

EVOLUTIONARILY STABLE MORPHOLOGIES IN PEA POPULATIONS¹

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Abstract.— We investigated the hypothesis that plant form can dramatically affect plant competitive ability, and that forms with dense canopies can invade populations of plants with more open canopies regardless of initial relative frequencies. Under controlled field conditions, we examined the effects of plant form on growth rate, size variation, mortality, and reproduction in high-density monocultures and mixtures of two morphologically distinct varieties of peas. These two varieties differ genetically at only the *afila* locus. In high-density monocultures and mixtures, peas with finely dissected, minute leaflets (*af/af*) grew more slowly and produced fewer seeds than *Af/–* individuals with large leaflets that cast more shade on neighbors. After as few as four generations, mixtures begun with 10% *Af/–* peas would be expected to evolve to *Af/–* monocultures. We conclude that an increase in morphological complexity (e.g., virtually leafless to leafy) can have dramatic ecological and evolutionary impacts on plant population dynamics.

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The evolution of elaborate, broad-leaved canopies and tall stature in terrestrial vascular plants has been attributed to selection for increased light-gathering ability among competing individuals (e.g., Horn, 1971; Givnish, 1982; Stewart, 1983; Niklas and Kerchner, 1984; Ellison, 1989). Computer simulation models strongly support the notion that for primitive and derived morphologies, increased light-gathering associated with elaborated canopies and increasing plant stature confers a selective advantage for such plants associated with their ability to overtop and outshade their neighbors (Niklas and Kerchner, 1984; Ellison and Niklas, 1988). Comparative studies among modern plant taxa support this hypothesis, and the results from these studies are particularly robust for the over 250,000 species of angiosperms (reviewed by Givnish, 1987). For early terrestrial vascular plants, there is inferential support for this hypothesis from studies of the fossil record and from computer simulations. With an appropriate model system this hypothesis can be experimentally examined under controlled conditions.

We experimentally examined the null hypothesis that leaf form confers no competitive advantage in mixed populations of

plants with differing leaf morphologies. In particular, we asked if a single-locus mutation that results in a morphological shift from virtual leaflessness to leafiness can invade a population of leafless individuals irrespective of the initial frequency of the mutation in the population. In other words, is leaflessness or leafiness an evolutionarily stable morphology?

METHODS

The Peas

Two dwarf isogenic lines of “New Line Early Perfection” peas were used in these experiments: the mutants *acacia* and *parsley-leaved* (Marx, 1974, 1987; Snoad, 1974). These two varieties differ only at the *afila* (*af*) locus (Kujala, 1953; Goldenberg, 1965; Gottschalk, 1972; Marx, 1974; Snoad, 1974) and were recessive at both the *stipule* (*st*) and *tendrilled* (*tl*) loci (*acacia* peas: *Af/–*; *st/st*; *tl/tl*, *parsley-leaved* peas: *af/af*; *st/st*; *tl/tl*). Although differing at only a single locus, these two genotypes have very different forms. The *acacia* peas have large, flat leaflets characteristic of cultivated vining peas, but lack the stipules and tendrils (imparipinnate leaves: Makasheva, 1983). The *parsley-leaved* peas also lack stipules and tendrils, and have numerous minute leaflets where the tendrils normally would be. These kind of leaves (multiple imparipinnate leaves: Makasheva, 1983), form as a result of interactions between the recessive alleles *af* and *tl* (Gould et al., 1986). For stylistic convenience, herein we will refer to the *aca-*

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cia as 'leafy' because of their large, flat leaflets, and the *parsley-leaved* ones as 'leafless' when discussing these two varieties. We emphasize that other investigations of 'leafless' peas have used the genotype *af/af; st/st; Tl/-* (Hedley and Ambrose, 1981; Butcher, 1983; Hedley et al., 1983; Ambrose and Hedley, 1984), and that the *parsley-leaved* mutant that we use is not completely leafless (Makasheva, 1983; Marx, 1987; Ellison and Rabinowitz, 1989).

We chose to use these two varieties because they have radically different leaf morphologies that could lead to distinct differences in relative competitive abilities. Unlike tendrilled peas, these two varieties, which lack tendrils, are easily separated in the field. Consequently, we also could accurately assess *individual* variation in plant performance.

These two varieties differ significantly ($P < 0.05$, *t*-test) in leaf area. The total leaf area (leaflets + rachides) of the compound leaves of the leafy variety is more than twice that of the leafless peas (leafy— 12.7 ± 2.35 cm² [SD]; leafless— 6.2 ± 1.45 cm² [Ellison and Rabinowitz, 1989]).

One would expect that such a dramatic reduction in leaf area would also affect CO₂ photoassimilate level in the plants. However, Harvey (1972, 1974) found that for these and other varieties of morphologically altered peas, there was no difference among varieties in the rate of CO₂ uptake per unit area of leaf. Hedley and Ambrose (1979) provide data showing that the yield of these varieties is not limited by photoassimilate availability. Hedley and Ambrose (1981) report that in England, leafless and semi-leafless varieties out-yield (per unit area of land) leafy varieties. In the United States, however, the reverse has been found (Glover, 1980; Hedley and Ambrose, 1981). These authors attribute yield differences in the two countries to the different genetic backgrounds into which these mutants have been introduced. However, they do not report reproduction on a per-plant basis. Since leafless peas are often planted at higher densities than leafy ones (Hedley and Ambrose, 1981), differences in total yield may simply reflect planting densities, and not individual plant performance. In fact, Ellison and Rabinowitz (1989) found that when individ-

ually-grown, the two varieties used in this study produced equivalent numbers of seeds per individual and had similar growth rates.

The two varieties that we studied also do not differ in germination rate, although leafy pea seeds are, on average, 0.02 g heavier than leafless ones (Ellison and Rabinowitz, 1989). Neither variety forms *Rhizobium*-associated nodules (G. Marx, pers. comm.), and both varieties set seed cleistogamously. Further details on the biology of these varieties can be found in Gritton (1972), Marx (1974), Sharma (1972), Hedley and Ambrose (1981), Snoad (1981), Gould et al. (1986), and Ellison and Rabinowitz (1989).

Experimental Design

We grew peas in a substitutive design (De Wit, 1960) to test the hypothesis that for a background of fixed density, leafy peas can invade leafless ones regardless of initial frequency. We planted 196 peas into 32 50 × 50-cm quadrats (peas were evenly spaced in a 14 × 14 grid) in a 5 × 11-m common garden on Cornell University farmland. We chose this density because earlier studies had indicated that we could expect severe competition with 20–30% mortality at this density (Gritton and Eastin, 1968; Glover, 1980; Butcher, 1983; Ambrose and Hedley, 1984; Ellison and Rabinowitz, 1989). The garden was plowed on 1 May 1987, and peas were planted on 24 May. Seeds were pretreated with fungicide (Benomyl) to prevent damping off. Eight quadrats were leafy monocultures, eight were leafless monocultures, eight were mixed plantings of 90% leafy and 10% leafless, and eight were mixtures of 10% leafy and 90% leafless. The location of each genotype within mixtures was random. A one-row border of peas surrounded each quadrat. The percentage of the two varieties in the border was the same as in the quadrat. Quadrats were separated from each other by 1 m of bare soil.

Initially, the garden was covered with bird-netting to prevent predation of young seedlings. The netting uniformly reduced light availability by 15% throughout the garden. We removed the netting on 7 June 1987. During a two-week rainless period in early June, we watered the plants every other day. Plants were not fertilized or treated with insecticide. These plants were not notice-

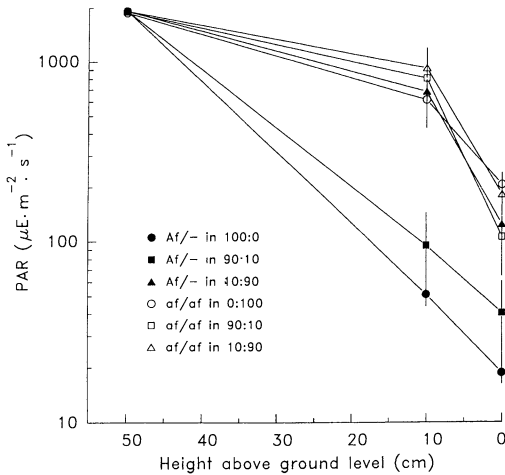


FIG. 1. PAR attenuation rate by the two genotypes (leafy: *Af/-*; leafless: *af/af*) in four planting backgrounds. Plotted points are means \pm 1 SE. See text for statistics.

ably damaged by insect herbivores during the experiment.

In dense, competing plant stands, competition for light is often intense and is responsible for determining size and reproductive inequality among individuals (Weiner and Thomas, 1986). As one measure of competitive ability of these peas, we measured light attenuation in the four planting backgrounds. At three randomly selected points within each monoculture, we measured the amount of available PAR ($\mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$) above the canopy, beneath the canopy at 10 cm above ground level, and at ground level. In mixtures, we measured available PAR under three randomly selected leafy peas, and under three randomly selected leafless peas.

Thirty, 45, and 60 days after planting, we measured plant height and counted the number of nodes on a subsample of all plants. We measured 20 randomly chosen plants in each monoculture quadrat, 20 randomly chosen plants of the dominant genotype in each mixture quadrat, and all of the minority genotype in each mixture quadrat. The randomly chosen plants were tagged at the first census with colored plastic bands, and these same plants were remeasured at the two subsequent censuses. We collected and counted the number of seeds produced by every plant at the end of the

experiment. Because these plants set seeds cleistogamously, differences in seed production can be attributed only to resource limitation (i.e., interplant competition), not to pollinator limitation.

Because we were interested in the invasibility of each genotype, the most important measure of plant success was seed production. Peas must dry completely (senescence) before seed set is complete. Therefore, to accurately assess reproductive success of these two genotypes, we could not harvest these plants prior to senescence, and consequently have no measure of plant biomass in this experiment. However, plant height and node number are highly correlated with biomass ($r^2 = 0.95$, $P < 0.0001$, *F*-test; Ellison and Rabinowitz, 1989).

All data were analyzed using SPSS/PC+ (version 2.0). Data were transformed when necessary to conform to the assumptions of parametric statistics. Throughout this paper, the planting background is referred to in ratio form, with the percent of *Af/-* peas given first (e.g., 10:90 is a mixture with 10% *Af/-* peas and 90% *af/af* peas).

RESULTS

Leafy peas attenuated light more rapidly than did leafless ones ($F_{[1,425]} = 14.83$, $P < 0.001$; Fig. 1). PAR availability declined significantly from above the canopy to ground level, regardless of genotype or planting background ($F_{[2,425]} = 464.77$, $P < 0.0001$; Fig. 1). Light attenuation rate increased with the proportion of leafy peas in the quadrat ($F_{[3,425]} = 3.19$, $P = 0.023$; Fig. 1). In mixed plantings, there was a significant height \times genotype interaction ($F_{[2,276]} = 4.59$, $P = 0.011$), indicating that the two genotypes differed in their attenuation rates. However, there was no significant genotype \times planting background interaction ($F_{[1,276]} = 1.22$, $P = 0.270$); e.g., leafy plants did not differ significantly in attenuation rate in the two mixtures. Overall attenuation rate did not differ between the two mixed plantings (height \times planting background: $F_{[2,276]} = 2.21$, $P = 0.112$).

Thirty days after sowing, the two genotypes were not significantly different in height or node number in any planting background (Fig. 2). Fifteen and 30 days later, however, the leafy peas were taller than the

Effects of genotype and planting background on growth

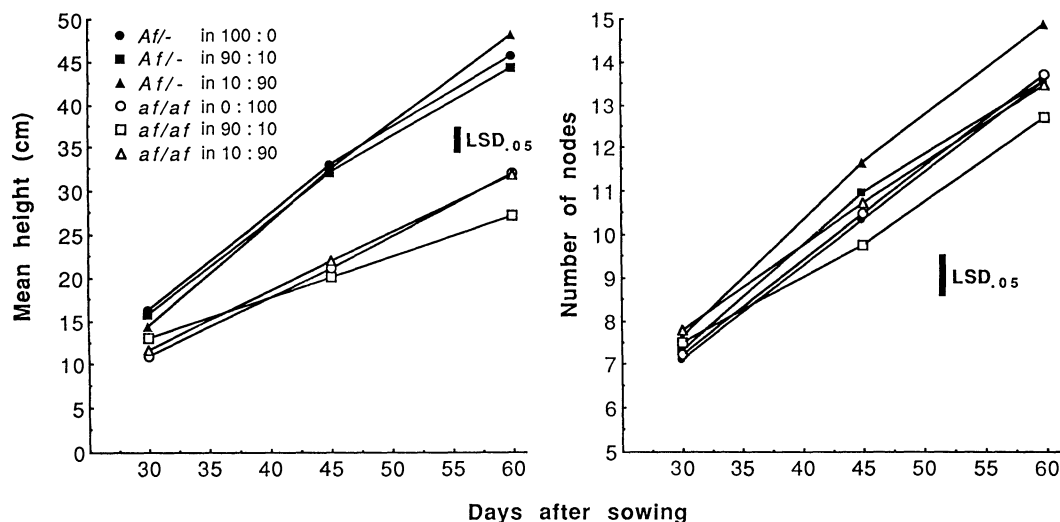


FIG. 2. Effects of plant genotype and planting background on height and node production. Values plotted are means for each sampling date. Statistics are given in Table 1 and text.

leafless ones in all planting backgrounds (Fig. 2). The fastest-growing peas were leafy ones growing in leafless-dominated (10:90) mixtures (Table 1). Leafy peas in monocultures and in 90:10 mixtures were growing at identical rates (Table 1). Leafless peas grew most slowly when they were the minority genotype (in 90:10 mixtures) and at identical rates in leafless monocultures and 10:90 mixtures (Table 1). Final number of nodes produced was greatest in leafy peas in 10:90, and least in leafless peas in 90:10 mixtures (Fig. 2). Among all other plantings, the two genotypes did not differ in node production.

The height distributions of plants in monocultures and mixtures became increasingly hierarchical (sensu Weiner and

Solbrig, 1984) over time, indicating that asymmetric competition for resources ("dominance and suppression" sensu Weiner and Thomas, 1986), where large individuals acquire a disproportionate share of available resources) was occurring in these populations (Fig. 3). Leafy and leafless peas initially had similar height distributions in mixtures. Forty-five and 60 days after sowing, however, leafy peas were found most commonly in the larger height classes, indicating that the leafy genotype was "dominant," while the leafless genotype was suppressed (Fig. 3).

Mortality differed between genotypes and among planting backgrounds (Table 2). Because there were no significant differences in mortality between quadrats within a

TABLE 1. Effects of genotype and planting background on growth rate. All regressions are statistically significant ($P < 0.0001$, F -test).

Background	Genotype	Growth rate ($\text{cm} \cdot \text{d}^{-1}$)	95% c.i.	r^2	Rank
100:0	<i>Af/-</i>	11.9	(10.1–13.6)	0.33	2
90:10	<i>Af/-</i>	12.0	(10.4–13.6)	0.37	2
90:10	<i>af/af</i>	3.6	(2.2–4.9)	0.09	4
10:90	<i>Af/-</i>	15.8	(14.2–17.5)	0.59	1
10:90	<i>af/af</i>	9.1	(8.0–10.3)	0.41	3
0:100	<i>af/af</i>	8.8	(7.5–10.0)	0.34	3

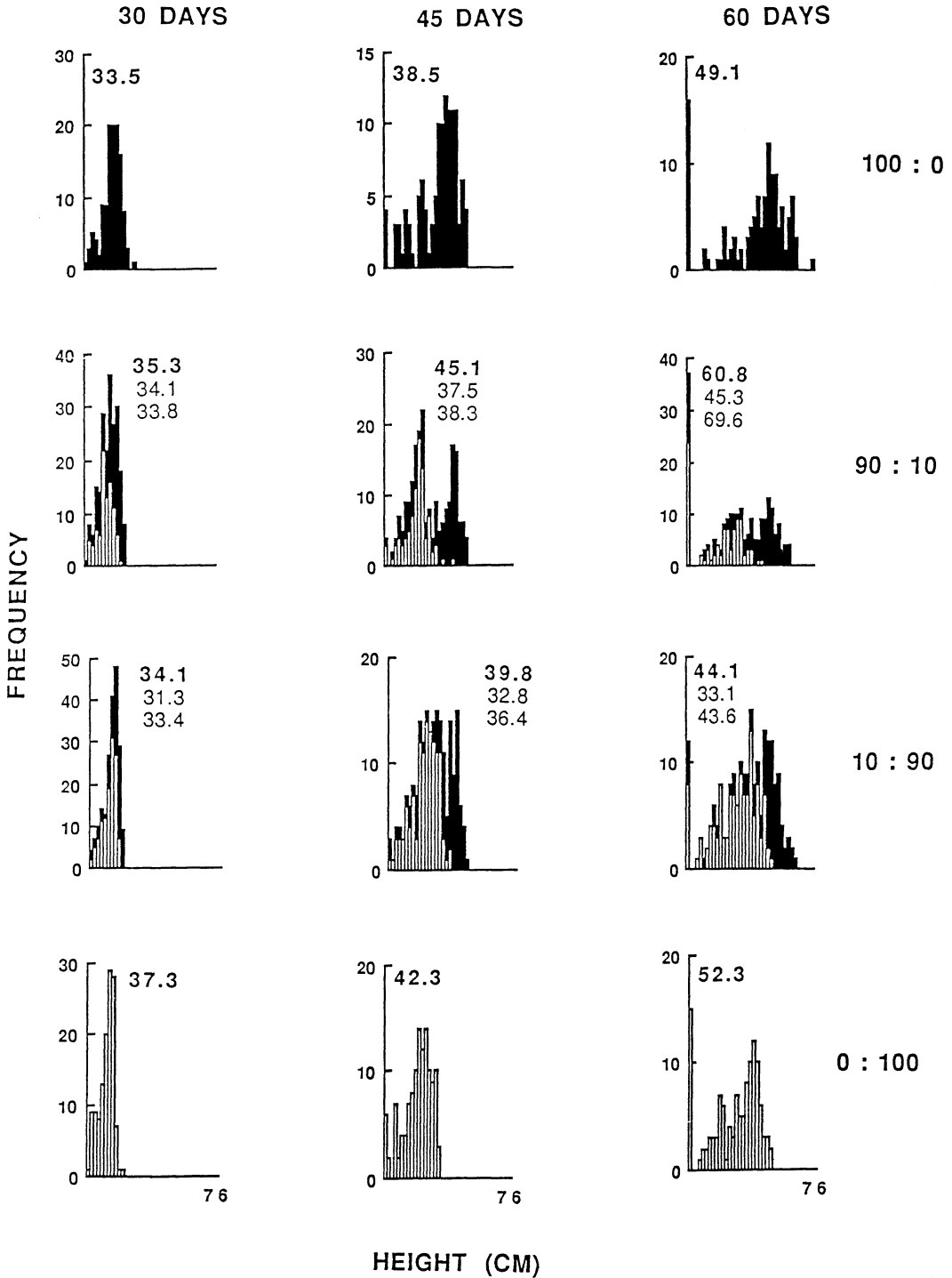


FIG. 3. Height distributions of the two genotypes in the four planting backgrounds (solid bars: leafy peas; open bars: leafless peas). The magnitude of size inequality is given by the distribution's CV. The CV of the entire distribution is given in bold type. For mixed plantings, the CV of leafy peas is given above the CV of leafless peas. Note changes in scale of the y-axes; x-axes of all histograms range from 0 to 76 cm in 2 cm intervals.

Pea production by leafy and leafless peas

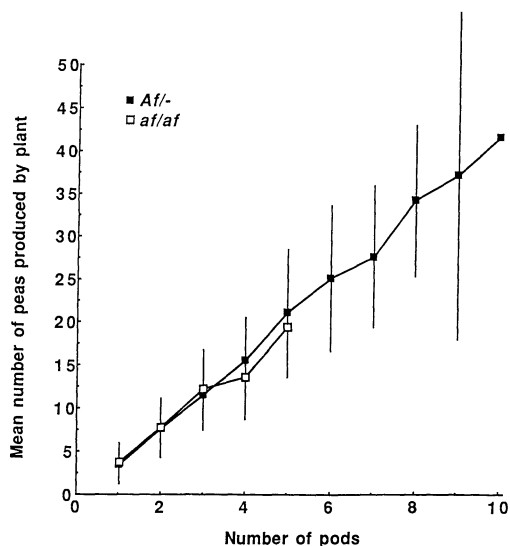


FIG. 4. Reproduction of leafy and leafless peas (mean \pm SD), pooled over planting backgrounds. Regardless of planting background or genotype, peas produced approximately four peas/pod. See Table 3 for reproductive statistics within different planting backgrounds.

treatment, we present mortality data pooled over the eight quadrats in each treatment. None of the leafy peas in 10:90 mixtures died in the course of the experiment, while in the converse quadrats, 24.6% of the leafless peas died when they were the rare genotype (Table 2). Mortality of leafless and leafy peas in monocultures did not differ significantly (Table 2). Leafy and leafless peas also had similar mortality in mixtures where they were the majority genotype.

Sixty-five days after sowing, pod production and plant senescence began. Pea production increased linearly with number of pods, indicating a constant number of peas produced per pod in all planting backgrounds (Fig. 4). However, no leafless plant produced more than 5 pods, while the maximum number of pods produced by a leafy plant was 10 (in a 10:90 mixture). There was a significant effect of planting background and genotype on the number of pods produced, and a significant interaction between planting background and genotype in mixtures on number of pods produced (Table 3). More leafy peas produced pods in

TABLE 2. Effects of genotype and planting background on mortality.

Back-ground*	Geno-type†	Number planted	Number germinated	Number alive at harvest (%)
100:0	<i>Af/-</i>	1,568	1,244	920 (74.0)
90:10	<i>Af/-</i>	1,408	1,158	835 (72.1)
90:10	<i>af/af</i>	160	130	98 (75.4)
10:90	<i>Af/-</i>	160	83	83 (100.0)
10:90	<i>af/af</i>	1,408	812	592 (72.9)
0:100	<i>af/af</i>	1,568	956	709 (74.1)

* Significant effect of planting background ($P < 0.01$, ANOVA).

† Significant effect of genotype ($P < 0.01$, ANOVA). Significant effect of background \times genotype in mixtures ($P < 0.05$, ANOVA).

10:90 mixtures than in any other planting background, while leafless peas performed best in leafless monocultures (Table 3). Maximal pod production increased inversely with frequency for the leafy genotype, and increased directly with frequency for the leafless genotype (Table 3).

DISCUSSION

Based on the results presented here, we reject the null hypothesis that leaf morphology does not affect plant competitive ability. In both monocultures and mixtures, leafy peas were larger, grew more rapidly, and produced more offspring than their leafless counterparts (Figs. 2–4, Tables 1 and 3). Changes in height distributions of these peas over time support the hypothesis that leafy peas are competitively superior to leafless ones.

In the absence of mortality, size distributions whose degree of inequality increases through time are considered to be evidence for asymmetric competition for light (Weiner and Thomas, 1986). No change, or a decrease in inequality over time, would be evidence for either symmetric competition for soil nutrients, or a reflection of the absence of competition and the predominant role of growth rate in determining size distribution shape (Turner and Rabinowitz, 1983; Weiner and Thomas, 1986). However, in populations where density-dependent mortality occurs, death of smaller, competitively inferior individuals can reduce the degree of inequality (Weiner and Thomas, 1986). We observed a reduction in inequality over time in quadrats where mortality was relatively high (cf. Table 2, Fig. 3).

TABLE 3. Number of pods produced per plant by each genotype in the four planting backgrounds.

Background*	Genotype†	Number of pods produced										Mean	C.V.	
		0	1	2	3	4	5	6	7	8	9			10
100:0	<i>Af/-</i>	534	143	90	75	45	23	7	3	0	0	0	0.98	71.0
90:10	<i>Af/-</i>	546	86	81	57	34	15	9	3	3	1	0	0.98	149.0
90:10	<i>af/af</i>	81	12	4	1	0	0	0	0	0	0	0	0.23	243.2
10:90	<i>Af/-</i>	17	5	5	8	15	13	9	7	4	1	1	0.88	172.3
10:90	<i>af/af</i>	396	96	67	25	5	3	0	0	0	0	0	0.57	167.8
0:100	<i>af/af</i>	400	133	113	49	12	2	0	0	0	0	0	0.80	135.2

* Significant effect of planting background ($P < 0.0001$, ANOVA).

† Significant effect of genotype ($P < 0.0001$, ANOVA). Significant effect of genotype \times background in mixtures ($P < 0.0001$, ANOVA).

While all quadrats showed evidence of dominance and suppression among plants (Fig. 3), leafy peas were the dominant individuals (in terms of height) in both 90:10 and 10:90 mixtures. Leafy peas attenuated light more rapidly than leafless ones in all planting backgrounds (Fig. 1). Hence, in mixtures of leafless and leafy peas, once leafy peas exceed leafless peas in height, the smaller, leafless individuals would rapidly be outshaded, and would die. As a result of these differences in light attenuation ability, leafless peas appear to suffer disproportionate mortality relative to their abundance when in mixtures (Table 2).

We have argued that plant form *sensu stricto* is responsible for observed differences in height growth and reproduction. Physiological differences in these varieties resulting from morphological changes could also be important, particularly if the two varieties differed in their relative photosynthetic efficiencies. Harvey (1974) found that imparipinnate and multiple imparipinnate leaves, which occur respectively in our leafy and leafless varieties, do not differ in the amount of photosynthetate exported on a per-leaf basis. Hedley and Ambrose (1979) illustrate that per plant seed production is not limited by photoassimilate availability. The primary carbon sources for ripening pea seeds are the leaflet immediately subtending the pod and the pod itself (Lovell and Lovell, 1970; Harvey, 1974). Therefore, it appears that possible physiological differences between these varieties do not significantly affect reproductive performance.

This is not to say that physiological factors are irrelevant. Leafless plants growing in the shade of leafy ones in 90:10 mixtures were much smaller than either genotype in

any other planting background. This result suggests that the shade cast by the leafy peas on the leafless ones significantly affected photosynthesis in the latter. Similarly, the plants least affected by shade (leafy in 10:90 mixtures) were the largest. Interactions between leaf size, shape, and orientation can affect photosynthesis (e.g., Givnish, 1982, 1984), and consequently, competitive ability. Further studies on interactions between pea leaf shape and orientation and leaf physiology could provide further data with which to assess the validity of our conclusions.

Based on total pea production, leafless peas would rapidly be replaced by leafy ones in mixtures regardless of initial frequency of the leafy genotype (Fig. 5). In leafy-dominated (90:10 mixtures, 99% of the seeds harvested were of the leafy genotype, while only 1% were of the leafless genotype. In leafless dominated (10:90) mixtures, 50% of the harvested peas were of the leafy genotype. If we assume a maximum possible production of 400 seeds per quadrat, and use the simple Lotka-Volterra two-species competition equations (e.g., Hutchinson, 1978), we would predict that in 10:90 mixtures, leafless peas would be replaced by leafy ones in only four generations (Fig. 5). A similar result was obtained by Glover (1980) in six-way mixtures of the leafless, semi-leafless, and leafy genotypes of peas described by Marx (1974). In our populations, virtual leaflessness is therefore not an evolutionarily stable morphology as it is invadable by leafy forms at all frequencies. On the other hand, with respect to these two genotypes, leafiness can be seen as an evolutionarily stable morphology because it is not invadable by the leafless peas under any conditions.

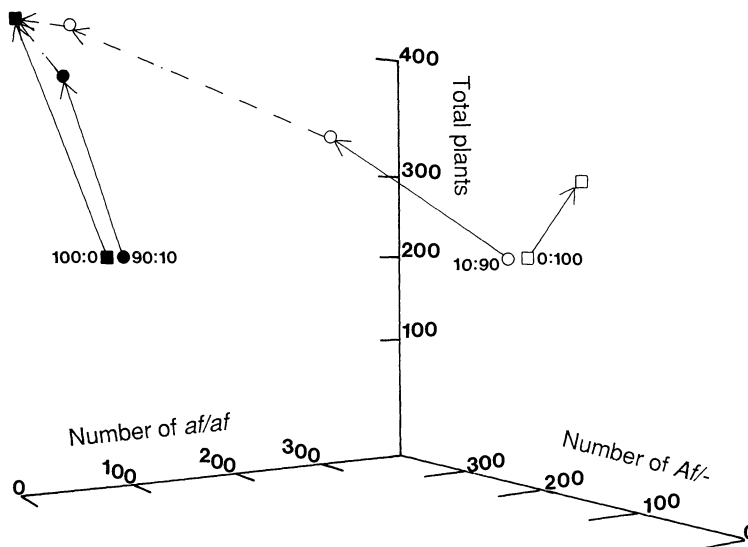


FIG. 5. Projection of population dynamics of mixtures of leafy and leafless peas, based on a maximum seed production of 400 peas/0.25 m². Solid lines represent data from this experiment, dotted lines are projections. (Figure drawn as a perspective plot and is not isometric.)

We do not mean to suggest that leafiness is either an evolutionarily stable morphology or an optimal morphology in *every* environment. Givnish (1987) summarized hundreds of studies on leaf and plant shape and illustrated convincingly that optimal leaf shapes vary with moisture, temperature, amount of irradiance, etc. Clearly, for example, broad-leaved plants would be selected against in hot, dry deserts (Givnish, 1979, 1987). The prevalence of the broad-leaved habit in numerous habitats, however, argues strongly that leafiness is selectively favored in equitable or predictably mesic regions. While this conclusion is not by itself surprising, given the large corpus of comparative data (Givnish, 1987), we have, for the first time, demonstrated experimentally that a single-locus mutation conferring leafiness would invade a population of virtually leafless conspecifics under controlled conditions. In light of available comparative data, these results strongly support the notion that leafiness is an evolutionarily stable morphology.

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