and teosinte to Tripsacum cannot be denied, however, as is well known from their crossability and cross-mapping studies. Chromosome differentiation in this case seems to be more important in the tactics of immediate divergence than in the ultimate strategy of wider speciation.

P. Chandravadana and W. C. Galinat

UNIVERSITY OF MILAN
Institute of Genetics, Milan, Italy

A second case of transposed duplication in chromosome 10

We have presented evidence that a nonparental strand isolated from heterozygous R-sk/r-r K10 plants carries a chromosome segment in duplicate, one segment in normal position and one transposed to a new position on the same chromosome (G. Gavazzi and G. Galli, MNL 48:106-112; Gavazzi, Heredity in press). The data to be presented refer to another strand, referred to as case 1 strand, isolated from R-st K10/r-r parents as a presumed intralocus recombinant carrying the P component of r-r linked to R-st. The parental genotype expressed in terms of the P and S components of the R locus is symbolized p S-st/P s, where the lower case letters p and s do not distinguish between presence of a recessive allele and absence of the gene component.

The transmission of case 1 strand as determined in heterozygotes with a normal strand is significantly lower than the expected 50%, amounting to about 17% and 43% in the male and female germ line respectively (Table 1). Furthermore, stippled kernels with BFB cycles are frequently observed in testcrosses of

Table 1. Observed segregation on ears obtained by reciprocal crosses of heterozygous P S-st/p s plants to a p s line.

Entering parent	Colorless	Stippled	Light stip.	BFB	Total seeds	Case 1 strand transmission
female	7583	5537	26	95	13241	42.73%
male	3074	622	-	16	3712	17.19%

P S-st/p s plants, while they are not observed when S-st is on a normal strand. The frequent occurrence of the cycles is suggestive of chromosome instability.

The P to S-st recombination value as determined in testcrosses of P S-st/p s females is much higher than expected, suggesting that P of case 1 strand is dislocated to a new position either distal or proximal to the R locus:

Gametes tested	Presumed strand constitution				% nonparental strands	
	P S-st	p s	p S-st	P s	S-st	s
7240	3623	3445	116	56	3.10 (2.33)*	1.60 (1.86)*

*Recombination values corrected for differential transmission of strands with the duplication.

Case 1 strand carries Mst distal to S-st. Its loss through crossing over leads to a light stippled phenotype. Accordingly if this strand carries P distal to R then the light stippled recombinants yielded by testcrosses of P S-st/p s females (see Table 1) should not carry P but they would still carry it if the latter is proximal to R.

Out of 18 presumed light stippled progeny tested, nine bred true. Eight of them lost P, while one retained it. This is the result expected if the gene

sequence of the strand is S-st - Mst - P. The putative light stippled originally isolated were 26 out of 5658. Their frequency, estimated on the basis of the result of their progeny test, amounts to 0.23%, a value much lower than the expected 5.7%, suggesting that crossing over in this chromosomal segment is hampered, possibly by the presence of a structural heterozygosity.

As to the three point testcross data of G S-st P/g p s females the following distribution of the g marker was observed:

Parentals				Recombinants				
S-st P		p s		S-st		p s P		n
G	g	G	g	G	g	G	g	
2374	5	105	3210	62	19	49	0	5814

The recombination value in the g - R region, as determined in our stocks, is about 19%. The results obtained with case 1 strand are unexpected. Among parentals, in fact, g recombinants are almost null in S-st P and only 3.16% in p s strands while among recombinants the frequency of S-st and s strands carrying g is about 23 and 0% respectively. These data are consistent with a model that depicts case 1 strand as a chromosome carrying a chromosomal region 20 or more units long, including the G and P markers, in duplicate--one region in normal position and one translocated distally to R.

The fact that none of the p s P recombinants carries the g marker suggests that the transposed duplication is inverted, as indicated below:

G S-st Mst P G

Evidence for the presence of a duplicated region in case 1 strand: Evidence in favor of the presence of the duplicated region was sought among the light stippled recombinants isolated in testcrosses of G S-st P/g p s females (see Table 1). If the duplicated segment of case 1 strand is distal to R then the light stippled recombinants should have a normal strand without the transposed duplication and they would thus show normal values of recombination in the G - R region. The results reported in Table 2 confirm this expectation.

Table 2. Recombination frequency for g - S-st as determined in testcrosses of stippled and light stippled plants to g p s males.

Aleurone phenotype	Recombination frequency (%)	No. seedlings	Inferred strand constitution
stippled	5.0	100	G S-st Mst P G
"	1.6	126	"
"	2.8	106	"
"	0.8	147	"
"	2.9	5814	"
light st.	26.1	199	G S-st mst
"	22.8	271	"
"	14.2	183	"
"	15.3	150	"
"	19.2	151	"
"	31.7	328	"
"	4.4	455	G S-st mst P G

Further data in favor of the hypothesis come from the analysis of a sample of plants derived from stippled kernels with BFB cycle in their endosperm. These kernels, derived from testcrosses of G S-st P/g p s plants, proved upon germination to have lost P in 8 out of 16 cases. Accordingly they have been used in testcrosses to g p s plants to see whether loss of P of case 1 strand is associated with re-establishment of normal transmission and g - R recombination values:

Case 1 strand	Stippled phenotype	Crossing over % g to S-st	Case 1 strand transmission ♀♀	Case 1 strand transmission ♂♂	Inferred strand constitution
standard*	standard	1.98	44.6	20.6	G S-st P G
deriv. -1	dark	15.10	50.5	51.1	G S-st
deriv. -2	dark	2.07	40.6	38.0	G S-st G
deriv. -3	standard	0.62	44.0	--	G S-st G
deriv. - 4	very dark	1.51	47.6	51.0	G S-st G

*standard refers to a strand carrying P; the four derivatives lost it.

The data indicate that only one of the four derivative strands lost a major portion of the entire translocated duplication while the remaining three retained a portion marked with G. The apparent association of loss of the duplication or part of it with an altered stippled expression remains, at present, unexplained. More data are necessary to confirm it and to understand what might be the relationship between the two events.

G. Gavazzi and Graziella Anzani

Postzygotic lethals as a genetic tool for the analysis of embryogenesis

Embryogenesis in higher plants is a complex process involving many steps whose identification and temporal sequence might be analyzed by means of gene mutations affecting embryo and endosperm morphology. Different mutants of this kind are known in corn. They are also easily inducible with chemical mutagens. The frequency of selfed M2 ears segregating for such mutants following a 0.1% EMS treatment to seeds amounts to about 25% (C. Colella and G. Gavazzi, MNL 47:111). The induced mutants are either viable or lethal. The former consist of etched, collapsed endosperm and small seeds while the latter include the same types as well as aborted seeds, germless and defective endosperm type. Post-zygotic lethals are expected to be mutants of genes whose activity is required in embryogenesis, in the metabolism of the resting seed, or in catabolic reactions of the germination process. They would also include nutritional mutants with blocks in essential metabolites not diffusible from maternal tissues or required by the embryo at a late differentiation stage when the vascular flow originating in the mother plant is interrupted. These mutants are often recognizable at an early stage of seed development. Immature embryos can thus be excised and forced to germinate on enriched media.

Growth on such media should allow survival of some mutants with a nutritional block or with lethality confined to late stages of embryogenesis that are bypassed by inducing precocious germination. Other mutants that might be rescued are those whose endosperm development is genetically blocked, like those with defective endosperm.

We isolated more than 70 postzygotic lethals and began their analysis by excising immature mutant embryos, 1-2 mm long, on M2 and M3 ears, and transferring them on both mineral and enriched media (Gavazzi et al., Z. Pflanzenphysiol. 75:381-391). The results so far obtained on a group of 11 mutants can be summarized as follows: