressivity of quantitative traits in the lines with differing states of *Bg-rbg* components suggests that transposable elements can be responsible for significant modification and determination of the new regulatory links between genes, invoking the involvement of transposable elements in evolution.

Further studies of maize lines exhibiting change of state for components of the *Bg-rbg* system of transposable elements

--Koterniak, VV

Under genetic instability at the *opaque2* (*o2*) locus, conditioned by the *Bg-rbg* system of transposable elements, the receptor element *rbg* (contained in mutable responsive allele *o2-m(r)*) in

the presence of the regulatory element *Bg* can excise, causing reversion of the mutable allele to normal. Earlier we showed that by means of disruptive selection for whole endosperm revertants (WER, phenotypically normal kernels, formed as a result of reversion at the early stages of gametophyte or endosperm development), the frequency of *rbg* excision can be significantly and rapidly changed (MNL 73:76-79; Maydica 44:195-203, 1999).

Low and high WER content in the lines obtained under such selection (designated as LFWER and HFWER lines with *o2-lf; Bg-lf* and *o2-hf; Bg-hf* genotypes, respectively) was determined by change in state in the mutable responsive allele *o2-m(r):3449* and the regulatory element *Bg-3449*. Newly arisen alleles *o2-lf* and *o2-hf* were characterized by low and high rate of *rbg* excision respectively. The regulatory element *Bg-hf* contained in HFWER lines differed sharply from the *Bg-lf* in its ability to cause *rbg* excision at different doses (MNL 73:76-79; Maydica 44:195-203, 1999).

The efficiency of reverse selection for WER content. In 1997 (on the material obtained in 1995) we started the reverse selection for WER content (i. e. selection for WER increase in LFWER and WER decrease in HFWER lines). Results obtained after two years of selection indicated its effectiveness for WER decrease in HFWER lines and ineffectiveness for WER increase in LFWER lines (Maydica 44:195-203). Further selection confirmed these conclusions (Fig. 1). The higher stability of the *o2-lf* allele in relation to frequency of *rbg* excision indicates the lower level of organization of this allele in comparison to *o2-m(r):3449* and *o2-hf* alleles. Higher stability of *o2-lf* could be connected with the loss of some of its genetic properties, resembling in this respect the higher stability of the *o2* locus after the reversion of the mutable allele at this locus (Salamini, Cold Spring Harbor Symp. Quant. Bio. 45:467-476, 1981). Since the *o2-lf* retains its ability for reversion to normal we can assume that this loss did not affect the *o2* locus, but was caused by deletion in the *rbg* element contained in the *o2-lf* allele. In this connection it is necessary to mention that internal deletions in the nonautonomous (receptor) *dSpm* element of the *Spm/En* system can delay frequency and timing of excision of this element (see for example Schiefelbein et al., Proc. Natl. Acad. Sci. USA 82:4783-4787, 1985; Schwarz-Sommer et al., EMBO J. 4:2439-2443, 1985).

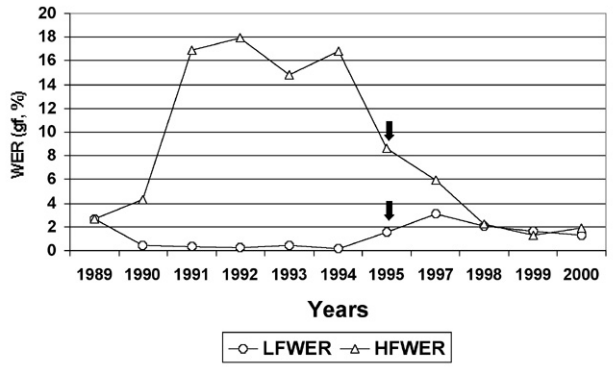

Figure 1. Gametic frequency (gf, %) of WER in a HFWER subline (pedigree of the 00-4518-10 ear) and in LFWER subline (pedigree of the 00-4514-3 ear) obtained under reverse selection for WER. Arrows indicate the ears from the progeny of which the reverse selection was started.

Low frequency of whole endosperm revertants can be conditioned by different genetic mechanisms. During reverse selection for WER frequency, it was observed that the limits of variation of WER frequency in the progeny of the HFWER ears with low revertant content equal to that of the LFWER lines were much higher in comparison with the variation of the same trait in LFWER families. Thus, after 3 cycles of reverse selection, variation of WER frequency in 2 HFWER reverse selection families was in the range of 0.56-12.31% (gametic frequency of WER in the ears from which they were originated was 2.27 and 2.28%). Variation of the same trait in reverse selection progenies of LFWER sublines was equal to 0-3.43% (these families originated from the ears with gametic WER frequency of 1.75 and 2.05%) (Fig. 2). Differences in variability of WER content could reflect different mechanisms of the control of low frequency of the *rbg* excision from the mutable alleles of the LFWER lines and the HFWER reverse selection sublines.

Expressivity of quantitative traits in lines differing with states of the Bg-rbg system components. We reported that lines obtained under disruptive selection for WER differed also in some quantitative traits: lines obtained under selection for high revertant content had higher kernel weight and volume, number of leaves, longer period from emergence to flowering (MNL 73:76-79; Maydica 44:195-203) and were more sensitive to herbicide application (MNL 74:57-58) in comparison to the lines obtained under selection for low revertant frequency.

We also observed that sensitivity to herbicide “Buctril D” in the lines obtained did not depend from the presence of the active regulatory element in these lines (MNL 74: 57-58).

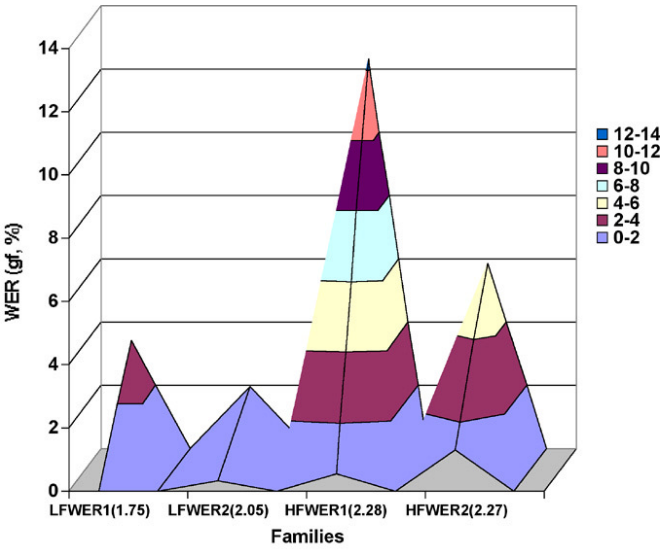

Fig. 2. Limits of WER gametic frequency in reverse selection families of LFWER and HFWER lines after 3 cycles of reverse selection for this trait (1999 year data). WER frequencies on progenitor ears are given in parentheses.

The mentioned differences of kernel weight and volume were observed on variegated kernels of the forms containing active regulatory elements. On the material obtained in 1999, we analyzed kernel weight and volume in LFWER and HFWER lines and their derivatives that lacked regulatory elements (*o2-lf; +Bg* and *o2-hf; +Bg* derivatives, respectively). (The methods of the analysis were described earlier (MNL 73:76-79)). Data obtained showed that superiority in kernel weight and volume of the lines obtained under selection for high revertant frequency was observed both on variegated and non-variegated kernels the latter formed on sublines lacking regulatory elements (Table 1).

Table 1. Values of some characteristics of variegated and non-variegated kernels of the lines with low and high WER frequency (with *o2-lf; Bg-lf* and *o2-hf; Bg-hf* genotypes, respectively) and their derivatives lacking regulatory elements (*o2-lf; +Bg* and *o2-hf; +Bg* genotypes, respectively).

Genotypes	Ears analyzed	50 kernel weight, g	50 kernel volume, cm^3	Kernel density, g/cm^3
variegated kernels				
o2-lf; Bg-lf	7	5.83a*	4.40a	1.326a
o2-hf; Bg-hf	8	7.05b	5.21b	1.354a
o2-hf; Bg-hf as % of *o2-lf; Bg-lf*		120.9	118.4	102.1
non-variegated kernels				
o2-lf; +Bg	14	5.89a	4.69c	1.257b
o2-hf; +Bg	16	6.69b	5.50b	1.216c
o2-hf; +Bg as % of *o2-lf; +Bg*		113.6	117.3	96.7

* For each trait a common letter at the means indicates insignificance of the differences between them (P≤0.05).

Higher values of kernel density observed with the *o2-lf; +Bg* derivatives most likely resulted from the action of polygenic modifiers which conditioned higher endosperm vitreousity. These modifiers apparently also lessened the differences in kernel weight between the LFWER and HFWER derivatives lacking regulatory elements. The results obtained indicate that the differences of the studied quantitative traits do not depend directly on WER content and on the presence of active regulatory elements in the lines studied.

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Chloroplast morphology, pigment content and fluorescence parameters in *virescent* mutants

--Marocco, A

Chlorophyll-deficient tissue is a frequent symptom in plants when they experience low temperature. These symptoms also arise in mutated populations of plants. The *virescent* character is a common genetic variant in pigmentation of higher plants for which a large number is known in maize. It is generally accepted that expression of this character is influenced by temperature sensitivity (reviewed by King, 1991 The Genetic Basis of Plant Physiological Processes, Oxford Univ. Press, 151-224). Since the cloning of genes affecting chloroplast development at low temperature may help application oriented activities in the field of temperature tolerance in maize, we developed gene tagging experiments for the *Virescent* genes of maize using the *Activator-Dissociation* transposable elements (Cerioli et al., 1995 Genet. Res. 66: 203-212). I have now examined the phenotypic expression of *virescent* mutations by analysing the chloroplast morphology, the pigment content and the fluorescence parameters in nine mutants grown at low temperature.

The *v1*, *v2*, *v3*, *v4*, *v13*, *v16*, *v18*, *v19* and *v26* mutants employed in this study are derived from progenitor stocks obtained from the Maize Genetics Cooperation Stock Center, University of Illinois, Urbana. All mutants are in the Oh43 background. Seeds were grown in a controlled environment chamber at 15 C under continuous light (80 Wm^{-2}).

Electron microscope inspection of the *virescent* leaf phenotype at the cellular level showed that cells in the leaf tissue contain few chloroplasts (Table 1), and these did not appear to be fully developed. Plastids contain poorly organised and aberrant thylakoids; the organelles generally are two-thirds the size of fully developed chloroplasts. The ungreened *virescent* leaves contained a variety of aberrant chloroplasts. The plastid types ranged from those with little internal structure on loosely constructed prolamellar bodies to those with nearly normal morphology. The distinctly abnormal plastids predominated in *v2*, *v4* and *v16*.

The level of photosynthetic pigments is severely reduced (Table 1). The *virescent* mutants were extremely deficient in chlorophyll, which was to near-normal level with Oh43 genotype. The *v1*, *v2*, *v3*, *v19* and *v26* leaves were relatively less deficient in chlorophyll b than in chlorophyll a, resulting in lower chlorophyll a/b ratios than for normal leaves. Leaves of *v4* and *v13* exhibited a substantial increase in chlorophyll a relative to the chlorophyll b content. Changes in the proportion of luteins and xanthophylls per unit weight in normal and *virescent* leaves were measured. Leaves of *v1*, *v19* and *v13* exhibited a decrease by 44%, 40% and 16%, respectively, in the lutein content compared to wild type. The lutein contents of *v2*, *v3*, *v4*, *v16*, *v18* and *v26* were 31% below the wild type. The levels of xanthophylls were higher in leaves of *v1*, *v13* and *v19* as compared to wild type. The mutations led to an increase in the relative levels from 53% to 70%. A strong reduction in the xanthophyll contents by more than 64% was observed in *v2*, *v3*, *v4*, *v16*, *v18* and *v26* mutants compared to normal leaves.

Fluorescence measurements were performed with a PAM 101 fluorimeter (Heinz Walz, Effeltrich, Germany). From an analysis of the fluorescence quenching parameters in the green tips of leaves, it is shown that all mutants possess a functioning, fully reversible, non-photochemical quenching mechanism (Table 1). This is most developed in the *v13*, *v18* and *v19* mutants. These three mutants also have a relatively high primary photochemical yield for photosystem II and a functioning photosystem I, as indicated by the high photochemical quenching capacity. Together the chlorotic phenotype and the molecular identification will provide a foundation to investigate the pathway for this mechanism of cold susceptibility.

The various *virescent* mutations are characterised by different stages of chloroplast development. I hypothesize a model where *V2*, *V4* and *V16* loci are located upstream, followed by *V1*, *V3* and *V26*. Mutations in *V13*, *V18* and *V19* loci may control the downstream pathway. The leaves of ungreened *virescents* contain a reduced amount of total chorophyll. The relatively greater deficiency in chlorophyll a reduces the chlorophyll a/b ratio below normal in most of the mutations. This difference can not be regarded as a distinctive characteristic of all *virescent* mutants as reported for the *v18* mutant (Chollet and Paolillo, 1972 Z. Pflanzenphysiol. 68: 30-44). In fact, the ratio is considerably higher in *v4* and *v13* leaves. The total content of carotenoids was affected to a much lesser extent, if at all, by the mutations. It

Table 1. Plastid measurements, chlorophyll content and *in vivo* chlorophyll fluorescence in normal and *virescent* leaves grown at 15 C. Data are means of 5-7 replicates, each representing a different plant ± SE.

Genotype	Plastid number [a]	Plastid size (μm)	Chlorophyll a+b	Fv/Fm
v1	5.0 ±1.0	3.3 ± 0.2 x 2.4 ± 0.3	44.0±1.0	0.32
v2	4.0 ±0.6	5.5 0.8 ± x 2.5 ± 0.4	10.0 ±0.1	0.12
v3	4.7 ±0.8	4.0 ± 0.7 x 2.0 ± 0.0	37.7±0.7	n.d.
v4	3.5 ±0.5	4.0 ± 0.7 x 2.0 ± 0.0	17.7 ±0.4	n.d.
v13	5.7 ±1.0	6.8 ± 0.8 x 4.3 ± 0.3	102.0±1.7	0.67
v16	3.9 ±0.5	4.0 ± 0.5 x 2.5 ± 0.2	traces	0.09
v18	3.0 ±0.0	6.0 ± 1.0 x 2.5 ± 0.3	7.8 ±0.1	0.52
v19	4.4 ±0.5	6.0 ± 0.6 x 3.0 ± 0.4	67.0±0.8	0.62
V26	3.9 ±0.5	6.0 ± 0.5 x 3.0 ± 0.1	13.3 ±0.1	0.35
Oh43	6.1±0.7	4.5 ± 0.4 x 3.0 ± 0.2	3,000 ±9.4	0.81

[a] Each entry represents the average of measurements obtained by analysing 20 cells.

seems, therefore, that mutant leaves attempt to protect themselves against damage from excessive light by increasing the carotenoids/chlorophyll a+b ratio (Haldimann et al., 1995 Physiol. Plant. 95:409-414). In this context it is interesting that all mutants possess a significant, reversible, non-photochemical quenching capacity. From the point of view of the photosynthetic characteristics determined by PAM fluorescence measurements, the most interesting mutants are *v13*, *v18* and *v19*. These mutants not only have a relatively high PSII quantum efficiency for primary energy conversion when grown under cold stress conditions, but evidently also have an actively functioning PSI, as indicated by the high values for photochemical quenching. In addition, these three mutants also possess the most effective non-photochemical quenching mechanism(s), which is thought to provide protection against excess photon absorption by PSII. Even more important is the finding that the mutations induced important changes in the photosynthetic quantum conversion. Photosystem II appears to be correctly assembled in the *v13*, *v18* and *v19* mutants because the F_v/F_m, ϕ_p, ϕ_n and ϕ_{tot} were higher than wild type. In these mutants the protections against low temperature and excessive light is ensured by the ϕ_p and ϕ_n processes.

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Oat-maize chromosome manipulation for the physical mapping of maize sequences

--Kynast, RG, Okagaki, RJ, Odland, WE, Stec, A, Russell, CD, Zaia, H, Livingston, SM, Rines, HW, Phillips, RL

We have developed a complete set of oat-maize chromosome additions to map maize sequences and study expression of maize genes in the genetic background of oats. A total of 37 monosomic and disomic addition lines that involve five oat (chromosome recipient) and three maize (chromosome donor) lines were generated, as described in detail by Riera-Lizarazu et al. (TAG 93:123-135, 1996), and recovered and identified as described in detail by Kynast et al. (Plant Physiol, in press, 2001). Because each recovered addition line represents its own distinct retention event, we developed a nomenclature for identification of the addition lines. **OMAxy.z** is an abbreviation for Oat-Maize Addition extended by three alpha numericals. The x position indicates the maize chromosome constitution, which will be d for disomic or m for monosomic. The **y** position is the number of the maize chromosome that is added, namely 1 to 10. The **z** position is a number that identifies a particular version of the maize chromosome that traces back to the original recovery event. Table 1 summarizes the identity and status of addition lines that are currently available to the scientific community. Fertile lines include a total of 30 single disomic additions (2n = 6x+2 = 44) for maize chromosomes 1, 2, 3, 4, 6, 7, 8, and 9, one single monosomic addition (2n = 6x+1 = 43) for maize chromosome 8, and two double disomic additions (2n = 6x+2+2 = 46) for maize chromosomes 1+9 and 4+6. Four original haploid additions are maintained as tiller-clones because in those recovered haploid monosomic additions (n = 3x+1 = 22), the added maize chromosome did not transmit to the F2 offspring. The clones include one addition plant with maize chromosome 1, two addition plants each with maize chromosome 5, and one addition plant with maize chromosome 10.

Table 1: Available oat-maize chromosome addition lines with their female and male parents

Added maize chromosome	Oat line (Female Parent)	Maize line (Male Parent)	Number of F1 plants (Tiller-clones)	Number of different fertile lines
1	Preakness	Seneca 60	1	
	Starter	Seneca 60		1
2	Starter	Seneca 60		6
	Starter	*bz1 mum-9*		1
3	Preakness	Seneca 60		1
	Sun II	Seneca 60		1
4	Starter	Seneca 60		5
	Starter	A188		2
5	Starter	Seneca 60	1	
	F1 hybrid	Seneca 60	1	
6	Starter	Seneca 60		2
7	Starter	Seneca 60		3
	GAF Park	Seneca 60		1
8	Starter	*bz1 mum-9*		1
	GAF Park	Seneca 60		1
9	Starter	Seneca 60		5
	GAF Park	Seneca 60		1
10	GAF Park	Seneca 60	1	
1 + 9	Starter	Seneca 60		1
4 + 6	Starter	Seneca 60		1

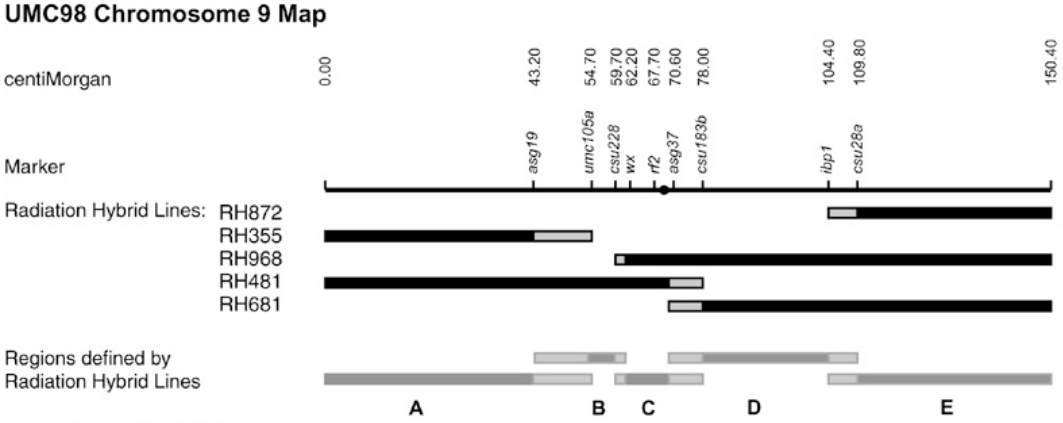
We evaluated the practicability of OMAs for physical mapping with 50 molecular markers that had been previously placed on linkage maps by Southern hybridization. Primer pairs were designed for the 50 markers and used for PCR analysis against the genomic DNAs of a complete set of OMAs. Forty-eight markers mapped to their expected chromosome. The two remaining markers were cloned and sequenced. They appeared to identify duplicates of previously genetically mapped loci. Four duplicate loci were identified that had not been previously mapped.

For evaluating the mapping of new maize sequences, primers have been designed and tested for EST sequences from ZmDB (http:www.zmdb.iastate.edu/) and for STS sequences derived from unmethylated regions of the maize genome described by Rabinowicz et al. (Nature Genet 23:305-308, 1999). To date, 300 EST and 50 STS markers have been mapped to chromosome. These markers include 72 on chromosome 1, 47 on chromosome 2, 45 on chromosome 3, 42 on chromosome 4, 56 on chromosome 5, 46 on chromosome 6, 43 on chromosome 7, 52 on chromosome 8, 42 on chromosome 9, and 20 on chromosome 10. Of these markers, 75% mapped to one chromosome, 20% mapped to two chromosomes, and 5% mapped to three to nine chromosomes.

Mapping at high resolution is possible with oat-maize radiation hybrids (RHs) through the use of panels of lines created by radiation-induced breakage. These lines contain chromosome rearrangements and sub-chromosomal segments of maize DNA. The first RH panel was made from an OMA maize chromosome 9 line and has been described by Riera-Lizarazu et al. (Genetics 156:327-339, 2000).

Two types of panels are being assembled for future mapping with RHs for maize chromosome 9. The first is a high-resolution panel with more than 40 lines that can give a mapping resolution of

We have five RH lines for chromosome 9 that may prove useful for making low resolution maps. Several lines appear to retain one contiguous stretch of maize DNA. For example, the chromosome 9 radiation hybrid line RH355 retained the distal tip from the short arm of chromosome 9 translocated onto an oat chromosome. Any maize sequence present in this line must be located in the distal end of chromosome 9. This strategy may allow us to rapidly place hundreds or thousands of sequences to discrete regions of the chromosome.



The black bars show the regions of chromosome 9 retained by these RH lines. The light gray bars indicate the regions of uncertainty, *e.g.* csu28a is the last marker present, and ibp1 is the first marker missing in RH872.

The charcoal gray bars show the regions defined by the five radiation hybrid lines. The light gray bars again indicate the regions of uncertainty. A few sequences were mapped to demonstrate how this approach would work.

Figure 1: Low resolution radiation hybrid maps

approximately 5 Mbp. The second panel is a low-resolution panel of five lines that have overlapping segments and can allocate sequences to discrete locations on the chromosome. Figure 1 is a graphic representation of how this latter panel is designed. The strategy of the low-resolution panel is to map hundreds or thousands of sequences to chromosomal regions.

Initial RH panels are being evaluated for maize chromosomes 2 and 4. Both of these panels have more than 30 candidate lines that have been identified as containing maize segments and are currently being characterized with markers to evaluate their usefulness. Monosomic OMA seed have been produced, irradiated, and are being grown for characterization of RHs for maize chromosomes 3, 6, and 7.

New technologies are being employed and evaluated to create higher throughput efficiency for identifying sequences in OMA and RH lines. These technologies include using robotics to process samples, Invader Assay (Third Wave Technologies, Inc.), and microarrays. The use of OMA and RH lines in conjunction with these technologies can provide an efficient and reliable means to map thousands of maize sequences to chromosome and discrete segments within a chromosome.

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In vivo and in vitro endospermogenesis in parthenogenetical maize lines

--Alatortseva, TA, Tyrnov, VS

Morphogenesis in vitro is known to depend significantly on genotypical, epigenetical, karyotypical and other peculiarities of explant. The specificity of the female gametophyte structure, consisting of cells with different functions and ploidy, has to be taken into account for in vitro culture of ovaries, both fertilized and unfertilized. The ploidy of embryo sac elements can change significantly. For example, two haploid polar nuclei form a central nucleus with ploidy 2n after fusion; after its fertilisation the initial endosperm nucleus has 3n ploidy.

Endosperm development is of interest for: a) its trophic, morphogenetical and regulatory functions in relation to the embryo; b) its role in parthenogenesis; c) the possibility of production from apomictic endosperm haploid cells and tissues or homozygous diploid ones; d) its positive or negative influence on embryogenesis and regeneration in vitro.

We investigated parthenogenetical line AT-1, described earlier (Tyrnov, MNL 71:73-74, 1997). Unfertilized ovaries, 1 to 17 days after appearance of silks, were used as explants.

MS medium modified by sucrose, vitamins and 2,4-D was added. Culture was in the dark at a temperature of about 25 C. A portion of ovaries was used for cytoembryological analysis before plating onto medium and during the culture period (after 3, 7, 14, 21 days). This allowed us to follow the course of embryological and morphogenetical processes. In vivo as well as in vitro, we regularly observed the following events: 1) Egg's division and development of embryo from bicellular to globular. A number of multicellular embryos appear with increasing ovary age. Different ovaries of the same age can include proembryos of different developmental stages. Embryo development to the globular stage can proceed without endosperm formation. 2) Division only of the central cell. 3) Division of both the central cell and egg.

In the last two cases the first division of the central cell is preceded by fusion of polar nuclei. This situation was observed in 7-8 days ovaries. The in vivo and in vitro ovary ages are determined as days after silk appearance.

17-18 days after silk appearance, endosperm is multinuclear.

Usually karyokinesis is not followed by cytokinesis (cellularization), and the endosperm appears cenocyte. In some cases, fragments of nuclear or cellular endosperm were observed. If endospermogenesis and embryogenesis proceed together in embryo sac, the last one begins earlier and passes ahead of embryo development. At the moment of fusion of polar nuclei, the embryo can contain from 2 to 100 cells.

The analysis of stages of ovaries, cultured in vitro, demonstrated that the presence of both processes (endospermogenesis and embryogenesis) leads to their mutual inhibition. Embryos stop development at the globular stage. In addition, at the same stage, many embryo-like structures begin to form on the surface. They do not reach the stage of mature embryoid and are not able to form plantlets when plated on regeneration medium.

The development of embryos continues in the absence of endospermal tissue. They can form plantlets or produce by gemmagenesis a great number of embryoids, able to produce plantlets.

Thus, it can be suggested, that in unfertilized ovaries in vitro there is a special type of interrelationship between haploid embryo and endosperm.

A negative influence of endosperm on embryo can be conditioned by some circumstances. We suggest the following possibilities: 1) Endosperm, by enveloping the embryo, is either a barrier, or competitor for nutrient substances. 2) Anomalous characters of endosperm, by its ploidy and variable developmental timing lead to anomalies of embryogenesis. 3) If the endosperm realizes a regulatory role by means of physiologically active substances, its interrelation with endogenic factors from its surroundings can give undesirable effects for embryogenesis.

Reproduction of haploid and diploid maize forms in vitro

--Alatortseva, TA, Tyrnov, VS

In many cases, for biotechnological manipulations, strains with stable regeneration potential are needed. Technologies are important for producing regenerants from either haploid or diploid maize independently of both genotype and ploidy. Sometimes only one form can be used, if its regeneration potential is high enough and stable. It can be used as a recipient of certain genes. The use of haploid plants as donors of explants is advisable, because in that case the effects of both dominant and recessive genes are manifested.

Taking into account the statements above, we have carried out an investigation on maize.

Diploid embryos: The mature embryos of four maize lines (AT-1, UV-98, HPL-1 and HPL-52) were cultured on modified medium MS, containing different concentrations of 2,4-D and sucrose.

We ascertained that the spectrum of new formations, appearing in the process of culturing explants of different lines is not always identical. Practically all germinating embryos are able to form globular structures on the surface of the coleoptile, and sometimes on leaves. The development of globes can be realized in two directions: by way of formation of rhizogenic callus, or by differentiation of globes in embryo-like structures. The last ones form the new generation by gemmagenesis. As a result embryogenic complexes (EGC) are formed. EGCs, when extracted from test-tubes, disintegrate easily into pieces, including a great number of embryoids of the different origin. Some embryoids in EGC complement give rise to plantlets still on initial medium, or they germinate after passage on medium without 2,4-D, but with IAA and kinetin (1.0 mg/l). On fresh medium with 2.0 mg/l 2,4-D actively growing regenerable strains can be produced. It should be noticed that in the given conditions of culturing only embryos of AT-1 line are able to form EGC and give plantlets. The best results for this line were obtained on medium containing 1.0 mg/l 2,4-D and 4% sucrose and 3.0 mg/l 2,4-D and 6% sucrose. Diploid embryos of the lines UV-98, HPL-1 and HPL-52 produce exclusively globes, giving rhizogenic callus.

Haploid embryos: From kernels of the line UV-98, produced with use of haploinducers, haploid embryos were isolated and cultured on medium containing 2.0 mg/l 2,4-D and 2.0% sucrose. In contrast to diploid embryos, haploid ones gave rise to EGC embryoids which developed in plantlets.

Unpollinated ovaries: Ovaries of 15 lines and hybrids, including sexual forms and forms with elements of apomixis were cultured on nutrient medium, containing also a different correlation of 2,4-D and sucrose.

Regenerants were produced only in line AT-1, having a predisposition to reduced parthenogenesis. The ovaries of other lines on all tested mediums degenerated after approximately 7 days from the beginning of culturing.

In ovaries, line AT-1 and its hybrids autonomously formed parthenogenetical proembryos with a great number of globular structures on their surface, which later transform into embryoids. As a result of this EGC appeared, like that for zygotic embryos of line AT-1.

Embryogenesis and regeneration can proceed on initial medium. The concentrations 2,4-D - 2.0 mg/l and 5-9% sucrose were most optimal for induction of the above-mentioned processes.

Consequently, maximal regeneration potential is characteristic of line AT-1. Differentiated embryos isolated from dry kernels and haploid parthenogenetical proembryos developing inside unpollinated ovaries, are able to produce practically countless numbers of plantlets of embryoid origin. The visible differences in regeneration ability of haploid and diploid embryos have not been established. In addition we were able to demonstrate an example of haploid embryos from line UV-98 and the possibility of producing in vitro regenerants from embryos originating from pollination of donor ears by haplo-inducing pollen.

Thus, two different technologies of producing haploid strains and regenerants can be presented. The first combines culturing of unpollinated ovaries with a genetically conditioned predisposition to reduced parthenogenesis. The second combines culturing with producing kernels with haploid embryos, obtained after pollination by a specially created pollinator - haplo-inducer.

Estimation of parthenogenesis frequency on the grounds of genetical and embryological data

--Tyrnov, VS, Smolkina, YV, Titovets, VV

We have investigated the line AT-3, described before (Tyrnov, MNL 71:73-74, 1997), characterized by pseudogamous reduced parthenogenesis. The frequency of this phenomenon depend on delays in pollination and can reach 50-100%.

In these experiments, we pollinated a week after appearance of silks. We used the pollen of a purple tester; matroclinic haploids and diploids were diagnosed by colour and plant morphology.

For embryological analysis the ears were fixed in acetoalcohol 7-8 days after appearance of silks. Enzymatic maceration of ovaries was used for isolation of embryo sacs. The usual frequency of haploid plants reached 12.1%, with 6.7% of haploids in monoembryonic seedlings, and 5.4% in twins and triplets. The frequency

of diploid matroclinic plants was small, about 0.2%.

Among twins the following cytological types were revealed: n-n, n-n-n, n-2n, n-2n-n, n-n-2n, 2n-2n. Diploid twins were mainly of hybrid origin. Only one was matroclinic.

Approximately 100 embryo sacs from each ear were examined cytoembryologically. In all, 535 embryo sacs were examined. Non-typical, for maize, events included: 1) autonomous embryo - 16.3%; 2) autonomous endosperm - 4.7%; 3) some eggs - 11.2%; 4) egg-like synergids - 7.1%; 5) additional embryo sacs - 3.2%.

The above embryological peculiarities were manifested independently or in combination as follows: a) separate or simultaneous embryo- and endospermogenesis; b) globular embryo + one or some eggs; c) one or some globular embryos; d) some eggs + two synergids; e) egg + egg-like synergids; f) two embryos + two eggs + two synergids.

Apparent additional embryo sacs were observed in the region of antipodal disposition. They were in different stages of formation (from unicellular to 5-6-cellular) and reached one half the size of a normal embryo sac. They may be of aposporic origin. However this question needs additional investigation.

Observation showed formation of mono- and polyembryonic haploids, even triplets of n-n-n type. The potential opportunities for egg-like synergids remain unclear: are these cells able to produce embryos or not? The high frequency (more than 7%) of egg-like synergids in parthenogenetical lines indicates an obvious connection of this phenomenon with parthenogenesis. It could be used as an indicator of embryo capability for parthenogenesis.

As a whole, the frequency of phenomena connected with parthenogenesis on an embryological level is significantly higher (about 40%) than the frequency of their manifestation in plants (about 12-13%). This can be explained by an earlier discovery that endospermogenesis in lines of the AT series does complete (Enaleeva, Tyrnov, MNL 71:74-75, 1997), so that a portion of autonomous embryos perish. In addition, embryogenesis also probably can not always complete, since a rather great number of seeds without embryos (approximately from 1 to 20%) was observed.

This work was supported by a grant from the Russian Foundation for basic Research.

Change of quantitative traits of androgenic maize plants

--Zavalishina, AN, Tyrnov, VS, Nekrasov, AM

It has been shown that androgenic haploids, obtained by the method of androgenesis in vivo after pollination by a nucleus donor and then diploidized, reveal changes in the pigmentation of plants. The nucleus donor has brown colour pigment controlled by genes *a1 B1 Pl1 R1*. While displacing the genome of the nucleus donor in other cytoplasms there appear plants of light brown, tan and green colours. This testifies to expression changes of nuclear genes *B1*, *Pl1* (MNL 69:120-121, 1995; MNL 72:74-75, 1998). These changes have a strongly pronounced phenotypical manifestation, and their inheritance is subject to certain regularities analogous to paramutation of *B1* and *Pl1* genes. Further investigation of the diploid generation of androgenic haploids has shown that besides pigmentation other quantitative traits can be changed. The results of the changes of such traits as plant height and length of first ear are presented in this article.

Generations of androgenic plants having a nucleus from a BMS line with nuclear genes *a1 B1 Pl1 R1* and cytoplasms of two different stocks: N-type from line HPL1 - N(HPL1) and T-type from line AT - T(AT) were used in the experiment. From BMS in cytoplasm T(AT), besides the generation of brown coloured plants, the generations of light brown and two green plants were used. The generations of two plants were used from BMS in cytoplasm N (HPL1). All the generations were obtained after pollination by a nucleus donor. The nucleus donor BMS-line was used as control. This line was aligned according to the quantitative traits and plant colour. We have been observing this line for 20 years.

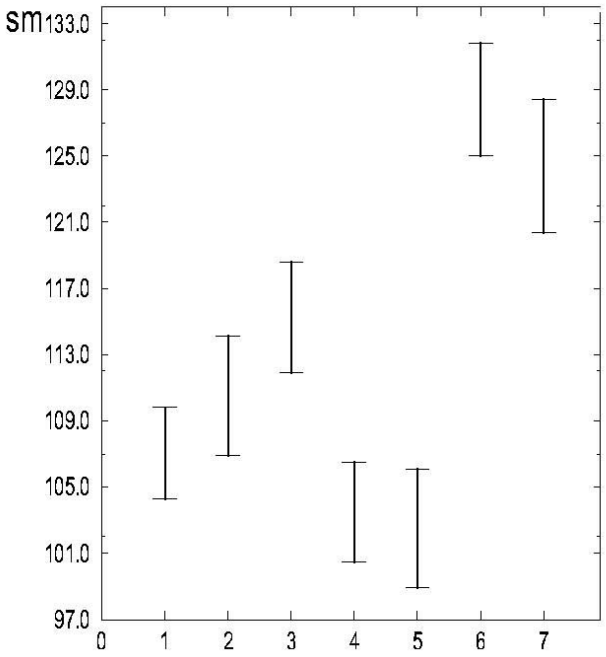

Figure 1. Plant height confidence intervals.

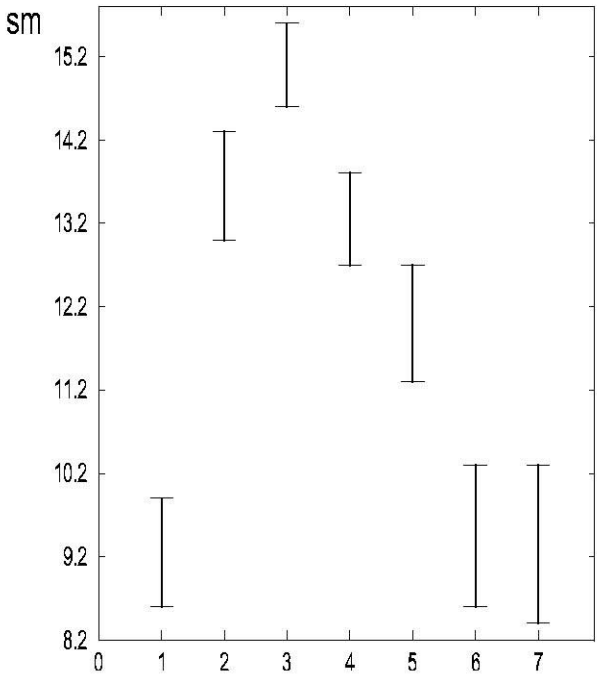

Figure 2. Ear length confidence intervals.

In Figure 1 confidence intervals of plant height, and in Figure 2 confidence intervals of length of the first ear are presented. Both BMS plant generations in cytoplasm N (HPL1) differ greatly by 20-25% according to the height of the plant of the nucleus donor. In the BMS generation in cytoplasm T(AT) we can observe variations in plant height. The generation of light brown plants exceeds by 10% in height the generation of both green plants, which seem to be 5% shorter than plants of the nucleus donor. If we take the length of the ear, the picture is different. BMS in cytoplasm T(AT) differs slightly from the nucleus donor, but BMS in cytoplasm T(AT) in all variants exceeds by 20-50% the nucleus donor. In particular, in the generation of light brown colour plants the ears are 1.5 times greater than the ears of the donor. From this it follows that traits can be altered: they can be reduced and enhanced by the choice of the proper source of cytoplasm.

The results testify to the important role of cytoplasm in the change of most important quantitative traits. They can be useful for revealing the reasons and mechanisms of genome instability, trait variability, and loss of sort quality. Productivity improvement due to cytoplasm is of great interest. It is necessary to discover and study new sources of cytoplasm which can lead to trait change in the necessary direction.

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Modifications in the amino acid content of callus obtained from immature maize embryos under stress conditions

--Urechean, V, Naidin, C

Amino acid composition for callus initiated from immature maize embryos in stress conditions was determined by the Moore and Steine method for an inbred line (W 153R) and a hybrid Lc 15 x L 649 (Table 1).

For the control medium variant (MT), the calli were cultivated for one month on solid medium NBMCo (N_6 - macroelements, Chu, 1978; B_5 - microelements, Gamborg, 1968; MS - vitamins, Murashige-Skoog, 1962) added with: 30 g/l saccharose; 7.0 g/l agar; without hormones; pH = 5.8.

For S_1 the calli were treated with salt solution (5 g/l NaCl) for one hour, then cultivated on the same medium NBMCo for one month.

A_1 - the calli were taken over the solid medium variant A_1 (1 μM ABA) where they were cultivated for one month.

M_2 - the calli were taken over the solid medium variant M_2 (530 mM mannitol) where they were cultivated for one month.

The composition of the culture medium influences both the callus mass (m) and the quantity of amino acids. For the callus belonging to the genotype W 153R, the salt solution S_1 causes both the diminution of the callus mass and a lower percentage content of amino acids. Levels of individual amino acids varied independently. The content of aspartic acid and tyrosine increased obviously and the content of threonine, glycine, and alanine diminished significantly. Other amino acids had little variation. On mannitol medium, although the callus mass is greater, the total content of amino acids is lower (4.39%), and the amino acids' relation with the control variant is very different. The proline was diminished, and glutamic acid, lysine and aspartic acid increased.

Table 1. Modifications in the amino acid content of the callus obtained from immature maize embryos for an inbred line and a hybrid under stress conditions (S_1; A_1;M_2) (mg/100 g dry matter)

AMINO ACID	W 153R				Lc 15 x L 649		
	MT m = 65.6 mg	S_1 m = 51.9 mg	A_1 m = 35.4 mg	M_2 m = 92.9 mg	M_t m = 56.7 mg	S_1 m = 26.6 mg	A_1 m = 29.7 mg
ASPARTIC ACID	417.0	579.0	326.0	718.0	454.0	655.0	385.0
THREONINE	219.0	164.0	207.0	165.0	107.0	136.0	151.0
SERINE	183.0	171.0	198.0	152.0	108.0	145.0	230.0
GLUTAMIC ACID	1026.0	1048.0	690.0	808.0	801.0	892.0	824.0
PROLINE	168.0	159.0	272.0	117.0	167.0	416.0	520.0
GLYCINE	529.0	381.0	257.0	204.0	324.0	371.0	301.0
ALANINE	676.0	309.0	320.0	196.0	249.0	350.0	413.0
METHIONINE	119.0	131.0	142.0	76.0	121.0	131.0	85.0
VALINE	212.0	198.0	200.0	176.0	195.0	345.0	232.0
ISOLEUCINE	141.0	154.0	167.0	145.0	142.0	404.0	191.0
LEUCINE	204.0	188.0	223.0	215.0	200.0	388.0	262.0
PHENYLALANINE	670.0	710.0	287.0	408.0	502.0	552.0	384.0
TYROSINE	321.0	449.0	381.0	373.0	369.0	724.0	450.0
HISTIDINE	190.0	174.0	263.0	153.0	126.0	472.0	291.0
LYSINE	210.0	197.0	219.0	173.0	199.0	438.0	449.0
ARGININE	320.0	351.0	561.0	246.0	324.0	728.0	740.0
CYSTEINE	109.0	125.0	144.0	68.0	113.0	-	59.0
TOTAL AMINO ACIDS %	5.71	5.49	4.86	4.39	4.50	7.15	5.97
PRO/TAA %	2.94	2.90	5.60	2.66	3.71	5.82	8.71
GLU/TAA %	17.97	19.09	14.20	18.40	17.80	12.48	13.80
LYS/TAA %	3.68	3.59	4.51	3.94	4.42	6.13	7.88
ASP/TAA	7.31	10.55	6.71	16.34	10.08	9.16	6.0

PRO - proline; GLU - glutamic acid; LYS - lysine; ASP - aspartic acid; TAA - total amino acids; S_1 - salt solution treatment (1h) - 5 g/l NaCl;
A_1 - 1 μM ABA solid medium; M_2 - 100mM mannitol solid medium

ABA leads to a severe diminution of glutamic acid and to a slight increase of proline and arginine.

In the case of the hybrid genotype Lc 15 x L 649 the results show a different behaviour. The treatment with salt solution leads to a severe diminution of the callus mass, but the total content of amino acids is strikingly higher, and for each amino acid. At the same time, a modification of the relation between the amino acids can be observed, namely glutamic and aspartic acids diminish in comparison with the other amino acids, and lysine and proline levels increase. On the ABA medium there was a significant increase of proline and a diminution of aspartic acid in comparison with the other amino acids.

These results show that the metabolic response of the callus exposed to the stress factors (NaCl, abscisic acid and mannitol) is specific to the genotype.

Metabolic modifications of the reserve substances from the mature maize embryos exposed to in vitro culture conditions

--Urechean, V, Naidin, C

The first reference to the use of the complete mature zygotic embryos as a type of explant to obtain embryogenic callus belongs to Green and collaborators (Crop Science 14:54-58, 1974), who showed the role of meristematic cells placed in the embryo and the culture medium.

In order to induce somatic embryogenesis, we often resort to the supplementation of the culture medium with the organic nitrogen supplied by L-proline (6 - 9 - 12 - 25 mM/l), glutamine (8 - 25 mM/l), glycine (0,1 mM/l) or L - asparagine (0,03 mM/l), depending on the relation between the reducer and the reduced nitrogen.

In order to observe the metabolic high tide of the reserve substances from the explant cultured in vitro and also the accumulation of the amino acids from the callus, we determined the amino acid content of the explanted mature embryos and the various em-

bryogenic callus through the Moore and Steine method (Table 1).

Initiation of the callus was achieved on NBMCd solid medium (N_6 - macroelements, Chu, 1978; B_5 - microelements, Gamborg, 1968; MS - vitamins, Murashige-Skoog, 1962), added with 3.0 mg/l 2,4 D; 30 g/l saccharose; 7.0 g/l agar; pH = 5.8.

To induce somatic embryogenesis, calli were transferred onto $NBMC_3$ solid medium (N_6 - macroelements, Chu, 1978; B_5 - microelements, Gamborg, 1968; MS - vitamins, Murashige-Skoog, 1962), with: 1.0 mg/l kinetin; 30 g/l saccharose; 7.0 g/l agar; pH = 5.8 for 3 weeks.

Dry weight (m) was used to assess the size and development of the callus. We observed significant modifications in the content of each amino acid.

Larger embryo mass is, correlates with a higher percentage content of amino acids:

Lc 15 (m = 20.3 mg) - 11.61 g protein amino acids/ 100 g dry weight;

Lc 464 (m = 17.8 mg) - 10.93 g protein amino acids/ 100 g dry weight.

The amino acid content clearly diminishes at the same time as the callus size as follows:

Lc 3 (m = 21.3 mg) - 10.85 g protein amino acids/ 100 g dry weight;

W 153R (m = 25.7 mg) - 7.31 g protein amino acids/ 100 g dry weight;

Lc 15 (m = 44.1 mg) - 6.25 g protein amino acids/ 100 g dry weight;

Lc 3 x A 188 (m = 72.2 mg) - 4.24 g protein amino acids/ 100 g dry weight.

These findings show that, for growth and differentiation of the callus, an important part of amino acids initially contained in the embryo is consumed. On the other hand, we find that all the analysed calli have lower content of proline, valine, glycine, histidine, lysine and arginine, suggesting that the transformation of these into other amino acids or compounds of a different nature (alkaloids, anthocyanins, hormones, etc). The higher the amino acid content in the explant, the better the chances of a vigorous embryogenic callus capable of supporting the regeneration ability.

On this basis we suggest that the changes in callus amino acids are a sign of metabolic processing and can be used to select callus genotypes with a higher performance in culture. It is evident that a callus obtained from the hybrid (Lc 3 x A 188) explant exhibits heterosis characteristic of the F1 generation even under conditions of in vitro culture.

Table 1. The content in amino acids of the mature embryos and the embryogenic callus obtained from 5 genotypes of maize (Zea mays L.) (mg/ 100 g dry weight).

AMINO ACID	MATURE EMBRYOS		EMBRYO-GENIC CALLUS			
	Lc 15	Lc 464	Lc 3	Lc 15	W 153 R	Lc 3 x A188
	m = 20.3 mg	m = 17.8 mg	m = 21.3 mg	m = 44.1 mg	m = 25.7 mg	m = 72.2 mg
ASPARTIC ACID	674.8	205.0	814.7	958.8	508.8	605.7
THREONINE	271.9	361.0	340.1	198.8	156.3	52.3
SERINE	395.1	473.0	470.2	270.9	270.7	234.5
GLUTAMIC ACID	1239.8	1834.0	1399.2	684.8	1507.0	518.4
PROLINE	1877.5	1336.0	606.6	487.6	336.5	218.0
GLYCINE	496.3	649.0	473.0	330.1	301.0	291.5
ALANINE	448.1	501.0	748.7	316.9	958.6	296.0
METHIONINE	164.1	152.0	205.5	152.9	246.9	140.9
VALINE	650.4	518.0	403.8	206.6	175.1	146.6
ISOLEUCINE	441.7	420.0	698.9	184.6	201.1	115.5
LEUCINE	633.9	564.0	694.8	356.9	391.3	268.0
PHENYLALANINE	724.9	610.0	1309.2	498.5	662.4	350.7
TYROSINE	652.5	651.0	694.3	400.1	502.0	248.2
HISTIDINE	790.5	729.0	482.6	282.1	319.4	180.6
LYSINE	762.4	688.0	576.8	350.8	272.9	227.2
ARGININE	1290.9	1129.0	698.9	443.4	425.7	272.0
CYSTEINE	94.5	107.0	228.8	128.1	72.5	73.5
TOTAL AMINO ACIDS %	11.61	10.93	10.85	6.25	7.31	4.24
PRO/TAA %	16.17	12.22	5.59	7.80	4.60	5.14
GLU/TAA %	10.68	16.78	12.90	10.94	20.62	12.23
LYS/TAA %	6.57	6.29	5.31	5.61	3.73	5.36

PRO - proline; GLU - glutamic acid; LYS - lysine; TAA - total amino acids;

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In vitro colchicine - mediated doubling of corn maternal haploids

--Nedev, T, Gadeva, P, Krapchev, B, Kruleva, M

Experiments have been made with colchicine, dimethyl sulfoxide (DMSO), and Tween 80® (Fluka AG, Buchs SG) to optimize dose treatment combination for double halpoidization (DH) plants. Maternal haploids were derived from dry seeds. Corn genotype, Ig1IRL - 93 - 18/8 - 6 x A 654, was used in this investigation. Seeds were surface sterilized with 70% ethanol, followed by sodium hypochloride solution, washed a few times with autoclaved tap water and transferred onto three variants of artificial medium: colchicine; colchicine plus DMSO; colchicine plus DMSO plus Tween 80®. Different concentrations and different durations for components of variants were examined. Regarding procedures for colchicine preparation, concentration, and treatment duration, please see our publication in Maize Genetics Cooperation Newsletter No 73. After treatment, seeds were rinsed with sterile water and transferred onto medium free of colchicine to promote germination. The ploidy status of the plants obtained was determined by chromosome counting of germinated root tip cells. Experiments performed have shown that variations of chromosome number, including aneuploidy, diploidy and polyploidy were observed. Depending on combination used, different percentages of DH plants were obtained. Considering the total number of cells counted, the colchicine (for the best concentration and treatment duration, please see our publication in Maize Genetics Cooperation Newsletter No 73), DMSO and Tween 80® medium was very effective. The greater frequency of DH plants on the colchicine plus DMSO plus Tween 80® medium is probably due to slow penetration of these substances, which maybe favors and allows more doubling. From our point of view, these results clearly demonstrate the high potential of such treatment in acting as a chromosome doubling agent.

In summary, the results of this study suggest that the combination of colchicine plus DMSO plus Tween 80® optimized chromosome doubling of corn dry seeds of genotype Ig1IRL - 93 - 18/8 - 6 x A 654.

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TAICHUNG, TAIWAN
National Chung Hsing University

A novel structure of the B-10 chromosome of TB-10L6
--Cheng, Y-M, Lin, B-Y

The B chromosome consists of two unequal arms. The long arm comprises, proximal to distal, a centric knob, a proximal euchromatic region, four distal heterochromatic regions (1, 2, 3, and 4) and a distal euchromatic tip (Lin, Genetics 92:931-945, 1979). The B breakpoint of TB-10L6 is located in the proximal euchromatic region (Lin, Genetics 90: 613-627, 1978). Accordingly, the 10-B chromosome contains the distal portion of the proximal euchromatic region, all four heterochromatic regions and the distal euchromatic tip; the B-10 chromosome carries the centric knob and the proximal portion of the proximal euchromatic region. The predicted pachytene structure of heterozygous TB-10L6 is a trivalent with a complete pairing in two arms and no pairing in the third, because the B part of 10-B and B-10 are not homologous.

Such pachytene structure was not observed in this study. Instead, of the 18 cells with a clear standard structure of 10-B and B-10 mentioned above, a T-configuration with two arms completely paired and the third arm partly paired was detected (Figure 1). The distal portions of the proximal euchromatic region of B-10 and heterochromatic region 3 of 10–B pair together (I, Figure 1). This pairing brings the portion of 10L adjacent to the breakpoint and heterochromatic region 2 in close association (II, Figure 1), leaving the unpaired portion of 10L to form a single-strand loop (III, Figure 1). The pairing between two different B parts were documented previously by Longley (Longley, Am. J. Bot. 43:18-22, 1956). He observed in heterozygous TB-9La a pairing between the proximal euchromatic region and the distal euchromatic tip of the B long arm in a reversed fashion, which he termed “dyscentric pairing”. An exchange in the paired region resulted in the formation of a small chromosome carrying the centromeric knob and two tiny euchromatic arms. No such “dyscentric pairing” was observed in this study.

Seven other cells possessed an unexpected heterozygous structure. In those cells, the B-containing arm of the T-configuration had a standard 10-B and an anomalous B-10 which had a complete pairing at the end (I, Figures 2 and 3). The paired portions, identical in both chromosomes, included heterochromatic regions 3, 4, and the distal euchromatic tip, leaving heterochromatic regions 1 and 2 unpaired (II, Figure 3). In other words, the B-10 of these cells did not carry the expected B-structure; i.e., the centric knob and the proximal euchromatic region. Instead, its B-portion covers only heterochromatic regions 3 and 4 but not the centric knob and the proximal euchromatic region.. Such a B-10 structure is reminiscent of an early finding by Lin (Lin, MNL 60:54, 1986). He observed an acentric B-10 chromosome in the hyperploid of TB-10L19 and suggested a premeiotic origin. The current observation seems to be consistent with his supposition. In a premeiotic division, the proximal euchromatic region and heterochromatic region 3 may pair (I, Figure 1), and an exchange in this region would result in an acentric B-10 that carried heterochromatic regions 3 and 4 (I, Figure 3) but not regions 1 and 2 (II, Figure 3). Further work is needed to substantiate this supposition.

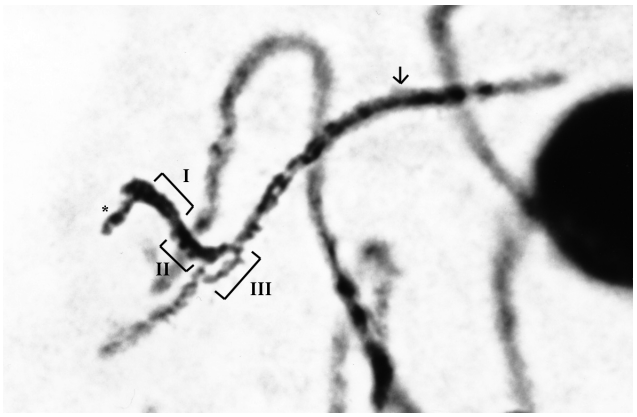

Figure 1. Chromosome pairing of a heterozygous TB-10L6 with an excepted B-10 structure. Arrow, centromere 10; *, the centric knob; I, pairing between heterochromatic region 3 and the proximal euchromatic region; II, association of heterochromatic region 2 with part of 10L; III, unpaired portion of 10L.

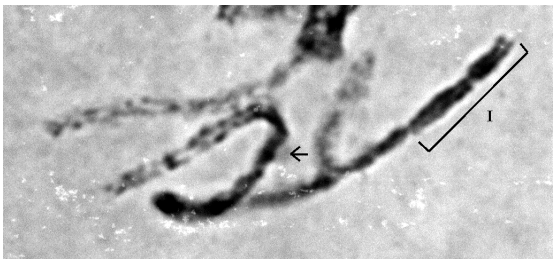

Figure 2. Chromosome pairing of a heterozygous TB-10L6 with an unexpected B-10 structure. Only the distal portion of the B-containing arm is focused. The distal portions of 10-B and B-10 have an identical structure, comprising heterochromatic regions 3, 4, and the distal euchromatic tip. Arrow, centromere 10; I, complete pairing of the heterochromatic regions 3 and 4 plus the distal euchromatic tip of 10-B and B-10.

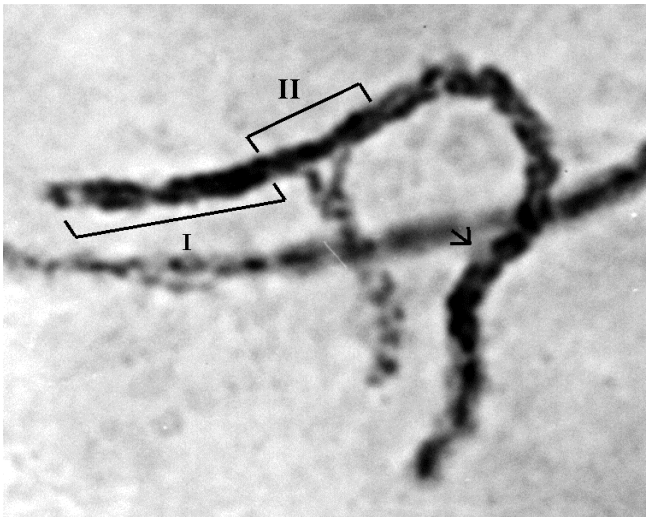

Figure 3. Chromosome pairing of a heterozygous TB-10L6 with an unexpected B-10 structure. All three arms are focused. The distal portions of 10-B and B-10 have an identical structure, consisting of heterochromatic regions 3, 4, and the distal euchromatic tip. Arrow, centromere 10; I, complete pairing of heterochromatic regions 3 and 4 plus the distal euchromatic tip of 10-B and B-10; II, unpaired heterochromatic regions 1 and 2 of 10-B.

Mutual mapping of RFLPs and 33 B-10L translocations

--Cheng, Y-M, Lin, B-Y

Hypoploids and hyperploids, produced by crossing B73 with pollen of B-10L translocations present in the W22 background (Lin, MNL 48: 182-184, 1972), were used to map RFLPs. Because the hypoploid, but not hyperploid, is deficient of the distal portion of 10L, the absence of the paternal signal indicates an RFLP position distal to the breakpoint. By the same rationale, the presence of the paternal signal implies a proximal position. Altogether, 7 RFLPs were analyzed against this set of translocations, and they divide the set into six groups. The most proximal group includes four translocations (TB-10L19, TB-10L26, TB-10L22, and TB-10L7), and the most distal one has a single translocation (TB-10L32) (Figure 1).

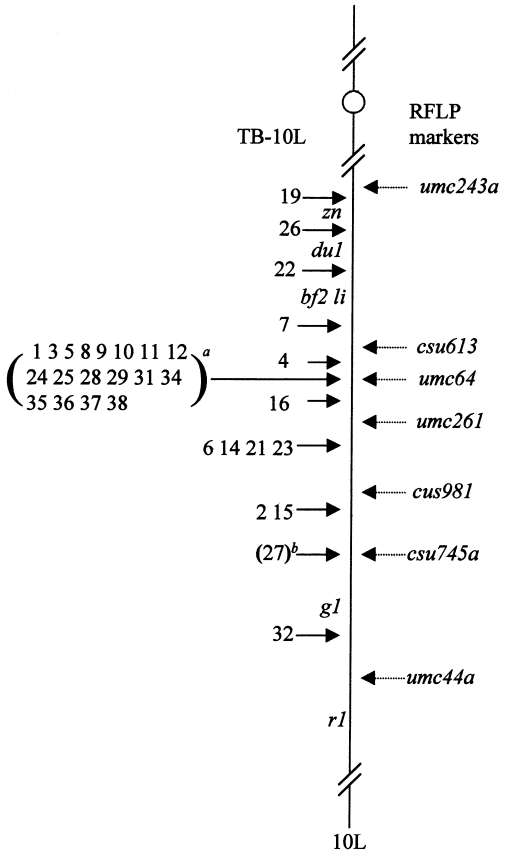

Figure 1. Map position of 33 B-10L translocations. [a, b] indicate that no polymorphic parental signals for *umc64* ([a]) and *csu745a* ([b]) were detected in hyperploids of the translocations in parentheses.

Cytological 10L breakpoint of B-10L translocations

--Cheng, Y-M, Lin, B-Y

Pachytene structure of ten heterozygous B-10L translocations was determined. Three chromosomes (10, 10-B, and B-10) are expected to pair in a T-configuration, and the point where three arms meet is the location of the breakpoint (for details see the separate article of this issue). The break-position is represented by the ratio of the length between the centromere and the breakpoint to that of 10L. Each value is the average of at least three cells. The result conforms to the previously published data on linkage of this region (Lin, MNL 48: 182-184, 1974) with the exception of TB-10L9 and TB-10L12. The linkage data place the two translocations proximal to TB-10L16, but the cytological data place them distal to TB-10L11. Also, the order of the two breakpoints is reversed in the two maps. This discrepancy may be due partly to small sample sizes of the linkage analysis.

Table 1. Cytological breakpoint of ten B-10L translocations

Translocations	Breakpoint on 10L	Average	Lin's data[a]
TB-10L19	0.07, 0.04, 0.07, 0.06	0.06	1.30
TB-10L20	0.08, 0.08, 0.10	0.09	0.98
TB-10L22	0.12, 0.12, 0.09, 0.06, 0.11	0.10	0.98
TB-10L1	0.23, 0.24, 0.20	0.22	0.80
TB-10L16	0.25, 0.34, 0.28	0.29	0.40
TB-10L11	0.29, 0.27, 0.29, 0.37	0.31	0.33
TB-10L12	0.60, 0.40, 0.47	0.49	0.41
TB-10L9	0.55, 0.45, 0.56	0.52	0.61
TB-10L6	0.53, 0.60, 0.58, 0.59	0.58	0.32
TB-10L21	0.72, 0.77, 0.68, 0.69, 0.73	0.72	0.30

[a] recombination ratio of breakpoint-*R*/ *g-R* (from Lin, 1974)

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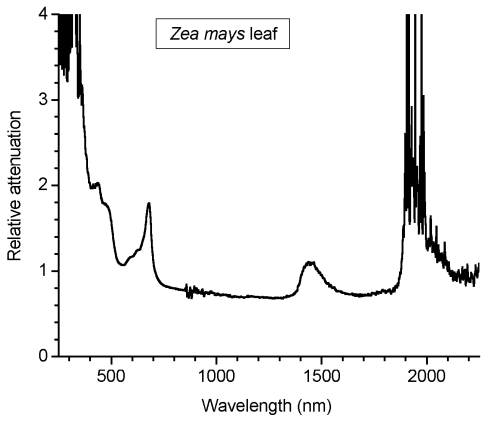
Optical density of leaf

--Lin, B-L, Cheng, P-c, Sun, C-K

Recent development in laser technologies offers a number of wavelength choices in multi-photon fluorescence and harmonic generation microscopy. In order to assist in the selection of excitation wavelengths and suitable fluorescent probes, we measured the light attenuation of leaf in the spectral range of 250-2250nm. The spectrum covers UV, visible and extended IR range to include the emission wavelengths of Ti-sapphire (800nm), Nd-glass (1064nm), Cr-forsterite (1270nm), Cr-YAG (1500nm), Er-glass (1550nm) and other ultra-fast IR lasers, as well as the emission wavelengths of harmonic generations (second and third harmonic) and fluorescence probes. A Hitachi spectrometer equipped with a scattered light integrator was used in this study to measure the attenuation of maize leaf (field grown mature leaf). Therefore, the attenuation spectrum is mainly the result of



absorption properties of leaf with minimum scattering contribution. In order to minimize the scattering contribution due to air spaces in the mesophyll, water logged leaf was used in the measurement.

The Figure shows the attenuation spectrum (Cheng et al., SPIE Proceedings, vol. 4262) of maize leaf. Note the high attenuation in UV as the result of proteins and other organic compounds. The attenuation in the blue and red spectral region is the result of chlorophylls and other photosynthetic pigments. The attenuation in the IR range (>1400nm) is mainly due to the presence of water in the leaf tissue. The translucent window of maize leaf suitable for light microscopy is within the spectral range of 350-1400nm.

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TALLAHASSEE, FLORIDA
Florida State University

Tom Thumb, a useful popcorn

--Bass, HW, Kang, LC, Eyzaguirre, A

We have been working with an extra-early yellow popcorn for several years and report here on some of the desirable attributes of this variety called Tom Thumb. Tom Thumb can be propagated by self or open pollination and appears to be a stable inbred. We have adopted Tom Thumb as one of our regular "'lab rats" because of its 1) extremely rapid life cycle, 2) tolerance to greenhouse growth throughout the year in Tallahassee, 3) uniformity of growth habit, and 4) good seed set as shown in Figure 1. The seed are available from the Maize Stock Center, but we routinely work with seed purchased from Johnny's Selected Seeds (johnnyseeds.com, Albion ME). As stated in their 2001 home garden catalog entry on Tom Thumb, "85 days, extra-early, yellow popcorn. Refined from a genuine New Hampshire heirloom by the late Prof. E. M. Meader, University of New Hampshire and Johnny's Selected Seeds. Matures even in the Far North. The plants are dwarf, only 3 1/2' tall, and bear 1 or 2 ears 3-4" long." We counted the leaf bearing nodes for plants (n=43) from the Fall 2000 greenhouse. Node number ranged from 8 to 11 with a mean of 10.

The plants are almost too quick and small for summer fields. They can be grown indoors in small pots at high density with relatively little supplemental lighting. The plants usually produce tillers that can be cut back to assist shoot capping on the main stalk. Tom Thumb offers a number of advantages as an experimental or educational line of maize. For instance, a seed mutagenesis experiment can produce dominant mutations (plant or seed) during a single academic quarter or semester. Also, Tom Thumb might be good for production of transgenic maize using genotype-independent protocols.

We are currently breeding meiotic mutations into the Tom Thumb background for use in our work on meiotic telomere functions. We have examined the pollen mother cells and found them to be suitable for FISH and immunocytochemical analysis of meiotic prophase. Figure 2 shows that telomeres and several knobs can be detected by 3D FISH carried out as previously described (Bass et al., J. Cell Biol., 137:5-18).

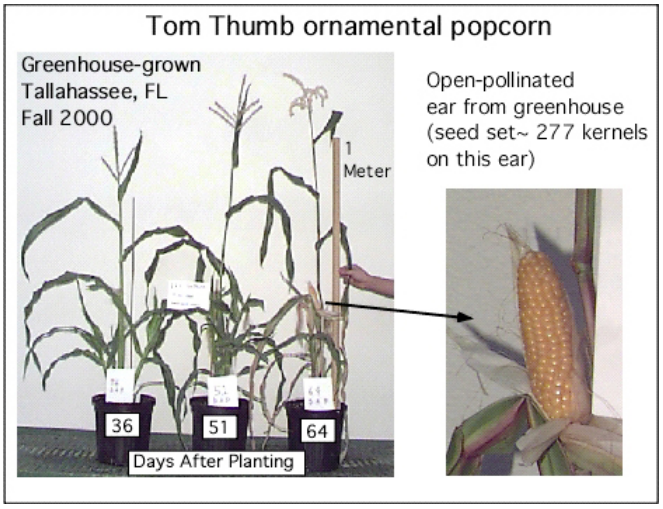

Figure 1.

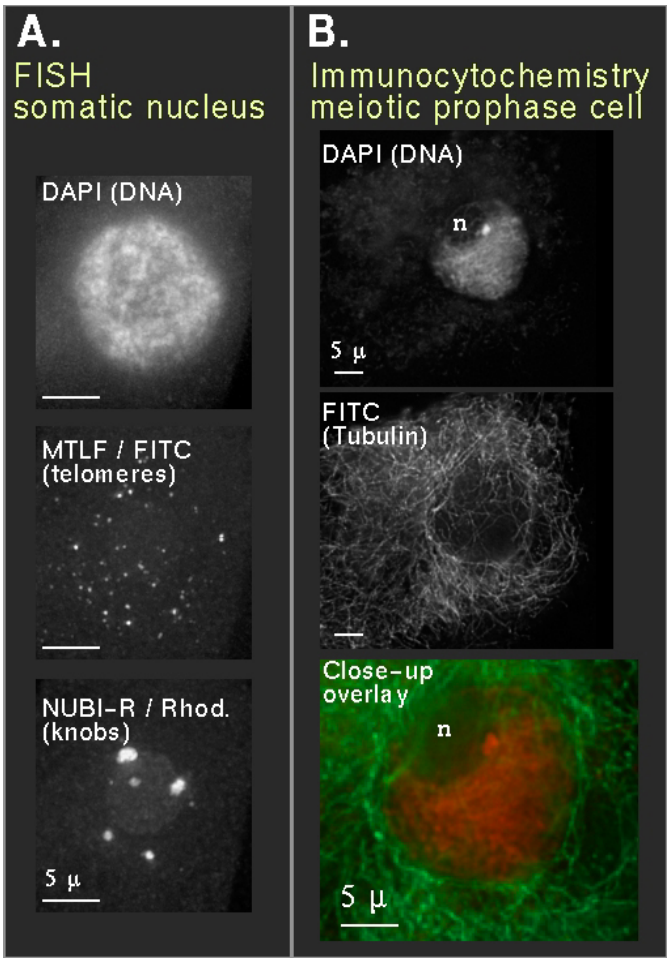

Figure 2.

We are collecting size-staged anthers of green-house grown Tom Thumb plants. The size classes are "A" < 0.5 mm; "B" 0.5-1.5 mm; "C" 1.5-2.5 mm; and "D" 2.5-3.5 mm. Figure 3 shows DAPI images of representative meiotic nuclei from A, B, and C size classes which contain anthers from premeiotic interphase plus early leptotene, leptotene plus zygotene, and zygotene plus

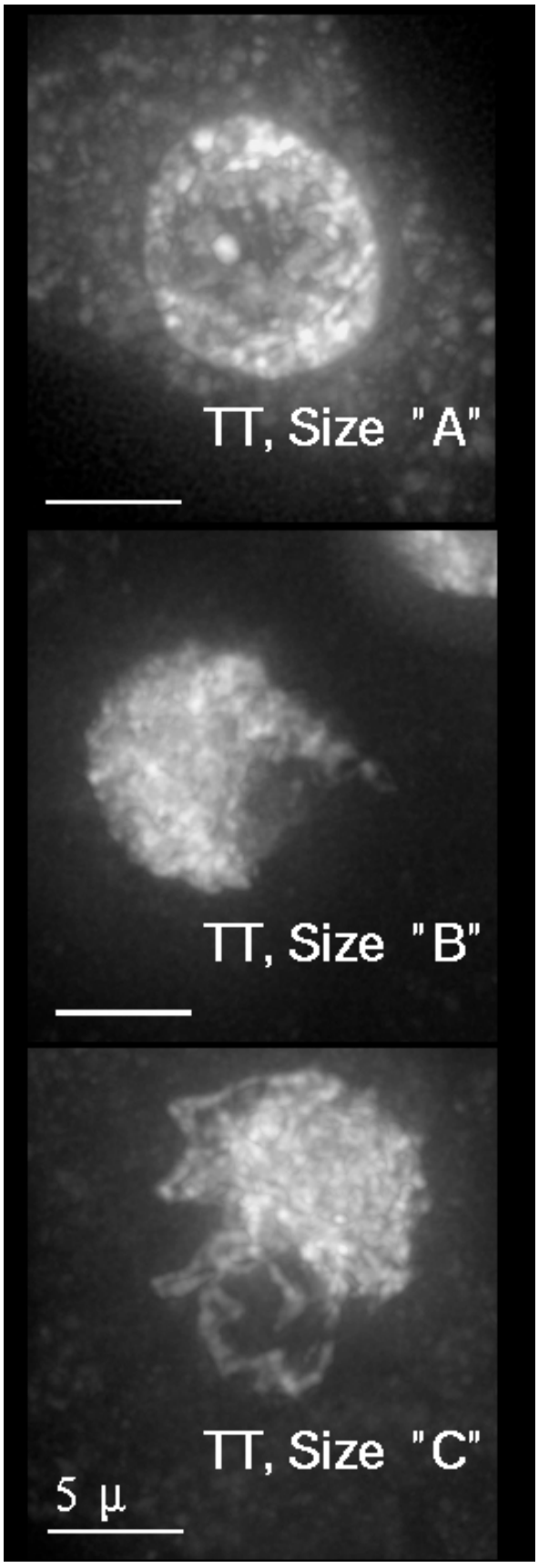

Figure 3.

pachytene, respectively. These anthers will provide mRNA preparations for microarray analysis of meiotic gene expression. Anthers from the larger floret are dissected in the greenhouse, measured on a ruler under a dissecting microscope, and frozen. Anthers are collected for four months at a time, then a new set of collections is started. Those shown in Figure 3 are from the first trimester of 2000 (Jan-April).

Variable distribution of meiotic homologs; on-line spinning projections of 3D data from chromosome painting and telomere FISH analysis of OMAd9.2

--Bass, HW, Bordoli, SJ

We have developed a 3D FISH system to study meiotic telomere behavior and homologous chromosome interactions during meiotic prophase (Bass et al., 1997, J. Cell Biol., 137:5-18). In a recent chromosome painting study, the 3D intranuclear distribution of homologs was characterized in pollen mother cells before and during meiotic prophase (Bass et al., 2000 J. Cell Sci. 113:1033-1042). Examination of deconvolution image data revealed a surprising diversity of homolog arrangements and dispositions, relative to each other, and relative to the position of the telomere cluster-defined bouquet. In particular, many bouquet-stage nuclei (mostly at zygotene) contained spatially separated homologs. This observation, along with the published measurements of interhomolog distances in well-preserved nuclei indicate that premeiotic pairing does not contribute much, if anything, to the zygotene synapsis that is required for proper homolog disjunction. Thus, the homology search appears to function during meiotic prophase, after chromosomes have reorganized into condensed and extended fibers, and largely coincident with the bouquet stage when the telomeres are clustered on the nuclear envelope.

Computer-assisted inspection of the 3D data conveys a great deal of information. In order to make the visual data more accessible, we have prepared an on-line supplemental data page for some of the meiotic nuclei analyzed by Bass et al., (2000). The web page, http://bio.fsu.edu/~bass/mv/bq2/, contains a table with links to Quicktime movies that can be downloaded or viewed with web browsers. For each movie, projections of the FISH signals are shown for the telomeres (purple) and the maize-9 homologs (green). The DAPI image, which marks the entire nucleus (42 oat plus 2 maize chromosomes), was omitted. Each movie is made from a cropped down cube of data in which a single spherical nucleus is centered.

This form of data display may be useful to researchers and educators who are interested in the native structure of meiotic chromosomes and the function of the telomere bouquet. The movies convey some of the spatial and topological aspects of meiotic chromosome pairing and synapsis. The original data are archived as DeltaVision image data (A.P.I. Seattle, WA) and the optical sections can be distributed as grey scale TIFF files upon request from HWB (bass@bio.fsu.edu).

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Novartis Seeds

Quantitative effects of loci *p1* and *a1* on the concentrations of maysin, apimaysin, methoxymaysin, and chlorogenic acid in maize silk tissue

--Guo, BZ, Zhang, ZJ, Butron, A, Widstrom, NW, Snook, ME, Lynch, RE, Plaisted, D

Among the natural products synthesized through the phenylpropanoid/flavonoid pathway in maize silk are C-glycosyl flavones, including maysin, apimaysin and methoxymaysin, and the phenylpropanoid chlorogenic acid which are antibiotic to corn earworm (Waiss et al., J. Econ. Entomol. 72:256-258, 1979; Elliger et al., Phytochemistry 19:293-297, 1980). Maysin concentration in maize silks is genetically controlled by quantitative trait loci (QTLs) including some of the well characterized flavonoid pathway genes such as *p1* and *a1*, and some relatively poorly understood loci as revealed by DNA markers (e.g. Styles & Ceska, Can. J. Cytol. 19:289-302, 1977; Styles & Ceska, Maydica 34:227-237, 1989; Byrne et al., PNAS 93:8820-8825, 1996; McMullen et al., PNAS 95:1996-2000, 1998; Grotewold et al., Plant Cell 10:721-740, 1998; Guo et al., J. Econ. Entomol., in press, 2001). The functional allele at the *p1* locus encodes a Myb- homologous protein that can bind to and activate transcription of the *a1* gene, as well as regulate the transcription of some other flavonoid pathway genes (Grotewold et al., Plant Cell 10:721-740, 1998; Bruce et al., Plant Cell 12:65-79, 2000). Homozygous recessive *a1* plus a dominant *p1* factor can enhance the accumulation of C-glycosyl flavones in silk tissue (Styles & Ceska, Can. J. Cytol. 19:289-302, 1977; Styles & Ceska, Maydica 34:227-237, 1989; Guo et al., J. Econ. Entomol., in press, 2001). Apimaysin is highly related to maysin structurally, differing only by a 3'-hydroxyl group (apimaysin 3'-H, maysin 3'-OH). It had been assumed that apimaysin and maysin share the same structural enzymes, except flavonoid 3'-hydroxylase, and require the same pools of metabolic precursors. However, Lee et al. (Genetics 149:1997-2006, 1998) suggested that the synthesis of apimaysin and maysin occurs independently. An apimaysin QTL did not affect maysin synthesis and a maysin QTL did not affect apimaysin synthesis in a F2 population (Lee et al., Genetics 149:1997-2006, 1998). Genetic mechanisms underlying the concentration of chlorogenic acid in maize silk are unknown. In cultured maize cells, Grotewold et al. (Plant Cell 10:721-740, 1998) observed a compound that was indistinguishable from chlorogenic acid in UV absorption spectrum. This compound accumulated when *p1* was expressed, suggesting that *p1* expression can affect the level of chlorogenic acid.

In the study presented here, we report further details about the quantitative genetic control over maysin, apimaysin and methoxymaysin, and chlorogenic acid. In particular, our results support the suggestion (Grotewold et al., 1998) that *p1* regulates the gene(s) required for the synthesis of chlorogenic acid. We present the evidence that the patterns of effects of *p1* and *a1* on apimaysin and methoxymaysin were very similar or identical to those on maysin in the (GE37 x 565) F2 population. We also detected two chromosome regions near RFLP markers *npi409* on the short arm of chromosome 5 and *umc132a* on the long arm of chromosome 6, respectively, which showed contrasting association with maysin and apimaysin and methoxymaysin, indicating that the syntheses of these flavonoids occur independently (Lee et al., Genetics 149:1997-2006, 1998).

The F2 population was derived from the cross between the inbred lines GE37 and 565. Inbred GE37 is a dent corn with a high concentration of C-glycosyl flavones (maysin, apimaysin and methoxymaysin) and chlorogenic acid in silk tissues. Inbred 565 is a *sh2*-sweet corn with essentially no C-glycosyl flavones and a low concentration of chlorogenic acid in silk tissues (Guo et al., J. Econ. Entomol. 92:746-753, 1999). The allelic constitution at the *p1* locus is *P1-wrb* (white pericarp, red cob, browning silk) for GE37 and *p1-www* (white pericarp, white cob, non- browning silk) for 565. Our testcrosses with an *a1* tester stock indicated that GE37 has functional *A1* allele and 565 has a non-functional *a1* allele at the *a1* locus. The 304 F2 plants used in this study were derived from two self-pollinated F1 plants, 142 plants from one F1 and 162 plants from the other. Leaf tissue was collected from F2 individuals, and from GE37, 565 and F1 at the mid-whorl stage for DNA preparation. The collected silks were prepared for extraction of maysin, apimaysin and methoxymaysin, and chlorogenic acid. The concentrations of these chemicals was determined by reverse-phase HPLC, and expressed as percent fresh silk weight. Apimaysin and methoxymaysin were not separately measured, instead they were measured together in mixture. Hereafter, we abbreviate the apimaysin and methoxymaysin as am-maysin. One hundred and two DNA probes were screened against the DNA samples of GE37, 565 and (GE37 x 565) F1 digested with the 13 enzymes of *Apa*I, *BamH*I, *Bgl*II, *Csp45*I, *Dra*I, *EcoR*I, *EcoR*V, *Hind*III, *Pst*I, *Sal*I, *Ssp*I, *Xba*I and *Xho*I. Probes which were polymorphic were used for genotyping F2 individuals.

Distribution of F2 individuals over concentration of flavones (maysin or am-maysin) showed that a large number of individuals had an extremely low concentration of the flavones (white bars in Figures 1 and 2). To further analyze the distribution patterns, we examined only F2 individuals that were heterozygous at the *p1* locus. The distribution of the *p1*-heterozygous individuals showed the absence of a large number of individuals with extremely low flavone concentration (black bars in Figures 1 and 2). All of the individuals with extremely low flavone (but not chlorogenic acid) concentration (white bars in Figures 1 and 2) were homozygous for the *p1* allele from parent 565, and the number of these individuals was about 1/4 of the whole population (86/304 for maysin and 83/304 for am-maysin). Few F2 individuals had an extremely low concentration of chlorogenic acid (Figure 3). In all cases, a significant number of individuals were observed with higher chemical concentration than that of GE37, indicating a transgressive segregation occurred. The chromosome positions of *p1*, *a1*, *npi409* and *umc132a* were confirmed on the short arm of chromosome 1, the long arm of chromosome 3, the short arm of chromosome 5 and the long arm of chromosome 6, respectively, by using MAPMAKER/EXP 3.0. In expressing the association between loci and chemical concentrations, multi-locus models were constructed in a stepwise way to best explain variation for chemical concentrations. The significant locus (*p1*) that had the highest R^2 was included in the modelling. Then each of the remaining loci or markers was added, resulting in two-locus models from which the one was selected that had the highest R^2 and in which both loci (*p1* and *a1*)

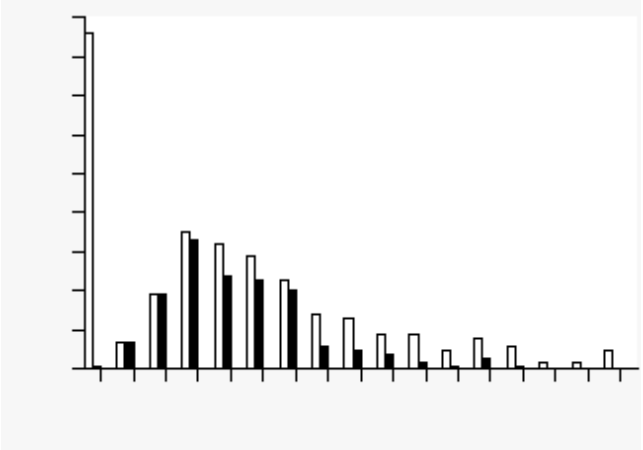

Figure 1. Frequency distribution of silk maysin concentrations in F2 population of (GE37 x 565). Black bars represent the F2 individuals that were heterozygous at the *p1* locus. White bars represent the total 304 F2 individuals that were homozygous or heterozygous at the *p1* locus.

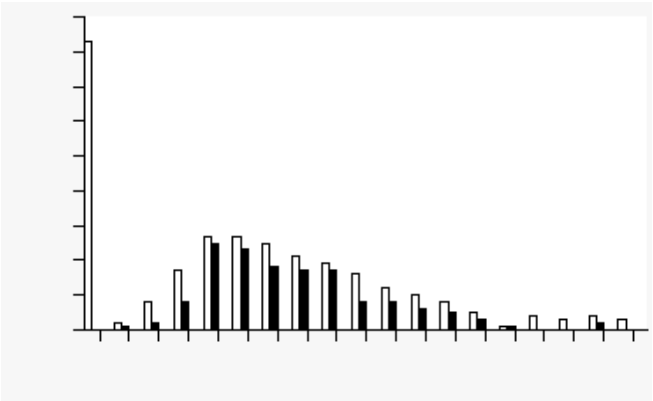

Figure 2. Frequency distribution of silk apimaysin and methoxy maysin maysin concentrations in F2 population of (GE37 x 565). Black bars represent the F2 individuals that were heterozygous at the *p1* locus. White bars represent the total 304 F2 individuals that were homozygous or heterozygous at the *p1* locus.

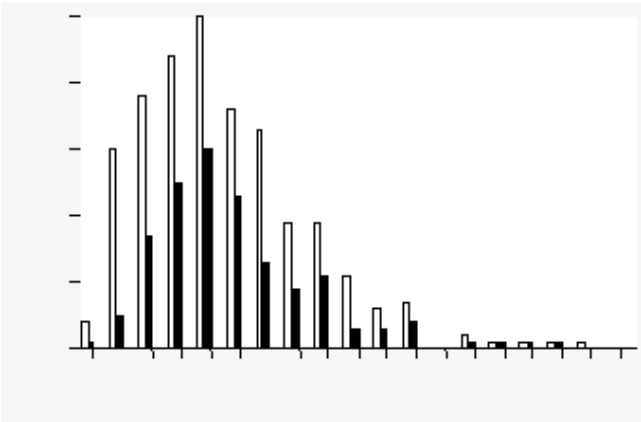

Figure 3. Frequency distribution of silk chlorogenic acid concentrations in F2 population of (GE37 x 565). Black bars represent the F2 individuals that were heterozygous at the *p1* locus. White bars represent the total 304 F2 individuals that were homozygous or heterozygous at the *p1* locus.

were significant. The interaction between the two loci (*p1* and *a1*) was added to the model and it was observed that all three terms (*p1*, *a1* and *p1* x *a1*) in the model were significant (P<0.01). Each of the remaining loci or markers was added to the model, resulting in three-locus models from which one was selected that had the highest R^2 and in which all terms (*p1*, *a1*, *p1*x*a1* and *npi409*) were significant. Interaction between *npi409* and *p1* or *a1* was not found to be significant. Due to the limited population size (304 individuals), three-way interaction was not tested, and no other locus or marker could be added to the model at 0.01 level. Therefore, for maysin the best multi-locus model included *p1*, *a1*, *npi409* and *p1*x *a1*, accounting for 61.0%, 6.4%, 1.3% and 1.7%, respectively, and 70.4% in total of maysin variation (Table 1). Using the same procedure, the best multi-locus models were constructed for am-maysin and chlorogenic acid (Table 1). For am-maysin, the best multi-locus model included *p1*, *a1*, *umc132a* and *p1*x*a1*, accounting for 64.5%, 8.4%, 1.0% and 2.1%, respectively, and 76.0% in total of am-maysin variation. For chlorogenic acid, the best multi-locus model included *p1* and *a1*, accounting for 12.5% and 4.7%, respectively, and 17.2% in total of chlorogenic acid variation.

We noticed that *npi409* was included in the best multi-locus model for maysin, whereas *umc132a* was included in the best multi-locus model for am-maysin. To further show the associations of *npi409* and *umc132a* with maysin and am-maysin levels, four-locus models including *p1*, *a1*, *npi409* and *umc132a* were constructed for both maysin and am-maysin (Table 2). In the four-locus model for maysin, *npi409* had significant association (*P* = 0.0059) with maysin, while *umc132a* had nearly no association (*P* = 0.7389) with maysin. However, in the four-locus model for am-maysin *npi409* had nearly no association (*P* = 0.4829) with am-maysin, while *umc132a* had significant association (*P* = 0.0062) with am-maysin. Interactions involving *npi409* or *umc132a* were not significant (data not shown) in these four-locus models.

Table 1. Multi-locus models of flavonoid pathway loci or associated RFLP markers that best explained the variation for maysin, apimaysin and methoxymaysin, and chlorogenic acid concentration in the F2 population of (GE37 x 565).

Locus/RFLP marker or interaction	Chromosome location[a]	Significance	$R^{2\,b}$	Parent contributing higher value allele
Maysin				
p1	1S	*P* < 0.0001	61.0	GE37
a1	3L	*P* < 0.0001	6.4	565
npi409	5S	*P* = 0.0027	1.3	565
p1 x *a1*		*P* = 0.0043	1.7	
Total			70.4	
Apimaysin and methoxymaysin				
p1	1S	*P* < 0.0001	64.5	GE37
a1	3L	*P* < 0.0001	8.4	565
umc132a	6L	*P* = 0.0062	1.0	GE37
p1 x *a1*		*P* = 0.0002	2.1	
Total			76.0	
Chlorogenic acid				
p1	1S	*P* < 0.0001	12.5	GE37
a1	3L	*P* = 0.0005	4.7	GE37

[1] The 1, 3, 5 and 6 are chromosome number. S and L represent short arm and long arm of the chromosome, respectively.
[2] Percent chemical variation explained.

Table 2. Contrasting associations of *npi409* and *umc132a* with maysin or apimaysin and methoxymaysin in (GE37 x 565) F2 population.

Locus/RFLP marker or interaction	Maysin	Apimaysin and methoxy-maysin
npi409	*P* = 0.0059	*P* = 0.4829
ucm132a	*P* = 0.7389	*P* = 0.0062
p1	*P* < 0.0001	*P* < 0.0001
a1	*P* < 0.0001	*P* < 0.0001
p1 x *a1*	*P* = 0.0042	*P* = 0.0002

At the *p1* locus, mean maysin concentrations were 1.018%, 0.554% and 0.003% fresh silk weight for homozygous GE37, heterozygous GE37/565, and homozygous 565, respectively (Table 3), indicating that the effect of *p1* on maysin was additive. At the *a1* locus, the mean of the 565 homozygous class was higher than those of GE37/565 heterozygous and GE37 homozygous classes for both maysin and am-maysin concentrations, while there was no significant difference between the means of GE37/565 heterozygous and GE37 homozygous classes, indicating that *a1* acts in recessive mode for high maysin and am-maysin. On chlorogenic acid *a1* showed an additive effect. The genotype class means of *p1* x *a1* interaction showed that *a1* increases maysin or am-maysin concentrations only when the *a1* allele from 565 is homozygous and at least one *p1* allele from GE37 is presented. The *npi409* marker represents a locus that acts in recessive mode for high maysin, i.e. the mean of 565 homozygous class (0.620) was significantly higher than those of GE37 homozygous (0.471) or GE37/565 heterozygous (0.484) classes. The *umc132a* marker represents a locus that acts in an additive mode for am-maysin.

The F2 population of (GE37 (565) showed polymorphism at both the *p1* and *a1* loci, in contrast to the F2 population of (GT114 (GT119) reported by Byrne et al. (PNAS93:8820- 8825, 1996) that did not show polymorphism at the *a1* locus. Using an F2 population derived from SC102 (high maysin dent corn) and B31857 (low maysin *sh2* sweet corn) parents, Guo et al. (J. Econ. Entomol. in press, 2001) reported that *p1* was not polymorphic in this population. A flanking marker *npi286* to *p1* corresponded with 25.6% of the silk maysin variance and *a1* (accounted for 15.7% of the silk maysin variance) in this population (Guo et al., 2001). In the study reported here, we found further details about the roles of *p1*, *a1*, and the interaction between *p1* and *a1* in quantitatively genetic control over maysin, am-maysin, and chlorogenic acid, as well as confirmed that *p1* and *a1* are major QTLs controlling maysin concentration. Our results confirm the report by Grotewold et al. (1998) that *p1* regulates the gene(s) required for the synthesis of chlorogenic acid. We present evidence that maysin and am-maysin synthesis share genes, including *p1* and *a1* in the (GE37 (565) population, in contrast to results with the population of (GT114 (NC7A) reported by Lee et al. (1998) in which the syntheses of apimaysin and maysin occurred independently. In addition, we detected two chromosome regions near RFLP markers *npi409* on the short arm of chromosome 5 and *umc132a* on the long arm of chromosome 6, respectively, which showed contrasting associations with maysin and am-maysin, indicating that the syntheses of these flavonoids are independent.

Table 3. Levels of maysin, apimaysin and methoxymaysin, and chlorogenic acid in the F2 population of (GE37 x 565).

Locus/RFLP marker or interaction	Genotype[1]	Maysin (% silk fresh weight)	Apimaysin and methoxymaysin (% silk fresh weight)	Chlorogenic acid (% silk fresh weight)
p1	A	1.018a[2]	0.111a	0.066a
	H	0.554b	0.079b	0.055b
	B	0.003c	0.007c	0.037c
a1	A	0.460a	0.057a	0.065a
	H	0.423a	0.055a	0.052b
	B	0.692b	0.085b	0.041c
npi409	A	0.471a		
	H	0.484a		
	B	0.620b		
umc132a	A		0.076a	
	H		0.066b	
	B		0.055c	
p1 *a1*	A A	0.808a	0.105a	
	A H	0.847a	0.087a	
	A B	1.299b	0.141b	
	H A	0.465a	0.069a	
	H H	0.428a	0.063a	
	H B	0.769b	0.106b	
	B A	0.007a	0.006a	
	B H	0.006a	0.005a	
	B B	0.008a	0.009a	

*A, B and H represent homozygotes for the GE37 allele, homozygotes for the 565 allele, and heterozygotes, respectively.
** Significant level is $P < 0.01$. Within each group of comparisons, means followed by the same letter are not significantly different.

URBANA, ILLINOIS
Maize Genetics Cooperation • Stock Center

Allelism testing of miscellaneous stocks in Maize COOP phenotype only collection

--Jackson, JD

This report summarizes allele testing of miscellaneous stocks characterized by phenotype only, in the Maize Genetics COOP Stock Center collection. Some of these mutants have been found in other COOP stocks and some have been sent in by cooperators over the years. In most cases crosses were made between known heterozygotes and homozygous plants. Plants were scored at the seedling stage and again at maturity. Proposed new designations have been assigned to these alleles. The stocks with positive tests have been increased and placed on the 2001 stocklist. It is expected that with further sorting and allelism testing of mutations characterized by phenotype only, additional alleles of characterized mutants will be discovered and placed in the main collection.

previous designation	allelism test with *ws3*	allelism test with *g1*	allelism test with *g2*	new designation
v-N2260*	negative: (+/v*) x *ws3*; *v** x *ws3*	negative	negative	--

previous designation	allelism test with *zn2*	allelism test with *zb1*	allelism test with *zb4*	new designation
zn-4-6(4461)*	positive: *zn2* x *zb**	----	----	*zn2*-4-6(4461)
zb-94-234*	positive: (+/*zb**) x *zn2*; *zn2* x *zb**	negative	negative	*zn2-94-234:* MGCSC stock number: U140I

note: *zn2-94-234* from *ub1* stock

previous designation	allelism test with *ra1*	allelism test with *ra2*	new designation	MGCSC: stock number
ra-PI184279*	positive: (+/*ra**) x *ra1*	negative	*ra1-PI184279*	708AB
ra-PI239103*	positive: (+/*ra**) x *ra1*	negative	*ra1-PI239103*	708AC
ra-PI267181***	positive: (+/*ra**) x *ra1*	negative	*ra1-PI267181*	708AD
ra-PI267184*	positive: (+/*ra**) x *ra1*	negative	*ra1-PI267184*	708AE
ra-63-3359*	positive: (+/*ra**) x *ra1*	negative	*ra1-63-3359*	*708AF*

ra-D*	negative: *(+/ra*)* x *ra1*	positive: *(+/ra*) x ra2*	*ra2-D*	308G
ra-412*	negative: *(+/ra*)* x *ra1*	negative: *(+/ra*) x ra2*	--	--

note: tassels of all new *ra1* alleles have good ramosa phenotype. Ears of *ra1-Pl* alleles have extreme ramosa phenotype.
**: *gs1-Pl267181* may segregate in this stock.

previous designation	allelism test with *gs1*	new designation	MGCSC: stock number
gs-Pl267181*	positive: *(gs1* x *gs*)*	*gs1-Pl2671811***	109C

note: *ra1-Pl267181* may segregate in this stock.

previous designation	allelism test with *ij1*	new designation	MGCSC: stock number
str-60-2454-20*	positive: *(+/ij1)* x *str**	*ij1-60-2454-20*	711C

Additional linkage tests of non-waxy (*Waxy1*) reciprocal translocations involving chromosome 9 at the MGCSC

--Jackson, JD, Stinard, P, Zimmerman, S

Approximately one acre each year is devoted to the propagation of the large collection of A-A translocation stocks. In this collection is a series of *Waxy1*-linked translocations that are used for mapping unplaced mutants. Each translocation is maintained in separate M14 and W23 inbred backgrounds which are crossed together to produce vigorous F1's to fill seed requests. Over the years, pedigree and classification problems arose during the propagation of these stocks. We have been able to sort through the problem ones, and can now supply good sources proven by linkage tests to include the correct translocated chromosomes.

Previously we reported the linkage results for some of these stocks (MNL72:79-81; MNL73:86-88; MNL74:67). Below is a summary of additional translocation stocks we have completed testing.

Table 1. *Wx1* T4-9b (4L.90; 9L.29)

A) The F1 source showed linkage of *wx1* with *c2*.

2 point linkage data for *c2-Wx1* T4-9b
Testcross: [*C2 Wx1* T4-9b x *c2 wx1* N] x *c2 wx1* N

source: 87-998 x 996^F1

Region	Phenotype	No.	Totals
0	+ Wx	829	
	cl wx	1039	1868
1	cl Wx	100	
	+ wx	287	387

% recombination *c2-wx1*= 17.2 ±0.8

Table 2. *Wx1* T6-9(4505) (6L.13; 9ctr.)

A) The F1 source showed linkage of *wx1* with *y1*:

2 point linkage data for *Y1-Wx1* T6-9(4505)
Testcross: [*Y1 Wx1* T6-9(4505) x *y1 wx1* N] x *y1 wx1* N

source: 87-1027 x 1025 ^F1

Region	Phenotype	No.	Totals
0	+ Wx	1391	
	y wx	1468	2859
1	y Wx	204	
	+ wx	187	391

% recombination *y1-wx1* = 12.0±0.6

Table 3. *Wx1* T7-9a (7L.63; 9S.07)

A) The F1 source showed linkage of *wx1* with *gl1*:

2 point linkage data for *gl1-Wx1* T7-9a
Testcross: [*Gl1 Wx1* T7-9a x *gl1 wx1* N] x *gl1 wx1* N

source: 87-1038 x 1036^F1

Region	Phenotype	No.	Totals
0	+ Wx	955	
	gl wx	846	1801
1	gl Wx	186	
	+ wx	173	359

% recombination *gl1-wx1* = 16.6±0.8

Table 4. *Wx1* T8-9d (8L.09; 9L.16)

A) The M14 source showed linkage of *wx1* with *v16*:

2 point linkage data for *v16-Wx1* T8-9d
Testcross: [*V16 Wx1* T8-9d x *v16 wx1* N] x *v16 wx1* N

source: 888-999-1001 x same bulk #1^M14

Region	Phenotype	No.	Totals
0	+ Wx	263	
	v wx	221	484
1	v Wx	141	
	+ wx	133	274

% recombination *v16-wx1*=36.1±1.7

B) The W23 source showed linkage of *wx1* with *v16*:

2 point linkage data for *v16-Wx1* T8-9d
Testcross: [*V16 Wx1* T8-9d x *v16 wx1* N] x *v16 wx1* N

source: 82-157-2@^W23

Region	Phenotype	No.	Totals
0	+ Wx	575	
	v wx	521	1096
1	v Wx	239	
	+ wx	189	428

% recombination *v16-wx1*=28.1±1.2

Table 5. *Wx1* T8-9(6673) (8L.35; 9S.31)

A) The M14 source showed linkage of *wx1* with *v16*:

2 point linkage data for *v16-Wx1* T8-9(6673)
Testcross: [*V16 Wx1* T8-9(6673) x *v16 wx1* N] x *v16 wx1* N

source: 87-1715-1 x sib^M14

Region	Phenotype	No.	Totals
0	+ Wx	554	
	v wx	428	982
1	v Wx	139	
	+ wx	182	321

% recombination *v16-wx1*=24.6±1.2

B) The W23 source showed linkage of *wx1* with *v16*:

2 point linkage data for *v16-Wx1* T8-9(6673)
Testcross: [*V16 Wx1* T8-9(6673) x *v16 wx1* N] x *v16 wx1* N

source: 87-1716-1 x sib^W23

Region	Phenotype	No.	Totals
0	+ Wx	445	
	v wx	375	820
1	v Wx	208	
	+ wx	186	394

% recombination *v16-wx1*=32.5±1.3

Additional linkage tests of *waxy1* marked reciprocal translocations at the MGCSC

--Jackson, JD, Stinard, P, Zimmerman, S

In the collection of A-A translocation stocks maintained at MGCSC is a series of *waxy1*-linked translocations that are used for mapping unplaced mutants. Also new *wx1*-linked translocations are being introduced into this series and are in a conversion program to transfer each translocation to the inbred backgrounds M14 and W23. These inbreds are then crossed together to produce vigorous F1's to fill seed requests. Over the years, pedigree and classification problems arose during the propagation of these stocks. We have been able to sort through the problem ones, and can now supply good sources proven by linkage tests to include the correct translocated chromosomes. Additional pedigree information on bad sources is available should anyone want to check on samples supplied to them previously by the Stock Center.

Previously we reported the linkage results for some of these stocks (MNL72:81-82; MNL73:88-89; MNL74:67-69). Below is a summary of additional translocation stocks for which we have completed testing. Additional translocation stocks will be tested as time allows.

Table 1. *wx1* T3-9c (3L.09; 9L.12)

A) The M14 source showed linkage of *wx1* with *vp1:*

3 point linkage data for *vp1-wx1* T3-9c
Modified backcross: [*Vp1 wx1* N x [*vp1 Wx1* N x *Vp1 wx1* T3-9c]]@

source: 93-481-1 ^M14

Region	Phenotype	No.	Totals
0	vp N Wx	129	
	+ T wx	108	237
1	+ N Wx	18	
	vp T wx	9	27
2	+ T Wx	4	
	vp N wx	1	5
1+2	vp T Wx	2	
	+ N wx	0	2

% recombination *vp1-wx1* =13.3±2.1
% recombination *vp1*-T=10.7±1.9
% recombination T-*wx1*=2.6±1.

B) The W23 source showed linkage of *wx1* with *vp1:*

3 point linkage data for *vp1-wx1* T3-9c
Modified backcross: [*Vp1 wx1* N x [*vp1 Wx1* N x *Vp1 wx1* T3-9c]]@

source: 94-1893-1 ^W23

Region	Phenotype	No.	Totals
0	vp N Wx	153	
	+ T wx	170	323
1	+ N Wx	17	
	vp T wx	10	27
2	+ T Wx	1	
	vp N wx	1	2
1+2	vp T Wx	2	
	+ N wx	2	4

% recombination *vp1-wx1* =10.4±1.6
% recombination *vp1*-T=8.7±1.5
% recombination T-*wx1*=1.7+0.7

C) Combined data for M14 & W23 sources.

3 point linkage data for *vp1-wx1* T3-9c
Modified backcross: [*Vp1 wx1* N x [*vp1 Wx1* N x *Vp1 wx1* T3-9c]]@

combined M14 & W23 data

Region	Phenotype	No.	Totals
0	vp N Wx	278	
	+ T wx	282	560
1	+ N Wx	35	
	vp T wx	19	54
2	+ T Wx	5	
	vp N wx	2	7
1+2	vp T Wx	4	
	+ N wx	2	6

% recombination *vp1-wx1* =11.6+1.3
% recombination *vp1*-T=9.6+1.1
% recombination T-*wx1*=2.1+0.4

The following linkage relationship was established: *vp1* – 9.6 - T – 2.1 - *wx1*. These data are consistent with the % recombination *vp1-wx1* = 11.06+0.62 in Robertson, D.S. 1955. Genetics 40:745-760. These could also be consistent with the breakpoints determined by Dr. C. R. Burnham and students, University of Minnesota.

Table 2. *wx1* T4-9g (4S.27; 9L.27)

A) The F1 source showed linkage of *wx1* with *su1*.

2 point linkage data for *su1-wx1* T4-9g
Testcross: [*Su1 wx1* T4-9g x *su1 Wx1* N] x *su1 wx1* N

source: 93-444-2 x 445 F1 of ^M14 x ^W23

Region	Phenotype	No.	Totals
0	+ wx	749	
	su Wx	741	1490
1	+ Wx	241	
	su wx	23	264

% recombination *su1-wx1* =15.1+.09

B) The M14 source showed linkage of *wx1* with *su1*:

2 point linkage data for *su1-wx1* T4-9g
Testcross: [*Su1 wx1* T4-9g x *su1 Wx1* N] x *su1 wx1* N

source: 93-482-1 x SIB^M14

Region	Phenotype	No.	Totals
0	+ wx	810	
	su Wx	818	1625
1	+ Wx	247	
	su wx	18	265

% recombination *su1-wx1* =14.0+0.8

C) The W23 source showed linkage of *wx1* with *su1*:

2 point linkage data for *su1-wx1* T4-9g
Testcross: [*Su1 wx1* T4-9g x *su1 Wx1* N] x *su1 wx1* N

source: 92-405-1 x SIB^W23

Region	Phenotype	No.	Totals
0	+ wx	1007	
	su Wx	998	2005
1	+ Wx	284	
	su wx	31	315

% recombination su1-wx1=13.6±0.7

Table 3. *wx1* T4-9e (4S.53; 9L.26)

A) The F1 source showed linkage of *wx1* with *su1*.

2 point linkage data for *su1-wx1* T4-9e
Testcross: [*Su1 wx1* T4-9e x *su1 Wx1* N] x *su1 wx1* N

source: 93W-1389-1 x 1390-9 F1 of ^M14 x ^W23

Region	Phenotype	No.	Totals
0	+ wx	478	
	su Wx	604	1082
1	+ Wx	70	
	su wx	19	89

% recombination *su1-wx1* =7.6±0.8

B) The M14 source showed linkage of *wx1* with *su1*:

2 point linkage data for *su1-wx1* T4-9e
Testcross: [*Su1 wx1* T4-9e x *su1 Wx1* N] x *su1 wx1* N

source: 92H-470-1 x SIB^M14

Region	Phenotype	No.	Totals
0	+ wx	934	
	su Wx	1052	1986
1	+ Wx	39	
	su wx	10	49

% recombination *su1-wx1* =2.4±0.3

C) The W23 source showed linkage of *wx1* with *su1*:

2 point linkage data for *su1-wx1* T4-9e
Testcross: [*Su1 wx1* T4-9e x *su1 Wx1* N] x *su1 wx1* N

source: 93W-1390-9@^W23

Region	Phenotype	No.	Totals
0	+ wx	1018	
	su Wx	1033	2051
1	+ Wx	72	
	su wx	37	109

% recombination *su1-wx1* =5.0±0.5

Table 4. *wx1* T4-9(5657) ((4L.33; 9S.25)

A) The F1 source showed linkage of *wx1* with *gl4*:

2 point linkage data for *gl4-wx1* T4-9(5657)
Testcross: [*Gl4 wx1* T4-9(5657) x *gl4 Wx1* N] x *gl4 wx1* N

source: 87-870 x 872^F1

Region	Phenotype	No.	Totals
0	gl Wx	240	
	+ wx	225	465
1	+ Wx	12	
	gl wx	5	17

% recombination *gl4-wx1*= 3.5±0.8

B) The W23 source showed linkage of *wx1* with *gl4*:

2 point linkage data for *gl4-wx1* T4-9(5657)
Testcross: [*Gl4 wx1* T4-9(5657) x *gl4 Wx1* N] x *gl4 wx1* N

source: 92H-471-7^W23

Region	Phenotype	No.	Totals
0	gl Wx	92	
	+ wx	83	175
1	+ Wx	10	
	gl wx	3	13

% recombination *gl4-wx1*=6.9±1.9

C) The M14 source was not tested.

Table 5. *wx1* T5-9(4817) (5L.06; 9S.07)

A) The F1 source showed linkage of *wx1* with *a2*:

2 point linkage data for *a2-wx1* T5-9(4817)
Testcross: [*A2 wx1* T5-9(4817) x *a2 Wx1* N] x *a2 wx1* N

source: 933-450-1 x 451^F1

Region	Phenotype	No.	Totals
0	a Wx	494	
	+ wx	421	915
1	+ Wx	63	
	a wx	27	90

% recombination *a2-wx1* =9.0±0.9

B) The M14 source showed linkage of *wx1* with *a2*:

2 point linkage data for *a2-wx1* T5-9(4817)
Testcross: [*A2 wx1* T5-9(4817) x *a2 Wx1* N] x *a2 wx1* N

source: 87-884 x SIB ^M14

Region	Phenotype	No.	Totals
0	a Wx	1006	
	+ wx	959	1965
1	+ Wx	133	
	a wx	49	182

% recombination *a2-wx1* =8.5±0.6

C) The W23 source showed linkage of *wx1* with *a2*.

2 point linkage data for *a2-wx1* T5-9(4817)
Testcross: [*A2 wx1* T5-9(4817) x *a2 Wx1* N] x *a2 wx1* N

source: 92-412-1 x SIB ^W23

Region	Phenotype	No.	Totals
0	a Wx	802	
	+ wx	781	1583
1	+ Wx	104	
	a wx	47	151

% recombination *a2-wx1* =8.7±0.7

Table 6. *wx1* T5-9d (5L.14; 9L.10)

A) The F1 source showed linkage of *wx1* with *gl8*:

2 point linkage data for *gl8-wx1* T5-9d
Testcross: [*Gl8 wx1* T5-9d x *gl8 Wx1* N] x *gl8 wx1* N

source:93-452-3 x 453 ^F1

Region	Phenotype	No.	Totals
0	gl Wx	598	
	+ wx	565	1163
1	+ Wx	193	
	gl wx	111	304

% recombination *gl8-wx1*= 20.7±1.1

B) The M14 source showed linkage of *wx1* with *gl8*:

2 point linkage data for *gl8-wx1* T5-9d
Testcross: [*Gl8 wx1* T5-9d x *gl8 Wx1* N] x *gl8 wx1* N

source: 93-483-1 x SIB ^M14

Region	Phenotype	No.	Totals
0	gl Wx	864	
	+ wx	819	1683
1	+ Wx	220	
	gl wx	147	367

% recombination *gl8-wx1*=17.9±08

C) The W23 source showed linkage of *wx1* with *gl8* .

2 point linkage data for *gl8-wx1* T5-9d
Testcross: [*Gl8 wx1* T5-9d x *gl8 Wx1* N] x *gl8 wx1* N

source: 93W-1414-3@^W23

Region	Phenotype	No.	Totals
0	gl Wx	430	
	+ wx	419	849
1	+ Wx	159	
	gl wx	91	250

% recombination *gl8-wx1*=22.7±1.3

Table 7. *wx1* T8-9d (8L.09; 9L.16)

A) The F1 source showed linkage of *wx1* with *v16*:

2 point linkage data for *v16-wx1* T8-9d
Testcross: [*V16 wx1* T8-9d x *v16 Wx1* N] x *v16 wx1* N

source: 93-470-1 x 471^F1

Region	Phenotype	No.	Totals
0	v Wx	356	
	+ wx	336	692
1	+ Wx	200	
	v wx	109	309

% recombination *v16-wx1*=30.9±1.5

B) The M14 source showed linkage of *wx1* with *v16*:

2 point linkage data for *v16-wx1* T8-9d
Testcross: [*V16 wx1* T8-9d x *v16 Wx1* N] x *v16 wx1* N

source: 93-490-1@^M14

Region	Phenotype	No.	Totals
0	v Wx	600	
	+ wx	492	1092
1	+ Wx	158	
	v wx	81	239

% recombination *v16-wx1*=18.0±1.1

C) The W23 source showed linkage of *wx1* with *v16*:

2 point linkage data for *v16-wx1* T8-9d
Testcross: [*V16 wx1* T8-9d x *v16 Wx1* N] x *v16 wx1* N

source: 92H-483-1 x SIB^W23

Region	Phenotype	No.	Totals
0	v Wx	451	
	+ wx	410	861
1	+ Wx	146	
	v wx	95	241

% recombination *v16-wx1*=21.9±1.2

Table 8. *wx1* T8-9(6673) (8L.35; 9S.31)

A) The F1 source showed linkage of *wx1* with *v16*:

2 point linkage data for *v16-wx1* T8-9(6673)
Testcross: [*V16 wx1* T8-9(6673) x *v16 Wx1* N] x *v16 wx1* N

source: 93-472-1 x 473^F1

Region	Phenotype	No.	Totals
0	v Wx	643	
	+ wx	542	1185
1	+ Wx	141	
	v wx	111	252

% recombination *v16-wx1*=17.5±1.0

B) The M14 source showed linkage of *wx1* with *v16*:

2 point linkage data for *v16-wx1* T8-9(6673)
Testcross: [*V16 wx1* T8-9(6673) x *v16 Wx1* N] x *v16 wx1* N

source: 93-433-1 x SIB^M14

Region	Phenotype	No.	Totals
0	v Wx	403	
	+ wx	376	779
1	+ Wx	71	
	v wx	64	135

% recombination *v16-wx1*=14.8±1.2

C) The W23 source showed linkage of *wx1* with *v16*:

2 point linkage data for *v16-wx1* T8-9(6673)
Testcross: [*V16 wx1* T8-9(6673) x *v16 Wx1* N] x *v16 wx1* N

source: 93-491-1 x SIB^W23

Region	Phenotype	No.	Totals
0	v Wx	616	
	+ wx	592	1208
1	+ Wx	172	
	v wx	123	295

% recombination *v16-wx1*=19.6±1.0

Table 9. *wx1* T9-10(8630) (9S.28; 10L.37)

All *wx1* marked sources of T9-10(8630) showed no linkage with either *r1* or *g1*. New crossovers were obtained for both the M14 & W23 conversions.

A) The new M14 crossover sources showed linkage of *wx1* with *r1*.

2 point linkage data for *r1-wx1* T9-10(8630)
Testcross: [*r1 wx1* T9-10(8630) x *R1 Wx1* N] x *r1 wx1* N

source: 99-1463-3; from: 98-1139-2c/o^M14

Region	Phenotype	No.	Totals
0	+ Wx	766	
	r wx	648	1414
1	r Wx	115	
	+ wx	195	310

% recombination *r1-wx1*=18.0±0.9

source: 99-1463-5; from: 98-1139-2c/o^M14

Region	Phenotype	No.	Totals
0	+ Wx	779	
	r wx	571	1350
1	r Wx	90	
	+ wx	159	249

% recombination *r1-wx1*=15.6±0.9

B) The new M14 crossover sources showed linkage of *wx1* with *g1*.

2 point linkage data for *g1-wx1* T9-10(8630)
Testcross: [*G1 wx1* T9-10(8630) x *g1 Wx1* N] x *g1 wx1* N

source: 99-1463-2 from: 98-1139-2c/o^M14

Region	Phenotype	No.	Totals
0	g Wx	1458	
	+ wx	1254	2712
1	+ Wx	76	
	g wx	70	146

% recombination *g1-wx1* =5.1±0.4

source: 99-1463-5 from: 98-1139-2c/o^M14

Region	Phenotype	No.	Totals
0	g Wx	487	
	+ wx	463	950
1	+ Wx	17	
	g wx	11	28

% recombination *g1-wx1* =2.9±0.5

source: 99-1463-7 from: 98-1139-2c/o^M14

Region	Phenotype	No.	Totals
0	g Wx	195	
	+ wx	207	402
1	+ Wx	5	
	g wx	5	10

% recombination *g1-wx1* =2.4±0.8

source: 99-1464-3 from: 98-1139-2c/o^M14

Region	Phenotype	No.	Totals
0	g Wx	613	
	+ wx	586	1199
1	+ Wx	26	
	g wx	22	48

% recombination *g1-wx1* =3.8±0.5

source: 99-1464-6 from: 98-1139-2c/o^M14

Region	Phenotype	No.	Totals
0	g Wx	215	
	+ wx	221	436
1	+ Wx	8	
	g wx	7	15

% recombination *g1-wx1* =3.3±0.8

source: 99-1464-8 from: 98-1139-2c/o^M14

Region	Phenotype	No.	Totals
0	g Wx	696	
	+ wx	649	1345
1	+ Wx	22	
	g wx	13	35

% recombination *g1-wx1* =2.5±0.4

C) The new W23 crossover sources showed linkage of *wx1* with *g1*.

2 point linkage data for *g1-wx1* T9-10(8630)
Testcross: [*G1 wx1* T9-10(8630) x *g1 Wx1* N] x *g1 wx1* N

source: 99-1465-11 from: 98-1159-11c/o^W23

Region	Phenotype	No.	Totals
0	g Wx	513	
	+ wx	526	1040
1	+ Wx	8	
	g wx	11	19

% recombination *g1-wx1* =1.8±0.4

source: 99-1466-1 from: 98-1159-11c/o^W23

Region	Phenotype	No.	Totals
0	g Wx	494	
	+ wx	457	951
1	+ Wx	10	
	g wx	17	27

% recombination *g1-wx1* =2.8±0.5

source: 99-1468-2 from: 98-1159-11c/o^W23

Region	Phenotype	No.	Totals
0	g Wx	527	
	+ wx	463	990
1	+ Wx	11	
	g wx	22	33

% recombination *g1-wx1* =3.2±0.6

source: 99-1468-8 from: 98-1159-11c/o^W23

Region	Phenotype	No.	Totals
0	g Wx	246	
	+ wx	247	493
1	+ Wx	8	
	g wx	6	14

% recombination *g1-wx1* =2.8±0.7

source: 99-1468-11 from: 98-1159-11c/o^W23

Region	Phenotype	No.	Totals
0	g Wx	335	
	+ wx	661	645
1	+ Wx	8	
	g wx	8	16

% recombination *g1-wx1* =2.4±0.6

Preliminary two-point linkage data for *inr1* and *du1* on 10L

--Stinard, P

Inr1 is a dominant *R1* allele-specific aleurone color inhibitor that can be scored as pale or colorless aleurone in the presence of certain susceptible *R1* (*R1-S*) alleles. The recessive *inr1* allele provides full purple aleurone color in the presence of *R1-S*. Previous data (Stinard, P. 1999. MNL 73:89-90) had shown that *inr1* is located on the long arm of chromosome 10, distal to the TB-10L19 breakpoint (10L.00), but proximal to *g1*. In order to further refine the map location of *inr1*, a three-point linkage test involving the 10L markers *inr1*, *du1*, and *g1* was set up as indicated in Table 1. All stocks used in the crosses were homozygous for *wx1* in order to enhance the expression of *du1*. Kernels from these crosses will be planted at a later date and the resulting plants scored for *g1* in order to provide three-point linkage data. Preliminary two-point data involving only *inr1* and *du1* are presented in Table 1. These data indicate that *inr1* and *du1* are very tightly linked, with only an approximately 0.2 centimorgan distance between them. These data cannot be used to determine the global order of *inr1* and *du1* on chromosome 10. That determination will have to be made after the *g1* data are collected.

Table 1. Two-point linkage data for *inr1* and *du1*.
Testcross: (*Du1 Inr1 G1 R1-S wx1* X *du1 inr1 g1 R1-S wx1*) X *du1 inr1 g1 R1-S wx1*.

Reg.	Phenotype	No.	Totals
0	Inr1 Du1	4354	
	inr1 du1	4410	8764
1	Inr1 du1	7	
	inr1 Du1	8	15

% recombination *inr1--du1* = 0.17 +/- 0.04

A second *R1* allele-specific aleurone color inhibitor, *Inr2*, is located on 9L

--Stinard, P

As reported in last year's MNL (MNL 74:70-71), two *R1* allele-specific aleurone color inhibitors were isolated from the novelty maize variety "John Deere." One inhibitor, *Inr1*, had been previously mapped to the long arm of chromosome 10 (MNL 73:89-90) and an allele of *Inr1* is also found in the Maize Genetic Stock Center's *da1* stock. Here we report the mapping of the second inhibitor, *Inr2*, to the long arm of chromosome 9.

Because *Inr2* exhibits dominant inhibition of aleurone color, easily scored on the ear in the presence of appropriate *R1* alleles (herein referred to as *R1-S*, or susceptible alleles), we chose to map *inr2* using a set of *wx1* marked A-A translocations. Plants homozygous for *Inr2* and *R1-S* were crossed to a series of *wx1*-marked translocations in a colorless aleurone (*r1*) background. F1 plants were backcrossed by a homozygous *inr2 wx1 R1-S* line, and the resulting ears were scored for colorless (Inr) vs. colored (inr) and waxy (wx) vs. starchy (Wx) kernels (Table 1). In crosses involving *wx1 y1* T6-9e, some of the backcrosses were made by plants homozygous for *inr2*, *wx1*, *y1*, and *R1-S*, so three-point linkage data for *wx1*, *y1*, and *inr2* were obtained (Table 2). All crosses demonstrated linkage of *inr2* with *wx1*, indicating that

Table 1. Two point linkage data for *wx1 inr2* in crosses involving various A-A translocations.
Testcross: [*wx1* T *inr2 r1* / *Wx1* N *Inr2 R1-S*] X *wx1* N *inr2 R1-S*.

	Region 0		Region 1		
Translocation	*Wx Inr*	*wx inr*	*wx Inr*	*Wx inr*	% recombination *wx1--inr2*
T1-9(5622)	246	182	60	82	24.9 +/- 1.8
T1-9(8389)	292	289	47	49	14.1 +/- 1.3
T2-9c	215	385	120	69	24.0 +/- 1.5
T2-9b	177	131	48	86	30.3 +/- 2.2
T2-9d	205	200	34	83	22.4 +/- 1.8
T3-9(8447)	204	245	13	24	7.6 +/- 1.2
T3-9(8562)	75	74	16	8	13.9 +/- 2.6
T4-9(5657)	296	212	63	48	17.9 +/- 1.5
T5-9(022-11)	254	250	22	46	11.9 +/- 1.4
T5-9a	214	184	59	47	21.0 +/- 1.8
T7-9a	250	248	41	78	19.3 +/- 1.6
T8-9d	213	194	47	66	21.7 +/- 1.8

Table 2. Three point linkage data for *wx1 y1 inr2* in crosses involving T6-9e.
Testcross: (*wx1 y1* T6-9e *inr2 r1* / *Wx1 Y1* N *Inr2 R1-S*) X *wx1 y1* N *inr2 R1-S*.

Region	Phenotype	No.	Totals
0	wx y inr	459	
	Wx Y Inr	497	956
1	wx y Inr	125	
	Wx Y inr	99	224
2	wx Y Inr	29	
	Wx y inr	24	53
1 + 2	wx Y inr	9	
	Wx y Inr	10	19

% recombination *wx1--y1* = 5.8 +/- 0.7
% recombination *y1--inr2* = 19.4 +/- 1.1
% recombination *wx1--inr2* = 25.2 +/- 1.2

inr2 is located on chromosome 9. The distance between *wx1* and *inr2* showed variability (from 7.6 centimorgans to 30.3 centimorgans) depending upon which A-A translocation was used in the linkage cross. This kind of linkage variability is not unusual in crosses involving translocation stocks (E. B. Patterson, 1952. Ph.D. Thesis, California Institute of Technology). Furthermore, the production of viable duplicate-deficient eggs by adjacent disjunction when plants heterozygous for certain translocations are used as females in linkage crosses can also distort linkage data somewhat.

The linkage data obtained from the crosses with T6-9e (breakpoints 6L.18 9L.24) provide sufficient information to fix the location of *inr2* on chromosome 9 with respect to *wx1*. Because *y1* is located on the 9-6 chromosome very close to the breakpoint in T6-9e, and the gene order determined from the linkage data is clearly *wx1 y1 inr2*, *inr2* has to be located on 9L distal to the T6-9e 9L breakpoint (9L.24). If we take the T6-9e linkage data for the *wx1--inr2* distance (25.2 centimorgans) as a minimum value for the distance between *wx1* and *inr2*, *inr2* is located near or distal to *bk2* on 9L. Additional tests using B-A translocations and 9L linkage markers will be conducted to confirm and refine the location of *inr2* on 9L.

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Chromomere map of meiotic maize chromosome

--Caixeta, ET, Carvalho, CR

Computational and cytogenetic methods were used with the objective of mapping with high resolution, the longitudinal differentiation of maize chromosomes. Tassels of the line L-869 were collected and fixed in a methanol:acetic acid solution (3:1). Pollen mother cells were macerated with an enzymatic solution, prepared cytogenetically by the air-drying technique and later stained with a Giemsa solution. Meiotic figures were photomicrographed and digitized by means of a scanner or captured directly by a CCD video camera from microscope to a computer. The technique used allowed a visualization of well defined chromosomes that were spread out in the same focus level on the slide. The morphologic preservation of the bivalents and the almost absence of background or artifact resulted in high quality cytogenetic preparations. Digitized image analysis made the graphic plot of relative density of the chromosomes in 256 tones of gray scale possible. The profile of the gray value standards analyzed from these graphs revealed absolute and relative measures of the chromosomes. The longitudinal differentiations recognized by the centromere, knob, chromomeric and interchromomeric regions were precisely mapped throughout the meiotic chromosomes.

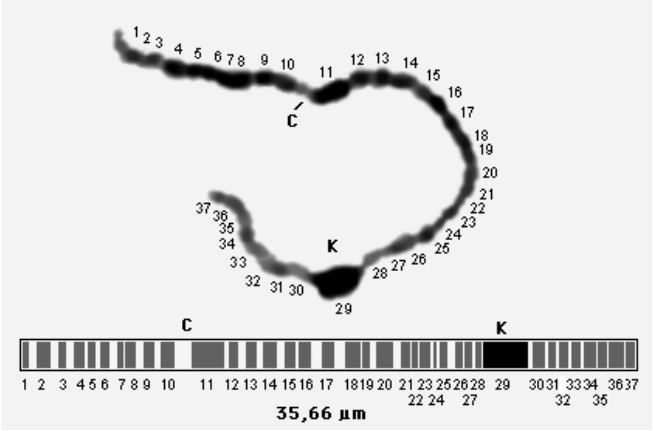

Figure 1. Maize pachytene chromosome number 7 and diagram showing chromomeres map. C = centromere, K=Knob.

A male transmissible deficiency induced by B chromosomes in maize

--Saraiva, LS, Carvalho, CR

Rhoades and Dempsey accumulated extensive data about the unusual phenomenon of interaction between B chromosomes and heterochromatic knobs on A chromosomes causing breaks and loss of markers on these chromosomes. This high-loss phenomenon occurs at the second microspore division and produces deficient chromosome. A survey was made for plants with deficient chromosomes transmissible through the gametes resulting from high loss. Because the *Yg2* locus is close to the terminal knob, selection of exceptional plants which have lost this locus identifies deficiencies of various lengths of 9S as well as for more complex rearrangements.

The high-loss strain used had several B chromosomes and chromosome 9 carried a large knob terminating the short arm. Marker genes on this arm included the dominant *Yg2* and *C* alleles with *Yg2* close to the knob. Pollen from the high-loss strain was applied to the silks of *yg2 c* tester plants and the *C* seeds produced were planted to search for deficient chromosomes due to non-correspondence between embryo and endosperm after the breaks occur at the second microspore division. The yellow green seedlings represented deficiencies of chromosome 9.

The cytological analysis of yellow green exception number 364-2 showed that it had one chromosome 9 with a small terminal knob and a knobless homologue. Because the high-loss strain used as the paternal parent was homozygous for a large knob in chromosome 9 and the *yg2* tester stock was homozygous for a small knob, the chromosome 9 constitution of plant 364-2 obviously arose by loss of the knob from the high-loss strain although cytologically there was no apparent or easily detectable deletion of the euchromatic tip. Pollen from this plant was completely fertile and uniform in size. Following pollination by a *c* male parent, an ear with 148 *C* and 145 *c* kernels was produced, showing a normal female transmission of the supposedly deficient chromosome, with the dominant *C* allele. Normal transmission was also obtained when plant 364-2 was used as the male in a test cross (55 *C*: 49 *c*).

To determine if the knobless chromosome 9 was in fact deficient, individuals of the presumably Df9 (deficient *Yg2*) *C*/ N9 *yg2 c* constitution were crossed as male and female parents with a stock homozygous for McClintock's wd chromosome and containing the Wd ring with the dominant *Yg2* and *Wd* alleles which cover the deficiency in the wd chromosome. Because the ring chromosome is somatically unstable and frequently lost, wd plants possessing the ring are green-white striped. The progenies of the above crosses were planted in the sandbench and seedlings were scored (Table 1).

Four phenotypic classes were observed. Chromosome 9 constitutions of these classes are as follow: white (Df9/*wd*), yellow

Table 1. Seedling classification of progenies from reciprocal crosses of Df9 *C*/N9 *yg2 c* plants with individuals homozygous for *wd* and containing the Wd ring (*). The Df9 was derived from plant 364-2.

	Number of seedlings	
Phenotype	Df *C*/N9 *yg2 c* as male	Df *C*/N9 *yg2 c* as female
White	91	111
Green-white striped	20	25
Green-yellow green striped	24	29
Yellow green	102	15

* Combined data from two ears for each kind of cross.

green (N9/*wd*), green-yellow green striped (N9/*wd* plus ring) and green-white striped (Df9/*wd* plus ring).

The occurrence of white and green-white striped seedlings means that plant 364-2 had a chromosome 9 deficient for the *Yg2* and *Wd* loci. The 1:1 ratios of white plus green-white striped versus yellow green plus green-yellow striped seedlings demonstrate the normal transmission of the deficient chromosome by both female and male gametes.

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Pictorial language for universal communication
--Galinat, WC

A visual art form such as a drawing, painting, photograph, sculpture or etching can be the summit at a mountaintop of information, the Rosetta Stone[1] dictionary for deciphering complex problems in all languages here on earth and throughout the Universe. Long before the invention of the written word to preserve and convey information, people painted and carved pictures (petroglyphs) on walls of caves and cliffs for all to understand, both then and many thousands of years later. The act of inscribing information by any means and the storage of it in libraries for retrieval made it possible to have a cultural evolution by which humans learned how to over-power and manipulate all other forms of life, including other humans. Visual art can convey more than just words. Like music, it can convey emotions from the heart.

People of different languages have told me that on viewing my popular drawing of a corn plant, they were deeply moved by a powerful feeling of beauty, awe and understanding. This drawing has been recognized worldwide in numerous publications and now, best of all, it will be immortalized in a marble etching magnified to seven feet tall, five feet wide, as delineated by the world renowned architect and artist, Larry Kirkland. The etching will be located on a marble wall in the lobby of the new National Academy of Science-National Research Counsel (NAS-NRC) building in Washington D.C. (Fig. 1).

Some history of this drawing needs to be recorded. It illustrates the structure of the Northern Flint race of maize. It was adapted from my earlier (1957) drawing for a Christmas card that included a Pilgrim and a bushel basket of eight-rowed ears (Fig. 2). I sent a copy to Henry A. Wallace (1958), who responded "Your drawing of the Pilgrim in action in the cornfield in October of 1621 is probably the most accurate that has thus far been made." On the second page of the card, I gave the following explanation of the illustration.

Corn and the Pilgrims

"After finding a large cache of seed corn at Corn Hill, Cape Cod, the Pilgrims recorded that it was "God's good providence that we found this Corne, for else we know not how we should have done." Later prosperity came to Plymouth Colony when they learned the Indian methods for the culture and use of corn. Investigation of this plant has now become scientific, thereby helping to extend "God's good providence to all of mankind."

Later, Wallace came to Harvard's Botanical Museum because he had a special message for me. He said "Your drawings of maize are more important than the words we use to describe them. Their pictorial language cuts across all other languages in a profound and beautiful manner without need of translation."

One result of my Northern Flint-Pilgrim Christmas card to Henry Wallace was an exchange of at least seven letters, from 1958 to 1963, between him at his Farvue Farm in South Salem, New York, and me at Harvard's Botanical Museum. To those younger than myself, some explanation of who Henry Wallace was is necessary.

Henry A. Wallace (1888-1965) was probably the greatest American since Thomas Jefferson. He was able to effectively combine being a scientist, politician, author, editor, and founder of the first company to develop, produce and sell hybrid corn seeds. As a politician, he was secretary of Agriculture from 1933 to 1940, Vice President from 1941 to 1945 and Secretary of Commerce in 1945 and 1946. He was a leader of those creating the first green revolution by putting the more productive hybrid corn on American farms. He was a special friend not only to maize farmers and maize breeders, but to all of humanity.

I have found that not everyone understands things as pictures but just in words and so I have added captions. The first wide distribution of my drawing of the morphology of maize with captions was in a chapter that I wrote on the "Botany and Origin of Maize" in the CIBA-GEIGY Maize Monograph 1979, Editor Ernst Hafliger, pg. 9. Basel, Switzerland. It has been used in other books such as Fussel, Betty, 1992. The Story of Corn. Pub. Alfred A. Knopf, Inc. NY. (pg. 61); In the CIMMYT book: Maize Seed Industries in Developing Countries 1998, Editor Michael Morris, Chap. 4, by Pandey, S. (pg. 60); In Neuffer, Coe, Wessler, Mutants of Maize 1997. (pg. 16), Pub. Cold Spring Harbor Lab. Press, Plainview, NY; On covers to books: Kiesselbach, T.A. 1999 - 50th Anniversary of: The Structure and Reproduction of Corn. Pub. Cold Spring Harbor Lab. Press. On covers or within: Proceedings (including the 1985 NE Corn Conference held in Waltham) Workshops, Newsletters: - all too numerous to mention. It has been embossed on "T" shirts (Scott Poethig, Univ. Penn, Philadelphia) and I would like to see my corn plant transferred to stained glass windows (Fig. 3).

If there is a special power of communication in my corn artwork, especially in the marble etched reproduction (7'X5') on a wall in the lobby to the new NAS-NRC building in Washington D.C. where the world's best scientists come to discuss the past and future, I am honored. Even so, I always feel sad that my illustration work falls so far short of truly expressing the gorgeous beauty and harmony that I see expressed in the phenotypes assembled under natural evolution over the millenniums, both for survival in nature and under domestication over a relatively short time for human survival. The origin, evolution and diversification of maize is especially rapid and miraculous because it is a diverse diploid that

[1] A black basalt stone found in 1799 that bears an inscription in hieroglyphics, demotic characters, and Greek and is celebrated for having given the first clue to the understanding of Egyptian hieroglyphics.

Morphology of Maize

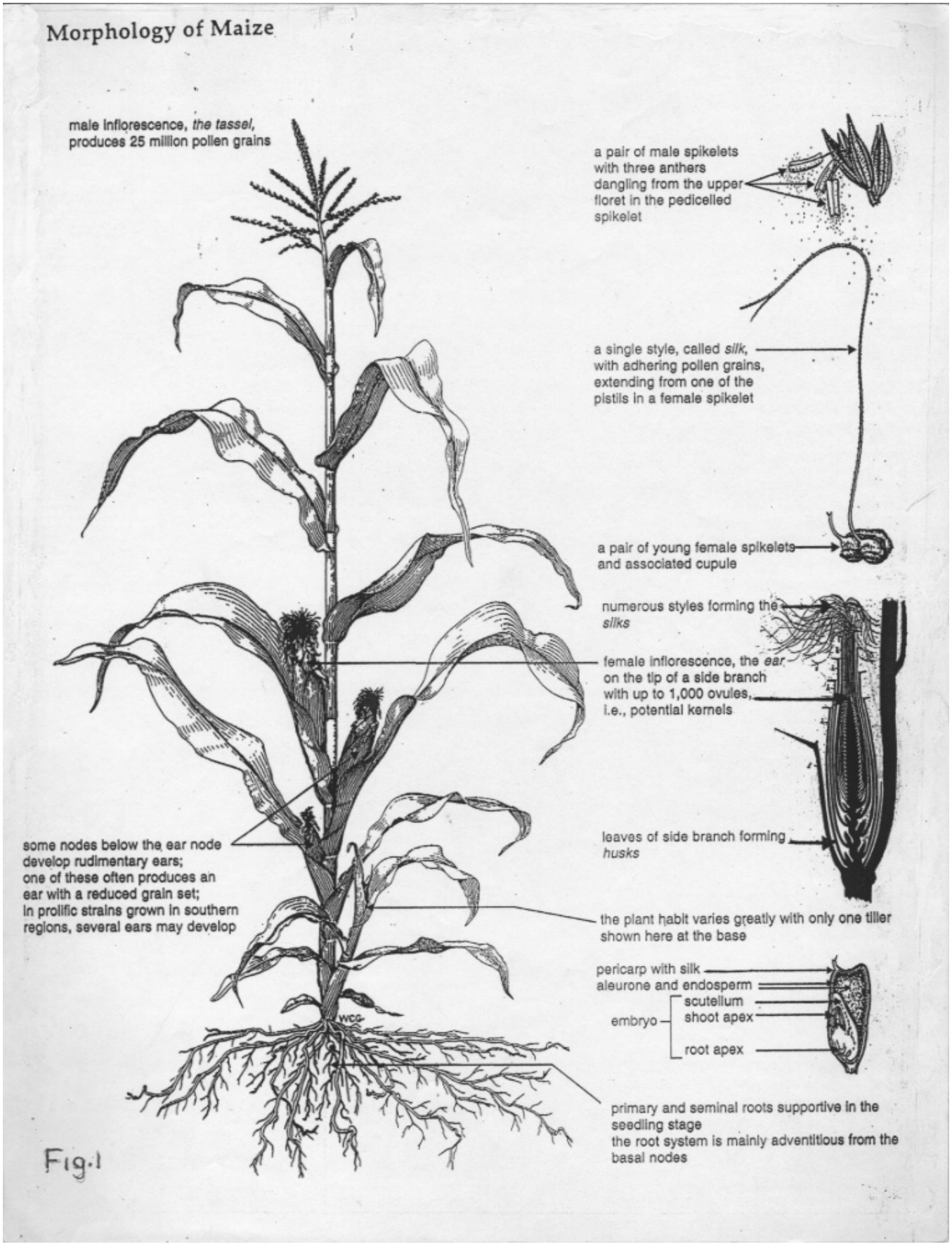
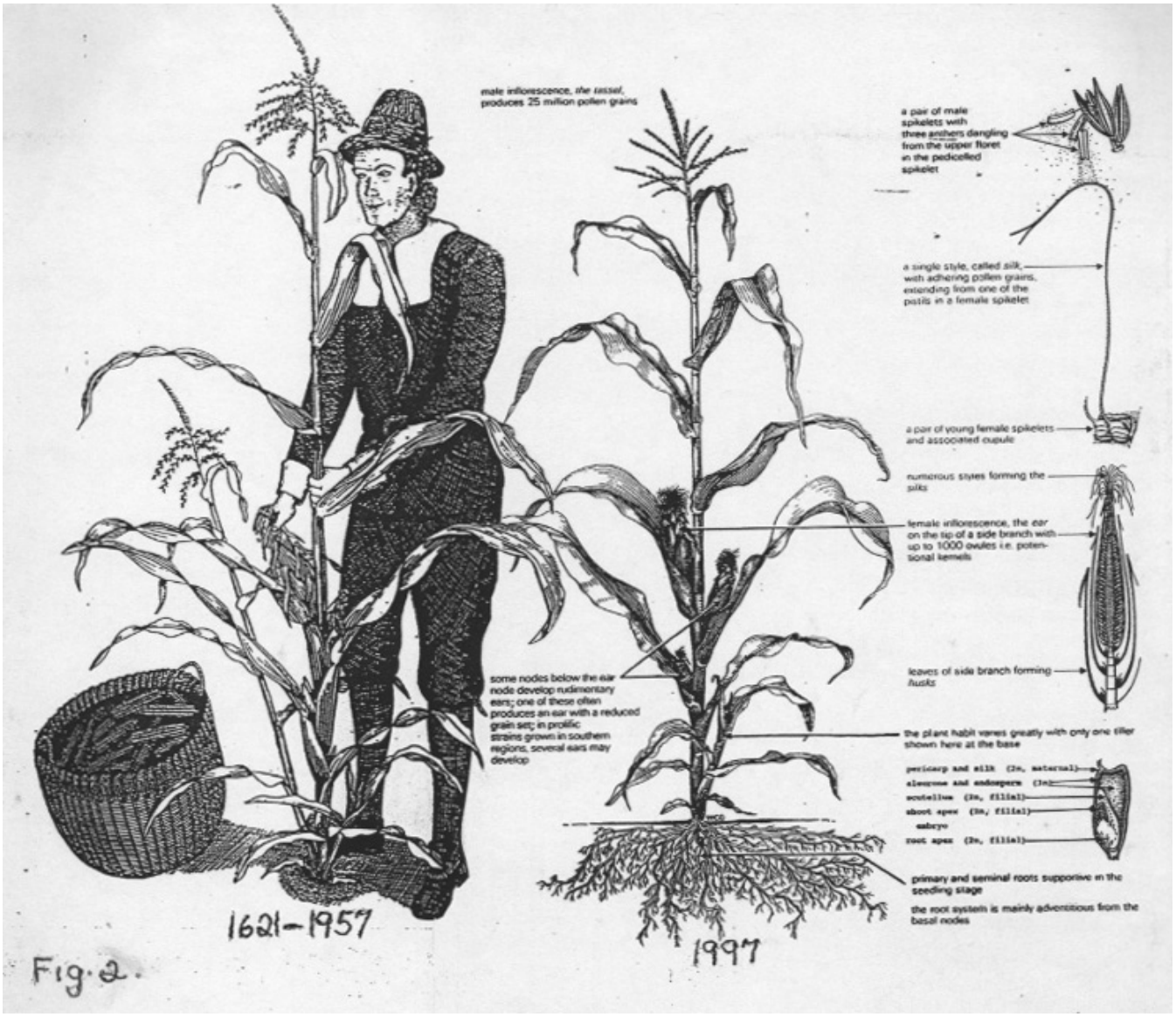


Fig. 1


male inflorescence, *the tassel*, produces 25 million pollen grains
a pair of male spikelets with three anthers dangling from the upper floret in the pedicelled spikelet
a single style, called *silk*, with adhering pollen grains, extending from one of the pistils in a female spikelet
a pair of young female spikelets and associated cupule
numerous styles forming the silks
female inflorescence, the *ear* on the tip of a side branch with up to 1000 ovules i.e. potensional kernels
leaves of side branch forming *husks*
some nodes below the ear node develop rudimentary ears; one of these often produces an ear with a reduced grain set; in prolific strains grown in southern regions, several ears may develop
the plant habit varies greatly with only one tiller shown here at the base
pericarp and silk (2n, maternal)
aleurone and endosperm (3n)
scutellum (2n, filial)
shoot apex (2n, filial)
embryo
root apex (2n, filial)
primary and seminal roots supportive in the seedling stage
the root system is mainly adventitious from the basal nodes
1621–1957
1997
Fig. 2.

is usually outcrossed and undergoes rapid genetic recombination.

I can only optimistically hope that when scientists and politicians view my corn artwork in the new NAS-NRC building in Washington D.C., they may experience such deep emotion from its beauty and accuracy that a profound understanding will overpower their thinking with a strong dedication and determination to generate better support for both maize farmers and maize researchers.

Acknowledgment is given to the Federation of Massachusetts Farmers' Markets for the essential computer typing by Amy Todd.

A scenario for one of the teosinte origins of maize
--Galinat, WC[2]

When the mutant building-block genes for maize were still scattered around at random in wild populations of teosinte about 7000 or more years ago, the following scenario could account for one or more ancient origins of maize under a domestication of teosinte. For the purpose of this discussion, I shall give full credit to my vision of just one wise, observant, elderly Indian lady who happened to be a farmer-breeder. She observed that the seeds of both teosinte and *Tripsacum* were borne single because they had to fit tightly within a fruitcase designed for protection against hungry birds, insects and people (Galinat, 1970. U. Mass. A. E. S, Bul. 585). She also observed that the male spikelets borne higher up on the same axis were paired, free of fruitcases and free to dangle their anthers to scatter their load of pollen. She felt sorry for the solitary female spikelets locked in their fruitcase jails. If the male spikelets could be paired and free, so could domestic female spikelets. She thought this was a clear case of sex discrimination! She offered a gift or reward to any of the hundreds of gatherers of wild teosinte seed who would bring her ears of four-rowed teosinte – four-rowed due to paired female spikelets – just as free as the male spikelets. The four-rowed teosinte gatherers (men, women, children) came from miles away in all directions to give the wise lady their four-rowed ears of teosinte which she examined and, if good, paid the reward. Then one day some child handed her a four-rowed ear that had four rows of decussate single female spikelets. The wise lady glanced at the upper male region. The male spikelets remained paired but in four-ranks like the female region and the total now was eight male rows. She screamed "You dear child from the land of God's maize called teosinte have brought me a great treasure – the fantastic key to humanity's maize. A new cereal can now be bred that will result in an ever higher civilization of better fed, more thoughtful people who will cooperate with each other and live in peaceful harmony."

In her great wisdom, she carefully planted the two kinds of four-rowed teosinte in a special isolated garden. The one with four ranks of single spikelets was in a central area that she detasseled. All around it was her large collection of teosinte with paired female spikelets that would be the pollinators for the detasseled plants. Later she harvested the crossed seed from these female plants and the next growing season had the F1 hybrid in an isolated block. Then in the second year, the year of the F2 segregation, she found that 6.25% (1/16) of the plants carried the double recessive recombinant form a merger of the two different double rowing female pathways. These few pioneer plants were more than just the Adam and Eve of the first eight-rowed maize. They were destined to be progenitors to thousands of years of maize diversification and the best "Staff of Life" for humankind on planet Earth and throughout the Universe.

If my fictional story of the wise Indian lady as the mother of maize has not spoken clearly to you about my beautiful vision of corn's origin, then perhaps the languages of my poetry and artwork working together will communicate (Figs 1a & 1b).

Here you see,
How two kinds of four-rowed teosinte,
Became the key to maize's pedigree
When one morn, the first corn was born,
An amazing creation of recombination.

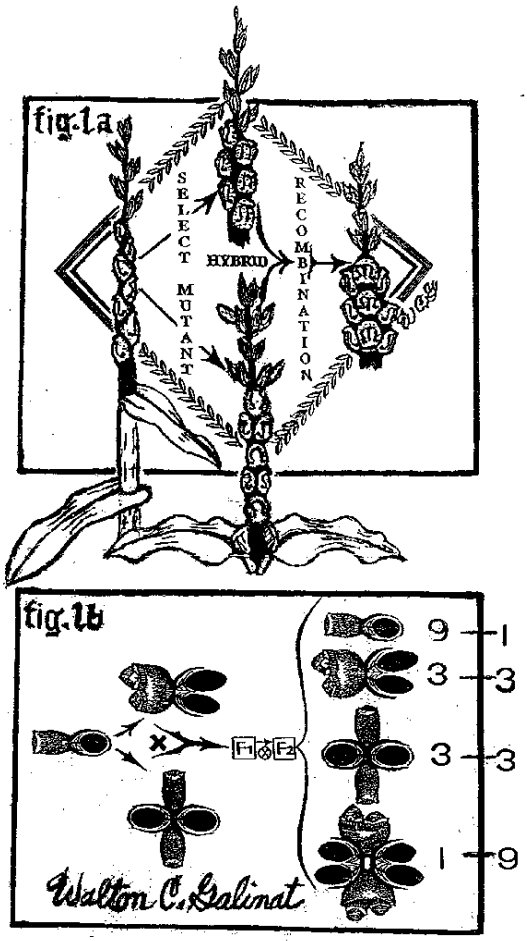


Figure 1a: Longitudinal views of teosinte, two different mutant kinds of four-rowed teosinte and a recombinant F2 double recessive eight-rowed maize. Notice the rowing of the male spikelets that are in the upper region above the female region and that the ear with four-ranks of single female spikelets has eight rows of male spikelets in the upper region as well as a pair of leaves just below the spike. The eight rowed ear of maize has eight rows of male spikelets.

Figure 1b: Cross-sectional views of just the female spikelets showing all four types of F2 segregants. The F2 frequency distribution ratios of 9:3:3:1 and 1:3:3:9 along the right hand edge represent a reversal of dominance with the teosinte background being the 9:3:3:1 and the maize background the 1:3:3:9. The architecture differences in ear structure of the two backgrounds reflect corresponding differences in energy sink capacity and this in turn controls the dominance of the genes involved.

[2] I was often accused by Paul Mangelsdorf of having an unfettered imagination, especially when he disagreed with me, and this fictional story may be just another example. But my fictional story here deals with real things and human nature to explain an accepted fact.

When the architecture of both the maize plant and its ears became designed to capture and then store a maximum of the photosynthetic energy, then the maize architecture became dominant over the primitive teosinte architecture. As a result, maize became important to the future of both humankind and our home planet.

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IV. MAIZE GENETICS COOPERATION STOCK CENTER

Maize Genetics Cooperation • Stock Center

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1,674 seed samples have been supplied in response to 252 requests, for 2000. Of these, a total of 85 requests were received from 20 foreign countries. Approximately 90% of our requests were received by electronic mail or through our order form on the World Wide Web.

We have added more stocks to our 'Phenotype Only' category of stocks. These are stocks that have been donated to the COOP over the years, and have been classified according to their mutant phenotype only. For the most part, these stocks have not as yet been allele tested, nor has their gene been located to a chromosome arm. While we expect that most of these will represent new alleles of known loci, some will represent unique, as yet undescribed loci. Over the past few years, some mutants in this class have been mapped and/or allele tested and where appropriate, the now characterized mutant stock was added to our main catalog. We are now listing all of these mutants to give cooperators that are interested in specific traits, easier access to these mutants. These now include many mutants from Gerry Neuffer's collection.

Approximately 6.2 acres of nursery were grown this summer at the Crop Sciences Research & Education Center located at the University of Illinois. Warm soil temperatures allowed for excellent emergence followed by optimal summer growing conditions. With additional water supplied by irrigation, we obtained good increases of most stocks grown this year

Special plantings were made of several categories of stocks:

1. We continue to grow a series of stocks donated to the COOP by Dr. Gerry Neuffer upon his retirement. Of the approximately 3000 stocks originally reported we have now been able to increase 256 characterized mutant stocks and add them to our main catalog listing. Approximately 640 others have been added to the phenotype only category including about 20 new mutants that were found during our summer growouts.
2. Plantings were also made from donated stocks from the collections of Don Auger (translocated Ac lines), Ed Coe (various genetic stocks), James Brewbaker (aphid resistant lines), Greg Doyle (inversions), Ina Golubovskaya (*dsy2* and *Mei1*), Al Kriz (globulin variants), Mario Motto (*opaque* and *glossy* alleles), Oliver Nelson (*bronze1* alleles and other mutants in his collection), Virginia Walbot (transposon-induced aleurone color mutant alleles), David Weber (Trisomic 8), and others. We expect to receive additional accessions of stocks from maize geneticists within the upcoming year and again request Cooperators to send us their stocks to insure their existence for future researchers.
3. We conducted allelism tests of several categories of mutants with similar phenotype or chromosome location. We found additional alleles of *sugary3, sugary4, yellow endosperm8*, *ramosa1, ramosa2, iojap1, green stripe1* and *zebra necrotic2*. In this manner, we hope to move stocks from our vast collection of unplaced uncharacterized mutants and integrate them into the main collection.
4. We conducted linkage tests of several mutants that had been placed to chromosome arm using B-A translocations or *waxy*-marked A-A translocations. More precise locations were determined for *inhibitor of r1* and *inhibitor of r2*.
5. Two acres were devoted to the propagation of the large collection of cytological variants, including A-A translocation stocks and inversions. In this collection is a series of *waxy1*-marked translocations that are used for mapping unplaced mutants. Over the years, pedigree and classification problems arose during the propagation of these stocks. We were able to sort through the problem ones, and we can now supply good sources proven by linkage tests to include the correct translocated chromosomes. Many additional translocation stocks were tested this last year. Results of these tests are reported in this issue of the Maize Genetics Cooperation Newsletter.
6. Stocks produced from the NSF project "Maize Gene Discovery, Sequencing and Phenotypic Analysis" (see: http://zmdb.iastate.edu/) were grown this summer. Approximately 60% of these represented plants that originally had to be outcrossed, and needed to be selfed to analyze for mutant segregation. The remaining 40% were seed increases that were planted from those families that originally yielded poorly. These increases help to maintain adequate seed stock to fill future requests.

We continue to grow a winter nursery of 0.5 acres at the Illinois Crop Improvement Association's facilities in Juana Díaz, Puerto Rico. We had an excellent winter crop last year, and all indications are that the crop will perform well this year as well. We plan to continue growing our winter nurseries at this location.

Philip continued his work on characterizing modifiers and inhibitors of certain *R1* alleles, and the inheritance and expression of the duplicate factor pairs *brn1 brn2* and *su3 su4*.

Janet continues with linkage testing and propagation of translocation stocks. She has finished sorting stocks into the 'Phenotype Only' category of stocks. Over the past year some mutants in this class have been allele tested and where appropriate, the now characterized mutant stock was added to our main catalog. Along with Shane she has sorted through the Neuffer collection and assigned each stock a drawer# and propagation status. All have been entered in a new database Shane set up to make retrieval of stocks easier.

The NSF project "Maize Gene Discovery, Sequencing and Phenotypic Analysis" generated 9419 stocks that were sent to the Stock Center. All of these stocks were then screened for ear and kernel mutants, samples from each family were sent to UC Berkeley for plant seedling screening and remaining seed was placed into cold storage until requested. Results from these screenings can be found at the ZmDB: Phenotype Database (http://zmfmdb.zool.iastate.edu/). Shane will work on the material generated this past summer, that is now arriving here. He will also be increasing stocks as necessary to maintain seed supply for requests and planting many of these stocks for the observation of adult plant traits. Our plan is to make this observation field available for maize genetics cooperators to visit and search for mutants that they are interested in. Details will be announced later.

Marty Sachs	Philip Stinard	Janet Day Jackson	Shane Zimmerman
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CHROMOSOME 1 MARKER

101A sr1 zb4 p1-ww
101B sr1 P1-wr
101C sr1 p1-ww
101D sr1 P1-rr
101F sr1 ts2 P1-rr
102A Ws4-N1589
102D Blh1-N1593
102F ms28
102G zb3
102H hcf6-N228B
102I hcf7-N1029D
103D vp5
103DA vp5-DR3076
103DB vp5-86GN4
103DC vp5-86GN3
103DD vp5-86GN6
103DE vp5-86GN11
103DF vp5-Mumm-1
103DG vp5-N81
103E zb4 ms17 p1-ww
104A Ts3
104F ms*-6034
104G ms*-6044
105A zb4 p1-ww
105B zb4 P1-wr
105C zb4 p1-ww br1
105E ms17 P1-wr
105F ms17 p1-ww
106B ts2 P1-rr
106C Glb1-0
106D Glb1-0; Glb2-0
107A P1-cr
107B P1-rr
107C P1-rw
107D P1-cw
107E P1-mm
107F P1-vv::Ac
107G P1-or
107H p1-ww
109A gs1-PI228173
109B gs1-PI262495
109C gs1-PI267181
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
111B hcf3-N846B
111C hcf3-N1242B
111D hcf44-N1278B
111F Les20-N2457
111G rs2
111H Les5-N1449
112B p1-ww br1 f1 bm2
112E as1
112H p1-ww br1
112I p1-ww br1 gs1 bm2
113B rd1
113BA rd1-Wasnok
113C br1 f1
113E br1 f1 Kn1
113K hm1; hm2
113L Hm1; hm2
114C br1 bm2
114D Vg1
114E Vg1; su1
114F br2 hm1; Hm2
114G br2 hm1; hm2
115C v22-8983
115CA v22-055-4
115E bz2-mVW2::Mu1
115F bz2-mVW4::MuDR
115J bz2-m::Ds; A1 A2 C1 C2 Pr1 R1
116A bz2-m::Ds; A1 A2 Ac C1 C2 Pr1 R1
116C an1 bm2
116D def(an1..bz2)-6923; A1 A2 Bz1 C1 C2 Pr1 R1
116G an1
116GA an1-93W1189
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
118CA lw1-3108
118CB lw1-6474
118J Adh1-3F1124r53
118K Adh1-1S5657; Adh2-33
118L Adh1-3F1124::Mu3
118M Adh1-3F1124r17
118N Adh1-lL14H; su1
118O Adh1-Cm
118P Adh1-FCm
118Q Adh1-Ct
119A Adh1-1S; Adh2-1P
119B vp8
119C gs1
119D gs1 bm2
119E Ts6
119F bm2
119H Adh1-FkF(gamma)25; Adh2-N
119J Adh1-Fm335::Ds1
119K Adh1-Fm335RV1
119L Adh1-2F11::Ds2
119M Adh1-1F725
120A id1
120B nec2-8147
120C ms9
120CA ms9-6032
120CB ms9-6037
120CC ms9-6042
120D ms12
120E v22-055-4 bm2
120F Mpl1-Sisco
120G Mpl1-Freeling
121A ms14
121AA ms14-6005
121B br2-mi8043
121C D8
121D lls1
121DA lls1-N501B
121E ty*-8446
121G ct2
121GA ct2-rd3
124A v*-5688
124B j*-5828
124C w*-8345
124CA w*-013-3
124CB w*-8245
124D v*-5588
124E w*-018-3
124F w*-4791
124G w*-6577
124H w*-8054
124I v*-032-3
124J v*-8943
125A Les2-N845A
125B Mpl1-Jenkins
125C hcf13-N1097B
125D hcf41-N1275C
125E hcf50-N1481
125F hcf2-N506C
125G hcf31-N1268B
126A bz2 gs1 bm2; A1 A2 Bz1 C1 C2 R1
126B id1-N2286A
126C dek1-N928A
126D dek1-N971
126E dek32-N1322A
126F o13
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
126N dek1-N1348
126O dek1-N1394
126P dek1-N1401
127A bz2 zb7-N101 bm2
127B dek1-N792
127C dek2-N1315A
127D dek22-N1113A
127E f1
127F Msc1-N791A
127G Tlr1-N1590
127I gt1
128A ij2-N8
128B l16-N515
128C l17-N544
128D pg15-N340B
128E pg16-N219
128G py2-N521A
128H spc2-N262A
129A w18-N495A
129AA w18-571C
129B wlu5-N266A
129C zb7-N101
129D emp1-R
129E ptd1-MS1568
129F dek*-MS2115
129G dek*-MS6214
130A o10-N1356
130B cp3-N888A
130BA cp3-N888A; mn4-N888C
130C id1-NA972
130D dek1-PB388
130E dek1-DR1129
130F ht4
6502A P1-ww-4Co63
6502C P1-ovov-CFS-29
6502D P1-rr(11)-CFS-33
6502E P1-rr(10)-CFS-36
6502F P1-rr(4-5)-CFS-47
6502G P1-rr(9)-CFS-53
6502I P1-rr(8-9)-CFS-75
6502K P1-vv-CFS-96
6502L P1-vv-CFS-110
6502M P1-vv-CFS-116
6502N P1-ovov-CFS-124
6502O P1-vv-CFS-138
6502P P1-rr(7)-CFS-140
6502Q P1-vv-CFS-155
6502R P1-o-grained-red-CFS-167
6502S P1-r pale(8)-CFS-181
6502T P1-rr(9)-CFS-186
6502V P1-vv-CFS-245
6502W P1-vv-CFS-246
6502X P1-vv-CFS-249
6502Y P1-vv-CFS-252
6502Z P1-vv-CFS-255
6502ZA P1-vv-CFS-256
6502ZB P1-vv-CFS-259
6503A P1-rr(11)-CFS-272
6503B P1-vv-CFS-273
6503C P1-vv-CFS-278
6503D P1-vv-CFS-279
6503E P1-vv-CFS-281
6503F P1-vv-CFS-282
6503G P1-vv-CFS-283
6503H P1-vv-CFS-284
6503I P1-r pale(5)-CFS-285
6503J P1-vv-CFS-286 (Brazil)
6503K P1-mm-CFS-286
6503L P1-mm-CFS-287
6503M P1-mm-CFS-289
6503N P1-mm-CFS-290
6503O P1-mm-CFS-291
6503P P1-mm-CFS-292
6503R P1-mm-CFS-294
6503S P1-mm-CFS-297
6503T P1-mm-CFS-301
6503U P1-rw(9)-CFS-302
6503V P1-rr(11)-CFS-303
6503W P1-rr(10)-CFS-305
6503X P1-rr(10)-CFS-315
6503ZA P1-rr(2)-CFS-319
6503ZB P1-rr(8)-CFS-320
6503ZC P1-rr(7)-CFS-321
6504A P1-rw(8)-CFS-324
6504B P1-rw(6-7)-CFS-325
6504C P1-rr(9)-CFS-327
6504D P1-rw(7)-CFS-330
6504E P1-rw(9)-CFS-332
6504F P1-rw(8)-CFS-334
6504G P1-o-grained-red-CFS-335
6504H P1-rw(5-6)-CFS-336
6504I P1-rw(7-9)-CFS-342
6504J P1-rr(5)-CFS-345
6504K P1-rw(7)-CFS-350
6504L P1-rr-CFS-360
6504M P1-rw(5)-CFS-369
6504N P1-ww(1)-CFS-376
6504O P1-vv-CFS-497
6504Q P1-rr(11)-CFS-548

CHROMOSOME 2 MARKER

201A mrl1-IHO
201B hcf106-Mum1::Mu1; hcf106c
201C hcf106-Mum2::Mu1; hcf106c
201D hcf106-Mum3::Mu1; hcf106c
201F ws3 lg1 gl2 b1
201G sm2-Brawn180
201H sm2-Brawn189
201I sm2-Brawn190
201J sm2-Brawn191
201K sm2-Brawn188
202A lg1-PI200299
202B lg1-PI262493
202C lg1-32TaiTaiTaSarga
202D lg1-ZCXGRB
202E lg1-64-4

202F fl1-o8
202G lg1-56-3037-5
203B al1
203BA al1-Brawn
203BB al1-y3
203D al1 lg1
203G al1-y3 gl2
204A al1-lty3
204B hcf1-N490B
205A al1 lg1 gl2
205B lg1
205C lg1 gl2
205G al1 gl2 B1
206A lg1 gl2 B1
206C D10-N2428
206D Wrp1-NA1163
206E oro2
207A y11
208B lg1 gl2 B1 sk1
208C lg1 gl2 B1 sk1 v4
208D lg1 gl2 B1 v4
208E lg1 gl2 b1
208H gl2-Salamini
209A gl11-N352A
209E lg1 gl2 b1 sk1
209I gl2-Parker's Flint
210E gl2-3050-3
210F gl2-PI200291
210G gl2-PI239114
210H gl2-PI251009
210I gl2-PI251885
210J gl2-PI251930
210K gl2-PI262474
210L gl2-PI262493
210M gl2-PI267186
210N gl2-N718
210O gl2-N239
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::Bg Ch1
213H lg1 gl2 B1-v::Bg
214A wt1-PI251939
214B lg1 b1 gs2
214C d5
214D gl11 B1
214E B1 ts1
214J sk1
214L lg1 gl2 mn1
215A gl14
215B gl11
215C wt1
215CA wt1-N472A
215CB wt1-N666B
215CC wt1-N178C
215CD wt1-N136A
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
217I Les10-NA607
217J Les11-N1438
217K Les15-N2007
217L Les18-N2441
217M Les19-N2450
217N cpc1-N2284B
218A w3
218C w3 Ch1
218D Ht1-GE440
218DA Ht1-Ladyfinger
218DB Ht1
218E ba2
218G B1-Peru; A1 A2 C1 C2 r1-r
218GA B1-Peru; A1 A2 C1 C2 R1-r
218H w3-8686
218I w3-86GN12
218J w3-Kermicle-1
219A B1-Peru; A1 A2 C1 C2 r1-g
219B b1; A1 A2 C1 C2 r1-g
219C Ch1
219D Ht1 Ch1
219F B1-Peru; A1 A2 C1 C2 bz2 r1-g
219G B1-Bolivia-706B; A1 A2 C1 C2 r1-g
219H B1-Bolivia; A1 A2 C1 C2 Pl1-Rhoades 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
219K B1-S; R1-g pl1-McClintock
219L B1-S; R1-r pl1-McClintock
220A Les1-N843
220B ws3 lg1 gl2; Alien Addition T2-Tripsacum
220D hcf15-N1253A
220F os1
221A gs2
221AA gs2-0229
221C wlv1-N1860 Ch1
221G wlv1-N1860
224B v*-5537
224H whp1; A1 A2 C1 R1 c2 gl1 in1
224I ws3-7752
224J ijmos*-7335
224K glnec*-8495
224L ws3-8949
224M ws3-8991
224N ws3-8945
226A ws3-N2357
226B b1-m1::Ds1; A1 A2 C1 C2 r1-g
226C b1-md2::Ds1; A1 A2 C1 C2 r1-g
226D b1-Pm5; A1 A2 C1 C2 r1-g
226E b1-Perum216; A1 A2 C1 C2 r1-g
227A dek3-N1289
227B dek4-N1024A
227C dek16-N1414
227D dek23-N1428
227E Les4-N1375
227I nec4-N516B
227K et2-2352
227L et2-91g6290-26
228A l18-N1940
228B spt1-N464
228C ws3-N453A
228CA ws3-N605A
228E B1-Bh
228F ms33-6019
228G ms33-6024
228H ms33-6029
228I ms33-6038
228J ms33-6041
229A rf3 Ch1
229B v24-N424
229BA v24-N576A
229BB v24-N588A
229BC v24-N350
229C w3 rf3 Ch1
229E emp2-MS1047
229F dek*-MS1365
229G dek*-MS4160
229H dek*-MS2159
229J dek*-PIE

CHROMOSOME 3 MARKER

301A cr1
301B bif2-N2354
301C spc3-N553C
301D Wi2-N1540
301E rd4
302A d1-6016
302AA d1-N446
302AB d1-N339
302B d1 rt1
302E d1-tall
303A d1 rt1 Lg3-O
303F g2
303FA g2-pg14::I
303FB g2-v19
303FD g2-56-3040-14
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
305D d1 Rg1
305K d1 cl1; Clm1-4
306F ref1-MS1185
307A Sdw2-N1991
307C pm1
308B d1 ts4
308E ra2
308F ra2 Rg1
308G ra2-D
309A a1-m3::Ds Sh2
309B a1-m1-5718::dSpm
309C a1-m1-5719A1::dSpm
309D a1-m1-5719A1::dSpm; Mod Pr1
309E a1 Sh2; Spm-w
309F a1-m2-8417::dSpm
309G a1-m2(os)-o1
309H a1-m2-7991A-o2
309I a1-m2-7995::dSpm
309J a1-m2-7977B::dSpm
309K a1-m2-8012A-p1
309L a1 Sh2; Spm-s
309M a1-m1-5719A1::dSpm sh2
309N a1-m2-7995B
309O a1-m1-5996-4::dSpm
309P a1-m1-5719A1::dSpm; Spm-i
309Q a1-m5::Spm-w; Spm-s
309S a1-m2-8411A::Spm-w Sh2
309T a1-m2-7981B6::Spm-w
309U a1-m2-8409::Spm-i
309V a1-m5::Spm-w Sh2
309W a1-m2-8011::Spm-w Sh2
309X a1 Sh2; Spm-w-8745
309Y a1 Sh2; Spm-i
309Z a1-m1-5720-o2
310C ra2 lg2
310D Cg1
311A cl1
311AA cl1-N2
311B cl1; Clm1-2
311BA cl1-7716; Clm1-2
311C cl1; Clm1-3
311D cl1-p; Clm1-4
311E rt1
311F ys3
311G Lg3-O ys3
312A Les14-N2004
312B Les17-N2345
312D Lg3-O
312G brn1-R
312H g2 brn1-R
312I brn1-R cr1
312J brn1-R ra2 lg2
312K brn1-Nelson
312L brn1-3071
312M ms23
313A gl6
313AA gl6-gl7
313AB gl6-N672B
313D ms3
313DA ms3-6008
313DB ms3-6009
313DC ms3-6043
313DD ms3-6020
314A gl6 lg2 A1; A2 C1 C2 R1
314C gl6 lg2 a1-m et1; A2 C1 C2 Dt1 R1
314F Rg1 gl6 lg2
314G gl6 lg2
315B Rg1 gl6
315C Rg1
315D A1-b(P415); A2 C1 C2 R1
315I A1-m2(os)-p1
315J A1-m2(os)-r2
315K a1-m2-7991A-o1
315L a1-m2-7991A-p2
315M a1-m2-7991A-p3
315N a1-m2-7991A-p4
315O a1-m2-7991A-p4b
315P a1-m2-7991A-p5
315Q a1-m2-8010A-o2
315R A1-m3-r1a sh2-m1::Ds
315S a1-m5-o1
315T a1-m5-o2
315U A1-m5-r1
315V A1-m5-r4
315W A1-m5-r5
316A ts4
316B a1-N796
316C dek5-N1339A
316D a1-mt2
316E a1-mt3
316F a1-mt4
316G a1-mt5
316H a1-mt6
316I a1-mt7
316J a1-mt8
316K a1-mt11
316L a1-mt13
316M a1-mt15
316N a1-mt16
316O a1-mt18
316P a1-mt19
317F gl6 ts4 lg2
317I a1-m1-5996-4m::dSpm; Spm
317J a1-m2::Spm-s; Spm-w
317K a1-m2-7991A::Spm-s
317L a1-m2-8004::dSpm
317M a1-m2-8010A::Spm-s
317N a1-m2-8011::Spm-w
317O a1-m2-8012A
317P a1-m2-8147

317Q a1-m2-8167::dSpm
317R a1-m2-8414C
317S a1-m2-8549C
317T a1-m5::Spm-w Sh2
317U a1-m5::Spm-w sh2-1
317W a1-m1-5720::Spm
317X a1-m1-6078::dSpm
317Y a1-m2-8409-2
317Z A1 def-1260
318A ig1
318B ba1
318C y10-7748
318D hcf19-N1257A
318E sh2-N391B
318EA sh2-N2307
318F sh2-N2340
318G na1
318H vp1-Mc
318I y10-8624
319A lg2 A1-b(P415) et1; A2 C1 C2 Dt1 R1
319C lg2 a1-m et1; A2 C1 C2 R1 dt1
319D lg2 a1-m et1; A2 C1 C2 Dt1 R1
319F lg2 a1-st et1; A2 C1 C2 Dt1 R1
319G lg2 a1-st et1; dt1
320A lg2
320B lg2-PI184281
320C lg2 na1
320D lg2-podcorn
320E et1
320F A1 sh2; A2 C1 C2 R1 b1 pl1
320K sh2-94-1001-11
320L sh2-94-1001-58
320M sh2-94-1001-1003
320N a3-Styles; B1-b Pl1-Rhoades r1-g
320O a3-Styles; B1-b Pl1-Rhoades R1-nj
321A A1-d31; A2 C1 C2 R1
321B lg2 a1; A2 C1 C2 R1 dt1
321C lg2 A1-b(P415) et1; A2 C1 C2 R1 dt1
321D a1-m4::Ds; A2 C1 C2 R1
321E a1-rUq; A2 C1 C2 R1
321F a1-Mum1; A2 C1 C2 R1
321H a1-Mum3; A2 C1 C2 R1
321I a1-Mum4; A2 C1 C2 R1
321J a1-Mum5; A2 C1 C2 R1
321K a1-rUq; Uq1
321L a1-rUq(flow); Uq1
322A A1-d31 sh2; A2 C1 C2 R1 dt1
322B A1-d31 sh2; A2 C1 C2 Dt1 R1
322C A1-Mum3-Rev; A2 C1 C2 R1
322F a1-m; A2 C1 R1 b1 dt1 pl1
322I et1-24
322J et1-27
322K et1-34
322L et1-2162
322M et1-2320
322N et1-2424
322O et1-2457
322P et1-3191
322Q et1-3328
322R et1-5079
322S et1-84-6013
322T et1-88g-9733
322U et1-43
323A a1-m; A2 C1 C2 Dt1 R1
323D a1-m sh2; A2 C1 C2 Dt1 R1
323E a1-m et1; A2 C1 C2 Dt1 R1
323G a1-m1::rDt (Neuffer); A2 C1 C2 Dt1 R1
323H a1-st; A2 C1 C2 Mrh R1 dt1
323I a1-m1::rDt (Neuffer); A2 C1 C2 R1 dt1
324A a1-st; A2 C1 C2 Dt1 R1
324B a1-st sh2; A2 C1 C2 Dt1 R1
324E a1-st et1; A2 C1 C2 Dt1 R1
324G a1-st; A2 C1 C2 R1 dt1
324H a1 et1; A2 C1 C2 R1 dt1
324I a1-st et1; A2 C1 C2 R1 dt1
324J A2; C1 C2 R1 a1-sh2-del-Robertson
324K a1-Mus1; A2 C1 C2 R1
324L a1-Mus2; A2 C1 C2 R1
324M a1-Mus3
324N a1-Mus4
325A a1-p et1; A2 C1 C2 R1 dt1
325B a1-p et1; A2 B1 C1 C2 Dt1 Pl1 R1
325C a1-x1; A2 C1 C2 R1
325D a1-x3; A2 C1 C2 R1
325E A1 ga7; A2 C1 C2 R1
325G a3
325I a1-p; A2 C1 C2 Dt1 R1
325J a1-p; A2 C1 C2 Pr1 R1 dt1
325K a1-m3::Ds sh2-m1::Ds; A2 Ac C1 C2 R1
326A sh2-Elmore
326AA sh2-Garwood
326AB sh2-60-156
326B vp1
326BA vp1-Mum3
326BC vp1-86N6
326BD vp1-86GN14
326BE vp1-86GN18
326BF vp1-86GN19
326BG vp1-Mum2
326BH vp1-Mum1::Mu
326C Rp3
326D te1-1
326DA te1-Forester
326DB te1-Grogan
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
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 R1 dt1
330L a1-mrh; A2 C1 C2 R1
332B dek5-N874A
332C dek24-N1283
332D Wrk1-N1020
332F gl19-N169
332G dek6-N627D
332H dek17-N330D
332I Lxm1-N1600
332M Spc1-N1376
332N wlu1-N28
332S Mv1
333A dek5-25
333AA dek5-MS33
333B te1-Galinat
333C dek5-Briggs-1998-1

CHROMOSOME 4 MARKER

401A Rp4-a
401C Ga1 su1
401D Ga1-S
401E Ga1-S; y1
401I ga1 su1
401J Ga1-M
401K Ga1-S su1
402A st1
402D Ts5
402E ms30-6028
402F hcf23-N1261A
403A Ts5 fl2
403B Ts5 su1
403C su1-F37
403D su1-PI228183
404A su3-5081; su4-5081
404B su3-89-1303-18; su4-89-1303-18
404C su3-94-4079-6; su4-94-4079-6
404D su3-85-3113-11; su4-85-3113-11
405B la1-PI239110
405BB la1-Funk:2232
405BC la1-N2020
405BD la1-N2276B
405BE la1-PI184284
405D la1-R su1 gl3
405G la1-R su1 gl4
406C fl2
406CA fl2-DR9234
406D fl2 su1
407D su1
407DA su1-N86
407DB su1-N2316
407DC su1-BKG489-13
407DD su1-Pl
407DE su1-R2412
407DF su1-N896A
407DG su1-N1161A
407DH su1-N2313
407DI su1-N2314
407DJ su1-N959
407DK su1-N1968
407DL su1-N1994
407E su1-am
407F su1-am; du1
408B bm3-Burnham su1
408C su1 zb6
408E bm3-91598-3
408J su1 ra3
408K su1; se1
408L su1 zb6 Tu1
409A su1-st
409B su1-66
409C su1-P
409D su1-5051
409F su1-28510
409G su1-28511
409H su1-28512
409I su1-28513
409J su1-28515
409K su1-28516
409L su1-28517
409M su1-28518
409N su1-28519
409O su1-28520
409P su1-30394
409Q su1-30397
409R su1-30398
409S su1-30399
409T su1-30400
409U su1-30401
409V su1-Bn2
410D su1 zb6 gl3
410E su1-A3
410F su1-4582::Mu1
410G su1-8064
410H su1-2401
410I su1-3837
410J su1-7110
410K su1-2857
410L su1-2859
410M su1-90-1101.1
410N su1-83-3383-4
410O su1-87-2046-27
410P su1-85-3217-10
410Q su1-84-5167-6
410R su1-84-5267-18
410S su1-85-3436-29
411A su1-8908
411B su1 gl4 o1
411F gl7 su1 v17
412C su1 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; bm*-COOP
414A bt2
414AA bt2-Williams
414AB bt2-60-158
414AC bt2-9626
414AD bt2-5288
414B gl4
414BA gl4-Stadler
414BB gl4-gl16
414BD gl4-N525A
414C gl4 o1
414E de*-414E
415A j2
415B o1-N1243
415C o1-N1478A
415D bt2-8132
416A Tu1-A158
416B Tu1-l(1st)
416C Tu1-l(2nd)
416D Tu1-d
416E Tu1-md
416F Tu1 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 C2; A2 C1 R1 a1-m
419G Dt6 C2; A2 C1 R1 a1-m
419H c2-m1::Spm; A1 A2 C1 R1
419I c2-m2::dSpm c2-m3::Mpi1
419J c2-Mum1
419K c2-m2::dSpm; Spm-s
419L c2-m881058Y::IRMA; En Mod wx1-m8::Spm-I8
419M c2-m3::Mpi1
420A su1 Dt4 C2; A2 C1 R1 a1-m

420C nec*-rd
420CA nec*-016-15
420D yel*-8957
420F dp*-4301-43
420G w*-9005
420H Dt4 C2; A2 C1 R1 a1-m
424C gl3-64-4
424D gl3-56-3120-2
424E gl3-56-3129-27
424F gl3-60-2555
424G gl3-PI183683
424H gl3-PI251928
424I gl3-PI251938
424J gl3-PI254858
424K gl3-PI267180
424L gl3-PI267219
424M gl3-PI-311517
424N gl3-15
426A Gl5 Su1; gl20
426B gl3-PI251941
426D cp2-N1324A
427A cp2-o12
427AA cp2-N211C
427AB cp2-N1875A
427AC cp2-MS2608
427AD cp2-N912
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
428E wt2-N10
428F lw4; Lw3
428G bx1
428H gl5 su1; gl20
428L dsc1-MS2058

CHROMOSOME 5 MARKER

501A am1 a2; A1 C1 C2 R1
501B lu1
501D ms13
501E gl17
501F gl17-N260B
501G gl17 a2; A1 C1 C2 R1
501I am1
502B A2 ps1-Sprague pr1; A1 C1 C2 R1
502C D9-N2319
502D A2 bm1 pr1; A1 C1 C2 R1
502E Ms42-N2082
502F Nl2-N1445
502G A2 Bt1 ga10
502H hcf21-N1259A
503A A2 bm1 pr1 ys1; A1 C1 C2 R1
503B hcf43-N1277B
503C a2-mu1::Mu1
503D a2-mu2
503E a2-mu3::Mu3
504A A2 bt1 pr1; A1 C1 C2 R1
504C A2 bm1 pr1 zb1; A1 C1 C2 R1
504E A2 bt1; A1 C1 C2 R1
505B A2 pr1 ys1; A1 C1 C2 R1
505C A2 bt1 pr1 ga*-Rhoades; A1 C1 C2 R1
505D pr1-N1515A
505E pr1-N1527A
506A A2 v3 pr1; A1 C1 C2 R1
506B A2 pr1; A1 C1 C2 R1
506C A2 pr1 v2; A1 C1 C2 R1
506D na2 A2 pr1; A1 C1 C2 R1
506F A2 pr1 v12; A1 C1 C2 R1
506L A2 br3 pr1; A1 C1 C2 R1
507A a2; A1 C1 C2 R1
507AA a2-Mus2; A1 C1 C2 R1
507AB a2-Mus3; A1 C1 C2 R1
507AC a2-Mus1; A1 C1 C2 R1
507F a2 bm1 bt1 ga*-Rhoades; A1 C1 C2 R1
507G a2 bm1 bt1; A1 C1 C2 R1
507H A2 bv1 pr1; A1 C1 C2 R1
507I a2-m4::Ds; wx1-m7::Ac7
508A a2 bm1 bt1 pr1; A1 C1 C2 R1
508C a2 bm1 bt1 bv1 pr1; A1 C1 C2 R1
508F a2 bm1 pr1 ys1; A1 C1 C2 R1
508H a2-Mum1
508I a2-Mum2
508J a2-Mum3
508K a2-Mum4
508L bv1 pr1
509G a2-m1::dSpm Bt1
509H a2-m1(II)::dSpm(class II)
509I pr1-m1
509J pr1-m2
509K a2-m1(ps)
509L a2-m1::dSpm; Spm-s
509M a2-m5::dSpm
509N A2-m1(os)-r1
510A a2 bm1 pr1 v2; A1 C1 C2 R1
510D a2 pr1 gl8; A1 C1 C2 R1
510E a2 ae1 pr1 gl8; A1 C1 C2 R1
510G a2 bm1 pr1 eg1; A1 C1 C2 R1
511C a2 bt1 pr1; A1 C1 C2 R1
511F a2 bt1 Pr1 ga*-Rhoades; A1 C1 C2 R1
511H a2 bt1; A1 C1 C2 R1
512C a2 bt1 pr1 ga*-Rhoades; A1 C1 C2 R1
512D vp2-N1136B
512E Wi4-N2445A
512F pb4
512G gl8-N166A
512H v13
512I lw2-vp12
513A a2 pr1; A1 C1 C2 R1
513C a2 pr1 v2; A1 C1 C2 R1
513D A2 pr1 sh4; A1 C1 C2 R1
513E a2 pr1 v12; A1 C1 C2 R1
514A a2 bm1 pr1; A1 C1 C2 R1
514B ae1-PS1
514C ae1-PS2
514D ae1-PS3
514E ae1-PS4
514F ae1-PS5
514G ae1-PS6
514H ae1-PS7
514I ae1-PS8
514J ae1-PS9
514K ae1-PS10
514L ae1-PS11
514M Ae1-5180-r4
514N bt1-m1::dSpm
514O bt1-m2
514P bt1-m3::dSpm
514Q bt1-m4::Ds
514R Bt1-m1-r1
515A vp2
515AA vp2-DR5180
515AB a2 vp2-green mosaic; A1 C1 C2 R1
515C ps1-Sprague
515CA ps1-8776
515CB ps1-881565-2M
515CC ps1-N80
515CD ps1-8205
515D bm1
515E bt1-N1992
515F bt1-N2308
515G bt1-N2309
516B bt1-R
516BA bt1-Elmore
516BB bt1-C103
516BC bt1-Singleton
516BD bt1-sh3
516BE bt1-sh5
516BF bt1-Eldridge
516BH bt1-6-783-7
516BI bt1-Vineyard
516BJ bt1-T
516BK bt1-W187R
516BL bt1-3040
516BM bt1-N797A
516C ms5
516D td1 ae1
516DA td1-Nickerson
516G A2 bm1 pr1 yg1; A1 C1 C2 R1
517A v3
517AB v3-8982
517B ae1
517BA ae1-EMS
517BB ae1-PS12
517BC ae1-PS13
517BD ae1-PS14
517BE ae1-PS15
517BF ae1-PS16
517BH ae1-Elmore
517E ae1 pr1 gl8
518A sh4
518AA sh4-Rhoades
518AB sh4-o9
518B gl8-Salamini
518BA gl8-R
518BB gl8-6:COOP
518BC gl8-6:Salamini
518BD gl8-10:COOP
518BE gl8-PI180167
518C na2
518D lw2
519AA ys1-W23
519AB ys1-5344
519AC ys1-N755A
519AD ys1-74-1924-1
519B eg1
519C v2
519D yg1
519E A2 pr1 yg1; A1 C1 C2 R1
519F A2 pr1 gl8; A1 C1 C2 R1
519H zb1
519I zb1-2
520A hcf38-N1273
520B v12
520C br3
520F A2 Dap1; A1 C1 C2 R1
520G A2 pr1 Dap1; A1 C1 C2 R1
520H Dap1-2
520I ae1-1979-7
520J ae1-MOEWS
520K ae1-1981-MuT
521A nec3-N409
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
521NA lnec*-8549
521P lw3; Lw4
524A v*-PI267226
524B les*-3F-3330
527A dek18-N931A
527B dek9-N1365
527C dek26-N1331
527D dek27-N1380A
527E grt1-N1308B
527F nec7-N756B
527G dek33-N1299
527H Msc2-N1124B
527I ppg1-N199
527J nec6-N493
528A Hsf1-N1595
528B wgs1-N206B
528C anl1-N1634
528CA anl1-330C
528E prg1-MS8186
528F ren1-MS807
528H dek*-MS2146
528I dek*-MS1182
529A anl1-N1643
529B anl1-N1645
529C anl1-N1671
529D anl1-N1685
529E anl1-N1691
529F anl1-N1673

CHROMOSOME 6 MARKER

601C rgd1 y1
601F po1-ms6 y1 pl1
601H rhm1 rgd1 y1
601I rhm1 y1 l11
601J Wsm1 Mdm1; Wsm2 Wsm3
601K wsm1 mdm1; wsm2 wsm3
601L Mdm1 y1
602A po1-ms6 wi1 y1
602C y1
602D rhm1 Y1
602J y1-w-mut
602K y1-gbl
602L y1-pb1
602M y1-8549
602N y1-Caspar
602O y1-0317
602P y1-129E
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-Brawn1
604F y1 si1-mssi
604FA y1 si1-ts8
604FB y1 si1-Sam
604H y1 ms1
604HA y1 ms1-Robertson
604I Y1 ms1
604IA ms1-6050
605A wi1 y1
605C y1 pg11; Wx1 pg12
605E wi1 Y1 Pl1
605F wi1 Y1 pl1
605G l3
606A Y1 pg11-4484; Wx1 pg12-

4484
606AA pg11-8925; pg12-8925
606AB pg11-48-040-8; pg12-48-040-8
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; Wx1 pg12
607A y1 Pl1-Bh1; A1 A2 C2 R1 c1 sh1 wx1
607C y1 su2
607E y1 pl1 su2 v7
607H y1 Pl1-Bh1; A1 A2 C2 R1 Wx1 c1 sh1
607I y1 Pl1-Bh1; A1 A2 C2 R1 c1 sh1 skb1 wx1
607J sm1-Brawn168
607K sm1-Brawn178
607L sm1-Brawn184
608A gs3-N268
608C sbd1-N2292
608D Les13-N2003
608F y1 pl1 w1
608G Y1 l11
609D Y1 su2
609DA Y1 su2-89-1273
609DB su2-PS1
609DC su2-PS2
609DD su2-1979-5
609DE su2-87-2279-12
609DF su2-1981
609DG su2-1982
609DH su2-0203
609DI su2-PI193430
609DJ su2-1979-1
609F ms1-Albertsen
610B Dt2 Pl1; A2 C1 C2 R1 a1-m
610F Y1 pl1 su2 v7
610G hcf34-N1269C
610H Y1 Dt2 pl1; A2 C1 C2 R1 a1-m
610I hcf36-N1271B
610J hcf48-N1282C
610K hcf26-N1263C
610L hcf323
610M hcf5-N510C
611A Pl1 sm1; P1-rr
611D Pt1
611E Y1 pl1 w1
611EA w1-7366
611I sm1 tan1-py1; P1-rr
611K Y1 Pl1 w1
611L w1; l1
611M afd1
611N sr4-N65A
611O o14-N924
612A w14
612B po1
612BA po1-ms6
612C l*-4923
612D oro1
612DA oro1-6474
612I tan1-py1
612J w14-8657
612K w14-8050
612L w14-6853
612M w14-025-12
612N w14-1-7(4302-31)
612O yel*-1-7(4302-31)
613A 2NOR y1; A1 C1 C2 R1 a2 bm1 pr1 v2 wx1
613D vms*-8522
613F w14-8613
613I tus*-5267
613J gm*-6372
613L w*-8954
613M yel*-039-13
613N yel*-7285
613O l*-4-6(4447)
613P yel*-8631
613T pg11-6656; pg12-6656
627A dek28-N1307A
627B dek19-N1296A
627C vp*-5111
627G dek*-MS1104; l*-1104

CHROMOSOME 7 MARKER

701B In1-D
701D o2
701E o2-Mum1
701F Hs1
702A o2 v5
702B o2 v5 ra1-Ref gl1
702I In1-Brawn
703A o2 v5 gl1
703B De*-B30
703C o2-m(r); Bg
703D o2 ra1-Ref gl1
703E o2-R; Bg
703F o2-m12::Spm
703G o2-m2::Ds; Ac
703H o2-m5::Ac
703J Rs1-O
703JA Rs1-1025::Mu6/7
703K Rs1-Z
704B o2 ra1-Ref gl1 sl1
704C o2-NA696
704D o2-NA697
704E gl1-m8
704F ms22-6036
704H o2-orange
705A o2 gl1
705B o2 gl1 sl1
705D o2 bd1
706A o2 sl1
706B vp9-Bot100
707A y8 v5 gl1
707B in1; A1 A2 C1 C2 R1 pr1
707C in1 gl1; A1 A2 C1 C2 R1 pr1
707D v5
707E vp9-R
707EA vp9-3111
707EB vp9-86GN9
707EC vp9-86GN15
707F y8 gl1
707G in1 gl1; A1 A2 C1 C2 Pr1 R1
708A ra1-Ref
708AA ra1-PI262495
708AB ra1-PI184279
708AC ra1-PI239103
708AD ra1-PI267181
708AE ra1-PI267184
708AF ra1-63-3359
708B bd1-N2355
708C o15-N1117
708D y8-lty2
709A gl1
709AA gl1-56-3013-20
709AB gl1-56-3122-7
709AC gl1-PI183644
709AD gl1-PI218043
709AE gl1-PI251652
709AF gl1-PI257507
709AG gl1-Istra
709AH gl1-BMS
709AI gl1-7L
709AJ gl1-9:COOP
709AK gl1-N212
709AL gl1-N269
709AM gl1-N345B
709C gl1-m
710A gl1 Tp1
710B gl1 mn2
710E o5 gl1
710I gl1 Bn1
710J gl1-N271
710K gl1-dy
710L gl1-PI218038
711A Tp1
711B ij1-ref::Ds
711C ij1-60-2454-20
711G ts*-br
712A ms7
712AA ms7-6007
712B ms7 gl1
713A Bn1
713E Bn1 bd1
713H Bn1 ij1
713I bd1 Pn1
714A Pn1
714B o5
714BA o5-PS3038
714BB o5-N76B
714BC o5-N874B
714C o5-N1241
714D va1
715A Dt3; A2 C1 C2 R1 a1-m
715C gl1 Dt3; A2 C1 C2 R1 a1-m
716A v*-8647
716B yel*-7748
716C dlf1-N2389A
716D dlf1-N2461
716F Les9-N2008
727A dek11-N788
727B wlu2-N543A
727D v27-N590A
727DA v27-N53B
727DB v27-N413C
727E gl1-cgl
727F Rs4-N1606
727G Rs1-O o2 v5 ra1-Ref gl1
727H ms34-6004
727I ms34-6010
727J ms34-6013
727K ms34-6014
728A Px3-6
728B ptd2-MS3193
728C mn2-cp1
728D sh6-8601
728E sh6-N1295
728F ren2-NS326
728G dek*-MS2082
728H dek*-MS5153

CHROMOSOME 8 MARKER

801A gl18-g
801B v16
801I yel*-024-5
801K v16 ms8
802A rgh1-N1285
802B emp3-N1386A
802C Ht2
802G ms43
802H gl18-PI262473
802I gl18-PI262490
803A ms8
803B nec1-025-4
803D gl18-g ms8
803F nec1-7748
803G nec1-6697
804A v21-A552
804B dp*-8925
804C tb*-poey1013
805A fl3
805C gl18-g v21-A552
805E el1
805G ms8 j1
808A ct1
808B Lg4-O
808C Htn1
810A v16 j1; l1
810B j1
810C j1-JSM
827A dek20-N1392A
827B dek29-N1387A
827C Bif1-N1440
827CA Bif1-N2001
827D Sdw1-N1592
827E Clt1-N985
827F pro1-N1058
827G pro1-N1121A
827H pro1-N1528
827I pro1-N1533
827J wlu3-N203A
827K pro1
827L pro1-Tracy
828A ats1
828C pro1-N1154A
828D pro1-NA342
828E pro1-N1530

CHROMOSOME 9 MARKER

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 C2 R1
901H yg2 C1 Bz1; A1 A2 C2 R1
902A yg2 c1 sh1 bz1 wx1; A1 A2 C2 R1
902B yg2 c1 sh1 wx1; A1 A2 C2 R1
902C yg2 c1 sh1 wx1 gl15-Hayes; A1 A2 C2 R1
902D yg2 c1 sh1 Bz1 wx1 gl15 K9S-s; A1 A2 C2 R1
902E C1 sh1 Bz1-McC1; A1 A2 C2 R1
902G C1 sh1 bz1 wx1; A1 A2 C2 R1 Spm
902I bz1-m13CS1
902J bz1-m13CS3
902K bz1-m13CS4
902L bz1-m13CS5
902M bz1-m13CS6
902N bz1-m13CS7
903A C1 sh1 bz1; A1 A2 C2 R1
903B C1 sh1 bz1 wx1; A1 A2 C2 R1
903D C1-I sh1 bz1 wx1; A1 A2 C2 R1
903E bz1-m13CS8
903F bz1-m13CS10
903G bz1-m13CS11
903H bz1-m13CS12
904B C1 sh1; A1 A2 C2 R1
904C C1 sh1 wx1; A1 A2 C2 R1
904D C1 wx1 ar1; A1 A2 C2 R1
904F C1 sh1 bz1 gl15 bm4; A1 A2 C2 R1
904G rgo1-Sarkar
905A C1 sh1 wx1 K9S-l; A1 A2 C2 R1

905C C1 bz1 Wx1; A1 A2 C2 R1
905D C1 sh1 wx1 K9S-I; A1 A2 C2 K10-I R1
905G C1 bz1 wx1; A1 A2 C2 R1
905H c1 sh1 wx1; A1 A2 C2 R1-scm2 b1
905I ms45-6040
906A C1 wx1; A1 A2 C2 DsI Pr1 R1 y1
906B C1 wx1; A1 A2 C2 DsI R1 Y1 pr1
906C C1-I Wx1; A1 A2 C2 DsI R1
906D C1-I; A1 A2 C2 R1
906G C1-I Sh1 Bz1 Wx1; DsI
906H C1 Sh1 bz1 wx1; Ac
907A C1 wx1; A1 A2 C2 R1
907E C1-I wx1; A1 A2 C2 R1 y1
907G c1-p; A1 A2 B1-b C2 R1 pl1
907H c1-n; A1 A2 C2 R1 b1 pl1
907I C1-S wx1; A1 A2 C2 R1
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
908G c1-mt13
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
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
909G hcf42-N1276B
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
910I sh1-bb1981 bz1-m4::Ds
910IA sh1-bb1981 bz1-m4::Ds; Ac
910L yg2-str
911A c1 wx1; A1 A2 C2 R1
911B c1 wx1 v1; A1 A2 C2 R1
911C c1 wx1 gl15-Hayes; A1 A2 C2 R1
911D Fas1
911E sem1-1364
911F def(Bf1..bm4)044-4
912A sh1
912AA sh1-1746
912AB sh1-9026-11
912AC sh1-3-6(6349)
912AD sh1-60-155
912AE sh1-EMS
912AF sh1-4020
912AG sh1-9552
912AH sh1-9626
912AI sh1-3017
912AJ sh1-6
912B sh1 wx1 v1
912E lo2
912H lo2 wx1
913C sh1 l7
913D sh1 l6
913E baf1
913F yg2-Mum1
913G yg2-Mum2
913H yg2-Mum3
913I yg2-Mum4
913J yg2-Mum5
913K yg2-Mum6
913L yg2-Mum7
913M yg2-Mum8
913N yg2-Mum9
913O yg2-DR83-106-3
913P yg2-DR83-106-5
914A wx1 d3-COOP
914B dek12-N1054
914K Wc1-ly; Y1
914L bz1-Mus1
914M bz1-Mus2
914N bz1-Mus3
914O bz1-Mus5
914P bz1-Mus6
914Q bz1-Mus7
914R bz1-Mus10
915A wx1
915B wx1-a
915C w11
915D wx1-N1050A
915E wx1-Alexander
915F wx1-N1240A
916A wx1 v1
916B wx1 v1-JRL
916C wx1 bk2
916E wx1 v1 gl15
916G Trn1-N1597
916H v31-N828
916I d3-8201
917A wx1 Bf1-ref
917C v1
917D ms2
917DA ms2-6002
917DB ms2-6012
917E gl15-Sprague
917EA gl15-Lambert
917EB gl15-KEW
917F d3-COOP
917FA d3-d2
917FB d3-015-12
917FC d3-072-7
917FD d3-8054
917FF d3-d2-Harberd
917FG d3-d2-Phillips
917FH d3-N660B
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 l6
919D l7
919G l6; l1
919I Bf1-DR-046-1
919J bz1-Mum9; MuDR
919K bz1-Mum4::Mu1
919L bz1-Mum1
919M bz1-Mum2
919N bz1-Mum3
919O bz1-Mum5
919P bz1-Mum6
919Q bz1-Mum7
919R bz1-Mum8
919S bz1-Mum9
919T bz1-Mum10
919U bz1-Mum11
919V bz1-Mum12
919W bz1-Mum15
919X bz1-Mum16
919Y bz1-Mum18
920A yel*-034-16
920B w*-4889
920C w*-8889
920E w*-8950
920F w*-9000
920G Tp3L-9SRhoades
920L ygzb*-5588
920M wnl*-034-5
920N pyd1
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::Ds
923ZA wx1-m6R
923ZB wx1-m6NR
923ZC wx1-m8::Spm-I8
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
924E wd1 C1 sh1 bz1
924F C1 Sh1 sh1 Bz1 bz1 wx1 tiny fragment 9
924G C1-I Bz1; Ac DsI
924H c1 sh1 bz1 wx1; Ac
925A bz1-m1::Ds wx1-m9::Ac
925B wx1-m9::Ds; Ac
925C bz1-m2::Ac
925D Wx1-m9r1
925E bz1-m2(DII)::Ds wx1-m6::Ds
925F C1 sh1 bz1 wx1-m8::Spm-I8
925H bz1-m2(DI)::Ds wx1; R1-sc
925I c1-m2::Ds Wx1; Ac
925J c1-m858::dSpm wx1
925K c1-m1::Ds
926A sh1-m5933::Ds
926B Sh1-r3(5933)
926C Sh1-r6(5933)
926D Sh1-r7(5933)
926E Sh1-r8(5933)
926F Sh1-r9(5933)
926G Sh1-r10(5933)
926H Sh1-r11(5933)
926I sh1-m6233::Ds
926J Sh1-r1(6233)
926K Sh1-r2(6233)
926L C1-I sh1-m6258::Ds
926M Sh1-m6258-r1
926N Sh1-r6795-1
926O bz1-m5::Ac
926P Bz1-wm::Ds1
926Q Bz1-m1-p
926R Bz1-m2-r1
926S Bz1-m2(DII)-r1
926T Bz1-m2(DII)-r2
926U Bz1-m2(DII)-r3
926V sh1-bb1981 Bz1-m4-p1
926W sh1-bb1981 Bz1-m4-r6851
926X sh1-bb1981 Bz1-m4-r7840B
926Y sh1-bb1981 Bz1-m4-r8332
926Z Bz1-m5-p1
926ZA Bz1-m5-r1
926ZB Bz1-m5-r2
927A dek12-N873
927B dek13-N744
927C dek30-N1391
927D Les8-N2005
927E Zb8-N1443
927H C1 Dt7; A2 C2 R1 a1-r
927I G6-N1585
927K Rld1-N1990
927L Rld1-N1441
928A yg2-N27
928AA yg2-N585
928AB yg2-N697
928AC yg2-N610
928B wlu4-N41A
928C ms20
928G c1-m5::Spm wx1-m8::Spm-I8; A1 A2 C2 R1
928H wx1-m7::Ac7
928I C1 bz1-mut::rMut; A1 A2 Bz2 C2 Mut R1
928J C1 bz1-(r)d; A1 A2 C2 R1
928K C1 Sh1 bz1-s; A1 A2 C2 Mut R1
928L ms45-6006
928M ms35-6011
928N ms35-6018
928O ms*-6021
928P ms*-6022
928Q ms35-6027
928R ms35-6031
928S ms*-6046
928T ms*-6047
929E Dp9
930A wx1-Mum1
930B wx1-Mum2
930C wx1-Mum3
930D wx1-Mum4
930E wx1-Mum5::Mu
930F wx1-Mum6
930G wx1-Mum7
930H wx1-Mum8
930I wx1-Mum9
930J wx1-Mum10
930K wx1-Mum11
930L wx1-Mus16
930M wx1-Mus181
930N wx1-Mus215
931A Wx1-m5::Ds
931B wx1-m6::Ds
931C wx1-m6-o1
931D Wx1-m7-i1
931E Wx1-m8-r10
931F Wx1-m9-r3
931G Wx1-m9-r4
931H wd1-Mus1
931I wd1-Mus2
931J wd1-Mus3
931K wd1-Mus4
931L wd1-Mus5
931M wd1-Mus6

CHROMOSOME 10 MARKER

X01A oy1-Anderson
X01AA oy1-yg
X01AB oy1-8923
X01B oy1 R1; A1 A2 C1 C2
X01C oy1 bf2
X01E oy1 bf2 R1; A1 A2 C1 C2
X02C oy1 zn1 R1; A1 A2 C1 C2
X02E oy1 du1 r1; A1 A2 C1 C2
X02G oy1 zn1
X02H Oy1-N1459
X02I Oy1-N1538
X02J Oy1-N1583
X02K Oy1-N1588
X02L Oy1-N1989
X03A sr3
X03B Og1
X03D Og1 R1; A1 A2 C1 C2
X03E oy1 y9
X03F Inr1-Ref
X04A Og1 du1 R1; A1 A2 C1 C2
X04B ms11
X04BA ms11-6051
X04D bf2
X04DA bf2-N185A
X04E du1-8501
X04F du1-8802
X05A Og*-0376
X05B Gs4-N1439
X05E bf2 sr2
X05G bf2 g1 R1-r; A1 A2 C1 C2
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
X07CA y9-y12
X07D nl1
X08A vp10
X08B vp10-86GN5
X08C vp10-TX8552
X08F li1
X08FA li1-IL90-243Tco
X09B li1 g1 R1; A1 A2 C1 C2
X09EA g1-g4
X09EB g1-56-3005-24
X09EC g1-1-7(X-55-16)
X09ED g1-68-609-13
X09EE g1-ws2
X09EF g1-PI262473
X09F ms10
X09FA ms10-6001
X09FB ms10-6035
X09G li1 g1 r1; A1 A2 C1 C2
X10A du1
X10AA du1-PS1
X10AB du1-PS2
X10AC du1-PS3
X10AD du1-PS6
X10AE du1-PS4
X10AF du1-PS5
X10AG du1-8801
X10AH du1-84-5350-31
X10D du1 g1 r1; A1 A2 C1 C2
X10F zn1
X10FA zn1-N25
X10G du1 v18
X11A zn1 g1
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; A1 A2 C1 C2
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
X13E g1 r1-ch; A1 A2 C1 C2 wx1
X13G R1-p
X13H R1-b
X14A r1-r lsr1-Ej; A1 A2 C1 C2
X14E r1; A1 A2 C1 C2 wx1
X14F v18 r1; A1 A2 C1 C2
X14I r1-sc:m3::Ds
X14J R1-nj::Ac
X14K r1-Del902
X14L r1-g; 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
X15F lsr1 R1-g sr2
X15G isr1 r1-g sr2
X15H isr1 R1-r:PI302369
X15HA isr1 R1-r:PI302369 sr2
X15I isr1 R1-nj Mst1
X16B r1 K10-I; A1 A2 C1 C2
X16C R1-ch; A1 A2 C1 C2 Pl1
X16CA R1-ch
X16D r1 sr2; A1 A2 C1 C2
X16E r1 K10-II; A1 A2 C1 C2
X16F R1 K10-II; 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-lsk; 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-scm2; A1 A2 C1 C2 bz2
X18H R1-nj; A1 A2 C1 C2 bz2
X18I r1; A1 A2 C1 C2
X19A R1-sc:124
X19B w2
X19BA w2-Burnham
X19BB w2-2221
X19C l1 w2
X19D o7
X19E R1-r Lc1-Ecuador; b1
X19F r1 w2
X19G r1-n19 Lc1; b1
X19H r1-g:e Lc1; b1
X20B l1
X20C v18
X20I R1-d:Arapaho
X20J R1-d:Catspaw
X24A cm1
X24B lep*-8691
X24C v*-8574
X25A R1-scm2; A2 C1 C2 a1-st
X25B R1-scm2; A1 A2 C1 c2
X25C R1-sc:122; A1 A2 C1 C2 pr1
X25D R1-scm2; A1 C1 C2 a2
X25E R1-scm2; A1 A2 C2 c1
X26A r1-X1 / R1; A1 A2 C1 C2
X26B R1-scm2; A1 A2 C1 C2
X26C R1-sc:122; A1 A2 C1 C2
X26D R1-sc:5691; A1 A2 C1 C2
X26E R1-scm2; A1 A2 C1 C2 pr1 wx1
X26F R1-scm2; A1 A2 C1 C2 ln1-D
X26G R1-scm2; A1 A2 C1 c2-m2::dSpm
X26H R1-scm2; A1 A2 C1 C2 wx1
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 l19-N425
X27J l13-N59A
X27K v29-N418
X27L Les12-N1453
X28B R1-scm2; 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-scm2; A2 C1 C2 a1-m1-5719::dSpm
X28J R1-scm2; A1 A2 C1 C2 bz1
X29A ren3-MS1339
X29B dek*-MS2181
X29C cr4-N590C
X29D cr4-N647
X29E cr4-N411

UNPLACED GENES

U140A aph1
U140AA Aph1
U140C l4
U140G ms22
U140H ms24
U140I zn2-94-234
U240A Les7-N1461
U240D o11
U240E zn2
U240F zn2-PI251887
U240G zn2-PI236997
U240H zn2-PI239110
U240I zn2-56-3012-10
U340D ws1-COOP ws2-COOP
U340DA ws1-Pawnee ws2-Pawnee
U340H oro4
U440B gl13
U440C hcf49-N1480
U440D ub1-76C
U440E frz1
U440F mg1-Sprague
U540A dv1
U540B dy1
U640A dsy1-Doyle
U640B dsy1-Russian
U640C pam1
U640D pam2
U640E ada1
U640F atn1 Adh1-1S5657
U740A abs1-PI254851
U740C lty1
U740F pi1 pi2
U740G Fbr1-N1602
U740H ad2-N2356A
U840A csp1-NA1173
U840D Les21-N1442
U840F agt1
U840G Wi3-N1614
U840H nld1-N2346
U840I Mc1
U840J hcf16
U940A Ht3
U940B dsy1
U940D hcf11-N1250A
U940E hcf17
U940F hcf73
U940G Glb2-0
U940C v25-N17

MULTIPLE GENES

M141A A1 A2 B1 C1 C2 Pl1 Pr1 R1-g
M141AA A1 A2 B1 C1 C2 Pl1-Rhoades Pr1 R1-g
M141B A1 A2 B1 C1 C2 pl1 Pr1 R1-g
M142A A1 A2 b1 C1 C2 pl1 R1-r
M142B a1 A2 b1 C1 C2 pl1 R1-r
M142C A1 a2 b1 C1 C2 pl1 R1-r
M142D A1 A2 b1 bz1 C1 C2 pl1 R1-r
M142E A1 A2 b1 bz2 C1 C2 pl1 R1-r
M142F A1 A2 b1 c1-p C2 pl1 R1-r
M142G A1 A2 b1 C1-I C2 pl1 R1-r
M142H A1 A2 b1 C1 c2 pl1 R1-r
M142I A1 A2 b1 C1 C2-ldfm pl1 R1-r
M142J A1 A2 b1 C1 C2-ldf1(Active-1) pl1 R1-r
M142K A1 A2 b1 C1 C2 pl1 pr1 R1-r
M142L A1 A2 b1 C1 C2 gl1 in1 pl1 R1-r
M142M A1 A2 b1 C1 C2 In1-D pl1 R1-r
M142N A1 a2 bt1 C1 C2 pr1 R1
M142O C1 sh1 bz1 wx1; A1 A2 C2 R1-r
M142P c1 sh1 wx1; A1 A2 C2 R1-r
M142Q yg2 c1 sh1 wx1; A1 A2 C2 R1-g
M142R A1 A2 C1-I C2 R1-r wx1
M142S su1 c2; A1 A2 C1 R1-r
M142T A1 A2 b1 C1 C2 pl1 r1-g
M142U A1 A2 b1 C1 C2 pl1 r1-r
M142V A1 A2 C1 C2 R1-nj
M142W A1 A2 C1 C2 R1-st
M142X A1 A2 b1 C1 C2 Pl1 r1-g
M142Y A1 A2 B1 C1 C2 Pl1 r1-g
M142Z a1-st A2 b1 C1 C2 pl1 R1-scm2
M142ZA A1 a2 b1 C1 C2 pl1 R1-scm2
M142ZB b1 bz1 C1 pl1 R1-scm2 sh1
M142ZC A1 A2 b1 bz2 C1 C2 pl1 R1-scm2
M142ZD A1 A2 b1 c1-n C2 pl1 R1-scm2
M142ZE A1 A2 b1 c1-p C2 pl1 R1-scm2
M241A A1 A2 B1 C1 C2 Pl1 Pr1 r1-g
M241C A1 A2 B1 C1 C2 Pl1 Pr1 R1-r
M241D A1 A2 b1 C1 C2 Pl1-Rhoades r1-g
M242A A1 A2 b1 C1 c2 pl1 R1-scm2
M242B A1 A2 b1 C1 C2 pl1 pr1 R1-scm2
M242C in1 gl1; A1 A2 b1 C1 C2 pl1 R1-scm2
M242D a1 sh2; A2 b1 C1 C2 pl1 R1-scm2
M242E c1 sh1 wx1; A1 A2 b1 C2 pl1 R1-scm2
M242F su1 c2; A1 A2 b1 C1 pl1 R1-scm2
M242G A1 A2 b1 C1 C2 pl1 R1-scm2

M242H A1 A2 b1 C1 C2 pl1 r1-g
M242I A1 A2 b1 C1 C2 pl1 r1-r
M340A A1 A2 B1 c1 C2 pl1 Pr1 R1-g
M340B A1 A2 B1 c1 C2 Pl1 Pr1 R1-g
M340C A1 A2 b1 c1 C2 pl1 Pr1 R1-g
M341B A1 A2 B1 C1 C2 pl1 Pr1 R1-r
M341C A1 A2 b1 C1 C2 Pl1 Pr1 R1-r
M341CA A1 A2 b1 C1 C2 Pl1-Rhoades Pr1 R1-r
M341D A1 A2 B1 c1 C2 Pl1 Pr1 R1-r
M341F A1 A2 b1 C1 C2 pl1 Pr1 R1-r
M441B A1 A2 B1 C1 C2 pl1 Pr1 R1-r wx1
M441D A1 A2 B1 C1 C2 Pl1 Pr1 r1-r
M441F A1 A2 b1 C1 C2 pl1 Pr1 R1-g wx1
M541B A1 A2 b1 C1 C2 pl1 Pr1 R1-g
M541F a1 A2 C1 C2 R1-nj
M541G A1 a2 C1 C2 R1-nj
M541H A1 A2 c1 C2 R1-nj
M541I A1 A2 C1-I C2 R1-nj
M541J A1 A2 C1 c2 R1-nj
M541K A1 A2 C1 C2-Idf1(Active-1) R1-nj
M541L A1 A2 bz1 C1 C2 Pr1 R1-nj
M541M A1 A2 Bz1 C1 C2 pr1 R1-nj
M541N A1 A2 C1 C2 gl1 in1 R1-nj
M541O A1 A2 C1 C2 In1-D R1-nj
M541P ae1 wx1
M641C A1 A2 b1 C1 C2 pl1 Pr1 R1-r wx1
M641D A1 A2 C1 C2 Pr1 r1 wx1 y1
M641E A1 A2 C1 C2 r1-g wx1 y1
M641F r1-g y1; A1 A2 C1 C2
M741A A1 A2 b1 C1 C2 pl1 Pr1 r1-g wx1
M741B Stock 6; A1 A2 B1 C1 C2 Pl1 R1-r
M741C Stock 6; A1 A2 B1 C1 C2 pl1 R1-r
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
M741I Stock 6; A1 A2 C1 C2 R1
M841A A1 A2 C1 C2 pr1 R1 su1
M841B f1 wx1
M841C v4 wx1
M841D v2 wx1
M841F A1 A2 bz2 C1 C2 R1-scm2 wx1
M841G A1 A2 C1 c2 R1-scm2 wx1
M841H gl6 wx1
M841I su1 wx1
M841J v16 wx1
M841K gl4 wx1
M841L gl2 lg1 wx1
M941A A1 A2 c1 C2 Pr1 R1 wx1 y1
M941B Mangelsdorf's tester; a1 bm2 g1 gl1 j1 lg1 pr1 su1 wx1 y1
M941BA Mangelsdorf's tester + R1-nj
M941C a1 Dt1 gl2 lg1 wt1
M941D gl1 wx1 y1
M941E gl8-R wx1 y1
MX40A A1 A2 C1 C2 P1-vv::Ac r1-sc:m3::Ds
MX40B A1 A2 Ac2 bz2-m::Ds C1 C2 R1
MX40C A1 A2 C1 C2 r1-sc:m3::Ds trAc8168
MX40D P1-vv::Ac r1
MX41A A1 A2 C1 C2 gl1 pr1 R1 wx1 y1
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

TRISOMIC

123A trisomic 1.
223A trisomic 2
328A trisomic 3
422A trisomic 4
523A trisomic 5
615A trisomic 6
718A trisomic 7
807A trisomic 8
922A trisomic 9
X23A trisomic 10

TETRAPLOID

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

CYTOPLASMIC STERILE/RESTORER

C736A R213 (N); mito-N Rf1 rf2
C736AB R213 (T) Sterile; cms-T Rf1 rf2
C736B Ky21 (N); mito-N Rf1 Rf2 Rf3 RfC
C736C B37 (N); mito-N rf1 Rf2 rf3 rfC
C736CA B37 (T) Sterile; cms-T rf1 Rf2
C736CB B37 (T) Restored; cms-T Rf1 Rf2
C736E Tr (N); mito-N Rf3 rfC rfT
C736F W23 (N); mito-N rf1 Rf2 rf3 RfC
C736FA W23 (N); mito-N rf1 Rf2 rf3 RfC
C736G B73 (N); mito-N rf1 Rf2 rf3 rfC
C736H L317 (N); mito-N rf3 RfC rfT
C836A Wf9 (T) Sterile; cms-T rf1 rf2
C836B Wf9 (N); mito-N rf1 rf2 rf3 rfC
C836C Wf9 (T) Restored; cms-T Rf1 Rf2 rf3 rfC
C836D Wf9 (S) Sterile; cms-S rf1 rf2 rf3 rfC
C836E Mo17 (T) Sterile; cms-T rf1 Rf2 rf3 rfC
C836F Mo17 (N); mito-N rf1 Rf2 rf3 rfC
C836G Mo17 (C) Sterile; cms-C rf1 Rf2 rf3 rfC
C836H Mo17 (S) Sterile; cms-S rf1 Rf2 rf3 rfC
C936D K55 (N); mito-N Rf1 Rf2 rf3 RfC
C936DA K55 (N); mito-N Rf1 Rf2 rf3 RfC
C936F N6 (N); mito-N rf1 Rf2 rf3 RfC
C936FA N6 (N); mito-N rf1 Rf2 rf3 RfC
C936G N6 (T) Sterile; cms-T rf1 Rf2
C936H N6 (T) Restored; cms-T Rf1 Rf2
C936I SK2 (N); mito-N rf1 Rf2 rf3 rfC
C936J SK2 (T) Sterile; cms-T rf1 Rf2
C936K SK2 (T) Restored; cms-T Rf1 Rf2
C936M 38-11 (N); mito-N rf1 Rf2 rf3 rfC
CX36A N6 (C) Restored; cms-C rf1 Rf2 rf3 RfC
CX36B N6 (S) Sterile; cms-S rf1 Rf2 rf3 RfC
CX36C B37 (C) Sterile; cms-C rf1 Rf2 rf3 rfC
CX36D B37 (S) Sterile; cms-S rf1 Rf2 rf3 rfC

CYTOPLASMIC TRAIT

C337A NCS2
C337B NCS3

TOOLKIT

T0318AA TB-3Ld lg1; ig1R1-nj
T0318AB cms-L; ig1 R1-nj
T0318AC cms-MY; ig1 R1-nj
T0318AD cms-ME; ig1 R1-nj
T0318AE cms-S; ig1 R1-nj
T0318AF cms-SD; ig1 R1-nj
T0318AG cms-VG; ig1 R1-nj
T0318AH cms-CA; ig1 R1-nj
T0318AI cms-C; ig1 R1-nj
T0318AJ cms-Q; ig1 R1-nj
T0940A Hi-II Parent A (for producing embryogenic callus cultures)
T0940B Hi-II Parent B (for producing embryogenic callus cultures)
T0940C Hi-II A x B (for producing embryogenic callus cultures)
T0940D KYS (for chromosome observations in pachytene microsporocytes)
T0940E Mu off; a1-Mum2 A2 C1 C2 R1
T3302A Inv1m; P1-vv::Ac bz2-m::Ds
T3302C T1-2b; P1-vv::Ac bz2-m::Ds
T3302D T1-2(036-7); P1-vv::Ac bz2-m::Ds
T3302E T1-2c; P1-vv::Ac bz2-m::Ds
T3302F T1-3(5883); P1-vv::Ac bz2-m::Ds
T3302G T1-3k; P1-vv::Ac bz2-m::Ds
T3302H T1-3(5597); P1-vv::Ac bz2-m::Ds
T3302I T1-3(5982); P1-vv::Ac bz2-m::Ds
T3302J T1-4i; P1-vv::Ac bz2-m::Ds
T3302K T1-4(064-20); P1-vv::Ac bz2-m::Ds
T3302L T1-4(4308); P1-vv::Ac bz2-m::Ds
T3302M T1-4(8602); P1-vv::Ac bz2-m::Ds
T3302N T1-4b; P1-vv::Ac bz2-m::Ds
T3302O T1-5(5525); P1-vv::Ac bz2-m::Ds
T3303A T1-5(6899); P1-vv::Ac bz2-m::Ds
T3303B T1-5b; P1-vv::Ac bz2-m::Ds
T3303C T1-5(4613); P1-vv::Ac bz2-m::Ds
T3303D T1-5(5045); P1-vv::Ac bz2-m::Ds
T3303E T1-5(043-15); P1-vv::Ac bz2-m::Ds
T3303F T1-5(5512); P1-vv::Ac bz2-m::Ds
T3303I T1-6(028-13); P1-vv::Ac bz2-m::Ds
T3303J T1-6(7352); P1-vv::Ac bz2-m::Ds
T3303K T1-6(7097); P1-vv::Ac bz2-m::Ds
T3303L T1-7(4405); P1-vv::Ac bz2-m::Ds
T3303M T1-7i; P1-vv::Ac bz2-m::Ds
T3303N T1-7(4837); P1-vv::Ac bz2-m::Ds
T3303O T1-7(010-12); P1-vv::Ac bz2-m::Ds
T3304A T1-8(6591); P1-vv::Ac bz2-m::Ds
T3304B T1-8(4685); P1-vv::Ac bz2-m::Ds

T3304C T1-8(4307-4); P1-vv::Ac bz2-m::Ds
T3304D T1-9(7535); P1-vv::Ac bz2-m::Ds
T3304E T1-9(8302); P1-vv::Ac bz2-m::Ds
T3304F T1-9(6762); P1-vv::Ac bz2-m::Ds
T3304G T1-10g; P1-vv::Ac bz2-m::Ds
T3304H T1-10f; P1-vv::Ac bz2-m::Ds
T3304I bz2-m::Ds
T3304J Inv1m; P1-vv::Ac r1-sc:m3::Ds
T3304K Inv1a; P1-vv::Ac r1-sc:m3::Ds
T3304M T1-2c; P1-vv::Ac r1-sc:m3::Ds
T3305A T1-3(5597); P1-vv::Ac r1-sc:m3::Ds
T3305B T1-4i; P1-vv::Ac r1-sc:m3::Ds
T3305C T1-4(064-20); P1-vv::Ac r1-sc:m3::Ds
T3305F T1-4b; P1-vv::Ac r1-sc:m3::Ds
T3305H T1-5(6899); P1-vv::Ac r1-sc:m3::Ds
T3305J T1-5(4613); P1-vv::Ac r1-sc:m3::Ds
T3305M T1-6(5495); P1-vv::Ac r1-sc:m3::Ds
T3305N T1-6e; P1-vv::Ac r1-sc:m3::Ds
T3305O T1-6(028-13); P1-vv::Ac r1-sc:m3::Ds
T3306C T1-7(4444); P1-vv::Ac r1-sc:m3::Ds
T3306D T1-7(4405); P1-vv::Ac r1-sc:m3::Ds
T3306H T1-8(6591); P1-vv::Ac r1-sc:m3::Ds
T3306L T1-9(8302); P1-vv::Ac r1-sc:m3::Ds
T3306M T1-9(6762); P1-vv::Ac r1-sc:m3::Ds
T3306N T1-10g; P1-vv::Ac r1-sc:m3::Ds
T3307A trAc8178
T3307D trAc8163
T3307F trAc8183
T3308A trAc8200
T3308B trAc6076
T3308D trAc8175
T3308E trAc8193
T3308F trAc8179
T3308G trAc8181
T3308H trAc8186
T3309A trAc8196
T3309B trAc6062
T3309C trAc6063
T3309D trAc8172
T3309E trAc8184
T3310A trAc8161
T3310B trAc8173
T3310D trAc8190
T3310E trAc8194
T3310F trAc8185
T3311A trAc8162
T3311B trAc8182
T3311D trAc6059
T3311F trAc8180
T3312A Ds-1S1 P1-vv::Ac Dek1
T3312B Ds-1S2 P1-vv::Ac Dek1
T3312C Ds-1S3 P1-vv::Ac Dek1
T3312D Ds-1S4 P1-vv::Ac Dek1
T3312E Ds-1L1 P1-vv::Ac Bz2
T3312F Ds-1L3 Bz2; Ac
T3312G Ds-2S1 B1-Peru; P1-vv::Ac
T3312I Ds-2S3 B1-Peru; P1-vv::Ac
T3312J Ds-2S4; P1-vv::Ac
T3312L Ds-3L1 A1 Sh2; P1-vv::Ac
T3312M Ds-3L2 A1 Sh2; P1-vv::Ac
T3312O Ds-4L1 C2; P1-vv::Ac
T3312P Ds-4L3 C2; P1-vv::Ac
T3312Q Ds-4L4 C2; P1-vv::Ac
T3312S Ds-4L6 C2; P1-vv::Ac
T3312T Ds-4L7 C2; P1-vv::Ac
T3312U Ds-5L1 A2 Pr1 Bt1; P1-vv::Ac
T3312V Ds-5S1 A2 Pr1 Bt1; P1-vv::Ac
T3312W Ds-5S2 A2 Pr1 Bt1; P1-vv::Ac
T3312Y Ds-9S1 C1-I wx1; Ac
T3312Z Ds-10L2 R1-sc; P1-vv::Ac

B-A TRANSLOCATIONS (BASIC SET)

122A TB-1La
122B TB-1Sb
222A TB-1Sb-2L4464
222B TB-3La-2S6270
327A TB-3La
327B TB-3Sb
421A TB-4Sa
423E TB-4Lf
522A TB-5La
522C TB-5Sc
614B TB-6Sa
614C TB-6Lc
717A TB-7Lb
719A TB-7Sc
809A TB-8Lc
922B TB-9Lc Wc1
922D TB-9Sd
X21B TB-10L19
X22A TB-10Sc

B-A TRANSLOCATIONS (OTHERS)

122C TB1-Lc
126G TB-1Sb P1-vv::Ac bz2-m::Ds A1 A2 Bz1 C1 C2 R1
221I TB-2Sa B1-Peru
221J TB-2Sb
225A TB-3La-2L7285
225B TB-1Sb-2Lc
320P TB-1La-3Le
320Q TB-5La-3L(1)
320R TB-5La-3L(2)
320S TB-5La-3L(3)
327C TB-3Lc
327D TB-3Ld
329Z T3-B(La); T3-B(Sb)
331A TB-1La-3L5267
331B TB-1La-3L4759-3
331C TB-1La-3L5242
331E TB-3Lf
331F TB-3Lg
331G TB-3Lh
331H TB-3Li
331I TB-3Lj
331J TB-3Lk
331K TB-3Ll
331L TB-3Lm
420B TB-9Sb-4L6504
420I TB-9Sb-4L6222
421B TB-1La-4L4692
421C TB-7Lb-4L4698
423A TB-4Lb
423B TB-4Lc
423C TB-4Ld
423D TB-4Le
423F TB-1Sb-2L4464-4f
425A TB-4Sg
425B TB-4Lh
425C TB-4Li
428I Dt6 TB-4Sa
522B TB-5Lb
522D TB-5Ld
528D TB-1La-5S8041
614A TB-6Lb
627E TB-6Lc Dt2; A2 C1 C2 R1 a1-m
720A TB-7Lb Dt3; a1-m1::rDt (Neuffer)
806A TB-8La
806B TB-8Lb
921A TB-9La
921B TB-9Sb
921C TB-9Lc
922C TB-9Sb C1-I
929A IsoB9-9 isochromosome Type 1
929B IsoB9-9 isochromosome Type 2
929C T9-B(La); T9-B(Sb)
929D IsoB9-9 isochromosome (original)
929F T9-B (La + Sb)
929G TB-9Sb; T9-8(4453)
929H TB-9Sb; T9-3(6722)
929I TB-9Sb-1866
929J TB-9Sb-1852
929K TB-9Sb-2150
929L TB-9Sb-14
929M TB-9Sb-2010
TX40D TB-1Sb P1-vv::Ac r1-sc:m3::Ds
TX40E TB-3La a1-m Dt1
TX40F TB-8Lc Ac2 bz2-m::Ds
TX40G TB-9Sd a1-m Dt1
TX40H TB-9Lc trAc8168 r1-sc:m3::Ds
TX40I TB-10L18 P1-vv::Ac r1-sc:m3::Ds
X21A TB-10La
X21C TB-10Ld
X22B T1La-B-10L18
X22C TB-10Lb
X30A TB-10L1
X30B TB-10L2
X30C TB-10L3
X30D TB-10L4
X30E TB-10L5
X30F TB-10L6
X30G TB-10L7
X31A TB-10L8
X31B TB-10L9
X31C TB-10L10
X31D TB-10L11
X31E TB-10L12
X31G TB-10L14
X31H TB-10L15
X31I TB-10L16
X31J TB-10L17
X32A TB-10L18
X32C TB-10L20
X32D TB-10L21
X32E TB-10L22
X32F TB-10L23
X32G TB-10L24
X32H TB-10L25
X32I TB-10L26
X32J TB-10L27
X32K TB-10L28
X33A TB-10L29
X33B TB-10L30
X33C TB-10L31
X33D TB-10L32
X33E TB-10L33
X33F TB-10L34
X33G TB-10L35
X33H TB-10L36
X34A TB-10L37
X34B TB-10L38

INVERSION

I143A Inv1a (1.S.30; 1.L.50)
I143B Inv1c (1.S.30; 1.L.01)
I143C Inv1d (1.L.55; 1.L.92)
I143D Inv1k (1.L.46; 1.L.82)
I243A Inv2b (2S.06; 2L.05)
I243B Inv2h (2L.13; 2L.51)
I444A Inv2a (2S.70; 2L.80)
I343A Inv3a (3L.38; 3L.95)
I343B Inv3b (3L.21; 3L.70)
I343C Inv3c (3L.05; 3L.95)
I343D Inv3(8582) (3S.55; 3L.82)
I443A Inv4b (4S.10; 4L.12)
I443B Inv4c (4S.89; 4L.62)
I443C Inv4a (4L.30; 4L.90)
I443D Inv4d (4L.40; 4L.96)
I443E Inv4f (4L.17; 4L.63)
I543A Inv4e (4L.16; 4L.81)
I543B Inv5a (5S.05; 5L.72)
I743A Inv5(8623) (5S.67; 5L.69)
I743B Inv6d (6S.70; 6L.33)
I743C Inv6(3712) (6S.76; 6L.63)
I743D Inv6a (6S.76; 6L.63)
I843A Inv6e (6S.80; 6L.32)
I943A Inv7f (7L.17; 7L.61)
I943B Inv7(8540) (7L.12; 7L.92)
I943C Inv7(3717) (7S.32; 7L.30)
I943E Inv7a (7L.05; 7L.95)
IX43A Inv8a (8S.30; 8L.15)
I344A Inv9a (9S.70; 9L.90)
IX43B Inv9b (9S.05; 9L.87)

RECIPROCAL TRANSLOCATIONS (wx1 AND Wx1 MARKED)

wx01A T1-9c (9L.22; 1.S.48); wx1
wx01B T1-9(5622) (9L.12; 1.L.10); wx1
wx02A T1-9(4995) (9S.20; 1.L.19); wx1
wx02AA T1-9(4995) (9S.20; 1.L.19); wx1
wx03A T1-9(8389) (9L.13; 1.L.74); wx1
wx04A T2-9c (9S.33; 2S.49); wx1
wx05A T2-9b (9L.22; 2S.18); wx1
wx06A T2-9d (9L.27; 2L.83); wx1
wx07A T3-9(8447) (9L.14; 3S.44); wx1
wx08A T3-9c (9L.12; 3L.09); wx1
wx09A T3-9(8562) (9L.22; 3L.65); wx1
wx10A T4-9e (9L.26; 4S.53); wx1
wx11A T4-9g (9L.27; 4S.27); wx1
wx12A T4-9(5657) (9S.25; 4L.33);

wx1
wx13A T4-9b (9L.29; 4L.90); wx1
wx14A T5-9c (9L.10; 5S.07); wx1
wx14B T5-9(022-11) (9L.27; 5S.30); wx1
wx15A T5-9(4817) (9S.07; 5L.06); wx1
wx16A T5-9d (9L.10; 5L.14); wx1
wx17A T5-9a (9S.17; 5L.69); wx1
wx18A T6-9(4778) (9L.30; 6S.80); wx1
wx19A T6-9a (9L.40; 6S.79); wx1
wx19B T6-9e (9L.24; 6L.18); wx1
wx20A T6-9b (9S.37; 6L.10); wx1 y1
wx21A T6-9(4505) (9ctr.00; 6L.13); wx1
wx22A T7-9(4363) (9ctr.00; 7ctr.00); wx1
wx23A T7-9a (9S.07; 7L.63); wx1
wx24A T8-9d (9S.16; 8L.09); wx1
wx25A T8-9(6673) (9S.31; 8L.35); wx1
wx26B T9-10(059-10) (9S.31; 10L.53); wx1
wx27A T9-10b (9S.13; 10S.40); wx1
Wx30A T1-9c (9L.22; 1.S.48); Wx1
Wx30B T1-9(4995) (9S.20; 1.L.19); Wx1
Wx30C T1-9(8389) (9L.13; 1.L.74); Wx1
Wx31A T2-9c (9S.33; 2S.49); Wx1
Wx31B T2-9b (9L.22; 2S.18); Wx1
Wx31C T2-9d (9L.27; 2L.83); Wx1
Wx32A T3-9(8447) (9L.14; 3S.44); Wx1
Wx32B T3-9(8562) (9L.22; 3L.65); Wx1
Wx32C T3-9c (9L.12; 3L.09); Wx1
Wx33A T4-9e (9L.26; 4S.53); Wx1
Wx33B T4-9(5657) (9S.25; 4L.33); Wx1
Wx33C T4-9g (9L.27; 4S.27); Wx1
Wx34A T5-9c (9L.10; 5S.07); Wx1
Wx34B T5-9(4817) (9S.07; 5L.06); Wx1
Wx34C T4-9b (9L.29; 4L.90); Wx1
Wx35A T5-9(8386) (9S.13; 5L.87); Wx1
Wx35B T5-9a (9S.17; 5L.69); Wx1
Wx35C T5-9d (9L.10; 5L.14); Wx1
Wx36A T6-9(4778) (9L.30; 6S.80); Wx1
Wx37A T6-9(8768) (9S.61; 6L.89); Wx1
Wx37B T7-9(4363) (9ctr.00; 7ctr.00); Wx1
Wx37C T6-9(4505) (9ctr.00; 6L.13); Wx1
Wx38A T7-9a (9S.07; 7L.63); Wx1
Wx38B T8-9d (9S.16; 8L.09); Wx1
Wx38C T8-9(6673) (9S.31; 8L.35); Wx1
Wx39A T9-10(8630) (9S.28; 10L.37); Wx1
Wx39B T9-10b (9S.13; 10S.40); Wx1

PHENOTYPE ONLY

Kernel Mutants

blotched aleurone
Bh*-86-1381-1
Bh-Tu*-Mumm

brittle endosperm
bt*-011-11
bt*-0601-Alexander
bt*-1979-14
bt*-1979-16
bt*-1982
bt*-4380
bt*-4539
bt*-4973
bt*-60-151
bt*-8101
bt*-8102
bt*-83-84-3541-1
bt*-84-4
bt*-84-5
bt*-84-5091-9
bt*-84-5257-1
bt*-84-6
bt*-85-3096-6
bt*-85-3098-15
bt*-85-3099-16
bt*-85-3372-27
bt*-87-2132-39
bt*-87-2297-1
bt*-87-88-2630-28
bt*-88-3177-14
bt*-88-3177-2
bt*-88-3177-7
bt*-8804
bt*-8805
bt*-89-1265-18
bt*-90286
bt*-A4109
bt*-Alexander
bt*-Briggs-1998-1
bt*-F-15
bt*-F-23
bt*-F-31
bt*-F-34
bt*-F-36
bt*-F-8
bt*-F10
bt*-Panzio
bt*-PetersonResHy
bt*-PI200197
bt*-PI251887
bt-gm*-84-5045-39
bt-gm*-85-3017-24
bt-sh*-PI251930

brown endosperm
brn*-1981-1
brn*-1981-2
brn*-1981-3
brn*-1981-4
brn*-84-23
brn-bt*-81-F-24

brown kernel
lt-brn-sml*-86-1302-37
bnk*-N747B

brown pericarp
bp*-PI183639

collapsed endosperm
cp*-N1076A
cp*-N1078B
cp*-N1092A
cp*-N1104B
cp*-N1275A
cp*-N1294
cp*-N1311C
cp*-N1313
cp*-N1319A
cp*-N1338
cp*-N1369
cp*-N1379A
cp*-N1385
cp*-N1393A
cp*-N1399A
cp*-N1430
cp*-N1436A
cp*-N2356B
cp*-N524E
cp*-N628
cp*-N863A
cp*-N886
cp*-N918A
cp*-N968A
cp*-N991

colored plumule
Pu*-1976-RYDCO

colorless aleurone
cl*-85-86-3559-1
cl*-86-1478-16
cl*-N1345A
cl*-N1346A
cl*-N720E
cl*-N795
cl*-N801
cl*-N818A
cl-crown-pale-base*-85-86-3558-23
r*-86-1590-6

colorless floury
clf*-N2425B

crumpled kernel
crp*-N1429A
crp*-N2207
dnj*-N1534

defective crown
dcr*-N1053A
dcr*-N1176B
dcr*-N1233A
dcr*-N1409
dcr*-N871A
dcr*-N925A

defective kernel
de*-1276
de*-17
De*-1976-RYDCO
de*-2080
de*-2192
de*-2424
de*-2915
de*-2919
de*-3188
de*-4309
de*-5044Hagie
de*-85-86-3567-35
de*-8505
de*-8507
de*-8508
de*-86-1472-6
de*-8808
de*-8809
de*-8810
de*-8811
de*-8818
de*-N1002A
de*-N1007A
de*-N1122A
de*-N1136A
de*-N1162
de*-N1166
de*-N1177A
de*-N1196
de*-N1310B
de*-N1336B
de*-N1390A
de*-N1400
de*-N1420
de*-N232B
de*-N260D
de*-N279B
de*-N296C
de*-N307D
de*-N400A
de*-N513B
de*-N528C
de*-N573A
de*-N660C
de*-N674A
de*-N748B
de*-N760B
de*-N877A
de*-N891A
de*-N903
de*-N929
de*-N979A
de-sml*-8813
de-sml*-8814
de-sml*-8815
de-sml*-8816
de-sml*-8817
def*-8101
def*-8102
def*-8103
def*-8104
def*-8105
def*-8106
def*-8107
def*-8108
def*-8109
def*-8110
def*-8111
def*-8112
def*-8113
def*-8114
def*-8116
def*-8118
def*-8119
def*-8120
def*-8121
def*-8122
def*-8123
def*-8125
def*-8126
def*-8127
def*-8128
def*-8130
def*-8131
def*-8132
def*-8134
def*-8136
def*-8137
def*-8138

def*-8201
def*-84-22
def*-84-28
def*-84-29
def*-84-30
def*-84-31
def*-84-37
def*-84-40
def*-84-41
def*-84-45
def*-84-48
def*-84-49
def*-84-53
def*-84-54
def*-84-58
def*-84-60
dek*-1979-32
dek*-1981-1
dek*-74-0060-4
dek*-84-14
dek*-86-1496-35
dek*-8902
dek*-8903
dek*-8904
dek*-99-6273-1
dek*-F-16
dek*-PS602
wrinkled-de*-86-1473-5
wrinkled-gm*-86-1582-32

dented kernel
dnt*-N1185A
dnt*-N1326
dnt*-N884A

dilute aleurone
dil*-N452D
dil*-N524C

discolored kernel
dsc*-N1084
dsc*-N749
pig*-84-5080-18
pig*-86-1178-6
pig-gm*-1979-51
pig-gm*-1979-52
pig-gm*-1979-9
pig-gm*-1981-A
pig-gm*-1981-B
pig-gm*-1982-3
pig-gm*-5020-14
pig-gm*-84-5078-10
pig-gm*-86-1200-3
pig-gm*-87-2275-15
pig-gm*-87-2305-22
pig-gm*-Briggs 1998-1
pig-gm*-Briggs 1998-2
pig-gm*-PI251930
ptd-dek*-1976-RYDCO
ptd-dek*-1981
ptd-dsc*-87-2490-22
sml-pig-gm*-88-89-3554-44

dull endosperm
du*-Sprague

etched endosperm
et*-3130
et*-3576
et*-5191
et*-6-9321-1
et*-73-766-1
et*-8-M-4
et*-84-5266-26
et*-84-5270-40
et*-85-86-3518-21
et*-86-1493-6
et*-8616
et*-87-2349-13
et*-88-89-3525-22
et*-88-89-3554-33
et*-89-90-1547-19
et*-89-90-1548-13
et*-Mu1767
et*-Mu2349
et-mutable*-87-2519-31
et*-N1361
et*-N164B
et*-N357C
et*-N403A
et*-N509A
et*-N514A
et*-N516C
et*-N518B
et*-N556A
et*-N561B
et*-N571A
et*-N586A
et*-N615A
et*-N617
et*-N629F
et*-N643A
et*-N670A
et*-N680C
et*-N701A
et*-N702A
et*-N723A
et*-N724D
et*-N745
et*-N76D
et*-N789
et*-N798A
et*-N818B
et*-N837A
et*-N861
et*-N864A
et*-N868A
Et*-N876A
et*-N953A
et*-N965
et*-Osturana
et-de*-88-89-3526-8
et-gm*-86-1475-34
et-gm*-86-87-1742-38
et-gm*-87-2502-19
granular-o*-84-5274-30
sml-et*-85-3522-29
su-sh-et*-98-1887-1

flint kernel
flint*-87-2126-22

floury endosperm
fl*-67-412
fl*-83-3386-19
fl*-84-44
fl*-8515
fl*-Mojo
fl*-N1145A
fl*-N1163
fl*-N1208A
fl*-N1287
fl*-N1308A
fl*-N1333B
fl*-N1426
fl*-N7B-65-1294
fl*-N872A
fl*-shoepeg
fl*-sucaxo
fl-cap*-1981
fl-cap*-66-519-1
fl-de*-8905
sml-fl-cap*-1981

germless
brn-gm*-85-3315-6
brn-gm*-85-86-3587-46
brn-gm*-85-86-3595-3
brn-gm*-86-1161-5
emb*-85-3100-32
emb*-85-3378-8
gm*-1387
gm*-1979-11
gm*-1979-53
gm*-5234
gm*-6372
gm*-8510
gm*-86-1011-2
gm*-86-1013-4
gm*-86-1097-3
gm*-86-1335-1
gm*-86-1591-7
gm*-86-87-1742-18
gm*-87-2456-9
gm*-N1303
gm*-N1311B
gm*-N1312
gm*-N1319B
gm*-N1390C
gm*-N198C
gm*-N869A
o-gm*-84-44
o-gm*-98-5733-1
pr-gm*-86-1109-1
sh-gm*-84-5045-32
sh-gm*-88-3082-4
sml-o-gm*-86-1323-4
sml-dsc-gm*-95W-240
w-o-gm*-85-3135-4
w-o-gm*-86-1349-1
w-o-gm*-88-3270-10
y-gm*-85-3288-28

glassy endosperm
ae*-84-7
ae*-92-1365-3
ae*-96-1449-1
ae*-Briggs 1998-1
ae*-Mu32

lemon white
lw*-1979-45
lw*-1979-46
lw*-1981
lw*-1998-1
lw*-1998-2
lw*-1998-4
lw*-73-2548
lw*-82-1
lw*-85-3076-28
lw*-85-3252-5
lw*-8509
lw*-8513
lw*-8514
lw*-86-87-1828-7
lw*-88-3177-2
lw*-89-90-3609-5
lw*-87-2407-36
lw*-B73
lw*-Funk-81-5
lw*-PI200203
pale-y*-83-84-3549-13
pale-y*-84-5082-33
pale-y*-84-5167-48
pale-y*-84-5288-19
pale-y*-85-3005-22
pale-y*-85-3006-30
pale-y*-85-3007-40
pale-y*-85-3010-40
pale-y*-85-3016-15
pale-y*-85-3017-31
pale-y*-85-3065-25
pale-y*-85-3069-6
pale-y*-85-3087-29
pale-y*-88-89-3551-35
pale-y*-89-1313-3
pale-y*-89-90-1525-23
pale-y*-90-3220-1
pale-y*-90-3220-26
w*-N677
wh*-BMS-Rhoades

marbled aleurone
Dap*-3
dap*-86-8126-2
Dap*-89-3177.0
Dap*-89-3177.5
Dap*-89-3178.3
Marbled*-Sprague

miniature kernel
mn*-1981-51
mn*-87-2215-17
mn*-87-2346-20
mn*-87-2347-36
mn*-87-2422-14
mn*-88-3177-2
mn*-88-89-3509-40
mn*-88-89-3564-25
mn*-N1536
mn*-N378C
mn*-PI239110
mn*-PI245132
sml-k*-97-4784-1

mosaic aleurone color
msc*-N593A

mottled aleurone
Mt*-2313
Mt*-65-2238
Mt*-N1343A
Mt*-Sprague

multiple aleurone layer
Mal*-Galinat
Mal*-Nelson
Mal*-PI515052

opaque endosperm
lrg-o-crown*-89-1275-17
o*-1979-54
o*-1981-11-Fox-19
o*-1981-3-Fox-7
o*-1981-5-Fox-9
o*-1981-6-Fox-10
o*-1981-8-Fox-15
o*-1982
o*-1982-2-Fox-13
o*-2-Fox-6
o*-3015
o*-73-798-1
o*-76GH-76
o*-8129
o*-82:288-1
o*-83-84-3549-39

o*-84-5025-15
o*-84-5025-17
o*-84-5025-8
o*-84-5044-35
o*-84-5091-13
o*-84-5094-4
o*-84-5095-23
o*-84-5117-16
o*-84-5261-37
o*-84-5270-40
o*-84-5282-27
o*-84-5295-13
o*-84-5321-28
o*-84-5324-29
o*-84-8a
o*-85-3084-8
o*-85-3088-3
o*-85-3335-35
o*-86-87-1767-10
o*-87-2285-33
o*-87-2350-2
o*-88-89-3550-27
o*-97-4784-6
o*-Briggs-1998-1
o*-BS20-Fox-3
o*-Fox-12
o*-N1008A
o*-N1037A
o*-N1046
o*-N1065A
o*-N1074A
o*-N1119A
o*-N1189A
o*-N1195A
o*-N1218
o*-N1228
o*-N1244A
o*-N1245
o*-N1298
o*-N1301
o*-N1310A
o*-N1320A
o*-N1355
o*-N1358
o*-N1422
o*-N436C
o*-N829C
o*-N870
o*-N885A
o*-N895
o*-N899
o*-N906A
o*-N930
o*-N938A
o*-N973
o*-N995A
o*-PI195245
o*-PI200285
o-de*-1981-9-Fox-18
o-dek*-6
o-dek*-87-2279-12
o-gm*-83-3398-6
o-gm*-84-33
o-sh*-86-1297-2
o-sh*-F1979-19
os*-2162
pro*-Mu1
sh-o*-87-2455-7
sml-o*-87-88-2692-5
sml-o*-PI195243

pale aleurone
pa*-N893A
pa*-N917A
pale-Cl*-86-1476-14
pale-Cl*-LGC65
pale-Cl-gm*-84-5251-1

pale aleurone, with pigmented sectors
pa-Cl*-m-86-1474-39
pa-Cl*-m-86-1478-4
pa-Cl*-m-87-2224-33

pale crown
pa-crown*-85-86-3558-23

pale yellow endosperm
al*-84-5020-32
pale-endo*-73-3
pale-endo*-73-4004
pale-y*-83-3382-16
pale-y*-83-3382-18
pale-y*-83-84-3548-25
pale-y*-84-5027-22
pale-y*-84-5103-16
pale-y*-84-5275-14
pale-y*-85-3016-30
pale-y*-85-3036-38
pale-y*-85-3042-7
pale-y*-85-3044-34
pale-y*-85-3134-46
pale-y*-85-3374-13
pale-y*-85-3377-2
pale-y*-85-3511-18
pale-y*-85-3562-31
pale-y*-85-86-3533-9
pale-y*-86-1151-7
pale-y*-86-1155-2
pale-y*-86-1155-3
pale-y*-86-87-1723-27
pale-y*-87-2160-16
pale-y*-87-2339-10
pale-y*-87-2350-2
pale-y*-87-2350-25
pale-Y*-87-2422-14
pale-y*-87-88-2679-1
pale-y-gm*-Rsssc-77-110
pale-y-o*-84-5288-2
pale-y-o*-86-1296-27
sml-y*-95-1930-2
y*-84-5272-12
y*-84-5288-1
y*-85-3041-2
y*-85-3078-41
y*-85-3087-12
y*-85-3125-7

pitted kernel
ptd*-N660E
ptd*-N738B
ptd*-N855A
ptd*-N901A
ptd*-N923

purple pericarp
Pl*-CFS-69

red aleurone
pr*-N707A
pr*-N850

red pericarp
r*-ch-Burbank-CFS-80
r*-ch-PI213730

red silk scar
red-silk-scar*-MTC

rough kernel
rgh*-N1060
rgh*-N1524
rgh*-N799A
rgh*-N802
rgh*-N882

shrunken kernel
pale-y-su-sh*-88-3133-28
sh*-1979-10
sh*-1982-2
sh*-2927-Mumm
sh*-2928-Mumm
sh*-83-3328-24
sh*-84-3
sh*-84-5248-20
sh*-84-5317-44
sh*-85-3045-7
sh*-85-3104-27
sh*-85-3112-20
sh*-85-3375-38
sh*-8502
sh*-8503
sh*-8506
sh*-8511
sh*-8517
sh*-86-1565-17
sh*-87-2045-25
sh*-87-2045-6
sh*-87-2050-1
sh*-87-2050-3
sh*-87-2213-19
sh*-87-2215-12
sh*-87-2355-29
sh*-87-2406-3
sh*-87-2496-21
sh*-88-89-3540-1
sh*-8806
sh*-8807
sh*-8906
sh*-8907
sh*-97P-29-5
sh*-Alexo1968
sh*-F-11
sh*-F-2
sh*-F-25
sh*-KERR
sh*-N1105B
sh*-N1320B
sh*-N1341
sh*-N1366
sh*-N1519B
sh*-N252B
sh*-N399A
sh*-N627A
sh*-N689
sh*-N741
sh*-N742
sh*-N750
sh*-N819
sh*-N849
Sh*-N881A
sh*-N887A
sh*-N911
sh*-RJL
sh-bt*-85-3392-31
sh-crown*-Briggs-1998-1
sh-de*-6607
sh-de*-RSSSC-117
sh-fl*-9180
sh-fl*-9392
sh-o*-87-2410-24
sh-wx*-F-18
su-sh*-F-5

small kernel
smk*-N1003
smk*-N1168A
smk*-N1203
smk*-N1529
smk*-N215D
smk*-N320
smk*-N433A
Smk*-N845B
smk*-N890A
smk*-N994A

spotted aleurone
cl-mut*-85-86-3564-1
cl-mut*-99-2170
coarse-mutable*-86-1417-7
Dt*-a; a1-m
Dt*-b; a1-m
Dt*-c; a1-m
Dt*-d; a1-m
Dt*-e; a1-m
Dt*-f; a1-m
Dt*-g; a1-m
Dt*-h; a1-m
Dt*-i; a1-m
spk*-N600Ce
spk*-N687A

sugary kernel
su*-1979-8
su*-83-3383-21
su*-84-5350-2
su*-85-3133-32
su*-8504
su*-8803
su*-89-1279-14
su*-L874261
su*-N1040
su*-N236C
su*-N748A
su*-N817
su-sh*-F-22

viviparous kernel
pale-vp*-87-2286-1
pale-vp*-87-2286-18
pale-vp*-87-2286-2
pale-vp*-87-2286-25
pale-vp*-87-2286-3
pale-y*-84-5032-21
pale-y-vp*-83-3100-31
pale-y-vp*-83-3124-33
pale-y-vp*-84-5266-5
pale-y-vp*-85-3140-15
pale-y-vp*-85-3240-5
pale-y-vp*-85-3267-6
pale-y-vp*-85-3267-9
pale-y-vp*-85-3385-34
pale-y-vp*-86-1316-27
pale-y-vp*-88-3177-14
ps*-85-3288-28
ps*-85-3492-36
ps*-85-86-3567-1
ps*-86-1105-2
ps*-86-1352-4
ps*-86-1499-3
ps*-86-87-1742-18
ps*-89-90-1588-37
ps*-90-3222-27
ps*-90-91-8549-7
ps*-96-5032-6
ps*-98-5691-5
ps*-99-2157-1
ps*-Mu85-3061-21

ps*-Mu86-1105-1
vp(ps)*-86-1449-3
vp(ps)*-86-1565-17
vp*-0118
vp*-0315
vp*-2-8c
vp*-71-1367
vp*-73-30173
vp*-8101
vp*-8104
vp*-8106
vp*-8107
vp*-8108
vp*-8109
vp*-8110
vp*-8111
vp*-8112
vp*-8113
vp*-8114
vp*-8115
vp*-8116
vp*-8117
vp*-8201
vp*-8203
vp*-8204
vp*-8208
vp*-8209
vp*-8210
vp*-8211
vp*-84-5079-29
vp*-84-5279-29
vp*-84-5315-29
vp*-8418
vp*-8420
vp*-85-3011-11
vp*-85-3017-9
vp*-85-3040-29
vp*-85-3042-7
vp*-85-3099-16
vp*-85-3135-4
vp*-85-3182-6
vp*-85-3250-1
vp*-85-3339-25
vp*-85-3422-13
vp*-85-86-3567-20
vp*-86-1109-1
vp*-86-1407-15
vp*-86-1573-27
vp*-87-2146-18
vp*-87-2213-19
vp*-87-2224-3
vp*-87-2274-37
vp*-87-2299-1
vp*-87-2339-1
vp*-88-89-3555-1
vp*-88-89-8625-5
vp*-89-1181-8
vp*-89-1279-14
vp*-89-90-1561-18
vp*-92-1401-8
vp*-93-1017-2
vp*-95-2086-1
vp*-N702C
vp*-PI183642
vp*-PI185847
vp*-PI200204
vp*-PI254854
vp*-PI430482
vp-de*-87-2406-23
vp-dek*-99-2197-1
vp-Y*-86-1267-31
vp-Y*-86-1361-7
w-vp*-84-5020-4
w-vp*-85-3014-6
w-vp*-85-3304-13
w-vp*-91-1859-8
w-vp*-91-2544-7
w-vp*-92-1408-1
y-vp*-0730
y-vp*-1982-1
y-vp*-1982-2
y-vp*-2062-Coop
y-vp*-60-153
y-vp*-65-792
y-vp*-6961
y-vp*-73-2656
y-vp*-80-6118
y-vp*-81-5
y-vp*-8102
y-vp*-8103
y-vp*-8105
y-vp*-8206
y-vp*-8207
y-vp*-83-1A
y-vp*-83-3101-36
y-vp*-8336
y-vp*-84-13
y-vp*-8419
y-vp*-85-3572-30
y-vp*-8512
Y-vp*-87-2339-10
y-vp*-87-2340-36
y-vp*-8701
y-vp*-88-89-3563-33
y-vp*-88-89-3613-25
y-vp*-99-2226-1
y-vp*-Alexho68-195

waxy endosperm
wx*-0208
wx*-98-1406-6

white cap kernel
Wc*-1982-1
Wc*-Funk-81-22
Wc*-Funk-81-23
wc*-87-2307-1
Wc*-DC
wc*-N1349

white endosperm
y*-1981
y*-1982-3
y*-73-2
y*-73-2262-1
y*-73-2262-2
y*-73-2394
y*-73-324-1
y*-73-4035
y*-73-426
y*-84-8b
y*-87-2201-3
y*-Funk-81-12
y*-Funk-81-2
y*-Funk-81-20
y*-Funk-81-9
y*-Sprague
y*-syn-DOCI
y*-Williams-60-154

wrinkled kernel
wr*-N1389A
wr*-N156C
wr*-N612A

Seedling Mutants

aberrant seedling
abbt*-N454C
abbt*-N594B
abbt*-N595B
abbt*-N712B

adherent leaf
ad*-87-2285-18
ad*-N253
ad*-N273B
ad*-N316
ad*-N377B
ad*-N512B
ad*-N551B
ad*-N582
ad*-N605B
ad*-N640
ad*-N664
ad*-N682B
ad*-N877B
ad*-N984B

albino seedling
nlw*-85-3357-17
peach-albino-mutable*-87-2209-30
w*-002-12
w*-005-19
w*-009-6
w*-010-4
w*-011-11
w*-017-14-A
w*-017-14-B
w*-020-9
w*-034-16
w*-037-14
w*-039-15
w*-2065
w*-2246
w*-3858
w*-4670
w*-4873
w*-5201
w*-5255
w*-5267
w*-56-3003-12
w*-5602
w*-5622
w*-5787
w*-5863
w*-6293
w*-6504
w*-6575
w*-7165
w*-7219
w*-7281
w*-74-1674-1
w*-78-297-3
w*-8105W
w*-8129
w*-8147
w*-8201
w*-84-5205-46
w*-84-5222-30
w*-85-3359-11
w*-85-3552-25
w*-85-3559-30
w*-8529
w*-8549
w*-8569
w*-86-1078-6
w*-86-1265-30
w*-86-2222-5
w*-8630
w*-8635
w*-8637
w*-8670
w*-87-2215-8
w*-8963
w*-8977
w*-8992
w*-9235
w*-B-75
w*-BYD
w*-Canario Hembrilla Enano
w*-MontenegrinFlint
w*-N103
w*-N109
w*-N115
w*-N126A
w*-N137D
w*-N145
w*-N147B
w*-N167
w*-N176
w*-N178A
w*-N1834
w*-N1839
w*-N1854
w*-N1865
w*-N1890
w*-N191
w*-N1915
w*-N192
w*-N21A
w*-N22
w*-N23
w*-N24
w*-N278A
w*-N285
w*-N318
w*-N332
w*-N335
w*-N346A
w*-N355
w*-N364
w*-N367B
w*-N404
w*-N405A
w*-N413B
w*-N42
w*-N428B
w*-N430B
w*-N436A
w*-N456A
w*-N457
w*-N491B
w*-N5
w*-N509B
w*-N516A
w*-N524A
w*-N532
w*-N547A
w*-N558B
w*-N563A
w*-N569B
w*-N574
w*-N58
w*-N587C
w*-N593B
w*-N6
w*-N621B
w*-N627B
w*-N67A
w*-N682A
w*-N704
w*-N708A

w*-N727A
w*-N729A
w*-N736A
w*-N77
w*-N804B
w*-N829B
w*-N883B
w*-PI184276
w*-PI201543
w*-PI213747
w*-PI228176
w*-PI228179
w*-PI232965
w*-PI232968
w*-PI232972
w*-PI239103
w*-PI239110
w*-PI251009
w*-PI251885
w*-PI251930
w*-PI251932
w*-PI254851
w*-PI267162
w*-PI267179
w*-PI267204
w*-Singleton-16
w*-Singleton-22
w*-Singleton-24
w*-Singleton-25
w*-Singleton-31
w*-Tama
w*-wh-mut
wh*-053-4
wh*-2083
wh*-89-578-6

clasping leaf
clsp*-87-2320-9
clsp*-88-89-3522-1

flecked leaf
flk*-N564B
flk*-N570A
flk*-N630B

glossy leaf
gl*-218-1
gl*-32TaiTaiTaSarga
gl*-4339
gl*-5201
gl*-5249
gl*-56-3023-6
gl*-56-3023-9
gl*-56-3036-7
gl*-6
gl*-60-2484-8
gl*-63-2440-8
gl*-85-3095-12
gl*-8654
gl*-87-2215-8
gl*-87-2215-30
gl*-87-2278-34
gl*-88-3142-4
gl*-97P-261-5
gl*-Bizika
gl*-gl12
gl*-LGC-117
gl*-LGC-27
gl*-Loesch
gl*-Manglesdorf
gl*-Moritsa
gl*-N168
gl*-N203C
gl*-N356
gl*-N546C
gl*-N616A
gl*-N656A
gl*-N681A
gl*-N696E
gl*-PI184286
gl*-PI200203
gl*-PI228177
gl*-PI232974
gl*-PI239101
gl*-PI239110
gl*-PI251885
gl*-PI251933
gl*-PI262474
gl*-PI262476
gl*-PI262494
gl*-PI262500
gl*-PI267203
gl*-PI267209
gl*-PI267212
gl-nec*-N516D

high chlorophyll fluorescence
hcf*-88-3005-3

luteus yellow seedling
l*-009-6
l*-017-3
l*-025-4
l*-062-3
l*-2215
l*-2673
l*-4356
l*-4545
l*-4871
l*-5-9b[X-7-39]
l*-549-1 Derived Flint
l*-56-3003-12
l*-570-2 Cincantin
l*-5783-straw
l*-62-489-2
l*-6474
l*-6923
l*-6973
l*-7165
l*-7281
l*-73-563
l*-7748
l*-8321
l*-8376
l*-84-5225-33
l*-85-3215-2
l*-85-3225-4
l*-85-3457-40
l*-85-3513-1
l*-85-3541-20
l*-86-1112-1
l*-86-1354-9
l*-8634
l*-88-89-3555-13
l*-89-90-1552-10
l*-8966
l*-d-8694
l*-LGC-43
l*-N104
l*-N113
l*-N119
l*-N124B
l*-N129
l*-N137B
l*-N140
l*-N171A
l*-N175
l*-N1806B
l*-N1838
l*-N1878
l*-N188A
l*-N1908
l*-N1920
l*-N195
l*-N218
l*-N251
l*-N31
l*-N336
l*-N347
l*-N368B
l*-N392A
l*-N416A
l*-N438A
l*-N496B
l*-N52
l*-N523
l*-N606
l*-N612B
l*-N62
l*-N703
l*-N730
l*-PI183642
l*-PI183643
l*-PI193433
l*-PI193435
l*-PI193436
l*-PI195245
l*-PI213737
l*-PI213745
l*-PI218038
l*-PI239110
l*-PI239114
l*-PI251884
l*-PI254854
l*-PI262495
l*-PI267215
l*-PI267226
l*-Rumanian Flint
l*-Tama
l*-y wx 6-9b
pyg*-N761
y-l*-85-3234-6
y-l*-8910 Briggs
yd*-87-2278-34
yel*-5344
yel*-8721
yel*-8793
yg*-8962

orobanche
oro*-6577
oro*-69-9291-8
oro*-84-5080-15
oro*-85-3087-3
oro*-85-3106-41
oro*-85-3113-11
oro*-88-3237-31
oro*-88-89-3550-32

pale green seedling
pas*-90-3222-13
pg*-2142
pg*-6372
pg*-69-5079-2
pg*-6923
pg*-7122
pg*-8129
pg*-84-5234-29
pg*-8412
pg*-8911
pg*-8959
pg*-Caspar
pg*-N102
pg*-N11
pg*-N12
pg*-N123C
pg*-N127
pg*-N1389B
pg*-N146A
pg*-N147A
pg*-N150A
pg*-N155A
pg*-N156B
Pg*-N1604
pg*-N161
pg*-N181
pg*-N1822A
pg*-N1866
pg*-N1881
pg*-N1885
pg*-N1983
pg*-N213
pg*-N215B
pg*-N272C
pg*-N296A
pg*-N346B
pg*-N35
pg*-N357B
pg*-N361A
pg*-N362A
pg*-N375B
pg*-N379
pg*-N380
pg*-N381
pg*-N384B
pg*-N40
pg*-N408C
pg*-N417A
pg*-N421
pg*-N429B
pg*-N445
pg*-N452C
pg*-N459
pg*-N46
pg*-N469
pg*-N481
pg*-N484A
pg*-N506A
pg*-N507A
pg*-N511
pg*-N514B
pg*-N524B
pg*-N550
pg*-N556B
pg*-N558A
pg*-N570C
pg*-N59B
pg*-N590B
pg*-N596B
pg*-N597B
pg*-N600A
pg*-N603
pg*-N615B
pg*-N618
pg*-N619
pg*-N638
pg*-N639
pg*-N641
pg*-N660A
pg*-N663B
pg*-N673A
pg*-N683A
pg*-N686B
pg*-N701B
pg*-N719C
pg*-N71A

pg*-N724B
pg*-N73A
pg*-N855C
pg*-N884B
pg*-N896B
pg*-N906B
pg*-PI183648
pg*-PI193424
pg*-PI262473
pg*-PI262495
pg*-PI267162
pg*-PI267215
pg-nec*-RJL-6527

pale pale green seedling
ppg*-N1474B
ppg*-N1963
ppg*-N406A
ppg*-N427A
ppg*-N449
ppg*-N458B
ppg*-N881B

piebald leaf
pb*-2-7-4400
pb*-87-2442-5
pb*-N1386C

ragged seedling
rgd*-N203E
rgd*-N2290C
rgd*-N261B
rgd*-N378B

red seedling leaf
red-leaf*-86-1569-7

small seedling
d*-N155B
d*-N230A
d*-N254
d*-N266B
d*-N293B
d*-N408A
d*-N429A
d*-N526B
sms*-N1964
sms*-N1971
sms*-N204B
sms*-N311C
sms*-N369B
sms*-N566
sms*-N570B
sms*-N680B

translucent leaf
trans-leaf*-56-3122-7
trans-leaf*-68F-958
trans-leaf*-78-314
trans-leaf*-79-6533
trans-leaf*-PI228176

tube leaf
fused-leaves*-N36B
fused-leaves*-N835B
fused-leaves*-PI228170

virescent seedling
l*-N184
v*-002-17
v*-007-18
v*-022-17
v*-025-4
v*-037-5
v*-1-2(5376)
v*-1-9(5622)
v*-2-9(5257)
v*-388-Sprague
v*-4308
v*-4698
v*-5-10(5355)
v*-5287
v*-5413
v*-5575
v*-56-3012-10
v*-5828
v*-60-151
v*-60-2397-15
v*-65-1433
v*-7230
v*-7281
v*-7312
v*-74-1690-1
v*-74-1873-1
v*-74-1948-1
v*-8070
v*-8129
v*-8201
v*-8339
v*-8522
v*-8654
v*-8743
v*-8806
v*-8957
v*-8958
v*-9026
v*-Funk-84-13
v*-Funk-84-9
v*-leng
v*-LGC-111
v*-LGC-142
v*-LGC-98
v*-N1007B
v*-N110
v*-N114A
v*-N116
v*-N125
v*-N128
v*-N131
v*-N133
v*-N134
v*-N135A
v*-N158
v*-N16
v*-N179
v*-N1806A
v*-N187
v*-N1886
v*-N1912
v*-N1966
v*-N201
v*-N206A
v*-N229
v*-N243
v*-N245
v*-N246
v*-N26
v*-N260C
v*-N280
v*-N289
v*-N29
v*-N298
v*-N303
v*-N330B
v*-N34
v*-N341
v*-N352B
v*-N358C
v*-N376
v*-N378A
v*-N397
v*-N400B
v*-N41B
v*-N422B
v*-N463
v*-N467
v*-N473B
v*-N499
v*-N517
v*-N526A
v*-N529B
v*-N53A
v*-N54A
v*-N54B
v*-N55
v*-N560
v*-N587A
v*-N620
v*-N634A
v*-N64A
v*-N655A
v*-N65B
v*-N660D
v*-N661A
v*-N674B
v*-N678B
v*-N69A
v*-N698B
v*-N710B
v*-N713B
v*-N728
v*-N735
v*-N748C
v*-N779A
v*-N7B
v*-N806C
v*-N826
v*-N829A
v*-N84B
v*-N878B
v*-N891C
v*-N956C
v*-pb-3019-16
v*-PI180165
v*-PI180231
v*-PI183640
v*-PI185851
v*-PI195244
v*-PI195245
v*-PI200197
v*-PI200201
v*-PI218042
v*-PI228174
v*-PI228176
v*-PI232974
v*-PI236996
v*-PI239105
v*-PI239114
v*-PI239116
v*-PI251883
v*-PI251891
v*-PI251930
v*-PI254856
v*-PI262476
v*-PI262487
v*-PI262489
v*-PI267184
v*-PI267209
v*-PI267212
v*-PI270293
v*-Pollacsek
v*-RumanianFlint
v*-Singleton-22
v*-Singleton-34
Vsr*-N1447
wst*-N643B

white luteus seedling
wl*-N1
wl*-N126B
wl*-N1350B
wl*-N1384B
wl*-N165A
wl*-N18
wl*-N1803
wl*-N1857
wl*-N189
wl*-N1930
wl*-N1931
wl*-N1949
wl*-N217A
wl*-N221
wl*-N241
wl*-N255
wl*-N283A
wl*-N290
wl*-N299A
wl*-N313
wl*-N315
wl*-N345A
wl*-N358A
wl*-N362B
wl*-N38B
wl*-N4
wl*-N401
wl*-N408B
wl*-N415
wl*-N416B
wl*-N44
wl*-N448
wl*-N47
wl*-N500
wl*-N502B
wl*-N508
wl*-N538A
wl*-N551C
wl*-N554A
wl*-N567
wl*-N575A
wl*-N60
wl*-N629A
wl*-N636
wl*-N637A
wl*-N646
wl*-N663A
wl*-N686A
wl*-N698A
wl*-N709B
wl*-N720B
wl*-N758A
wl*-N998C

white margins
whm*-N1462

white striped seedling
ij-mos*-8624
stk*-N359B
str*-2104-4 EBP
str*-2116-1 EBP
str*-5120B-Teo
str*-6-10-4307
str*-78-314-4
str*-78-314-5
str*-84-5222-7
str*-86-1494-27

str*-PI262495
str-et*-PI184276

white tipped leaf
wt*-N308
wt*-N432A
wt*-N580B
wt*-N650A

yellow green leaf
pastel*-1-6-5495
pyg*-N1266A
pyg*-N223
pyg*-N321
yg*-0130
yg*-4369
yg*-4484
yg*-4889
yg*-5-8(5575)
yg*-56-3021-18
yg*-6697
yg*-68-1429
yg*-6853
yg*-74-1827-1
yg*-77-585
yg*-8105
yg*-8379
yg*-8622
yg*-8631
yg*-8682
yg*-8692
yg*-8946
yg*-910J
yg*-B73
yg*-Caspar
yg*-N1314B
yg*-N157A
yg*-N2246
Yg*-N2294
yg*-N37
yg*-N706B
yg*-N72
yg*-PI228174
yg*-PI239114
yg*-PI267224
yg*-Singleton -23
yg*-Singleton-30
yg-nec*-95-5320-7
yg-nec*-Singleton-29
Yg-str*-Mu

zebra striped seedling
zb*-89-3137-5
zb-gl*-2187

Plant Mutants

absence of leaf blade
bladeless*-87-2406-23

adherent tassel
ad*-N613B

albescent
al*-1479
al*-PI245132
wh top*-Bauman

barren stalk
ba*-1447
ba*-68-679-8
ba*-74-304-12
ba*-74-369-2
ba*-PI200290
ba*-PI218135
ba*-PI239105
ba*-PI251885
ba-ub*-94-4712

bleached leaf
Blh*-N1455
blh*-N2302B
blh*-N2359
Blh*-N2421
Bh*-SF98-12

blotched leaf
bl*-N1278A
bl*-N43
red leaf blotch*-PI213779
yel-spl*-N152

brachytic plant
br*-2180
br*-78-136KEW
br*-Brawn219-221
br*-Brawn227-229
br*-Brawn230
br*-Brawn231-233
br*-Brawn235-237
br*-Brawn259-260
br*-Brawn261-262
br*-Brawn263-266
br*-Brawn267-268
br*-Brawn269-271
br*-Brawn272-273
br*-Brawn274-275
br*-OSIJEK-Yugoslavia
br*-PI228171
br*-PI239105
br*-Singleton-8
br*-Singleton1969-252
td*-PI262476

brevis plant
bv*-N2283

brittle stalk
bk*-N888D

brown midrib
bm*-PI228174
bm*-PI251009
bm*-PI251893
bm*-PI251930
bm*-PI262480
bm*-PI262485
bm*-PI267186

burned leaf
les*-Funk-4
les*-PI262474

chromosome breaking
Chrom-breaking*-Mu

colored leaf
lc*-PI239110

crinkled leaf
cr*-97P-111
cr*-98-1698

crossbanded leaf
cb*-N1620A
Cb*-N2290B
cb*-N696D
cb*-N719A

defective tassel
Tp*-54-55-Jos
Tp*-PI213734
Tp*-Pk41-Jos
Tp*-T8-Jos
Tp*-Tenn61

dwarf plant
d*-018-3
d*-119
d*-136-220
d*-1821
d*-2108
d*-2201
d*-2447-8
d*-3-eared-JC
d*-3047
d*-5312
d*-56-3037-23
d*-60-2428
d*-64-4156-1
d*-74-1701-5
d*-75-6071-1
d*-76-1304-9
d*-76-2186
d*-78-282-3
d*-78-286-1
d*-78-286-5
d*-85-3081-33
d*-87-2198-36
d*-gl11
d*-Brawn254-258
d*-MarovacWhiteDent
d*-N1352B
d*-N1883
d*-N1895
d*-N203D
d*-N2295
d*-N282
d*-N454A
d*-N518A
d*-N549B
d*-N604
d*-N699B
d*-N994B
d*-PI180231
d*-PI183644
d*-PI184286
d*-PI200303
d*-PI213769
d*-PI228169
d*-PI228171
d*-PI239110
d*-PI245132
d*-PI251652
d*-PI251656
d*-PI251885
d*-PI254854
d*-PI262495
d*-PI267219
d*-rosette
d*-shlf-9-436-1
d*-su
d*-su2
d*-Teo
d*-ts1

erect leaf
dge*-N2410

gritty leaf
gtl*-N2297

green striped leaf
gs*-98-5700-5
gs*-N359A

knotted husks
mwp*-Nelson

lesion
les*-2119
les*-74-1873-9
les*-ats
Les*-N1378
les*-N2290A
Les*-N2420
Les*-N502C

liguleless
Lg*-64-36
lg*-PI228170

male sterile
Ms*-2471
ms*-6015
ms*-6025
ms*-6026
ms*-6033
ms*-6039
ms*-6045
ms*-6048
ms*-6049
ms*-6052
ms*-6053
ms*-6054
ms*-6055
ms*-6057
ms*-6058
ms*-6059
ms*-6060
ms*-6061
ms*-6062
ms*-6064
ms*-6065
ms*-6066
ms*-N2415
Ms*-N2474
ms*-N2484
ms*-N352C
ms*-PI217219
ms-si*-355

many tillers
tlr*-N2243

multiple midrib
multiple-midrib*-87-2406-23

narrow leaf
nl*-5688
nl*-N232A
nl*-N410B
nl*-N462B
nl*-N625
nl*-N727B
nl*-N732A
nl*-PI245132
stf*-N601

necrotic leaf
ll*-N248A
ll*-N417D
nec*-011-7
nec*-017-3
nec*-4871
nec*-4889

nec*-5588 early
nec*-5619
nec*-5876
nec*-77-574-1
nec*-8624
nec*-8737
nec*-fraz
nec*-N1119B
nec*-N1185B
nec*-N1487
nec*-N193
nec*-N200B
nec*-N215F
nec*-N283B
nec*-N419
nec*-N430A
nec*-N468
nec*-N490A
nec*-N510A
nec*-N541B
nec*-N545B
nec*-N559
nec*-N562
nec*-N581
nec*-N596C
nec*-N599A
nec*-N650D
nec*-N712C
nec*-PI228174
nec*-PI267184
nec*-Vasco
nec-pg*-PI239116
shootless*-99-677-6

oil yellow plant
oy*-N2360A

pale green plant
pg*-56-3012-10
pg*-8321
pg*-Hy2 Nob 7-5
pg*-LGC-61

patched leaf
ptc*-N238A
ptc*-N611

pigmy plant
py*-N656B
py*-N714

ramosa
ra*-412E
ra*-4889

rolled leaf
rld*-N1405B
rld*-N1525

small plant
d*-N1074C
d*-N137C
d*-N149
d*-N164A
d*-N188B
D*-N2023
d*-N208B
d*-N210
d*-N262C
d*-N287B
d*-N305
d*-N328
d*-N394
d*-N524D
d*-N528B
d*-N553D
d*-N707B
D*-N987B
smp*-N121
smp*-N135B
smp*-N153B
smp*-N156A
smp*-N1954
smp*-N272A
smp*-N306
smp*-N586B
smp*-N600B
smp*-N602
Smp*-N842

speckled leaf
spc*-N112
spc*-N198B
spc*-N357A
spc*-N370

spotted leaf
les*-74-1820-6
spt*-N278B
spt*-N412A
spt*-N579B

stiff leaf
stf*-N1092C
stf*-N235B

streaked leaf
stk*-N351
stk*-N368A
stk*-N433B
stk*-N584A
stk*-N587D
stk*-N670B
stk*-N777B
stk*-N835A
stk*-N925B

striate leaf
Sr*-N2430
sr*-N675B

stubby plant
stb*-N938C

tassel seed
ts*-0174
ts*-69-Alex-MO17
ts*-Anderson
Ts*-N1374
ts*-N2409
ts*-PI200203
ts*-PI251881
ts*-PI267209
ts*-Sprague

tasselless
tls*-Funk
tls*-Va35

tiny plant
ty*-N215A
ty*-N326C

white sheath
ws*-N1979
ws*-N537D

white stripe leaf
ij*-N504A
li*-PI262476
str*-PI262474
wst*-N248B
wst*-N413A
wst*-N548
wst*-N564A
wst*-N696B

yellow stripe leaf
gs*-68-1354
ys*-1479
ys*-5-8(5575)
ys*-67-2403
ys*-68-1354
ys*-8912
ys*-N326A
ys*-PI-262172
ys*-PI-262475
ys*-PI228180
ys*-whorled

zebra necrotic leaf
zn*-8637
zn*-N230B
zn*-N342A
zn*-N372A
zn*-N451
zn*-N571D

Ear Mutants

distichous ear
distichous*-68-1227

distorted segregation
off-ratio*-85-3255-6
off-ratio*-86-1155-1
wx-off-ratio*-86-1110-4

polytypic ear
pt*-McClintock
pt*-Mu

reduced pollen fertility
ga*-0188
ga*-0213
ga*-3615
ga*-91-5197-2
ga*-94-764
Ga*-Yugoslavia

silky
si*-0443
si*-0503
si*-0648
si*-8104

tunicate
Tu*-5090B

unpaired rows
up*-Shirer

V. MAIZE GENOME DATABASE

www.agron.missouri.edu

MaizeDB has been busy integrating data from the published literature and from the new plant genome projects. WWW sites of interest to cooperators are summarized on p. iv of this Newsletter. While our goal remains to provide access to a comprehensive genome resource, we are engaging in interoperability with other data repositories such as the NCBI databases, and other maize and plant genome databases. The focus is genetically defined loci (17558 records) and maps (874) complete with documentation and functional annotation. Documentation includes the tools used, notably genetic stocks and source germplasm (21,534) and probes (151,579,aka markers, clones, primers), sources and availability, map scores (8610) and recombination data (1950). Functional annotation includes agronomic traits (565), phenotypic variations (1001), locus expression and properties, and gene products (1359). Literature citations (62,465), including authors, with addresses (5523), are considered key documentation. In this report we present the highlights, a brief summary of Maize Conference 2001 feedback, a report on recent data types, and a table summarizing interoperability status with some major external database repositories.

Highlights this year:

- major feedback from the maize genetics community, posted on the homepage
- redesign of home page, featuring easier access routes in a central location
- full text search of the entire www site (Google)
- comparative map graphic utility in collaboration with the Rice Genome Program, Tsukuba Japan
- user accesses up 60% over last year, at 8000 accesses/day.

Note: these accesses were via MaizeDB services (browse utilities, forms, full text searches). They do not include the new Google site search (an additional 25%) nor indexing activities by Internet robots and spiders.

Feedback synopsis.

We are delighted to report the success of the Maize Genetics Executive Committee Chair, Jeff Bennetzen, in eliciting a wide response from the community at the 2001 Maize Genetics Conference at Lake Geneva, WI. Thank you Jeff! We have in the past relied on our own sense, based on interactions with other genome and related databases on the Internet and a steady trickle of advice from the community. The Maize Conference 2001 feedback indicated an interest in retrieving data by graphical map displays (15% of responses), in comparative genomics (30%), in retrieval of map information for a particular nucleotide sequence (30%) and generally in easier, friendlier access (40%). We have made a start on addressing community wishes, (see highlights above). We will soon be implementing a graphical view of the genetically anchored BACs, and, additionally, a BLAST utility that returns map information in a custom report.

We are quite concerned that many of you find the MaizeDB interface difficult to navigate. We hope changes instituted this year will help, as well as those in progress. Consider our new utilities and rearrangings as first drafts, ready to be polished, embellished or surgically transformed based on your ongoing inputs and our resources. *Especially try Google first for efficient searches.*

Summary of recent datatypes.

SSR markers. Simple Sequence Repeats. Currently we represent data for 1735 SSR, for which 590 were discovered in public cDNA sequences. Data have been integrated from the Maize Mapping Project (US), Maize Mapping Consortium (EU), Pioneer, NC State, and the Brookhaven National Laboratory Acemaz. We are in contact with the Doebley maize evolution project and with CIMMYT regarding their SSR diversity data. Dynamic data summaries, organized by bin locations, and detailed map snapshots are provided by the SSR link in the database sidebar. A comparative map tool, featured in a central box on our home page, permits dynamic comparison of map coordinates for SSR mapped in distinct populations, as well as with other major maize maps.

ESTs, Expressed Sequence Tags: cDNA sequences most often deposited in the dbEST division of GenBank (NCBI, National Center for Biotechnology Information). Currently 112,582 cDNA GenBank accessions for some 66,996 clones are represented in MaizeDB and are linked to maps and other genetic and genomic information. Note that Google searches find all accessions. Of these 1,172 have genetic map locations.

EST Data flow: NCBI (GenBank) regularly sends files to MaizeDB with new ESTs or updates. MaizeDB processes these and imports information about each clone, the library, the source and availability. The universal sequence accessions are used to form links to GenBank and to ZmDB (for clone submissions from Stanford.) Information needed to create links to ZmDB contigs and to the TIGR gene index is extracted using the ZmDB table-maker or downloaded from an ftp site (TIGR), processed and updated several times/year.

EST Data Access: *Zea mays*-specific BLAST searches of all entries in dbEST are currently supported at NCBI and ZmDB. Mapped clones are accessible by the MaizeDB Probe Browser, an alphabetical tabulation, which can be delimited by bin location(s); it lists map coordinates and has dynamic links to selected MaizeDB pages (images, probe details), as well as to GenBank, ZmDB and TIGR. The first few letters of the Probe name reflect source; acronyms relevant to ESTs include: *csu*, California State University, *isu*, Iowa State

University, *std*, Stanford University. One exception, EST clones developed by Tim Helentjaris, but mapped to a *uaz* probed site, are named by plate location, and begin with 1C, 2C, 5C, 6C or 7C. A complete list of institutional acronyms is provided on-line with the suggested guidelines for nomenclature, www.agron.missouri.edu/maize_nomenclature.html, and under locus names. With permission of Ginny Walbot, we mirror a set of trace files for the Stanford sequences, converted to various formats by Deverie Bongard-Pierce (Mass. General Hospital).

Unigene Overgo BAC (Bacterial Artificial Chromosome) Anchors.

Currently 4300 Unigene-Overgo primer pairs are represented in MaizeDB, complete with links to public sequences included in the assembly. These data were provided by the partnership of Dupont and Incyte Genomics with the Maize Mapping Project. We anticipate an additional 6000 Unigenes to be added summer 2001. Of the initial 4300 Unigenes, over 2200 have been anchored to either an *Eco*RI and/or *Hin*dIII BAC clone (B73 libraries) available from CUGI. These probes, of type 'Overgo', are listed with the public sequence accessions and clones that contribute to the Unigene. This process builds on the EST dataflow described. While DuPont EST and genomic data per se are not supplied to MaizeDB, DuPont EST and genomic data contribute (a) to refine the public consensus sequence, (b) to the assembly, often a collapse of multiple public assemblies, and (c) to mask repeat sequences. In MaizeDB, the assembly is linked to appropriate contributing (public) sequences, to map coordinates inherited from a public sequence, and to the corresponding ZmDB-computed Unigene clone. Of note, some 450,000 BAC clones, from 3 public libraries are in queue at CUGI for contig assignment, based on fingerprint and marker data. CUGI updates the BAC contig computation approximately monthly and incorporates marker data submissions processed at MaizeDB.

Access to marker data currently is via Google, by focused searches on the Probe form, or by exploring the CUGI site. In process: (a) tabular summaries with query access and overview; (b) a physical/genetic map graphical display; (c) a BLAST utility that will return genetic map information and links to relevant external databases, including CUGI, TIGR, and ZmDB.

MTM Mutator Stocks.

Of new genetic Stocks represented in MaizeDB, there are 8,436 from the Cold Spring Harbor resource , which include 24 kernel phenotypes. Files were provided by MTM on request by MaizeDB, and phenotypic descriptors have been harmonized with MaizeDB listings, largely provided by Gerry Neuffer and the Stock Center. To view phenotypes, and their MTM Stocks, see the MaizeDB side bar, What' s New, and scroll to July 2000._ If Mutator is known to be 'On' or 'Off' this is part of the Stock Name.

External Database Interoperability

Database[1]	**Data retrieved**[2]	**MaizeDB data linked**[3]	**Links**[4]
GenBank (EMBL,DDBJ)[5]	Sequences	Variation, Probes, Loci	116,980
PubMed	Abstracts, full text, links out	Reference	2,805
ZmDB[5]	Sequences, contigs, clones	Probe	135,369
TIGR	Gene index, paralogs	Probe	50,466
CUGI[5]	BAC contigs, clones	Probe	68,545
RiceGenes	Rice maps	Probe	367
GrainGenes	Triticeae maps	Probe	287
SwissProt[5]	Protein sequence, function	Gene Product	448
Enzyme	Reactions, sequences, pathways	Gene Product	329
ProSite	Motif sequence and function	Term (Protein Feature)	1035
GRIN[5]	Germplasm evaluations, other	Stocks	3348
MTM	Descriptions, images	Stocks	8436

[1]Database www sites are provided on p.iv of this Newsletter.

[2]Data retrieved from the external database from the MaizeDB-created link

[3]Entities or data classes in MaizeDB with links to the external database listed

[4]Number of distinct accessions in MaizeDB for a given site. Thus multiple links of a GenBank accession to EMBL or DDBJ are counted once. Similarly, two distinct records, for example a Variation and a Probe with a link to the same GenBank accession, are also counted once.

[5]These databases have reciprocal links with MaizeDB.

Mary Polacco
Ed Coe
July 2001

VII. AUTHOR INDEX
(* identifies articles authored in this Newsletter)

This newsletter shares current research on genetics, cytogenetics, molecular biology, and genomics of maize. Information is shared by Cooperators with the understanding that it will not be used in publications without their specific consent.

Send your notes for the 2002 Maize Genetics Cooperation Newsletter now, anytime before January 1. Your MNL Notes will go on the Web verbatim promptly, and will be prepared for printing in the annual issue. Be concise, not formal, but include specific data, tables, observations and methods. Check MaizeDB for the most current information on submission of notes. Send your notes as attachments or as the text of an email addressed to Newsletter@chaco.agron.missouri.edu (we will acknowledge receipt, and will contact you further if necessary). If email is not feasible, please mail a double-spaced, letter-quality copy of your note, preferably with a disk containing the electronic version. Please follow the simple style used in this issue (city /institution title /--authors; tab paragraphs; give citations with authors' initials --e.g., Maizer, BA et al., J Hered 35:35, 1995, or supply a bibliography). Figures, charts and tables should be compact and camera-ready, and supplied in electronic form (jpg or gif) if possible. To separate columns in tables, please tab instead of using spaces, to ensure quality tabulations on the web. Your MNL Notes will go on the Web verbatim promptly, and will be prepared for printing in the annual issue. Mailing address:

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SEND YOUR ITEMS ANYTIME; NOW IS YOUR BEST TIME

MNL 55ff. on line	MaizeDB - http://www.agron.missouri.edu
Author and Name Indexes (and see **MaizeDB**)	
Nos. 3 through 43	Appendix to MNL 44, 1970 (copies available)
Nos. 44 through 50	MNL 50:157
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 53:153
Nos. 54 to date	Annual in each issue
Stock Catalogs	Each issue and MaizeDB
Rules of Nomenclature (1995)	MNL69:182 and **MaizeDB** (1996 update)
Cytogenetic Working Maps	MNL 52:129-145; 59:159; 60:149 and **MaizeDB**
Gene List	MNL69:191; 70:99 and **MaizeDB**
Clone List	MNL 65:106; 65:145; 69:232 and **MaizeDB**
Working Linkage Maps	MNL69:191; 70:118; 72:118 and **MaizeDB**
Plastid Genetic Map	MNL 69:268 and **MaizeDB**
Mitochondrial Genetic Maps	MNL 70:133 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 report 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, and advice or help you received, when you publish.

MaizeDB needs Cooperators (this means you) to:

(1) Look up "your favorite gene or expression" in **MaizeDB** (see section V in this Newsletter) and send refinements and updates to polaccom@missouri.edu, coee@missouri.edu, or db_request@chaco.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) Provide probe or primer information per http://www.agron.missouri.edu/cgi-bin/sybgw_mdb/mdb3/Probe/query; fingerprint data and fragment sizes are significantly useful to colleagues.

May you find a Unique corn in MM!