A THREE-POINT LINKAGE ANALYSIS INVOLVING Am-1 — A f - ~ I

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This article adds to the unfolding account of the am-1 and am-2 genes and their associated seed disorders (6,7,8). With respect to flower and axil color, both genes exert seemingly an identical effect. Moreover, plants that are homozygous recessive for both am-1 and am-2 cannot be distinguished, on the basis of flower phenotype, from plants that carry either gene alone. However, the two genes may be distinguished one from another on the basis of the seed disorder with which each is peculiarly associated. They may also be distinguished by their linkage relations, although thus far only am-1 has been mapped. The linkage relations of am-1 are considered here.

All four of the loci relevant to this discussion, viz. A, Af, I, Am-1 . are known to reside in chromosome 1, but _ is widely separated from the other three. Am-1, discovered by de Haan (1), was found by Wellensiek (10) to be linked with I at a map distance of about 26 units. Lamprecht (4) confirmed the linkage but found widely varying crossover values, ranging from a low of 9% to a high of 48%. Still, the mean of all his crosses (28*) was close to that reported by Wellensiek. Linkage values between.Af and X were reported by Khangildin (3), Snoad (9), and Kielpinski (2) to be 45, 14, and 8 percent, respectively. Finally, Marx (5) reported a relatively tight linkage between _f and Am-1 (7-8%). Together, the foregoing two-point tests suggest the following order and approximate map distances:

Am-1 8 Af 10 I

Apparently this is the first report of a three-point cross involving the above loci. Reciprocal crosses were made between two lines with the following genotypes:

P1 a af i Am-1
P2 A Af I am-1 (sd-1)

F2 plants, 250 in all, were grown and scored in the greenhouse. Additional seeds from the same cross will be planted in the field in the summer of 1983, but the essence of the experiment is already revealed in the F2 data presented in Table 1. Moreover, there is usually less chance of misclassifying the yellow (I/-) vs. green (i/i) cotyledon difference in greenhouse-grown plants than in field-grown plants where the seeds often are subject to bleaching.

Two of the segregating traits in F2 could be discerned prior to flowering, viz. foliar architecture (Af vs. af) and axil color. Axils were either purple-violet (A Am-1). pink (A am-1), or colorless (a). No af am-1 F2 recombinants were recovered because the two genes were linked in repulsion and apparently there were too few plants to reveal crossovers. Since approximately one fourth of the population was recessive for a. and since the Am-1 locus is hypostatic to a, segregation for Am-1-am-1 could not he observed in a. plants, at least not directly.

At flowering, two classes of flower color could be distinguished: Purple-violet (A Am-1) and white (A am-1, and a). These two phenotypes were expected in an approximate ratio of 9 colored to 7 white. The observed ratio of 125:125 yielded a Chi-square value of 3.97 (1 d.f.), a value which is significant at 0.05 but not at 0.001.

All A. am-1 segregants exhibited the seed disorder and all such plants were homozygous for I (I/I)None of the a I/I segregants exhibited a seed disorder, yet, because of the close linkage between I and am-1, all or nearly all of the a. I/I segregants would be expected to be am-1. This, then, is a way to identify am-1 plants in an a. background and shows that expression of the seed disorder is blocked in a. plants. These results confirm progeny test results of A/a. am-1/am-1 sd-1 plants presented earlier (8). Thus a is epistatic to am-1 not only with respect to the flower color phenotype, but also with respect to the associated seed disorder. In contrast, b is hypostatic to am-1 and/or am-2 with respect to flower color (i.e. am-1 b and am-2 b. flowers are white) but epistatic to am-1 and/or am-2 with respect to their associated seed disorders. B-b_ did not segregate in the present crosses. This was predictable on the basis that the seeds of the am-1 parent exhibited the seed disorder and b. is thought to mask the expression of seed disorder in am-1 plants just as it does in am-2 plants.

Because of the way this cross was constituted, the linkage relations among Am-1 --Af--I allow one to use the seed phenotype of one generation to reliably indicate the plant genotype of the ensuing generation. Thus, i/i F3 seeds (either A or a) can be expected to produce af F3 plants without the seed disorder. I/I seeds with A will produce Af am-1 plants with the seed disorder and I/I seeds with a will produce Af am-1 plants without the seed disorder. Heterozygous I/i (A/-) can be used as a continuing source of segregating genotypes and as aid in developing isogenic lines. The confidence that can be placed in these predictions is, of course, a function of the intensity of the linkages. In the present cross the probability of being correct is high because the observed linkage intensity between Am and I was considerably stronger than that reported previously. The af-i linkage gave an estimated recombination fraction of 3.7 + 1.2. Linkage chi-square for A vs. Af and I was non-significant.

Since my original source of am-1 (L-3 from Dr. Lamm) exhibited fair to poor seed set, I have selected for fully fertile, productive am-1 plants in order to be sure that the seed disorder is the direct, pleiotropic effect of am-1 and not the result of some other cause. Moreover, Lamprecht (4) suggested that am-1 plants were weaker than Am-1 plants, a suggestion I have not. been able to confirm. I now have fully fertile, productive am-1 lines which, as was the case in the populations discussed herein, give fully fertile F2 segregants in crosses.

The am-1 line used as a parent in the present crosses showed a strong expression of the seed disorder in the greenhouse but when grown in the field expression was considerably diminished. Upon return to the greenhouse expression of this line was again strong, as was the expression in all the A am-1 F2 segregants derived from the cross with the above line. Thus, the seea disorder phase of am-1 expression is influenced to some degree by the growth environment. What component(s) of the environment that may operate to effect these differences in expression remains unknown. Soil pH is one possibility.

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PLANT STATURE AS AFFECTED BY THE INTERACTION OF na AND le la cry^{c}

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Indirect evidence obtained in 1981 and 19 82 (1,2) indicated that the extreme dwarfing effect of _a is counteracted when na is combined with la cry^{c} (and presumably la. cry^{s}). Thus, when na. is present together with La and/or Cry, the plants are nana in phenotype, but when na is combined with la cry^{c} the plants are cryptodwarf. In effect, na is hypostatic to le la cry^{c}. This article offers direct confirmatory evidence favoring this hypothesis.

Seeds from 29 individual na wlo F2 segregants from entries C281-308 and C281-309 [see (2)] were planted in greenhouse flats filled with quartz sand and the resulting seedlings were scored for the marker wlo and for plant stature. The na and WL 1329 parents were included as controls. If the epistatic effect of na is overridden in an le. la cry^{c} background and if, as the F2 data showed, the cry^{c} allele segregated in F2, then it follows that some of na wlo F2 segregants should segregate for cryptodwarf plants. The progeny tests Bear this out. Nineteen of 29 F3 progenies tested had one or more cryptodwarf plants (Table 1), very close to the expected 2:1 ratio. Collectively, the segregating progenies contained 197 nana plants and 53 cryptodwarfs. All ratios must, of course, be interpreted in the light of the small size of the individual progenies. All plants manifested the wlo phenotype, thus verifying the classification for that gene in the F2 populations.

The F2 and F3 data together demonstrate that na is masked (at least in a gross morphological sense) in the presence of la. cry^{c}. By extension, the effect of na is modified by the dosage of alleles at La and Cry. Hence, some of the F2 and F3 segregants that fit the description of "compactum" may be the product of this gene interaction. In effect, the action of na is partially overcome in certain gene combinations.