

al., Proc. Natl. Acad. Sci. USA 94:7685-7690, 1997). Recent work in rice and wheat has found that *pbf1* does act as a transcriptional activator of storage proteins in vivo (Hwang et al., Plant Cell Physiol. 45:1509-1518, 2004). The association between *pbf1* and fruitcase weight could be a result of the role *pbf1* plays in the regulation of storage proteins. Although these associations seem biologically plausible given what is known, further work will be needed to validate that these genes do contribute to natural variation of fruitcase weight in teosinte.

Given the small percentage of associations found to be significant after correction for multiple-testing (< 0.2%), we hypothesize that there are many false negatives among our results. It is likely that our model, which was conservative in regard to controlling the false positive rate due to population structure, led to an increase in the number of false negative associations. We have made our datafiles available on <http://www.panzea.org>, as well as deposited seed from these and other teosinte populations with the U. S. Department of Agriculture North Central Regional Plant Introduction Station in Ames, Iowa, to encourage future teosinte association mapping studies which have the potential to detect genuine biological associations which were not detected in this study.

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Evidence of interaction between mutants of different *emp* genes

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The symbol *emp* (*empty pericarp*) refers to the phenotype of a group of defective kernel mutants with drastic reduction in endosperm tissue production. Here we report an analysis of the allelic relationship of nine *emp* mutants. They have different origins, thus representing independent mutational events. Originally

they were isolated in populations carrying an active *MuDR* or *Spm* and they all behave as single gene mutants. To establish their allelic relationship we made crosses of each mutant with the others. For each of the pairwise combinations of the nine mutants, pollen from 10-20 plants of a given mutant whose heterozygous condition was ascertained by selfing, was applied to the silks of plants representing the selfed progeny of +/-*emp* parents of a different *emp* isolate. The resulting ears were then scored for visual evidence of mutant segregation. If only wild-type seeds are observed in all ears produced by this cross, the two mutants are not considered to be allelic, whereas if some of the ears yield mutants in about one-quarter of the seeds this is taken as evidence of allelism. Wild-type seeds are then tested further in F2 and F3, the expectation being that ears should be recovered segregating 3 to 1 for the mutant, or not segregating in a 3 to 1 ratio. If the F2 obtained by selfing non-mutant plants of the F1 progeny includes ears segregating an excess of mutants (30-40%), this segregation value, approaching a 9 to 7 ratio, is taken as evidence of heterozygosity for two *emp* mutants in the parental F1 plant, thus defining two genes. The results of these tests, presented in Tables 1 and 2, are generally concordant in their conclusions. In two cases, however, where enough data have been collected, the results obtained in F1 and in F2/F3 lead to contrasting conclusions, i.e., one gene as inferred from the lack of complementation observed in F1, and two genes based on the observation of a segregation close to a 9 to 7 ratio, which is expected when the heterozygous *emp* F1 plants identify two genes.

These intriguing results seem to suggest an interaction between different *emp* mutants. Technically similar events are referred to in the literature as second site non-complementation (SSNC). There are 3 possible explanations for these events: interaction between two different mutant proteins leading to a toxic product, the mutant form of one protein sequestering the wild-type

Table 1. Results of the complementation test involving nine independently isolated *emp* mutants. + and - indicate complementation and non-complementation, respectively. Signs in parentheses refer to dubious results that need further validation.

♀↓	♂→	<i>emp4</i>	<i>emp8075</i>	<i>emp8077</i>	<i>emp8300</i>	<i>emp8376</i>	<i>emp8971</i>	<i>emp9106</i>	<i>empDAP3</i>	<i>emp9475</i>
<i>emp4</i>		-	+	+	+	+	+	+	+	-
<i>emp8075</i>			-	+	(-)	(-)	+	+	+	(-)
<i>emp8077</i>				-	+	+	+	-	+	+
<i>emp8300</i>					-	+	(-)	-	+	+
<i>emp8376</i>						-	+	+	(+)	+
<i>emp8971</i>							-	+	(+)	-
<i>emp9106</i>								-	+	+
<i>empDAP3</i>									-	+
<i>emp9475</i>										-

Table 2. Segregation in F2 and F3 of double mutants exhibiting non-complementation in the F1. Signs in parentheses refer to dubious results that need further validation.

Cross mode	Non complementation in F1 (# of ears)	Segregation > 30% in F2/F3 (# of ears)	Inferred number of genes from	
			F1	F2/F3
<i>emp4 x emp9475</i>	9/29	14/78	1	2
<i>emp8075 x emp8300</i>	1/22	6/27	(1)	2
<i>emp8075 x emp9475</i>	4/12	-	1	-
<i>emp8077 x emp9106</i>	14/28	4/35	1	(2)
<i>emp8300 x emp8971</i>	1/15	3/12	(2)	2
<i>emp8300 x emp9106</i>	9/29	5/36	1	2
<i>emp8376 x empDAP3</i>	(1)/13	2/18	2	2
<i>emp8971 x empDAP3</i>	2/20	0/6	1	1
<i>emp8971 x emp9475</i>	4/25	2/67	1	1

form of the other protein into an inactive complex, or combined haplo-insufficiency (Hawley and Gilliland, Genetics 174:5-15, 2006). We will test which of these possibilities applies to the cases reported here.

Desiccation tolerance of maize viviparous mutants

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In maize, desiccation tolerance is acquired by the embryo at a precise developmental stage between 20 and 25 DAP (days after pollination) and is probably related to the maturation process char-