INFLUENCE OF NON-ALLELIC INTERACTIONS ON THE PHENOTYPE OF na

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A preliminary experiment was conducted to study the linkage relations and interactions of nana (na) and microdwarf (lm), two genes known to reside in chromosome 6 (1,5,6). The na. parent derived from the na mutant isolated at Geneva (2); it also carried other chromosome 6 markers, viz. Arg. Pl, and wlo. WL 1329, obtained from Dr. Blixt, was used as a source of lm. In Blixt's inventory WL 1329, besiges being identified as lm, is listed in the "genotype" category as cry^{s}, but in the "origin" category as "microcryptodwarf". Unlike the na parent, WL 1329 is arg pl and Wlo. Thus the known or presumed genotypes of the two parents were:

(a) na wlo Arg Pl Lm le
(b) Na Wlo arg pl lm le

The populations also segregated and were scored for genes which were not relevant to the study, and, except to say that the genes segregated according to expectation, they will not be considered further. Each of two F_2 populations examined descended from an individual plant grown in the field. The two parents, additional F1 plants, and F2 populations then were planted at the same time and grown in the same glasshouse where they were fully classified and measured for internode length. Nodes to flower were also recorded. A four-point linkage analysis of Arg-Pl-Wlo-Na was performed on the combined populations and is presented in the following article. Arg or Pl are not immediately relevant to this article.

All F1's were classified as dwarf. The individual and combined F_2 distributions (Table 1) reaffirm the known linkage between na. and wlo. but the estimate of linkage intensity (10.8 ± 2.2) was somewhat higher than other estimates (2,3). The distributions do, in fact, appear disturbed, the Na wlo class being noticeably larger than the na Wlo class. Despite this, segregations for either gene in the individual and combined F2 populations were statistically not significantly different from expected.

Table 1. Joint segregation of phenotypes in two coupling-phase crosses involving na and wlo. The na wlo parent was a Geneva isolate; the Na Wlo parent was WL 1329.

A.	Na Wlo	Na wlo	na Wlo	na wlo	Total	Chi-squares Na (3:1)	Chi-squares Wlo (3:1)	Chi-squares Linkage	Recomb. fract.
C281-308	85	11	3	18	117	3.10	0.00		
309	68	10	2	23	103	0.03	2.72		
	153	21	5	41	220	1.96	1.19	99.56	10.2 ± 2.2

B.	Wlo Not long	Wlo "long"	wlo Not long	wlo "long"	Total	Chi-squares "Long" (3:1)	Chi-squares Wlo (3:1)	Linkage
C281-308	69	19	22	7	117	0.48	0.00	
309	51	19	23	10	103	0.55	2.72	
	120	38	45	17	220	0.00	1.19 n.s.	

The data suggest that the numerical imbalance of phenotypes might be explained by something other than chance or misclassification. Part B of Table 1 gives the Joint distribution between the Wlo-wlo locus and a phenotype designated "long". This designation is used to characterize F2 segregants that resembled the internode length and total height of plants of the WL 1329 parent. This, and the two other phenotypic classes (dwarf and nana). were determined visually and by measurement (Table 2). There were a total of 55 "long" plants in the combined F_2 populations, the number expeoted for a perfect 3:1. Thus "long" was inherited as a recessive character. Of the 55 "long" plants, 38 were associated with Wlo and 17 with wlo. indicating that "long" and wlo were independently inherited (linkage chi-square = 0.12[n.s.]).

Now, (a) since .na. is known to be rather tightly linked with wlo (2), and (b) since there were 17 "long" plants with wlo (too many to be considered as crossover products), it may be reasonable to suppose that the 17 "long" wlo plants carried na. but that the nana phenotype'was masked by the "long" phenotype. Therefore, by subtracting 17 (the "long" wlo segregants) from the Na wlo class in Table 1 A (21-17=4) and transferring them to the na wlo class (41+17=58), we are left with a distribution which shows the expected balance among the phenotypes. The adjusted distribution becomes 153:4:5:58 for the Na Wlo. Na wlo, na Wlo. na wlo classes, respectively. This produces an estimated recombination percentage of 4% between na and wlo. a figure which is consistent with estimates obtained in other crosses (2,3). Of course, this Juggling of the data would be highly inappropriate were it not for the known tight linkage between na and wlo.

On the basis of these assumptions, i.e. that na is hypostatic to "long" and that "long" is not linked with na, what then is the genie basis for the phenotype designated "long"? Although parental line WL 1329 is represented as carrying cry , its phenotype more closely resembles cryptodwarf (la cry) than it does "slender" (la cry). Moreover, the phenotype of the "long" F_2 plants closely approximated the phenotype of the parental WL 1329 plants (Table 2). There were no slender segregants. It would seem therefore that WL 1329 is cry rather than crv and that the genotype as given in Blixt's inventory is a typographical error. Even so, the presence of cryptodwarfs in F_2 implies that the na parent as well as WL 1329 were homozygous for la and that the Cry-cry alleles segregated in F2.

Still, WL 1329 is described as "microcryptodwarf", not as cryptodwarf, so we have yet to account for the purported presence of lm. a factor for internode shortening. But since the parental and F2 "long" plants resemble each other and both resemble ordinary cryptodwarrs, then it is appropriate to ask: where is lm? The F_2 populations give little hint of a segregation for this gene. However, many or most "long" plants had weak, thin stems and frequently the Initial shoot aborted at emergence and was replaced by a second shoot. Since Lindqvist (1) found 1m to be closely linked with wlo. there should have been evidence of repulsion phase linkage between wlo and la in the present crosses. None was detected.

Table 2. Mean length (cm) of each of the first five internodes, their sum, and the accumulated length of first nine internodes in parental lines and in the F_1's and F_2's of crosses of parental lines. F_2 populations are separated by cross and by length phenotype (dwarf, "long", and nana)

Population	Internode number[1] 1	2	3	4	5	Total	Sum of first nine internodes[2]	N
WL-1329 (P_1)	3.6	2.9	3.0	2.5	3.0	15.0	46.9	5
Nana (P_2)	1.3	0.9	1.1	1.4	1.6	6.2	16.5	7
WL-1329 x Nana (F_1)	1.6	1.5	2.3	3.0	4.1	12.5	44.2	21
Dwarf F_2 C281-308	1.6	1.6	2.1	3.0	3.8	12.1	49.7	70
309	1.5	1.4	2.1	2.8	3.5	11.4	45.8	49
"Long" F_2 C281-308	3.6	3.1	3.9	4.8	6.3	21.7	66.4	26
309	3.3	3.0	3.6	4.3	5.2	19.5	57.1	29
Nana F_2 C281-308	1.5	1.2	1.3	1.5	1.8	7.4	21.0	21
309	1.3	1.1	1.2	1.3	1.5	6.4	18.2	25

[1] Internode number based on second trifid bract counted as node 1. Thus length of internoce 1 is the distance (cm) between second trifid bract and first true leaf, internode 2 is the distance between first true leaf and second true leaf, etc.

[2] Total distance (cm) between node bearing the second trifid bract (node 1) and node 10.

The conclusion that cryptodwarf is epistatic to na is consistent with other observations which indicate that the na phenotype is subject to modification by genes at other loci (2). If this hypothesis is correct, then the ascending order of height for na plants is assumed to be: na La Cry, na La cry^c na La cry^s, na la Cry, na 1a cry^c, and na la. cry^s. Presumably, the presence of na cannot be visually detected in certain of the forgoing gene combinations. Since Wellensiek's na is extremely short, possibly it is Le na La Cry. It cannot be excluded, however, that Le itself shortens na. Obviously, the evidence developed in this experiment is not in accord with the assumption that WL 1329 carries Lm. If its presence was obscured by gene interactions and hence merely not detected, then perhaps a cross between WL 1329 and a known cryptodwarf would reveal its presence. It would be important that the two lines would have the same or similar flowering genotype since internode length is influenced by time and node of flowering.

We are left with the interesting proposition that La is dominant to le., that na is epistatic to Le and to le (4), but that na is hypostatic to combinations of le, la, cry^c and cry^s. As such this scheme is rife with implications in physiological genetics. For example, what is the phenotype of plants with the genotype Le. na la cry^s ?

1. Lindqvist, K. 1951. Hereditas 37:389-420.
2. Marx, G. A. 1981. PNL 13:35-37.
3. Marx, G. A. 1982. PNL 14:50-52.
4. Murfet, I. C. 1978. PNL 10:54-55.
5. Rasmusson, J. 1938. Hereditas 24:231-257.
6. Wellensiek, S. J. 1972. PNL 4:60.