2. An attempt to localize the lethal effects of A_1 deficiencies.

The lethality of the homozygous deficiencies $\underline{a\text{-}x_1}$ and $\underline{a\text{-}x_3}$ may be due to inviable endosperm and/or inviable embryo. Analysis of hypoploid endosperms and embryos produced by a pollen parent carrying the TB-3a translocation provides an opportunity to localize the lethal effects of Df $\underline{a\text{-}x_1}$ and Df $\underline{a\text{-}x_3}$. When, for example, an egg parent heterozygous for the $\underline{a\text{-}x_1}$ deficiency is crossed by a TB-3a pollen parent, the resulting hypoploid endosperm, $3(\underline{a\text{-}x_1})/3(\underline{a\text{-}x_1})/3^B$, is associated with hyperploid embryo, $3(\underline{a\text{-}x_1})/3^B/B3/B3$; and hyperploid endosperm, $3(\underline{a\text{-}x_1})/3(\underline{a\text{-}x_1})/3^B/B3/B3$, is associated with hypoploid embryo, $3(\underline{a\text{-}x_1})/3^B$.

In the studies reported here a single TB-3a pollen parent, hyperploid for the B^3 chromosome, was used as the TB-3a source. The following tables show the results of various crosses undertaken to study TB-3a hypoploid endosperm and embryo involving Df $\underline{a\text{-}x_1}$ and Df $\underline{a\text{-}x_3}$.

Table 1

Frequencies of endosperm types on four ears from the cross:

$3(a\ sh)/3(a\ sh) \times 3(a\ Sh)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$

	Endosperm phenotypes			
	A Sh	A sh	a Sh	a sh
Number of kernels	429	0	406	319
Frequency(%)	37.1	0	35.2	27.7

Table 2

Megaspore transmission of Df $\underline{a\text{-}x_1}$* in the cross:

$3(a\text{-}x_1)/3(A\ sh) \times 3(a\ sh)/3(a\ sh)$ (7 ears)

	Endosperm phenotypes	
	A sh	a sh
Number of kernels	1289	1380
Frequency(%)	48.3	51.7

*Df $\underline{a\text{-}x_1}$ and Df $\underline{a\text{-}x_3}$ are known to be deficient for both $\underline{A_1}$ and $\underline{Sh_2}$. Both are lethal to the sporophyte when homozygous. Hemizygotes with $\underline{a}$ and $\underline{sh}$ are viable and exhibit the recessive phenotypes.

Table 3

Frequencies of endosperm types on six ears from the cross:

$3(a\text{-}x_1)/3(A\ sh) \times 3(a\ Sh)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$

	Endosperm phenotypes			
	A Sh	A sh	a Sh	a sh
Number of kernels	1022	248	355	2
Frequency(%)	62.9	15.2	21.8	0.1
Expected frequency(%)*	54.1	13.4	18.2	14.3

*Calculated below from data on egg and pollen transmission in Tables 1 and 2:

$0.541 = 0.371 + (0.352 \times 0.483)$
$0.134 = 0.277 \times 0.483$
$0.182 = 0.352 \times 0.517$
$0.143 = 0.277 \times 0.517$

The two colorless, shrunken kernels registered in Table 3 have not been analyzed further. They represent either $3(\underline{a\text{-}x_1})/3(\underline{a\text{-}x_1})/3^B$ hypoploid endosperms, or $3(\underline{a\text{-}x_1})/3(\underline{a\text{-}x_1})/3(\underline{a}\ \underline{sh})$ endosperms resulting from contamination involving $\underline{a}\ \underline{sh}$ pollen. The frequency of colorless, shrunken kernels (hypoploid endosperms) involving Df $\underline{a\text{-}x_1}$ (Table 3, last column) is much lower than expected. Since kernels in this class should have hypoploid endosperms in which Df $\underline{a\text{-}x_1}$ is uncovered, but should possess hyperploid embryos in which the deficiency is not uncovered, the frequency of this class is expected to be normal if the lethal effect of this deficiency resides in the embryo but not in the endosperm. These results suggest, therefore, that Df $\underline{a\text{-}x_1}$ is lethal for endosperm tissue.

Kernels from the cross represented in Table 3 were not planted to study hypoploid plants, namely $3(\underline{a\text{-}x_1})/3^B$ and $3(\underline{A}\ \underline{sh})/3^B$. Instead, sample counts of normal and germless kernels were made on the assumption that even if the hypoploid embryo involving the deficiency is lethal, the associated hyperploid endosperm would develop normally resulting in a germless kernel. The results of this study are given in Table 4 where, for convenience, "Gm" refers to normal, and "gm" to germless kernels, as scored visually.

The increase in frequency of germless kernels when an egg parent heterozygous for the deficiency is crossed by the TB-3a pollen parent suggests that the hypoploid embryo involving the deficiency is inviable. It would appear then that Df $\underline{a\text{-}x_1}$ is lethal in the sporophyte as well as in the endosperm but that the lethal effect of such embryos does not extend to the associated hyperploid embryos.

Table 4

Sample counts of normal (Gm) and germless (gm) kernels from the indicated crosses.

Cross	Kernel phenotypes			
	A sh		a sh	
$3(a\text{-}x_1)/3(A\ sh) \times 3(a\ sh)/3(a\ sh)$	Gm	gm	Gm	gm
	181	0	179	0

$3(a\text{-}x_1)/3(A\ sh) \times 3(a\ Sh)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$

Kernel phenotypes							
A Sh		A sh		a Sh		a sh	
Gm	gm	Gm	gm	Gm	gm	Gm	gm
296	35	75	1	120	29	0	0

Analyses similar to those involving Df $\underline{a\text{-}x_1}$ were undertaken with Df $\underline{a\text{-}x_3}$. As Stadler and Roman pointed out, the latter deficiency is more drastic in its effects as it shows much reduced transmission through the female gametophyte and fails altogether to transmit through the male gametophyte. Essentially the same kind of analyses of Df $\underline{a\text{-}x_3}$ are presented in Tables 5 and 6 as are given for Df $\underline{a\text{-}x_1}$ in Tables 2 and 3.

Table 5

Megaspore transmission of Df $a\text{-}x_3$ in the cross:

$3(a\text{-}x_3)/3(A\ sh) \times 3(a\ sh)/3(a\ sh)$ (7 ears)

	Endosperm phenotypes	
	A sh	a sh
Number of kernels	1245	519
Frequency (%)	70.6	29.4

The absence of colorless, shrunken endosperms among the progeny of the cross in Table 6, where over 200 would be expected, indicates that $3(\underline{a\text{-}x_3})/3(\underline{a\text{-}x_3})/3^B$ hypoploid endosperm is inviable, and that Df $\underline{a\text{-}x_3}$, like Df $\underline{a\text{-}x_1}$, is lethal to endosperm tissue.

Table 6

Frequencies of endosperm types on 14 ears from the cross:

$3(a\text{-}x_3)/3(A\ sh) \times 3(a\ Sh)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$

	Endosperm phenotypes			
	A Sh	A sh	a Sh	a sh
Number of kernels	1732	552	223	0
Frequency(%)	69.1	22.0	8.9	0
Expected frequency(%)*	62.0	19.6	10.3	8.1

*Calculated below from data on egg and pollen transmission in Tables 1 and 5:

$0.620 = 0.371 + (0.352 \times 0.706)$
$0.196 = 0.277 \times 0.706$
$0.103 = 0.352 \times 0.294$
$0.081 = 0.277 \times 0.294$

Additional information on the viability of hypoploid endosperm and embryo involving Df $a\text{-}x_3$ is available from a different cross. Colorless, shrunken endosperms from the cross $3(a\text{-}x_3)/3(A\ Sh) \times 3(a\ sh)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$ are expected to be mainly $3(a\text{-}x_3)/3(a\text{-}x_3)/3(a\ sh)$ and $3(a\text{-}x_3)/3(a\text{-}x_3)/3^B$ in constitution. The former endosperm type should be associated with a $3(a\text{-}x_3)/3(a\ sh)$ sporophyte. The latter endosperm type, if viable, should be associated with a $3(a\text{-}x_3)/3^B/B^3(A\ Sh)/B^3(A\ Sh)$ sporophyte. These two types of sporophytes can be identified easily by crossing with $3(a\ sh)/3(a\ sh)$ plants. Nine out of twenty-nine colorless, shrunken kernels planted were analyzable. All nine individuals turned out to be $3(a\text{-}x_3)/3(a\ sh)$ plants, suggesting that the $3(a\text{-}x_3)/3(a\text{-}x_3)/3^B$ hypoploid endosperm is inviable. Purple, non-shrunken kernels from the same cross were also analyzed. Among sixty-three sporophytes tested, there were twenty-eight nonhypoploids, thirty-three $3(A\ sh)/3^B$ hypoploids and one unanalyzable hypoploid. No $3(a\text{-}x_3)/3^B$ hypoploid individuals were found. If no lethality is involved we expect (Table 5) 70.6% of the hypoploid sporophytes to be $3(A\ sh)/3^B$, and 29.4% to be $3(a\text{-}x_3)/3^B$ in constitution. The absence of the latter type of hypoploid sporophyte indicates that this constitution is inviable.

These data indicate that hypoploid endosperm and embryo involving the A_1 deficiencies are inviable, that is, that Df $a\text{-}x_1$ and Df $a\text{-}x_3$ are lethal to both the endosperm and the embryo.

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