

EFFECTS OF PLANT MORPHOLOGY AND EMERGENCE TIME ON SIZE HIERARCHY FORMATION IN EXPERIMENTAL POPULATIONS OF TWO VARIETIES OF CULTIVATED PEAS (*PISUM SATIVUM*)¹

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ABSTRACT

The effects of plant form and emergence time on size hierarchy formation in populations of two morphologically and genetically distinct varieties of peas (leafless and leafed) were studied. There were no significant differences in germinability between the two varieties, although leafless peas imbibed more rapidly than the leafed ones did. Monocultures of leafed and leafless peas were established at two densities: plants grown alone in small pots and plants grown at 576 m⁻². Time emergence was noted, and plant shape, biomass and seed production were measured at two-week intervals for ten weeks. Seedlings emerged continually over an eight-day period, and two cohorts of seedlings were distinguished (seedlings emerging 6-7 days after planting, and seedlings emerging > 7 days after planting). Dominance and suppression were observed in the high-density populations, and early-emerging plants had less hierarchical biomass distributions than did late-emerging ones. Although leafless peas were larger and suffered less mortality than leafed ones did at identical densities, there were no differences in the degree of size inequality between the two genotypes (emergence cohorts pooled), or within emergence cohorts between genotypes. The degree of size inequality increased with time among dominant individuals and decreased with time among suppressed individuals. These results broadly support Weiner and Thomas's (1986) hypothesis that plant form may affect the extent but not the existence of competitive asymmetry in plant populations.

THE PURSUIT of causal mechanisms that generate unequal size distributions ("size hierarchies") in plant monocultures has been a recurrent theme in plant population biology over the last thirty years (e.g., Koyama and Kira, 1956; Ford, 1975; Harper, 1977; Rabinowitz, 1979; Gates, 1982; Turner and Rabinowitz, 1983; Hara, 1984, 1986a, b; Weiner, 1985; Benjamin and Hardwick, 1986; Weiner and Thomas, 1986; Ellison, 1987a). Two hypoth-

eses that explain the genesis of size hierarchies in dense monocultures have been proposed: the dominance and suppression hypothesis, and the growth rate hypothesis (reviewed in Turner and Rabinowitz, 1983; Weiner and Thomas, 1986). Briefly, if dominance and suppression are occurring, then size distributions of individuals in dense, competing stands should be more hierarchical (*sensu* Weiner and Solbrig, 1984) than size distributions of noncompeting individuals. If, on the other hand, intrinsic differences in plant growth rate alone generate observed size hierarchies, there should be no difference between the degree of inequality among individuals of equal size in competing and noncompeting stands. While these two hypotheses are often considered to be mutually exclusive because each has a different predicted outcome (e.g., Turner and Rabinowitz, 1983), it is likely that growth rate and competitive effects interact to produce observed variation in plant sizes (Benjamin and Hardwick, 1986; Ellison, 1987a).

To date, of the dozens of studies that explicitly have examined hierarchy development in plant populations (reviewed in Benjamin and Hardwick, 1986; Ellison, 1986; Weiner and Thomas, 1986), only two have supported the growth rate hypothesis. Turner and Rabinowitz (1983) found no differences in the

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degree of inequality between competing and noncompeting populations of red fescue (*Festuca rubra*). Ellison (1987a) obtained similar results in populations of the succulent glasswort (*Salicornia europaea*) grown at densities ranging from 10 to 10,000 plants m^{-2} . Turner and Rabinowitz's (1983) study has been criticized because their populations were followed only for 44 days and may not have reached a size where competition for light was occurring (Weiner and Thomas, 1986). Ellison (1987a) followed his populations through seed set, however, and concluded that dominance and suppression were not occurring in glasswort stands, although competition for light does occur in these populations and affects plant growth rate (Ellison, 1987a; Ellison and Niklas, 1988).

Fescue and glasswort (in dense stands) have upright, unbranched morphologies. Lonsdale and Watkinson (1983), Ellison (1986, 1987a), and Weller (1987) presented some evidence that plant form can affect patterns of density-dependent mortality (self-thinning). However, less attention has been paid to the effects of morphology on size hierarchy formation. Ellison (1987a) surmised that growth form alone could determine the existence of dominance and suppression. Weiner and Thomas (1986), however, argued that "growth form cannot prevent dominance and suppression from occurring when plant size and density make light a limiting factor. Growth form may affect the extent, but not the existence, of the asymmetry." Studies such as Ellison's (1987a), Turner and Rabinowitz's (1983), and those reviewed by Benjamin and Hardwick (1986) and Weiner and Thomas (1986) may not be strictly comparable because the different species used may have very different requirements for growth and varying responses to experimental conditions that differ from experiment to experiment.

Size hierarchy development normally is examined in even-aged stands. In studies explicitly designed to examine size hierarchy development in herbaceous species, however, synchronous emergence has been used to describe emergence occurring over as few as three days (Mithen, Harper, and Weiner, 1985; Schmitt, Ehrhardt, and Cheo, 1986) to as many as 80 days (Matlack and Harper, 1986; Shaw and Antonovics, 1986). However, small differences in emergence time can affect final plant size substantially (e.g., Ross and Harper, 1972; Dolan and Sharitz, 1984; Fowler, 1984; Ellison, 1987b), and hence emergence time may affect hierarchy formation. To control for such differences and to further examine the role of

plant form and emergence time in plant population dynamics, we investigated the degree of size inequality and the responses to density in experimental populations of two cultivated varieties of peas (*Pisum sativum* L.) that differ at a single genetic locus but have radically different morphologies, leafy and leafless.

MATERIALS AND METHODS—*The peas*—Isogenic garden pea varieties were obtained from Dr. Earl Gritton (Dept. of Agronomy, University of Wisconsin, Madison, WI). Two dwarf lines of "New Line Early Perfection" peas were used in these experiments: "leafed" and "leafless" (Marx, 1974). Both genotypes lacked stipules and tendrils. The two varieties differed only at the *afilia* (*af*) locus (Gottschalk, 1972; Marx, 1974; Snoad, 1974), and were recessive at both the *st* and *tl* loci (Marx, 1974) (leafed peas: *Af/-*; *st/st*; *tl/tl*, leafless peas: *af/af*; *st/st*; *tl/tl*). Although differing at only a single locus, the two genotypes have very different forms (Fig. 1). The leafed peas look like normal peas, but lack the characteristic stipules and tendrils of vining peas (imparipinnate leaves: Makasheva, 1983). The "leafless" peas have numerous minute leaflets where the tendrils normally would be resulting from the interaction between the *af* and *tl* recessive genes (multiple imparipinnate leaves: Makasheva, 1983). Large leaflets and stipules are absent in the leafless variety. As a result of these differences in leaf form, the leaf areas of mature individuals of these two varieties (grown under long-day [14-hr light] conditions in an unheated greenhouse) are very different (Leafed: $\bar{x} = 12.7 \pm 1.05$ cm^2 (SE), $N = 5$; Leafless $\bar{x} = 6.2 \pm 0.65$ cm^2 (SE), $N = 5$). Although the minute leaflets of the leafless variety are located where tendrils normally would be, developmentally these small leaflets are true leaflets, not expanded tendrils (Gould, Cutter, and Young, 1986). Following the convention of Snoad (1974), we call the *af/af*; *st/st*; *tl/tl* variety "leafless" because it has double recessive alleles at the *af* and *st* loci while noting that it does, in fact, have minute leaflets (Marx, 1974; Fig. 1). These peas differ from leafless varieties studied by other investigators (e.g., Hedley and Ambrose, 1981; Butcher, 1983; Hedley, Ambrose, and Pyke, 1983; Ambrose and Hedley, 1984) in possessing two recessive alleles at the *tl* locus.

Germ̄inability—To determine variability among seeds and between genotypes, 150 seeds of each genotype were weighed (± 0.001 g) prior to planting. Because germination often differs between petri plate and soil trials (reviewed in

Matthews, 1977), and was variable in the density studies (see Results), we tested the germinability of each genotype following the protocol outlined by the International Seed Testing Association (1976). We tested 200 seeds of each genotype in 10 cm-diameter sterile glass petri dishes (20 seeds/dish). The seeds were germinated between two sheets of filter paper saturated with distilled water. The covered petri dishes were kept in a growth chamber at 18 C, 50% humidity, in a 12/12 hr photoperiod. We recorded daily the number of peas fully imbibed, and number germinated (radicles > 2 mm long) for 12 days. Distilled water was added daily to prevent desiccation.

Effects of density—Dried peas were sown 2 cm deep in sterile peat-perlite-vermiculite “Cornell Mix” (Department of Biometry and Plant Breeding, Cornell University, Ithaca, NY) at two densities: individually (non-competing) in 13 × 13 × 6 cm plastic pots (340 of each genotype, one per pot) and in dense stands of 72 seeds (equivalent to 576/m²) in 27 × 53 × 6 cm plastic flats (20 replicate flats of each genotype). In each flat, seeds were planted in 12 × 6 square arrays with 4 cm between each seed. All seeds were sown on 11 August 1986. Flats and pots were placed in an unheated greenhouse with no supplemental light. Plants were not fertilized. Once during the course of the experiment the plants were sprayed with Orthene (Ortho Corp.) to control aphids.

Seedlings emerged over a 10-day period beginning 6 days after planting. Two cohorts of seedlings were distinguished and marked with colored plastic rings. Early seedlings were defined as those seedlings that emerged 6–7 days after planting, while late seedlings were defined as those that emerged > 7 days after planting. Following the first flush of germination, few seedlings appeared until 13 days after planting. Those seedlings that emerged in between days 7 and 13 were included in the late emergence cohort. No emergence occurred > 15 days after planting.

Beginning two weeks after the first seedlings emerged, and every two weeks thereafter until pod production, we harvested 1/5 of the individually-grown plants and 1/5 of the plants in the high-density flats. Plants and flats were selected using a random number table. Only above-ground plant material was harvested. To reduce edge effects in the high-density flats, we did not harvest the outer border of plants (32 plants). We measured the height (± 1 mm), number of nodes, number of branches, and length of the primary rachis (from the stem to



Fig. 1. Drawing of the two varieties of peas used. Top: “leafed” pea (scale bar = 2 cm). Bottom: “leafless” pea (scale bar = 2 cm). (Drawn from two-wk-old seedlings by Beth Farnsworth.)

the insertion of the first leaflet; ± 1 mm) and counted the number of seeds produced by each plant. All harvested plants were dried (48 hr, 70 C) and individually weighed (± 0.001 g).

Data were analyzed using SYSTAT on an IBM PC-XT. Data were transformed when necessary to conform to the assumptions of parametric statistics (Sokal and Rohlf, 1981). Gini coefficients (G) (Weiner and Solbrig, 1984) were used as the measure of size inequality. G ranges from 0 in a population where all individuals are equal in size to 1 in an infinite population where only one individual has size

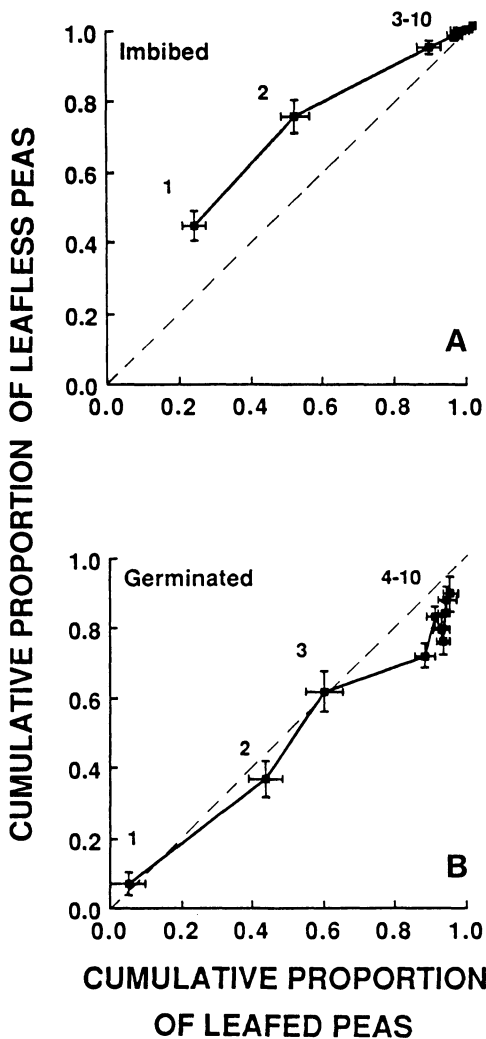


Fig. 2. Cumulative proportion of leafed and leafless peas that imbibed (top) or germinated (bottom) sampled at 1-day intervals ($\bar{x} \pm 1$ SE of 10 replicate petri dishes for each genotype). The number adjacent to each point is the sampling day. If the points fall along the dotted reference line drawn on each graph, then the peas are imbibing (germinating) at identical rates.

>0 (Weiner and Solbrig, 1984). One standard error (SE) is used throughout as the measure of variation, except when reporting Gini coefficients where bias-corrected, nonparametric, bootstrapped (1,000 bootstrap iterations) 95% confidence intervals (Efron, 1982; Dixon et al., 1987) are reported.

RESULTS—Petri plate germination trials—The two genotypes' seed mass frequency distributions were not significantly different from normal (Kolmogorov-Smirnov test for goodness-of-fit: Leafed— $D = 0.03$, $P > 0.15$; Leaf-

less— $D = 0.04$, $P > 0.15$), but seeds of the leafed genotype were significantly heavier than those of the leafless genotype (leafed: $\bar{x} = 0.201 \pm 0.004$ g; leafless: $\bar{x} = 0.183 \pm 0.004$ g; $F_{1,298} = 9.36$, $P = 0.024$, ANOVA). Peas began imbibing and germinating within 48 hr. Leafless pea seeds imbibed more rapidly than the leafed ones (Fig. 2A), but both varieties germinated at approximately the same rate (Fig. 2B). All of the peas imbibed within 9 days (Fig. 2A). However, only 95% of the leafed and 89% of the leafless peas had germinated after 12 days in the petri plates (Fig. 2B).

Effects of density: emergence—Virtually all of the individually-grown seeds emerged (leafless: 96%, leafed: 97%), but only 64% of the leafless and 60% of the leafed peas in the high-density flats emerged. In the individual pots, all seedlings emerged 6–7 days after planting (early cohort plants). In the high-density flats, 65% of the leafless seedlings were in the early cohort and 35% were in the late cohort, while 51% of the leafed seedlings were in the early cohort and 49% of the leafed seedlings were in the late cohort.

Effects of density: morphology—Through the first four harvests (8 weeks), the leafless plants were generally taller and had more nodes than the leafed ones in both density treatments ($P < 0.05$, ANOVA by harvest, pooled over emergence cohorts; Table 1). At the final harvest, however, there were no differences in height between the two genotypes at either density treatment ($P > 0.15$, ANOVA, Table 1). Leafless plants had more branches than leafed plants, but plants with more than one axillary branch were rare in these experimental populations. At the final harvest, height did not differ within genotypes between density treatments ($P > 0.10$, ANOVA). Although high-density plants had significantly more ($P < 0.05$, ANOVA) nodes than individually-grown ones, this difference was slight (one node; Table 1). Individually-grown plants had more branches than high-density plants ($P < 0.01$, ANOVA).

Within the high-density treatment, early-emerging individuals were significantly taller, had more nodes, and more often were branched than the late-emerging individuals in each genotype (Table 2). Early-emerging leafless and leafed peas rarely differed in height, number of nodes, or number of branches, and the same held true for late-emerging individuals (Table 2).

Primary rachis length did not differ among harvests, between densities, or between cohorts ($P > 0.10$, all cases), so differences in

TABLE 1. Morphological parameters (± 1 SE) for the two varieties of peas at each harvest. The values for each density treatment are pooled over emergence cohorts. Within each density, significantly different values ($P < 0.05$) are indicated by a * between them

Harvest		Individually-grown		High-density	
		Leafed	Leafless	Leafed	Leafless
1	Ht (cm)	10.3 \pm 0.23 *	12.1 \pm 0.18	7.7 \pm 0.35 *	10.4 \pm 0.43
	Nodes	6.4 \pm 0.09 *	7.2 \pm 0.09	5.4 \pm 0.24 *	6.5 \pm 0.26
	Branches	0.1 \pm 0.04 *	0.6 \pm 0.08	0.3 \pm 0.06 *	0.6 \pm 0.08
	N	60	60	92	91
2	Ht (cm)	12.6 \pm 0.28 *	13.7 \pm 0.25	11.4 \pm 0.43 *	13.9 \pm 0.38
	Nodes	7.9 \pm 0.14 *	8.5 \pm 0.12	7.6 \pm 0.24 *	8.1 \pm 0.23
	Branches	0.7 \pm 0.10 *	1.1 \pm 0.08	0.7 \pm 0.09	0.8 \pm 0.07
	N	65	65	103	102
3	Ht (cm)	13.6 \pm 0.34 *	15.0 \pm 0.37	14.3 \pm 0.56 *	16.5 \pm 0.38
	Nodes	8.9 \pm 0.17	9.2 \pm 0.20	9.5 \pm 0.31	9.8 \pm 0.25
	Branches	1.7 \pm 0.13	2.5 \pm 0.16	1.2 \pm 0.12 *	1.5 \pm 0.11
	N	65	65	88	108
4	Ht (cm)	18.7 \pm 0.53	18.7 \pm 0.47	17.2 \pm 0.70 *	20.2 \pm 0.59
	Nodes	8.9 \pm 0.20 *	9.9 \pm 0.30	9.9 \pm 0.42 *	11.4 \pm 0.47
	Branches	1.7 \pm 0.13	1.7 \pm 0.15	0.6 \pm 0.08	0.8 \pm 0.09
	N	65	65	86	98
5	Ht (cm)	20.1 \pm 0.55	20.7 \pm 0.49	19.9 \pm 0.83	21.2 \pm 0.63
	Nodes	8.5 \pm 0.23 *	9.3 \pm 0.31	10.9 \pm 0.44	11.7 \pm 0.43
	Branches	1.2 \pm 0.07 *	1.7 \pm 0.13	0.5 \pm 0.07 *	0.8 \pm 0.08
	N	65	65	66	94

rachis lengths were only assessed between genotypes. Leafless peas had significantly longer rachides than leafed peas (leafless: \bar{x} = 3.2 \pm 0.02 cm, N = 4,405 rachides; leafed: \bar{x} = 1.6 \pm 0.01 cm, N = 4,226 rachides; t = 76.73, P < 0.001).

Effects of density: biomass—Above-ground dry mass of individual plants increased over the course of the experiment, and individually-grown plants were significantly larger than high-density ones at all harvests (P < 0.001, ANOVA on log-transformed biomass data, pooled

TABLE 2. Morphological parameters (± 1 SE) for the high density treatments of the two varieties of peas at each harvest, separated by emergence cohort (definition of emergence cohort is given in text). Within each genotype, significantly different values ($P < 0.05$) are indicated by a * between them

Harvest		Leafed		Leafless	
		Early	Late	Early	Late
1	Ht (cm)	10.4 \pm 0.34 *	5.0 \pm 0.25	12.7 \pm 0.29 *	5.9 \pm 0.51
	Nodes	7.1 \pm 0.21 *	3.5 \pm 0.20	7.8 \pm 0.19 *	3.7 \pm 0.26
	Branches	0.2 \pm 0.08	0.3 \pm 0.08	0.8 \pm 0.10 *	0.4 \pm 0.10
	N	49	43	60	31
2	Ht (cm)	14.4 \pm 0.43 *	9.3 \pm 0.52	15.4 \pm 0.35 *	10.5 \pm 0.64
	Nodes	9.7 \pm 0.21 *	6.1 \pm 0.22	9.0 \pm 0.20 *	6.1 \pm 0.36
	Branches	1.1 \pm 0.19 *	0.5 \pm 0.08	0.8 \pm 0.087	0.7 \pm 0.12
	N	43	60	70	32
3	Ht (cm)	15.4 \pm 0.67 *	12.4 \pm 0.93	17.2 \pm 0.49 *	15.2 \pm 0.52
	Nodes	10.4 \pm 0.36 *	7.8 \pm 0.45	10.6 \pm 0.32 *	8.3 \pm 0.29
	Branches	1.5 \pm 0.15 *	0.6 \pm 0.16	1.7 \pm 0.14 *	0.9 \pm 0.15
	N	55	33	69	39
4	Ht (cm)	19.0 \pm 1.06 *	1.58 \pm 0.90	22.1 \pm 0.79 *	18.2 \pm 0.78
	Nodes	10.7 \pm 0.66	9.4 \pm 0.54	12.7 \pm 0.74 *	10.1 \pm 0.53
	Branches	0.9 \pm 0.13 *	0.3 \pm 0.07	0.9 \pm 0.13 *	0.6 \pm 0.11
	N	38	48	49	49
5	Ht (cm)	22.7 \pm 1.42 *	17.7 \pm 0.81	21.1 \pm 0.69	21.2 \pm 1.54
	Nodes	11.7 \pm 0.73 *	10.3 \pm 0.51	11.2 \pm 0.49 *	13.3 \pm 0.82
	Branches	0.7 \pm 0.11 *	0.3 \pm 0.08	0.9 \pm 0.09 *	0.3 \pm 0.12
	N	29	37	74	20

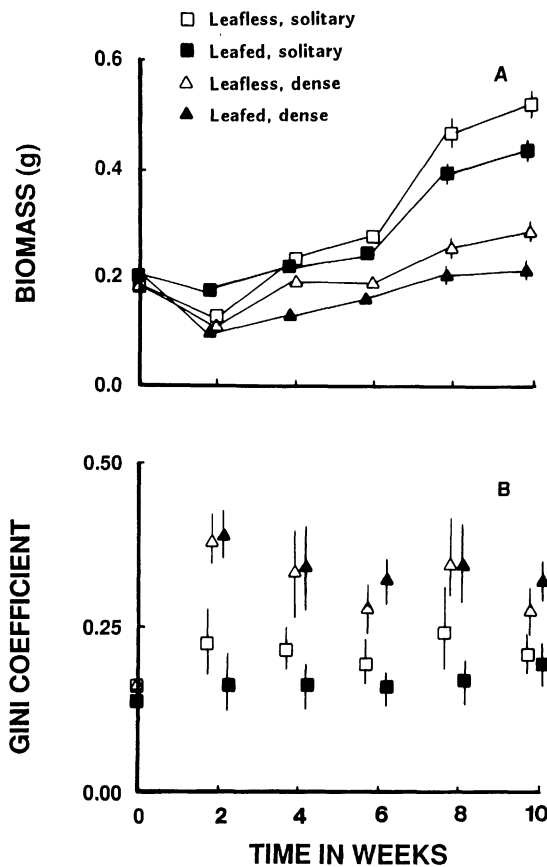


Fig. 3. A. Mean biomass (± 1 SE) of individual plants in the two density treatments (results pooled over emergence cohorts) at two-wk intervals. B. Gini coefficients (with bootstrapped 95% confidence intervals) for the populations at two-wk intervals. The point at week 0 is the seed mass (in A) and the seeds' Gini coefficient (in B). Error bars are shown when they exceed the diameter of the symbol. For each sampling date, points are spread across the x-axis so overlapping error bars can be distinguished.

over emergence cohorts; Fig. 3A). Mean biomass of the leafless plants was significantly greater than that of the leafed plants at the 2d through 5th harvests ($P < 0.025$, each harvest, ANOVA pooled over emergence cohorts; Fig. 3A). There was no significant interaction between genotype and density ($P > 0.05$, all harvests, ANOVA pooled over emergence cohorts). In the high-density flats, first cohort plants were significantly larger than second cohort ones at all harvests ($P < 0.001$, ANOVA pooled over genotypes; Fig. 4A), but there were no significant differences between genotypes' biomasses within each cohort ($P > 0.10$, ANOVA; Fig. 4A).

Two weeks into the experiment, high-den-

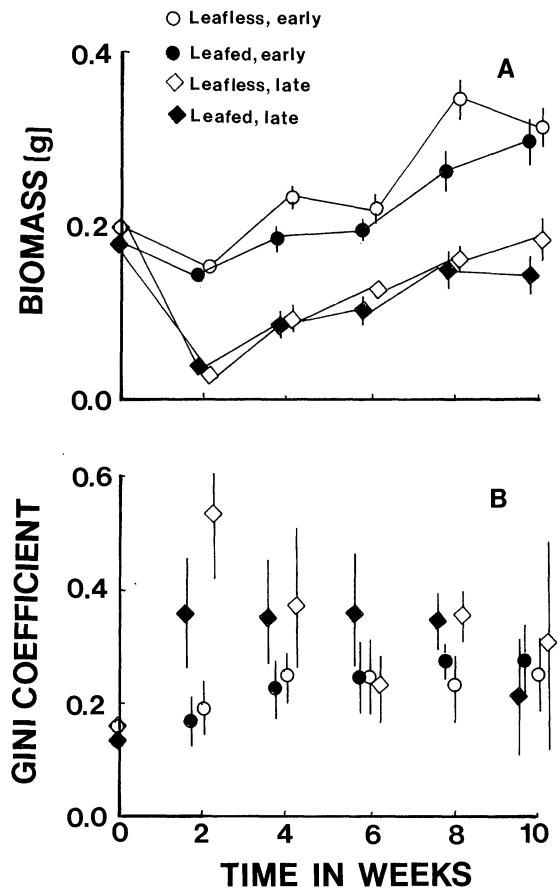


Fig. 4. A. Mean biomass (± 1 SE) of individual plants in the high-density treatment, separated by emergence cohort (early vs. late). B. Gini coefficients (with bootstrapped 95% confidence intervals) of high-density populations separated by emergence cohorts. The point at week 0 is the seed mass (in A) and the seeds' Gini coefficient (in B). Error bars are shown when they exceed the diameter of the symbol. For each sampling date, points are spread across the x-axis so overlapping error bars can be distinguished.

sity plots of both genotypes had biomass distributions that were significantly more unequal than individually-grown plants ($P < 0.05$ determined by nonoverlap of 95% confidence intervals; Fig. 3B) indicating that dominance and suppression were occurring among the high-density populations. Among the high-density plants, early-emerging plants had significantly less hierarchical biomass distributions than late-emerging plants ($P < 0.05$; Fig. 4B). The early-emerging high-density plants were neither more nor less hierarchical than the individually-grown ones, while the late-emerging plants' biomass distributions were significantly more unequal than those of the individually-grown plants (cf. Fig. 3B, 4B).

TABLE 3. Number of dead plants (% of total emerged in parentheses) in the high density populations

	Harvest				
	1	2	3	4	5
Leafless (emergence cohorts pooled)	0	0	2 (1.8)	4 (3.9)	10 (9.5)
Leafed (emergence cohorts pooled)	0	0	9 (9.3)	17 (16.5)	23 (23.1)
Leafless (1st cohort)	0	0	0	1 (2.0)	6 (7.4)
Leafed (1st cohort)	0	0	8 (12.7)	8 (17.4)	17 (36.9)
Leafless (2d cohort)	0	0	2 (4.8)	3 (5.7)	4 (16.6)
Leafed (2d cohort)	0	0	1 (2.9)	9 (15.8)	6 (14.3)

This pattern was observed consistently at all five harvests (Fig. 3B, 4B), but no increase in degree of size inequality was observed over the 10 weeks of the experiment even though biomass increased over the course of the experiment (Fig. 3A, 4A). In addition, within each density treatment, and within cohorts of the high-density treatments, the degree of inequality between biomass distributions of the two genotypes did not differ (Fig. 3B, 4B). Note that the value for *G* in Fig. 3B is not simply the sum of the values of *G* in Fig. 4B. Rather, as *G* is not additively decomposable, *G* was calculated for each germination cohort separately, and then *G* was recalculated for the entire high density population of each morphological type.

Effects of density: mortality—Plants did not die in the high-density flats until the third harvest (six weeks after emergence). Mortality was more severe among the leafed plants than among the leafless ones (Table 3). Among the leafless plants, more late-emerging plants died than did early-emerging ones by the 6th, 8th, and 10th weeks; mortality was more evenly distributed among emergence cohorts of the leafed peas (Table 3).

Effects of density: seed production—Seed production was very low in these experimental plants, probably due to the absence of fertilizer and the restricted rooting space in the pots and flats. No plant produced more than three pods. Among individually-grown plants, both genotypes produced equal numbers of seeds (Leafed: $\bar{x} = 3.5 \pm 0.33$, range = 0–12; Leafless: $\bar{x} = 3.5 \pm 0.27$, range = 0–13, $F_{1,128} = 0.001$, $P = 0.971$, ANOVA), while in the high-density treatment (pooled over emergence cohorts), the leafed plants produced significantly more peas than the leafless ones did (Leafed: $\bar{x} = 1.9 \pm 0.23$, range = 0–10; Leafless: $\bar{x} = 1.3 \pm 0.20$, range = 0–8, $F_{1,158} = 5.74$, $P = 0.02$, ANOVA). In the high-density populations, there were no significant differences in

pea production between emergence cohorts within genotypes (Leafed—early: $\bar{x} = 2.3 \pm 0.28$, late: $\bar{x} = 1.7 \pm 0.35$, $F_{1,64} = 2.03$, $P = 0.16$, ANOVA; Leafless—early: $\bar{x} = 1.2 \pm 0.22$, late: $\bar{x} = 1.9 \pm 0.43$, $F_{1,92} = 1.49$, $P = 0.23$, ANOVA).

The Gini coefficient was used to determine degree of inequality among individuals' seed production in the same way as this statistic was used on biomass distributions (The Gini coefficient of seed production will be referred to as G_{sp}). Seed production was distributed very unevenly among plants in the high-density populations. Pooled over emergence cohorts, the high-density leafless plants had significantly more unequal seed production distributions ($G_{sp} = 0.71$, 95% CI = 0.63–0.78) than high-density leafed plants ($G_{sp} = 0.51$, 95% CI = 0.43–0.61). In contrast, the individually-grown plants were much less hierarchical in seed production and G_{sp} did not differ between genotypes in this treatment (Leafed: $G_{sp} = 0.29$, 95% CI = 0.23–0.37; Leafless: $G_{sp} = 0.40$, 95% CI = 0.33–0.50). In the high-density leafed populations, early-emerging plants were significantly less hierarchical in seed production than late-emerging ones (early plants: $G_{sp} = 0.35$, 95% CI = 0.26–0.49; late plants: $G_{sp} = 0.63$, 95% CI = 0.53–0.77), while in the high-density leafless populations, there was no difference in the degree of hierarchy in seed production between emergence cohorts (early plants: $G_{sp} = 0.75$, 95% CI = 0.68–0.83; late plants: $G_{sp} = 0.58$, 95% CI = 0.43–0.76).

Biomass explained a small but significant portion of the variance in seed production in the individually-grown leafed population ($F_{1,63} = 23.14$, $P < 0.001$, $r^2 = 0.27$), the individually-grown leafless population ($F_{1,63} = 43.22$, $P < 0.001$, $r^2 = 0.41$), and the high-density leafless population (pooled over emergence cohorts: $F_{1,92} = 23.25$, $P < 0.001$, $r^2 = 0.20$). There was no significant relationship between plant biomass and seed production in the high-density leafed populations (pooled over emergence cohorts: $F_{1,64} = 2.34$, $P = 0.13$, $r^2 = 0.04$).

In the high-density leafless populations, emergence cohort also significantly affected seed production ($F_{1,91} = 11.86$, $P = 0.001$). Inclusion of emergence cohort in this regression model slightly increased the amount of variance explained by the model ($r^2 = 0.29$). The addition of emergence cohort as a factor affecting seed production did not, however, change the results in the high-density leafed population (effect of emergence cohort: $F_{1,63} = 0.39$, $P = 0.54$, $r^2 = 0.04$).

DISCUSSION—Our results indicate that dominance and suppression occur in dense populations of each morphological type. These data support Weiner and Thomas' (1986) hypothesis that plant form alone cannot prevent the occurrence of dominance and suppression. However, some of these results are at odds with a strict interpretation of the dominance and suppression hypothesis. Although size hierarchies are apparent in the high-density monocultures (pooled over emergence cohorts), the degree of inequality neither increased nor decreased through time (Fig. 3B) although plant biomass increased throughout the experiment. Large size hierarchies form in dense stands as a result of competition, and the fact that high-density plants are one-half the size of solitary ones is evidence that competition is occurring in the dense stands. Hara (1986b) and Weiner and Thomas (1986) have shown that if competition for aboveground resources (i.e., light) is the dominant interaction among plants, then resource preemption leading to dominance and suppression (larger size hierarchies with higher densities and increasing size hierarchies through time within density treatments) should be observed. If, on the other hand, competition for belowground resources (i.e., soil nutrients) dominates, resource depletion should result in overall lower mean size and size hierarchies should either decrease or not change with increases in density and through time within densities (Hara, 1986b; Weiner and Thomas, 1986).

Our results suggest that two-sided competition for nutrients occurred in the high-density flats and may have been more important in these populations than competition for light. Data from field experiments with these same genotypes indicate that the leafed peas' canopy blocks 97% of the incoming light (measured 10 cm above ground level), while the leafless canopy blocks only 68% of the available light ($P < 0.01$, t test; A. M. Ellison, D. Rabinowitz, and D. Vam Vikes, unpublished data).

Mortality was low in these greenhouse populations, and was more severe in smaller, late-

emerging plants (Table 3). Mohler, Marks, and Sprugel (1978) hypothesized that if the smaller (suppressed) plants in a population suffered disproportionate mortality then the degree of inequality in such populations should decrease over time. Although smaller individuals in our pea populations suffered greater mortality than larger ones, no overall decrease in the populations' degree of inequality was observed. In contrast, the growth rate hypothesis predicts that if plant growth rate alone determines variation in plant size, there should be no differences in the degree of inequality between density treatments (Turner and Rabinowitz, 1983; Uchmanski, 1985; Ellison, 1987a). It is clear from our data, however, that there are dominant and suppressed individuals in these experimental populations (Fig. 3). Although seeds of the two genotypes imbibe and germinate at similar rates (Fig. 2), germination of both genotypes occurs over two weeks. Most of the observed variation in plant size within genotypes appears to be a result of emergence time (Fig. 4), in agreement with the results of Ross and Harper (1972), Fowler (1984), and Ellison (1987b).

It is possible that rather than each monoculture behaving as a single population, the dominant and suppressed classes are behaving as distinct subpopulations. This notion is supported by the observed slight decrease in G in the late-emerging (suppressed) cohort (Fig. 4B) indicating that as a result of greater mortality in the second cohort, the size distribution evened out over time. In contrast, G increased slightly in the early-emerging (dominant) cohort (Fig. 4B) indicating more intense competition among these individuals.

Although dominance and suppression were observed in both leafed and leafless populations, mortality was lower and individual plant biomass higher in the leafless populations. If plant form played no role in the dynamics of these populations, we would expect that G would be greater in populations of equal densities but with larger individuals and/or less mortality. The absence of this result further supports Weiner and Thomas' (1986) hypothesis that although plant form may not prevent the occurrence of dominance and suppression, it can affect the extent of the asymmetry. The observed mortality in the high-density experimental populations also supports the notion that competition occurred in these populations.

These results can be only roughly compared with other studies of leafed and leafless peas (e.g., Hedley and Ambrose, 1981; Butcher, 1983; Hedley et al., 1983; Ambrose and Hed-

ley, 1984) as these investigators used genotypes without double-recessive alleles at the *tl* locus. These studies also used substantially lower densities (Weiner and Thomas, 1986). However, our data are similar to data from these other studies. For three varieties of leafless peas (one isogenic line and two cultivars, Filby and Barton) growing at 133 plants m^{-2} (with nitrogen fertilization), Butcher (1983) reported G values of 0.31, 0.31, and 0.26 respectively, and for three varieties of leafed peas (one isogenic line and two cultivars, Birte and Puget) at the same density, G was 0.31, 0.34, and 0.32 respectively. Weiner and Thomas (1986) reanalyzed data of Hedley and colleagues (1983) and found $G = 0.17, 0.21,$ and 0.24 for leafless (*af/af; st/st*) plants grown at 100, 204, and 277 m^{-2} , respectively. Hedley et al.'s (1983) data are comparable to ours in that G increased with increasing density. As with our data, both Butcher's (1983) and Hedley et al.'s (1983) data indicate less hierarchical size structures in populations of leafless peas relative to leafed populations.

Peas are ideal plants to use in investigations of the effects of plant form on population dynamics. Peas are easily obtained and grown, and the genetic bases of many morphological variants are well understood. The results presented here illustrate that a small genetic change (one allele) that has dramatic effects on plant form can also alter population size structure. The extended emergence period of peas allowed us to examine the combined effects of morphology and emergence time on pea population dynamics. The results obtained do not fit easily into the predictions of either the dominance and suppression or the growth rate hypothesis, and effects of the interaction between plant architecture and time of emergence on population dynamics deserve further study.

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