simultaneously to the $\underline{Ht}_1$ gene (chromosome 2-121) and rust-resistant gene $\underline{Rp}_1$ (chromosome 10-0), from different sources. The Ht source, a conversion of Illinois sweet corn inbred 101t, is not aphid resistant. The Rp source, a hybrid of W22 x B14A, is the more probable origin of resistance.

Resistance is recessive in all crosses we have made, and segregates monogenically in the crosses evaluated to date. A preliminary gene designation is the symbol aph. The possibility of linkage to the $\underline{Rp}_1$ locus is suggested in one set of testcrosses, which segregated as follows: 43 resistant to both, 27 susceptible to both, 90 resistant only to rust and 80 resistant only to aphids.

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1. Mutations that restore fertility to S male-sterile maize.

Exceptional male-fertile plants arising from crosses involving S male-sterile shrunken-2 inbred lines and their corresponding isogenic maintainer lines are under continuing study. The majority of these male-fertile exceptions involve cytoplasmic "mutations" in that the male-fertile trait is not pollen transmissible (Genetics 71: 607, 1972). However, we have recently reported on four independently-occurring mutations which restore fertility in S sterile cytoplasm and are pollen transmissible (MGNL 47: 50, 1973, Theoret. Appl. Genetics 43: 109, 1973). Analyses of these four nuclear restorer mutations have continued and two additional cases have been identified and are also being characterized. These six changes arose in the same strains in which the numerous cases involving cytoplasmic "mutations" were identified. The mode of restoration observed for the six newly-arisen nuclear restorers is gametophytic, as it is with the standard S restorer $\underline{Rf}_3$, rather than sporophytic, which is characteristic of the T restorers $\underline{Rf}_1$ and $\underline{Rf}_2$.

We have examined the progeny of crosses designed to determine whether the six nuclear restorer genes, designated I through VI, are allelic with the standard S restorer gene of inbred line CE1. If a particular newly-arisen restorer gene in question is allelic with $\underline{Rf_3}$, crosses of plants carrying the new restorer gene in S cytoplasm with pollen from inbred line CE1 should produce some progeny with all normal pollen. Nonallelism, on the other hand, would be indicated by the presence of plants with 25% aborted pollen. On the basis of pollen analyses of these progeny, none of the six new restorer genes is allelic with $\underline{Rf_3}$. Testcross progeny from plants with 25% pollen abortion are now being grown to confirm this observation.

Studies were also carried out to determine whether the six nuclear restorer genes resulted from mutation of the same gene locus. Crosses were made between plants carrying the different new restorer genes in S sterile cytoplasm. Here again, allelism would be indicated by the occurrence of plants with all normal pollen and nonallelism by the occurrence of plants with 25% aborted grains. Of the 15 possible combinations involving the six new restorers, pollen checks of all but two combinations indicated that plants with 25% aborted pollen were present and thus that the restorer genes involved in these crosses are nonallelic. The two remaining combinations, II with V, and II with VI, were poorly represented in the test and are subject to further analysis. As in the cases involving the $\underline{Rf_3}$ hybrids, it is expected that progeny tests will confirm the suspected genotypes of plants with 25% pollen abortion.

Further indication of differences among the new restorer genes is apparent from a study of their patterns of fertility restoration in F_1 hybrids with various inbred line female parents carrying S male-sterile cytoplasm (Table 1). Restorers I and II are clearly different from restorers III through VI; they are distinguished from one another on the basis of their fertility restoration patterns in crosses with R853, WF9 and I153 S male-sterile inbred lines. Further tests are underway to obtain a more complete picture of the fertility restoration patterns of these new restorers.

In the process of preparing seed for the 1973 summer planting, reduced kernels were observed on many of the ears which also segregated

Table 1

Restoration patterns of six new S restorers. Testcross progeny indicated as F (male-fertile) or S (male-sterile).

cmsS inbred line female parent	Male parent restorer strain					
	I	II	III	IV	V	VI
R839	S	S	F	F	F	F
M825	F	F	F	F	F	F
R853	S	F	F	F		
WF9	F	S	F	F	F	F
K55	S	S		F	F	
M14	S	S	F	F		
I11A	S	S	F			F
N6	S	S	F	F	F	F
I153	S	F	F	F		F

for a new restorer gene. In fact, reduced kernels were found on ears segregating for each of the new restorer genes except restorer IV. This is of special interest because, of the six cases under discussion here, restorer IV is the only one in which the restorer mutation occurred in nonsterile cytoplasm. Reduced kernels from some of the ears were planted separately from the normal ones in order to determine whether the reduced kernel phenotype could be correlated with the presence of a new restorer gene. A positive correlation was found for restorers II, III and VI. Restorers I and V require further testing.

Through analyses of progeny of self pollinations, attempts have been made to obtain plants homozygous for each of the new restorer genes in sterile cytoplasm. These could be identified as plants, with all normal pollen, whose crosses with maintainer pollen yield all male-fertile progeny. Such plants have been identified for restorer IV only. The new restorer genes carried by strains II and III are apparently lethal when homozygous; the others require further tests. Again, restorer IV, the only one of the six that arose in nonsterile cytoplasm, is the only one, of those so far tested, that exhibits normal behavior.

As noted above, preliminary evidence strongly suggests that the new restorer genes I through VI are not allelic. Linkage characteristics of these restorers are currently being investigated using the waxy translocation series. We are encouraged to believe that what would ordinarily be a laborious procedure may be greatly simplified through the use of a technique designed to identify linkage relationships in the pollen system. A brief description of this technique is presented elsewhere in this report.

Our search for additional new restorer genes has led to the preliminary identification of six new cases, and these are currently under investigation.

So far we have not been able to distinguish between two alternatives for the origin of male-fertile exceptions in plants with S-type male-sterile cytoplasm. We assume they arise either as a result of a qualitative change in a cytoplasmic entity of S male-sterile cytoplasm, or as the result of occasional transfer of normal cytoplasm through the male germ cells of maintainer pollen parents. In any case, from what we now know it is clear that the male fertile exceptions involve either a change at the cytoplasmic level, which is most often the case, or a change in the nucleus. Because the two kinds of male-fertile exceptions have arisen in the same strains, and in both cases are expressed initially as either entirely male-fertile plants or as sterile-fertile chimeras, we consider them to have a common origin. According to this scheme the male-fertile element has the characteristics of an episome. If the latter is fixed in the cytoplasm, the newly arisen male-fertile behaves as a maintainer strain; if it is fixed in the nucleus it behaves as a restorer strain. This interpretation is supported by preliminary evidence indicating that none of the six newly-arisen restorers is allelic with standard Rf_3, and that all appear to be nonallelic with each other. The differential behavior of the six new restorers may be the result of qualitative differences in the integrated "episome" or of modulations in its message based on differences in integration sites in the chromosomes. We are currently searching for evidence of transposition of the male-fertile element from chromosome to cytoplasm, and vice versa. We are also undertaking an intensive analysis of male-

fertile chimeras when they first make their appearance. There is some indication that both cytoplasmic and nuclear fixations of the male-fertile element are involved in individual chimeras. If this is confirmed in more extensive studies it will add strong support to the episome hypothesis.

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2. Sensitivity of pollen with Texas group male-sterile cytoplasms to Helminthosporium maydis race T pathotoxin.

The reaction of maize pollen carrying T or P male-sterile cytoplasm to the presence of Helminthosporium maydis race T pathotoxin in the germination medium has been reported previously (MGCNL 47: 49, 1973; Crop Science 13: 681, 1973). Pollen germination and growth are inhibited in the presence of the race T pathotoxin. Smith et al. (Crop Science 11: 772, 1971) have reported that plants carrying T, P, Q or HA male-sterile cytoplasm are susceptible to H. maydis race T. These four cytoplasms are members of the Texas group of male-sterile cytoplasms (Beckett, Crop Science 11: 724, 1971). Gracen (Plant Disease Reptr. 55: 938, 1971) has reported that RS male-sterile cytoplasm, found at Cornell in 1967, is also susceptible to race T.

We have studied the reaction of pollen of these five susceptible male-sterile cytoplasms carried in the two inbred lines NY821LERf and AyX187Y-2, to the race T pathotoxin. These inbred lines, with normal cytoplasm, and their five restored Texas group male-sterile versions were kindly provided by Dr. V. E. Gracen. Concentrations of race T pathotoxin which allow normal growth of pollen grains from NY821LERf and AyX187Y-2 inbred lines with normal cytoplasm inhibit germination and growth of pollen grains from the T, P, Q, HA and RS restored male-sterile versions of these two lines.

The T, P, Q, HA and RS male-sterile cytoplasms were identified in different and, so far as we are aware, unrelated strains of maize, and each is associated with enhanced susceptibility to race T of H. maydis. As noted above, race T pathotoxin inhibits germination of pollen from plants carrying these sterile cytoplasms. This would seem to indicate that the susceptibility and the male sterility associated with these