Inheritance of phenotypic plasticity in soft chess, *Bromus mollis* L. (Gramineae)

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Summary. Phenotypic plasticity, measured by the phenotypic variation of a genotype living under diverse environments, was shown to be under genetic control in annual grass, *Bromus mollis*. Genetic polymorphism and phenotypic plasticity appear to be alternative strategies of adaptation in plant populations.

The role of phenotypic plasticity in plant adaptation is widely recognized on the basis of a large number of observations: large phenotypic variation of an inbred or apomictic species, response of single plants and plant organs to heterogeneous environments, variations under density stress, modifiability of breeding system, and so on. Phenotypic plasticity, as opposed to developmental stability or homeostasis, is generally defined in terms of increased variation in quantitative traits expressed under a set of different environments (e.g. levels of moisture, fertilizer treatments, intensity of competition). In a variance partitioning model, this increase relates to the environmental and genotype-environment interaction terms. 3 questions must be answered in order to understand its evolutionary significance: 1. How is phenotypic plasticity related to the fitness of an individual? A simple operational criterion would be to measure the adaptive role of plasticity in terms of the range of environments under which a genotype can successfully complete its life cycle (survive and reproduce). 2. Would plastic responses in adaptation often be trait-specific and environment-specific? In a lucid review, Bradshaw[1] summarized evidence on this point; the answer is yes. In other words, a scramble of randomly chosen characters observed under a random set of environments would not yield any adaptive patterns in the phenotypic responses. 3. Is phenotypic plasticity inherited and do populations have genetic variance for plasticity upon which natural selection can act? This is particularly important now, since several adaptive strategy arguments suggest that genetic polymorphism and plasticity might be alternative ways to adapt to heterogeneous environments. Evolution of plasticity in certain inbreeding and colonizing plants is tempting to support such arguments[2,3]. Bradshaw[1] noted that genetics of plasticity is in need of much research. This study of variation in an annual grass, *Bromus mollis* L., reports an approach to the genetic studies of plasticity for quantitative variation.

Materials and methods. Genetic variation in 53 populations of *Bromus mollis* was described earlier by Moraes[4], using allozyme loci and a lemma hairiness locus. He had also grown 24 families from each of 8 populations to estimate the between-families (CV_b) and within-families (CV_w) components of quantitative variation. These 192 families were grown again in 1975 to score flowering time and other reproductive traits under 8 different environments (sandy loam vs. clay loam soils; 2 levels of fertilizer application; 2 photoperiods, 8 h and 12 h). Seed of each family was harvested separately. 20 families from each of 2 populations with low vs. high estimates of amounts of genetic variation, as measured by allozyme markers and between-families variance, were grown in 1976 (referred to as 'progeny' generation) under the same set of 8 environments and scored for quantitative variation. Regression of rank-ordered CV_w in progeny on the parental values measured the heritability of phenotypic plasticity.

Results and discussion. The table gives the estimates of polymorphism index[4,6] derived from frequency data at 11 loci, between-families variation (CV_b), and within-families variation (CV_w) for 8 populations and 3 characters. The first 2 are independent measures of genetic variation; estimates of CV_b and CV_w are largely measures of genetic and nongenetic components, since this species is highly selfpollinating and populations are highly homozygous (mean heterozygosity levels per locus less than 0.05). The distribution of CV_w values for 192 families as shown for 2 characters in figure 1 suggests a wide range of phenotypic responses of individual genotypes to their nursery environments. Time to flowering and panicle length are directly correlated with the relative reproductive rates and therefore measure adaptive responses. 2 populations (Nos 2 and 6 in the table), chosen for the lowest and highest levels of genetic polymorphism, provided estimates of CV_w in their

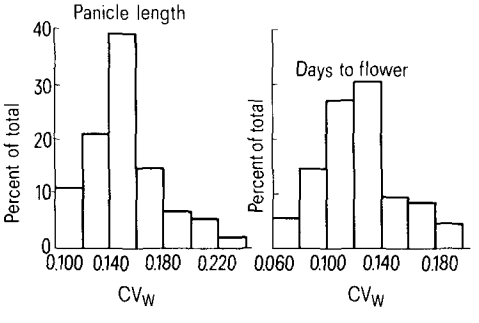

Fig. 1. Histograms showing the frequency distribution of CV_w (within-families coefficient of variation) in 192 families.

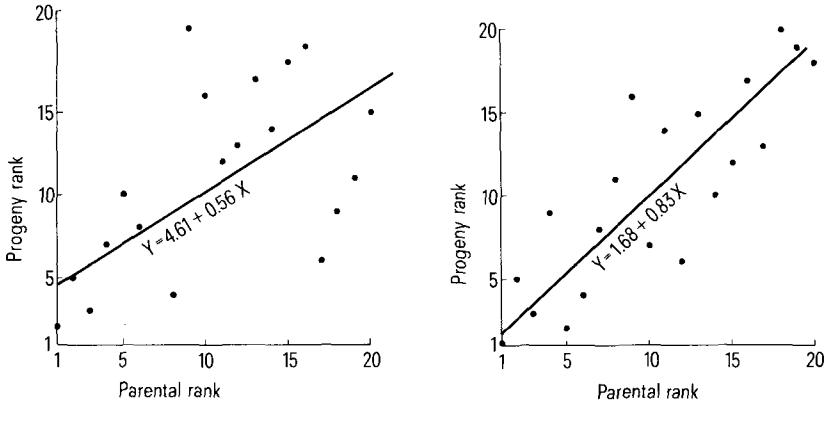

Fig. 2. Regression of CV_w in progeny on the parental values of CV_w, for days to flowering and based on 20 families drawn from population No. 2 (low genetic variation; ○, left) and No. 6 (high genetic variation; △, right). The estimates of CV_w are plotted by their rank orders.

Estimates of between- and within-family components of variation

Population	PI*	Culm height**		Panicle length**		Days to flowering	
		CV_b	CV_w	CV_b	CV_w	CV_b	CV_w
1	0.108	0.120	0.115	0.139	0.158	0.168	0.106
2	0.006	0.201	0.130	0.116	0.145	0.102	0.098
3	0.038	0.127	0.104	0.108	0.123	0.140	0.123
4	0.124	0.148	0.127	0.108	0.147	0.216	0.116
5	0.098	0.192	0.129	0.114	0.126	0.155	0.174
6	0.243	0.239	0.123	0.130	0.129	0.227	0.084
7	0.080	0.139	0.157	0.143	0.184	0.140	0.091
8	0.177	0.145	0.134	0.109	0.155	0.165	0.128
	Correlation coefficient (r)	0.08		0.59		−0.12	

* PI = polymorphism index based on allozyme variation at a total of 10 esterase and cathodal peroxidase loci and a locus for lemma hairiness. ** Data of Moraes[4].

progeny generation (1976). Rank orders of progeny CV_w are plotted against the rank orders in the parental generation (1975) for flowering time (figure 2). Estimates of regression coefficients were $b = 0.56 \pm 0.18$ (pop. 2) and 0.83 ± 0.14 (pop. 6). Both values of b are significant, suggesting a significant genetic determination of phenotypic plasticity in flowering time. Similar results were obtained for panicle length but regression coefficients for culm height were nonsignificant ($p > 0.10$).

Observations of greater genotype-specific plasticity in species with lower genetic variability were made earlier in 2 different genera of Gramineae: *Avena*[5,6] and *Bromus*[7], and in *Limnanthes*[8] (Limnanthaceae). In each case, a pair of congeners seemed to have alternative strategies of adaptation. Baker[3] had also provided a few such examples in weedy and nonweedy pairs of congeneric species. Both theoretical and experimental analyses of these examples in terms of natural selection for plasticity would be of considerable interest in plant evolution.

Inheritance of phenotypic plasticity is widely implied in the discussions of its evolution. It needs to be demonstrated and measured by appropriate experimental designs in quantitative genetics. Such experiments are likely to be difficult in ascertaining the control of environments, choice of characters, and interpretation of adaptive significance of nongenetic variation, but results of this study show that these are not unsurmountable problems.

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Larval necrophagy and photopigment phenocopying in *Musca domestica* (L.)[1]

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Summary. The intensity of photopigment modification in green-eyed house flies increased with increasing larval density and the relative frequency of +-type larvae. Phenocopying in these precursor deficient mutants resulted from the consumption of their dead 3rd instar +-type sibs.

The manipulation of insect photopigment expression in mutant strains by the transplantation of imaginal discs, the injection of body fluids or extracts, the feeding of pupae or adults, as well as the feeding of specific chemical precursors has been well-documented[3]. In *Drosophila* no modifications were induced by feeding or injecting photopigment deficient mutants with other mutant or +/+-larvae, and only boiled pupae containing the necessary precursors produced phenocopying[4]. While examining photopigment development in several Diptera species, Ward and Hammen[5] reported 'pink intermediates' among green-eyed house flies where the extent of modification was dependent upon the density and relative frequency of genotypes in the medium. This gn/gn-mutant accumulated tryptophan indicating a block in the first step of ommochrome synthesis: the oxidation of tryptophan to formyl-l-kynurenine. Their explanation was that the observed phenotypic variation resulted from +/+-larval excretory products contaminating the medium thereby conferring the necessary precursors to the mutants. The present observations of a gn/gn-strain[6] likewise produced offspring from hybrid and test crosses with phenotypes ranging from typical 'green' through several blends to a light red eye color. Genotypic ratios for these crosses approached the expected values when all eye

Table 1. Summary of simulated genetic crosses producing eye pigment modifications as a function of frequency and density dependence

Simulation	Initial density (+/+ : gn/gn)	Percent surviving +/+	Percent surviving gn/gn	Pigmentation index
$F_1 \times F_1$	30:10 (6)	43.3	40.0	1.13
	60:20 (6)	41.9	46.7	1.38
	120:40 (6)	35.8	40.8	1.58
+/gn × gn/gn	20:20 (4)	42.5	41.3	1.00
	40:40 (5)	37.0	35.0	1.19
	80:80 (5)	43.8	44.5	1.24

Vials were established with newly eclosed +/+- and gn/gn-larvae in the expected ratios from selfed F_1 and test crosses. Number of replicates is given in parentheses.