THE PLEIOTROPIC EFFECTS AND INTERACTIONS OF ar RESPECTFULLY REVISITED

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I have long been captivated by two early, landmark papers by Hans and Olof Tedin which describe the remarkable multiple effects of the flower color gene ar (1,2). Because the effects produced by ar are similar in some respects to those conferred by am-1 and am-2, two genes which have also occupied my attention for some time, I decided in 1979 to analyze anew the abstruse and artful antics of ar.

The flowers of ar plants have a distinct blue hue in contrast with the purple violet flowers of the wild type. Like several other flower color mutants, ar exerts a pleiotropic effect on axil color (also blue). Mutant ar also interferes with the expression of oh, a seed gene which normally produces self-colored reddish brown seed if A is also present. Oddly, ar in combination with b (pink flowers and axils) results in very pale pink flowers (in my hands white or nearly white whether cultivated in the field or glasshouse). Thus, neither ar nor b is epistatic to the other with respect to flower color; instead, the two genes interact to yield nearly colorless flowers. Though flower color is quenched in ar b plants, axil color is only slightly less pink than in plants carrying b alone. A more noteworthy feature of ar, however, is its pleiotropic effect on seed structure. Specifically, the hilum of seeds from ar plants is reduced to a narrow slit and the tracheid bundle (or bar) disappears. But with the introduction of the recessive seed gene, z, the hilum is restored to normal, without, incidentally, influencing flower or axil color. This suite of effects, involving site specificity, pleiotropy and interaction, provides a potentially powerful model for studies of gene regulation and expression. Moreover, as indicated above, the parallels between the ar b z system and the am-1, am-2, b system led me to acquaint myself with the former and, while gaining firsthand experience, to develop a series of desirable, genetically defined lines for use in further work.

WL 25[1/], the type line for ar, was used as a parent in the initial crosses made in 1979. Unfortunate1y , WL-25 is not only tall and late, but also shows poor pod and seed set . Although other more "friendly" ar lines were available in my collection, I wished to remove any doubt that the starting material was indeed ar. WL-25 also carries oh, the expression of which, due to the presence of ar, is partially inhibited. WL-25 was crossed with, my line C879-348 (le A Ar oh Cry st La B). The F1's and subsequent progenies from these crosses were characterized by extensive semi-steri1ity or complete sterility. Because of this, no meaningful data could he collected and therefore no details will be given, except to say that a progeny test oi one F2 segregant yielded an F3 progeny containing eight St plants and 73 st plants. Rigorous selection was practiced but it was not until the F_7 that a fully fertile, dwarf line carrying ar, oh, and B was isolated. Even so, the seeds in this line exhibited somewhat impaired development presumably owing to the effect of ar on the hilum structure of the seeds. Meanwhile, however, descendants from the original cross, starting with the F3, were used in new crosses with a series of other lines. Certain segregants from these second-order crosses were used in turn as parents in third-order crosses, so to date some 70 crosses and over 700 progenies have been grown and evaluated.

[1/] Seeds kindly supplied by Dr. Blixt. •

My observations agree in nearly all respects with those of H. and O. Tedin, but some details remain to be settled. A modest addition to their findings can be mentioned: in addition to z, genes a and b also restore normal hilum structure in ar plants. I have also introduced wa, a marker for genes ar and oh, and n and was, markers for z, into the system. Importantly, the material now at hand is "tamed", being represented by fertile dwarf lines which are easy to cultivate and in which the gene expressions are clear. A number of the lines are near isogenic for one or more relevant genes and thus are particularly favorable for demonstrating gene action and interaction. Finally, the material is well suited as parents for new crosses with genes in the am-1 and am-2 system, a project which is now underway.

1. Tedin, H. 1920. Hereditas 1:68-97.
2. Tedin, Hans and Tedin, Olof. 1928. Hereditas 11:1-62.

LINKAGE RELATIONSHIPS AMONG MARKERS IN CHROMOSOME 3 AND En, A GENE CONFERRING VIRUS RESISTANCE

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Two excellent seedling markers, apu and tac, recently were reported to be situated in chromosome 3, linked with st (4). The data did not reveal, however, if apu and tac lie towards the b or the M end of the chromosome, so new linkage tests were performed using b as an additional marker. F2 populations from the following crosses were scored in the field in 1984 (only the relevant genes being listed):

A B_ St apu Tac x A b st Apu tac (and reciprocal)
a B St apu tac x b st Apu Tac
a B St apu tac x A b st Apu Tac

The analysis (Table 1) confirms the placement of apu and tac in chromosome 3 and localizes tac in the M end of the chromosome. Although the orientation of apu is somewhat unclear from these data, the overall body of evidence indicates that apu also lies on the M side of st.

These findings, together with results from previous studies of chromosome 3 (2, 3), make it evident that suitable seedling markers are favorably spaced over nearly the entire length of the chromosome. This set the stage for three further linkage tests conducted in the greenhouse in the fall of 1984. They were designed to establish the relationships among morphological markers, certain isozyme markers, and the gene En conferring resistance to pea enation mosaic virus (PEMV).

Initially we determined the relationship between three morphological markers, st, apu, and tac, and two isozyme markers, Lap-2 and Aat-c (Table 2). Gel electrophoresis was performed using methods previously described (5). Linkage between Aat-c and Lap-2 is evident. Moreover, both isozyme markers showed linkage with tac and both evidently lie distal to tac.