

PLASTICITY VERSUS CANALIZATION: POPULATION DIFFERENCES IN THE TIMING OF SHADE-AVOIDANCE RESPONSES

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Abstract.—The reliability of environmental cues and costs of a fixed phenotype are two factors determining whether selection favors phenotypic plasticity or environmental specialization. This study examines the relationship between these two factors and the evolution of plant competitive strategies (plastic vs. fixed morphologies). In natural plant populations, shifts in light quality associated with foliar shade reliably indicate the presence of neighbors. These cues mediate plastic stem-elongation responses that often increase competitive ability and access to light. Using experimental light treatments (full sun, neutral shade, and foliar shade), genetic differences among populations of *Abutilon theophrasti* (velvetleaf) in average elongation and plasticity to foliar-shade cues were examined. Six populations, two from each of three site types (fields in continuous corn cultivation, fields undergoing corn-soy rotation, and weedy sites), were exposed to the light treatments at two stages in their life history. At the seedling stage, populations derived from cornfield sites exhibited higher, average elongation than populations from either rotating corn-soy fields or weedy areas. Because seedling elongation may delay shading of velvetleaf by corn, population differences may reflect adaptive responses to directional selection imposed by competitive conditions. However, the effects of simulated foliar shade on elongation were three times as great as the average population differences, and these comparatively higher levels of elongation were associated with an allocation cost. These results are consistent with the hypothesis that phenotypic plasticity may limit the evolution of specialists; reliable environmental cues enable individuals to facultatively adopt highly elongated, costly phenotypes in crowded patches while avoiding the costs of that phenotype in less crowded microsites. At later life-history stages, populations experiencing competition with corn exhibited lower plasticity to light quality than populations derived from weedy areas. Elongation at later nodes is maladaptive in cornfields because velvetleaf is ultimately incapable of overtopping corn; individuals that elongate therefore experience the cost of allocating to stems but fail to improve leaf exposure. The decreased responsiveness of cornfield populations to light quality is consistent with theoretical predictions in which reduced plasticity is favored when environmental cues fail to mediate an adaptive response.

Key words.—Adaptive plasticity, canalization, environmental cues, interspecific competition, shade-avoidance responses.

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Phenotypic plasticity and specialization are two modes of adaptation to environmental heterogeneity. When environmental conditions are coarse grained (i.e., when an individual experiences a single patch type), specialists with a fixed phenotype may evolve because a single phenotype consistently conveys the highest fitness (Levene 1953; Waddington 1957; Levins 1962, 1968). For instance, plant populations growing in competitive environments may evolve morphological attributes that enhance competitive ability (Horn 1971; Harper 1977). As environmental conditions become increasingly fine grained, such that both competitive and noncompetitive patches exist, selection is expected to favor phenotypic plasticity (Levins 1963; Bradshaw 1965; Lloyd 1984; Lively 1986, 1998; Sultan 1987; Schlichting and Levin 1990). Plasticity is selectively advantageous if reliable environmental cues exist (Levins 1963, 1968; Lively 1986, 1998) because individuals can adaptively match their phenotype to the level of competition they experience. Selection further favors plasticity if the alternative, competitive phenotype is costly (Lively 1986, 1998). When the competitive phenotype carries a high resource cost, individuals with fixed, competitive phenotypes experience reduced fitness in noncompetitive patches relative to plastic individuals.

Plants use light-quality cues associated with vegetative shade to detect neighbors and adopt competitive, elongated

phenotypes (Smith 1982; Casal and Smith 1989; Ballaré 1991; Schmitt and Wulff 1993). Because chlorophyll disproportionately absorbs wavelengths in the red region of the spectrum, light reflected off neighboring plants has a reduced ratio of red (630–690 nm) to far-red wavelengths (710–760 nm) in comparison to sunlight (Kasperbauer 1971; Holmes and Smith 1977; Smith et al. 1990). Light quality therefore provides a reliable indicator of neighbor proximity and the onset of competition for sunlight prior to direct shading. Plants detect light-quality cues via the phytochrome photoreceptors. These photoreceptors switch between active and inactive forms in response to shifts in red : far-red ratios of light (Morgan and Smith 1976, 1978; Casal and Smith 1989; Child and Smith 1987; Ballaré 1990; Quail 1991; Furuya 1993) and mediate a range of morphological responses, including elevated levels of stem elongation (Smith 1982; Schmitt and Wulff 1993; Smith and Whitelam 1997).

Stem elongation can enhance fitness under competitive conditions by affecting light interception. As internodes elongate, carbon allocation to stems increases. Relative allocation to leaves decreases as a result, which detrimentally affects whole-plant photosynthesis (Morgan and Smith 1978). The carbon cost of allocation to stems is offset under crowded conditions, because individuals that elongate often attain dominant positions in the size hierarchy and have higher lifetime light interception than shorter individuals (Smith 1982, 1994; Schmitt and Wulff 1993; Dudley and Schmitt 1996a; Weinig 2000). However, elongation is maladaptive when individuals are incapable of overtopping their neigh-

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bors; individuals that elongate incur the carbon cost of allocating to stems, but their leaves remain shaded (Weinig 2000). Under these conditions, light-quality cues are effectively unreliable. Although decreased red:far-red is correlated with the presence of neighbors, the positive correlation between elongation and fitness breaks down. Decreased plasticity to light quality is selected (Morgan and Smith 1979; Young 1981; Dudley and Schmitt 1996b).

Populations of many plant species experience both coarse- and fine-grained heterogeneity in competitive conditions (Harper 1977), and individual populations are likely to experience more or less reliable light-quality cues. The aim of this study was to answer the following questions. (1) Do populations derived from uniform and patchy environments differ in levels of stem elongation at early or later nodes? (2) Could selection to avoid the costs of a fixed, elongated phenotype limit the evolution of highly elongated, specialist genotypes? (3) Have population differences in plasticity to light-quality cues evolved? (4) Is population responsiveness to light quality correlated with the reliability of light-quality cues in the site of origin? This research examines growth responses of six populations of *Abutilon theophrasti* (velvetleaf), two from each of three site types (fields in continuous corn cultivation, fields undergoing corn-soy rotation, and weedy areas), to experimental light treatments in growth chamber and greenhouse experiments. At two stages in their life history, focal plants were exposed to either full-spectrum light, neutral shade, or simulated foliar shade, after which all internode lengths, biomass accumulation, and relative allocation to stems and leaves were measured.

Population Sites and Predicted Population Differences

Both soybeans and corn substantially reduce soil-level irradiance at some point in the season (McLachlan et al. 1993; Board and Harville 1996; Weinig 2000). Selection in soybean fields favors a discrete bout of elongation at later internodes because velvetleaf are able to grow taller than soybeans (Stoller and Woolley 1985; Regnier and Stoller 1989) and thereby improve light interception (Weinig 2000). Selection in cornfields may favor increased seedling elongation, which would delay shading of velvetleaf by corn plants. At later life-history stages, selection to decrease elongation is observed in cornfields because velvetleaf are incapable of overtopping corn and elongation fails to increase light interception (Weinig 2000). Directional selection is probably similar across microsites in cultivated fields because neighbor identity and neighbor proximity are unchanged. Selection may also be similar across growing seasons, depending on crop rotation schemes.

In some weedy areas, selection favors increases in stem elongation (Weinig 2000), but this selection probably varies across microsites and years. Velvetleaf seedlings in weedy areas may emerge in relatively dense stands of plants, but they may also in open patches and experience full sun. Neighbor identity is also variable.

In response to selection imposed by the competitive environment, populations from cornfields may have evolved higher, average elongation at the seedling stage relative to populations from disturbed, weedy areas (Table 1). At later

TABLE 1. Population differences predicted for average elongation and responsiveness to light-quality cues.

Site type	Average elongation	
	Seedling stage	Later stages
Disturbed, weedy areas	low	high
Rotating corn-soy fields	intermediate	intermediate
Continuous corn cultivation	high	low
Responsiveness to light-quality cues		
Site type	Seedling stage ¹	Later stages
Disturbed, weedy areas	—	high
Rotating corn-soy fields	—	intermediate
Continuous corn cultivation	—	low

¹ No a priori predictions exist for population differences in responsiveness of seedlings.

life-history stages, populations from fields in continuous corn cultivation may have both lower levels of average elongation and plasticity to light quality relative to populations from weedy areas (Table 1). Average elongation and relative plasticity of populations from fields undergoing rotating corn and soybean cultivation may be intermediate to populations from weedy areas and cornfields.

Population differences in elongation could evolve as a correlated response to selection acting on size and resulting changes in allometry rather than selection on stem elongation per se (Gould 1977; McKinney 1988). It is possible to distinguish between these two targets of selection by examining patterns of biomass accumulation and allocation. Populations with enhanced elongation are expected to have diminished leaf production. If populations with elevated elongation exhibit higher leaf production, and thus higher total biomass, then evolved internode differences may simply reflect a correlated response to selection on growth rate or size. If populations exhibit differences in life-history characters, for example, time to flowering, then selection on developmental rate may have occurred.

METHODS

Population Sources

Seeds used in this study were collected from two populations in each of three site types (i.e., weedy areas, fields undergoing corn-soy rotation, and fields undergoing continuous corn cultivation). The disturbed, weedy site type was represented by populations located at the Indiana University Faculty-Student Gardens and the Indiana University Aviaries in Bloomington, Indiana. Populations from the rotating corn-soy site type were located in Ames, Iowa and Bloomington, Indiana, and had been in cultivation for more than 75 years and 50 years, respectively. Populations experiencing continuous corn cultivation were located in Kokomo, Indiana, and Rosemont, Michigan, and had been in cultivation for about 20 years. Because velvetleaf is an annual with a short-lived seed bank (Baskin and Baskin 1973), the number of years in a location translates roughly into generations of selection. Gene flow among populations is likely to be low because the experimental populations were located at least several kilometers from one another and from populations in alternative site types. In addition, production of seeds from self-fertil-

ization approaches 97% in natural populations of velvetleaf (Andersen 1988), and seeds are passively dispersed from dehiscent capsules. Seeds from each population were obtained in 1996, and a subsample was subsequently grown for one generation in the greenhouse. The selfed progeny of the greenhouse-grown plants were used in this study in an effort to minimize potential maternal effects (Roach and Wulff 1986).

Growth Chamber Experiment: Experimental Design

The growth chamber experiment was used primarily to examine average population differences in seedling elongation and included only two light treatments: full-spectrum light and foliar shading. The full-spectrum treatment was established by placing clear, vinyl panels over the experimental plants. To simulate foliar shade, vinyl panels were airbrushed with pigments that reduce red light transmittance (Lee 1985; Dudley and Schmitt 1996b). A 3.5% solution of Hostperm Violet RL (American Hoechst, Inc., Coventry, RI) suspended in clear-finish varnish was sprayed onto 8-gauge, clear vinyl panels. Light spectral quality within each treatment was assessed using a LICOR 1600 spectroradiometer (Licor, Inc., Lincoln, NE). The ratio of red:far-red wavelengths was approximately 1.5 in the full-spectrum treatment and 0.4 under the simulated foliar-shade panels. Such ratios of red:far-red should affect elongation in a manner similar to direct sunlight and natural, vegetative canopies, respectively (Smith 1982).

Prior to planting, seeds were weighed and soaked in 60°C water for 10 min to minimize population differences in rate of germination. Fourteen seeds of each population were sown in randomized positions into each of four, celled trays filled with Metro-mix 360 (Scotts Company, Marysville, OH), after which the trays were placed in a Conviron (Pembina, ND) environmental chamber. The chamber was set for 11-h days with day/night temperatures of 24/17°C. Germination began after two days and was scored as date of hypocotyl emergence. When the first seedlings reached three days of age, two blocks were established. At each end of the chamber, one tray of seedlings was placed under a foliar-shade panel supported by chicken-wire fencing, whereas a second tray was placed under a clear vinyl panel similarly supported by chicken wire. Hypocotyl length was measured after four days under the treatment conditions and again six days later, after which individuals were harvested. Differences among populations and treatments in hypocotyl length were used to estimate the influence of these main effects on elongation, because differences in length should result from underlying differences in elongation. Leaf and stem tissues were separated, dried at 60°C for at least one week, and then weighed. The proportion of stem:total biomass was used to estimate the effects of elongation on allocation patterns.

Data Analysis

Comparisons were made between the first and second censuses of hypocotyl length to confirm that tissues were actively elongating during the treatment interval and, therefore, responsive to light conditions. Hypocotyl length of plants in

full light increased from $1.72 \text{ cm} \pm 0.03$ (SE) to 3.50 ± 0.04 between the pre- and posttreatment censuses.

Because the three-way interaction of block \times treatment \times population was nonsignificant for traits measured in the growth chamber ($P > 0.30$ for hypocotyl length at 13 days, total biomass), data from blocks were pooled. The effects of light environment and site type (i.e., weedy, rotating corn-soy, or continuous corn) were tested using three-way ANOVAs with treatment and site type as fixed effects and population nested within site type as a random effect (SPSS vers. 8.0; Norusis 1998). Error terms appropriate for hypothesis tests in mixed models were determined from the GLM procedure (SPSS vers. 8.0). Seed weight and germination date were included as covariates when significant at the $P < 0.15$ level.

Orthogonal contrasts were performed on the site-type effect and the site type \times treatment interaction to test a priori hypotheses regarding the effects of competitive history on elongation and growth responses. Site-type effects were partitioned into two contrasts testing whether populations derived from weedy areas differed from populations growing in cultivated fields (weedy areas vs. corn-soy fields and weedy areas vs. cornfields). Site type \times treatment interactions were partitioned into two similar orthogonal contrasts testing whether a population's site of origin affected the responsiveness of focal traits (e.g., internode lengths) to the light treatment. These contrasts assessed population responsiveness by comparing population differences observed in the full-light treatment with population differences measured in the foliar-shade treatment.

To determine the contribution of whole-plant growth to observed differences in hypocotyl length, a three-way ANCOVA for average hypocotyl length was performed with total biomass included as a covariate. If site-type effects diminish when the effects of biomass are controlled, then more elongated hypocotyls may have evolved as a correlated response to selection for accelerated growth rate or size rather than selection for greater hypocotyl elongation per se.

Greenhouse Experiment: Experimental Design

The greenhouse experiment was designed to test both population differences in average elongation and plasticity of elongation to light quality. Three light-treatments were included: full sunlight, neutral shade, and simulated foliar shade. The full-sunlight treatment and foliar-shade treatments were established by placing experimental plants under the vinyl panels described above. The neutral-shade treatment was set up through the use of shade cloths (Cornelia Inc, Cornelia, GA), which reduced incident light by 63%, but left light quality unchanged. Note that for this experiment the neutral-shade treatment served primarily as a control. Because the foliar-shade simulation involves an unavoidable, 60% reduction in total light, a neutral-shade group must be included to control for effects of irradiance. Differences between the full-sunlight and neutral-shade groups would reflect morphogenic responses to irradiance, whereas differences between the neutral- and foliar-shade groups should reveal responsiveness to light-quality cues.

On 22 March 1997, all seeds for the greenhouse study were

soaked and sown in germination trays as above. Germination began two days after planting and was scored as date of hypocotyl emergence. Seeds for this experiment were divided into two treatment cohorts that were exposed to light treatments at different ages. For the first cohort, 30–40 seedlings from five populations were included (one population from a cornfield, two from corn-soy fields, two from weedy areas). For cohort 2, a similar number of plants from four populations were used (two from corn-soy fields and two from weedy areas). The second cohort was limited to four populations because of space limitations in the greenhouse and the relatively larger size of older individuals. One week after germination began, seedlings in cohort 1 were transplanted into 4.5-in pots, whereas cohort 2 seedlings were moved to 5-in pots. Pots were randomized over all bench space in the greenhouse and were rotated every three days.

When plants were two weeks of age, cohort 1 individuals were censused for hypocotyl length and all internode lengths. These individuals were then moved into the light treatments, which were established by attaching the clear, neutral-shade, or foliar-shade panels to wooden frames on greenhouse benches. After four days under the light treatments, the length of all internodes and total height were measured. The same traits were measured once individuals had been under the treatments for 10 days. In the last three days of the treatment interval for cohort 1, some plants initiated flower buds. Individuals were assigned values between one and four such that the first individuals to produce buds were assigned a value of one, and those that failed to bud before the end of the treatment were given a value of four. Timing of bud appearance was used to estimate developmental rate. Following the treatment interval, all plants were harvested. Shoot and leaf tissues were separated and dried at 60°C for four days, at which point dry mass of each tissue was measured.

When the second cohort of plants was 4.5 weeks old, individuals were censused for all internode lengths and then placed in the experimental light treatments. After four days, cohort 2 individuals were censused for all internode lengths and total height. Following the treatment interval, above-ground tissues were collected, dried, and weighed as above.

For the greenhouse experiment, each light treatment was carried out on a single bench. Although treatment replication over the entire experimental area would have been desirable, this design was chosen because of the difficulty in fully separating light treatments. Light-treatment panels were arrayed several feet above the greenhouse benches. As a result, it was impossible to divide benches and fully isolate light environments such that each side of the bench received sunlight during all daylight hours. However, population rankings for seedling elongation were similar between the growth chamber and greenhouse experiments, as were the effects of full light relative to foliar shading (see Results). This suggests that the effects of experimental light treatments outweighed the effects of ambient environmental heterogeneity.

Data Analysis

In the greenhouse experiment, pretreatment censuses were again used to determine which internodes were actively elongating when the light treatments were applied. Hypocotyls

appeared almost fully expanded when the plants were two weeks of age, that is, when the light treatments were applied to cohort 1. Responsiveness of seedling elongation to light treatment was therefore determined using the average of the first and second internode lengths. To estimate responsiveness of later internodes, the average of the last internodes produced by each cohort was examined. For cohort 1, internodes 4–6 were measured. When cohort 1 plants were exposed to the treatments, only the first two internodes were present. Thus, internodes 4–6 must have been actively elongating in the treatment interval. For cohort 2, internodes 6–9 were used. Internodes 6–9 showed an average increase from $0.51 \text{ cm} \pm 0.03$ (SE) to 2.20 ± 0.07 , indicating that these internodes also were actively growing during the treatment interval.

Data were analyzed in a manner similar to the growth chamber experiment. Three-way mixed model ANOVAs were performed on the raw data for all traits. The data for time to flower-bud appearance failed to meet the ANOVA assumption of equal variances. However, tests performed on the raw data are presented because data transformations (Salisbury and Ross 1985) failed to reduce heteroscedasticity. Orthogonal contrasts were performed for main effects and site type \times treatment interactions to test a priori hypotheses regarding the effects of light quality and competitive history on elongation responses. The effects of light quality were tested by contrasting the neutral- and foliar-shade treatments. Site-type effects were partitioned as in the growth chamber experiment (weedy areas vs. corn-soy fields and weedy areas vs. cornfields). Site type \times treatment interactions were partitioned into two orthogonal contrasts testing whether a population's site of origin affected its responsiveness (e.g., in internode lengths) to light quality (weedy areas vs. corn-soy fields and weedy areas vs. cornfields). These contrasts assessed population responsiveness by comparing population differences observed in the neutral-shade treatment with population differences measured in the foliar-shade treatment. No contrasts were performed to determine differences among populations in responsiveness to light quantity because there were no a priori predictions regarding population differences in the morphogenic effects of irradiance.

For cohort 2, the effects of light environment on total biomass were impossible to determine because cohort 2 plants in the simulated foliar-shade treatment had senesced more leaves on average (2.8 ± 0.1) than individuals in the neutral-shade (1.7 ± 0.1) or full-light (1.3 ± 0.1) treatments. A one-way ANOVA was conducted to test the effects of population on biomass.

RESULTS

Growth Chamber Experiment

Light treatment significantly affected hypocotyl length (Table 2); on average, hypocotyls of individuals exposed to simulated foliar shade were twice as long as those of individuals grown under spectrally normal light (Fig. 1). Proportional allocation of biomass to stem tissues was also higher in individuals growing under foliar shade than in individuals growing under spectrally normal light (0.34 ± 0.00 vs. 0.20 ± 0.00 , respectively; Table 2). The shaded individuals

TABLE 2. Analysis of variance for traits measured in the growth chamber experiment, including hypocotyl length, biomass allocation (stem: total), total biomass, and ANCOVA for hypocotyl length with biomass as a covariate. Error mean squares (EMS) and error degrees of freedom (Edf) for each trait are as follows: hypocotyl length EMS = 0.169, Edf = 216; biomass allocation EMS = 7.21×10^{-4} , Edf = 217; total biomass EMS = 45.7, Edf = 217; ANCOVA for hypocotyl length EMS = 0.167, Edf = 215.

Effect	df	Hypocotyl length <i>F</i> -value	Biomass allocation <i>F</i> -value	Total biomass <i>F</i> -value	ANCOVA hypocotyl <i>F</i> -value
Treatment	1	2906.06***	1916.33***	338.54***	866.90***
Population(site type)	3	6.27	6.92	0.10	7.95
Site type	2	24.38*	0.04	164.15***	19.48*
Populations(site type)*treatment	2	0.61	0.72	1.18	0.49
Site type*treatment	3	0.10	2.45	1.70	0.28
Site type contrasts					
Weedy vs. corn	1	45.91**	0.01	397.25***	36.16**
Weedy vs. corn-soy	1	4.83	0.08	88.13**	4.02
Site type*treatment contrasts					
Weedy vs. corn	1	0.06	0.31	3.60	0.23
Weedy vs. corn-soy	1	0.16	1.73	1.65	0.32

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

also accumulated less biomass (17.2 ± 0.6 mg vs. 35.2 ± 0.6 mg; Table 2).

The cornfield site type exhibited significantly greater hypocotyl lengths on average than the weedy site type (Fig. 1; Table 2). Average hypocotyl lengths did not differ between the corn-soy and weedy site types (Table 2). The absence of significant two-way interactions demonstrates that neither populations nor site types differed in relative hypocotyl responsiveness to the light treatments (Table 2). Despite the fact that average hypocotyl lengths differed by 35% between the cornfield and weedy site types, proportional allocation of biomass to stem tissue did not differ among populations or site types (Table 2); all populations allocated between 26% and 27% of aboveground biomass to stem production. Thus, the comparatively large differences in hypocotyl length stimulated by the light treatment were associated with a trade-off between allocation to stems and leaves, whereas the smaller, genetically based population differences were not.

Site type affected total biomass accumulation (Table 2). Individuals from the weedy site type weighed significantly

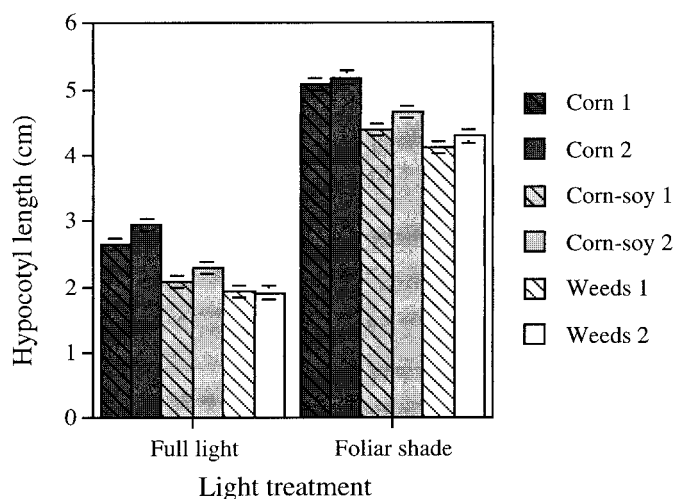


FIG. 1. Effects of light treatment and population on hypocotyl elongation observed in the growth chamber experiment. Means (\pm 1 SE) are shown.

less on average (22.3 ± 1.1 , 23.0 ± 1.1 mg) than those from both the cornfield (30.0 ± 1.1 , 29.6 ± 1.1 mg) and corn-soy site types (26.1 ± 1.1 , 26.2 ± 1.1 mg). The effect of site type on hypocotyl length remained significant in the ANCOVA including biomass as a covariate (Table 2), indicating that the observed differences in length were largely independent of differences in plant growth rate and size.

Greenhouse Experiment:

Elongation Responses and Biomass Allocation

In the greenhouse experiment, light treatment and site type significantly affected internode lengths and final height (summarized in Tables 3, 4). Following the four-day treatment interval for cohort 1, individuals exposed to simulated foliar shade had longer early internodes (internodes 1 and 2) than those grown under neutral shade (Table 5). Similar effects of light treatment were observed for later internodes measured both in cohort 1 (internodes 4–6) and in cohort 2 (internodes 6–9; Table 5).

Differences among site types in hypocotyl length observed prior to treatment application were somewhat less pronounced than in the growth chamber ($F = 10.96$; $df = 2, 2$; $P = 0.08$), but rankings for site type were identical between the two experiments. Individuals from the cornfield site type had longer hypocotyls on average than those from the weedy one ($F = 20.57$; $df = 1, 2$; $P = 0.04$), whereas hypocotyl length did not differ between the corn-soy and weedy site types ($F = 6.65$; $df = 1, 2$; $P = 0.12$; Fig. 2a). The cornfield site type had longer early internodes (internodes 1 and 2) than the weedy site type (Fig. 2b), but the length of these internodes did not differ between corn-soy and weedy site types (Fig. 2b). The site type \times treatment interaction was significant for internodes 1 and 2, and the contrasts indicated that responsiveness to light quality differed among site types (Table 3). The cornfield site type was significantly more responsive to foliar shade than the weedy one, but responsiveness did not differ between the corn-soy and weedy site types (Fig. 2c).

At later life-history stages, the rankings for site type were reversed. In cohort 1, the weedy site type had significantly longer late internodes (internodes 4–6) than both the cornfield

TABLE 3. Analysis of variance for traits measured in cohort 1 in the greenhouse experiment: early internode lengths (internodes 1 and 2), later internode lengths (internodes 4–6), seedling height (2.5 weeks of age), and final height (3.5 weeks of age). Error mean squares (EMS) and error degrees of freedom (Edf) for each trait were as follows: early internodes EMS = 4.29×10^{-2} , Edf = 508; late internodes EMS = 0.151, Edf = 483; seedling height EMS = 0.528, Edf = 492; final height EMS = 3.53, Edf = 489.

Effect	df	Internodes 1–2 <i>F</i> -value	Internodes 4–6 <i>F</i> -value	Seedling height <i>F</i> -value	Final height <i>F</i> -value
Treatment	2	2832.20***	158.17***	914.31***	537.82***
Population(site type)	2	6.19	1.72	14.93*	4.28
Site type	2	7.93†	50.24**	11.19†	2.99
Population(site type)*treatment	4	0.40	0.91	0.50	2.08
Site type*treatment	4	5.13*	9.04**	2.23	1.42
Treatment contrast					
Light quality	1	1474.25***	131.14***	435.82***	836.01***
Site type contrasts					
Weedy vs. corn	1	13.51*	52.67**	20.92*	0.79
Weedy vs. corn-soy	1	0.08	83.05**	6.39	3.62
Site type*treatment contrasts					
Weedy vs. corn	1	6.01*	9.45**	2.21	0.82
Weedy vs. corn-soy	1	0.78	3.48†	3.17	0.00

† $P < 0.08$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

and the corn-soy site types (Fig. 2d). In cohort 2, the weedy site type again exhibited longer late internodes (internodes 6–9) than the corn-soy site type (Fig. 2e). There was a significant site type \times treatment interaction for cohort 1 (Table 3) such that the weedy area showed heightened average responsiveness of internodes 4–6 to foliar shade relative to the cornfield (Fig. 2f). The weedy site type also tended to be more responsive than the corn-soy site type. For cohort 2, the site type \times treatment interaction for internodes 6–9 was non-significant (Table 4).

Population differences in average internode lengths translated into differences in overall height. At the first census for cohort 1, when plants were 2.5 weeks of age, individuals from the cornfield site type were taller on average than those from the weedy site type (Fig. 3a; Table 3). Differences in height between the corn-soy and weedy site types were not significant (Table 3). By the time cohort 1 plants had reached 3.5 weeks of age, rankings for site type had shifted, such that differences between the cornfield and weedy area were no longer significant (Fig. 3b; Table 3). Differences in height observed in cohort 2 between the weedy and corn-soy site types were nonsignificant (Fig. 3c; Table 4).

TABLE 4. Analysis of variance for traits measured in cohort 2 in the greenhouse experiment: later internode lengths (internodes 6–9) and final height (5 weeks of age). Error mean squares (EMS) and error degrees of freedom (Edf) for each trait are as follows: late internodes EMS = 0.718, Edf = 391; final height EMS = 13.5, Edf = 387.

Effect	df	Internodes 6–9 <i>F</i> -value	Final height <i>F</i> -value
Treatment	2	62.15**	59.88**
Population(site type)	2	1.84	1.19
Site type	1	25.24*	5.43
Population(site type)*treatment	4	0.97	1.91
Site type*treatment	2	0.45	0.41
Treatment contrast			
Light quality	1	74.8***	77.89***
Site type*treatment contrast			
Weedy vs. corn-soy	1	0.41	0.16

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

In comparison to individuals growing in neutral shade, individuals growing under foliar shade allocated a significantly higher proportion of total biomass to the production of stem relative to leaf tissue (Table 5; summarized in Table 6). Neither populations nor site types differed in biomass allocation patterns (Table 7). This result is similar to that of the growth chamber experiment; the comparatively large (60%) differences in height stimulated by light quality (Table 5) involved a trade-off between allocation to stems and leaves, whereas the smaller population differences in height did not.

Greenhouse Experiment: Growth and Developmental Rate

Individuals growing under simulated foliar shade unexpectedly accumulated slightly more aboveground biomass than those growing under neutral shade (Table 5; summarized in Table 6). However, the light-quality contrast was almost identical between the ANOVA for late internodes (Table 3) and the ANCOVA including biomass as a covariate ($F = 133.67$; $df = 1, 489$; $P < 0.001$), thus demonstrating that slight differences in plant biomass do not account for the effects of light quality on internode length.

Differences in total biomass were observed among populations in cohort 1 (Table 7). Populations in cohort 2 also differed in total biomass ($F = 11.94$; $df = 2, 390$; $P < 0.001$), but site types did not ($F = 0.91$; $df = 1, 2$; $P = 0.44$; Table 7). Thus, although the cornfield and corn-soy site types had shorter late internodes than the weedy area, they did not necessarily have lower biomass.

Individuals experiencing foliar shade initiated flower buds earlier than those under neutral shade (Table 5; summarized in Table 6). Neither populations nor site types differed in time to flower-bud appearance (Table 7). Populations did differ in plasticity of budding to foliar shade, but these differences did not generalize to site type (Fig. 4).

DISCUSSION

This study examined evolutionary responses to competitive environments that differed in the scale of environmental var-

TABLE 5. Treatment means (standard errors) for all traits measured in cohorts 1 and 2.

	Light environment		
	Full light	Neutral shade	Foliar shade
Internodes 1–2 (cm), cohort 1	0.86 (0.02)	0.92 (0.03)	1.90 (0.03)
Internodes 4–6 (cm), cohort 1	0.74 (0.03)	0.89 (0.03)	1.53 (0.03)
Internodes 6–9 (cm), cohort 2	1.74 (0.07)	1.88 (0.08)	2.78 (0.07)
Final height (cm), cohort 1	11.35 (0.15)	12.63 (0.15)	20.01 (0.15)
Biomass (stem:total), cohort 1	0.22 (0.00)	0.24 (0.00)	0.29 (0.00)
Total biomass (g), cohort 1	0.36 (0.01)	0.29 (0.01)	0.31 (0.01)
Date of budding, cohort 1	3.98 (0.05)	3.90 (0.05)	2.86 (0.04)

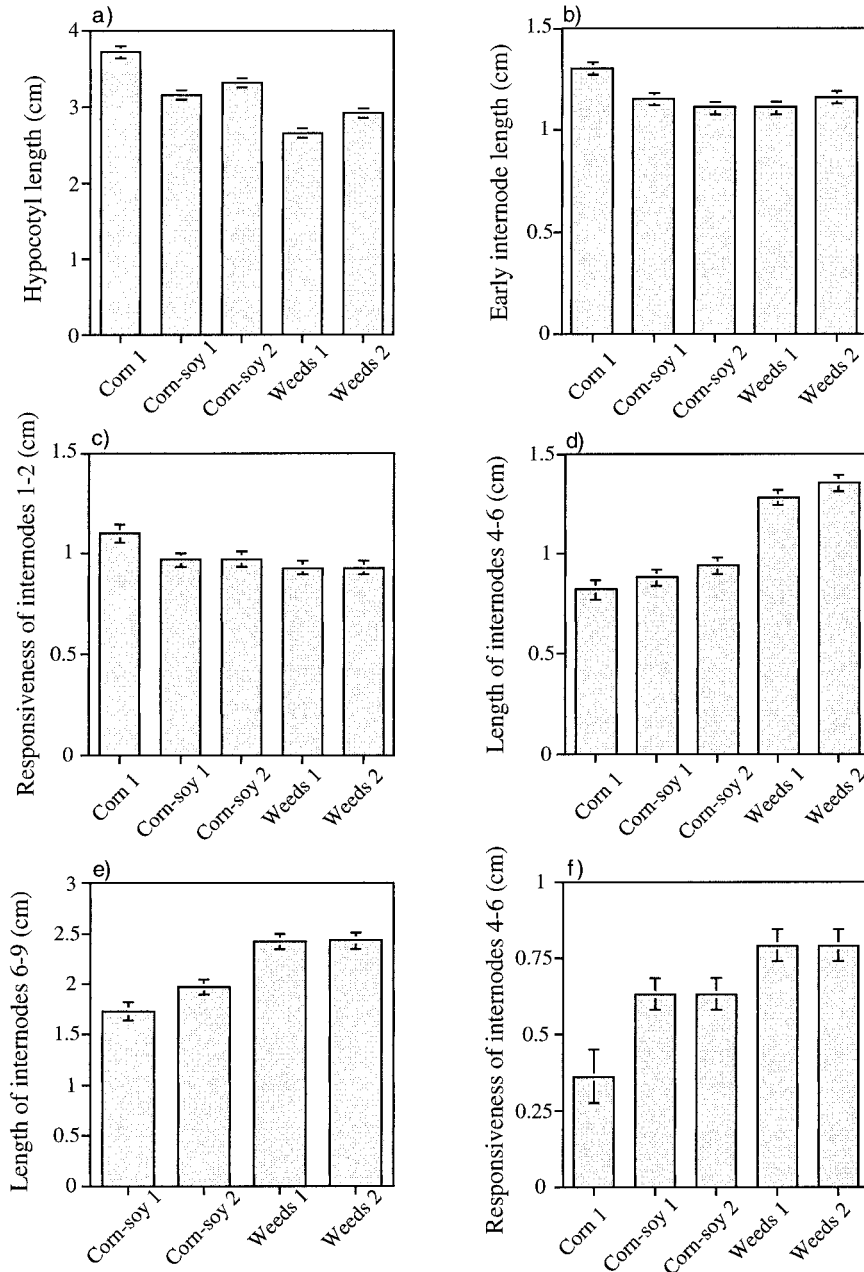


FIG. 2. Population differences observed in the greenhouse experiment for (a) average hypocotyl length; (b) average early internode lengths (internodes 1–2); (c) responsiveness of early internodes to light quality; (d) average late internode lengths of cohort 1 (internodes 4–6); (e) average late internode lengths of cohort 2 (internodes 6–9); and (f) responsiveness of late internodes measured in cohort 1 to light quality. Graphs of average lengths show population values averaged across light treatments (a, b, d, and e). Graphs of responsiveness depict length measurements in neutral shade subtracted from length measurements in foliar shade (c and f). Means (± 1 SE) are shown.

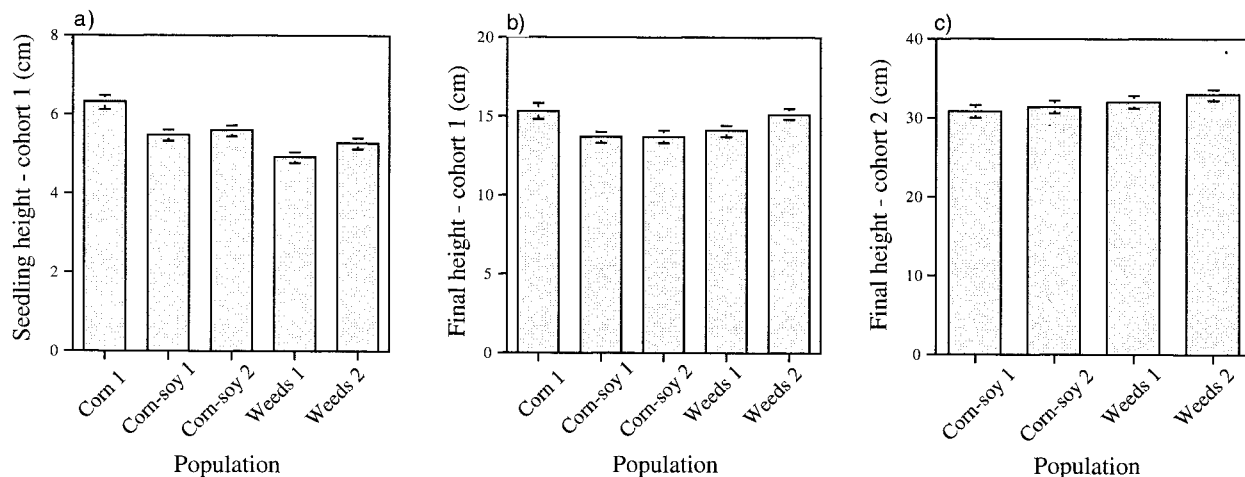


FIG. 3. Average population difference in height observed in the greenhouse experiment when plants were (a) 2.5 weeks of age, cohort 1; (b) 3.5 weeks of age, cohort 1; and (c) 5 weeks of age, cohort 2. Means (\pm 2 SE) are shown.

iability and the reliability of environmental cues. Average elongation at both early and later internodes differed between populations derived from homogeneous, cultivated-field sites and populations from patchy, weedy sites. Population rankings for average elongation were consistent with known patterns of phenotypic selection within each environment and support the hypothesis that the timing of elongation responses affects competitive ability (Weinig 2000). Plasticity to light quality also differed among populations such that those populations with a history of competition with corn were less responsive at later internodes than those from weedy sites. This result is consistent with the theoretical prediction that plasticity is selectively disadvantageous when environmental cues are unreliable. Given the known competitive history of the velvetleaf, the observed differences represent a very rapid evolutionary response. Velvetleaf was introduced to North America less than 200 years ago (Spencer 1984; Warwick and Black 1985). Because velvetleaf is an annual, it has experienced at most 200 generations of selection in cultivated

fields. Populations used in this study have a documented history of 20 generations of selection in cornfields and 75 years in rotating corn-soy fields. The discussion that follows addresses both the likelihood that interpopulation differences in elongation reflect adaptive differentiation and that plasticity to light-quality cues limits this differentiation.

Environmental Specialization

Interpopulation differences in elongation observed in this study probably reflect adaptive responses to competitive conditions. At the seedling stage, populations from cornfields exhibited greater elongation on average than populations from the weedy sites. Increased seedling elongation may be favored in cornfields because greater seedling height would delay shading of velvetleaf by corn. A previous study failed to detect selection to increase early elongation in cornfields (Weinig 2000), but significant nonlinear selection acting on other traits including late elongation and the combination of

TABLE 6. Analysis of variance for traits measured in cohort 1, including biomass allocation (stem:total), total biomass, ANCOVA for internodes 4–6 with biomass as a covariate, and time to budding. Error mean squares (EMS) and error degrees of freedom (Edf) for each trait are as follows: biomass allocation EMS = 6.7×10^{-4} , Edf = 492; total biomass EMS = 3.66×10^{-3} , Edf = 492; internodes 4–6 EMS = 0.110, Edf = 489; time to budding EMS = 0.299, Edf = 508.

Effect	df	Biomass allocation <i>F</i> -value	Total biomass <i>F</i> -value	ANCOVA internodes 4–6 <i>F</i> -value	Time to budding <i>F</i> -value
Treatment	2	304.58***	49.46***	264.72***	20.01**
Population(site type)	2	5.63	28.48**	1.94	0.99
Site type	2	2.93	0.14	51.51**	1.06
Population(site type)*treatment	4	1.10	0.81	0.90	10.07***
Site type*treatment	4	3.35	2.84	11.98**	1.11
Treatment contrast					
Light quality	1	249.90***	6.74**	133.67***	37.66**
Site type contrasts					
Weedy vs. corn	1	1.33	0.14	49.51*	0.26
Weedy vs. corn-soy	1	5.59	0.21	78.89**	2.12
Site type*treatment contrasts					
Weedy vs. corn	1	3.28	0.08	1.80	0.63
Weedy vs. corn-soy	1	0.42	3.20	12.22	3.09

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 7. Population means (standard errors) for proportional biomass allocation in cohort 1, total biomass in cohort 1, total biomass in cohort 2, and time to budding.

	Population origin				
	Cornfield	Corn-soy 1	Corn-soy 2	Weedy 1	Weedy 2
Biomass (stem:total)	0.246 (0.003)	0.247 (0.002)	0.238 (0.003)	0.252 (0.002)	0.260 (0.002)
Total biomass (g), cohort 1	0.31 (0.01)	0.29 (0.01)	0.34 (0.01)	0.31 (0.01)	0.34 (0.01)
Total biomass (g), cohort 2	na	0.79 (0.02)	0.91 (0.02)	0.77 (0.02)	0.82 (0.02)
Time to budding (days)	3.65 (0.07)	3.84 (0.05)	3.66 (0.06)	3.67 (0.05)	3.40 (0.05)

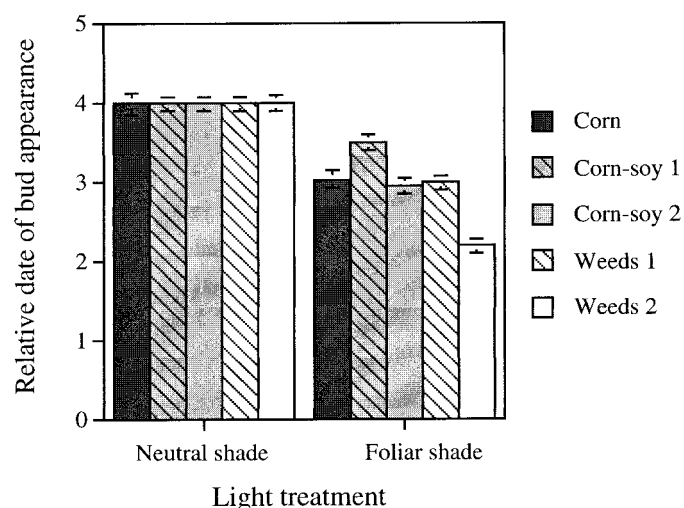
germination timing \times late elongation may have masked the fitness effects of elongation of early internodes (Brodie 1992). Competitive conditions favoring increased early elongation are expected to remain constant across microsites and growing seasons in cornfields because neighbor identity and neighbor proximity remain constant. In contrast, velvetleaf in weedy areas may emerge either in dense stands of seedlings or in relatively open, noncompetitive microsites such that the strength and direction of selection acting on elongation is variable.

Selection to increase seedling elongation may be accentuated in cornfields because velvetleaf are constrained to germinate synchronously with or later than the crop plants. Timing of germination and elongation generally interact in a complementary manner to increase competitive success (Weinig 2000). Early germination timing provides a head start to growth and enhances resource accumulation (Ross and Harper 1972; Harper and White 1974; Cook 1980; Fowler 1984; Kalisz 1986; Ellison 1987), whereas elongation raises an individual's position in the size hierarchy (Smith 1982; Ballaré 1991; Schmitt and Wulff 1993; Schmitt et al. 1995; Dudley and Schmitt 1996b). Velvetleaf in weedy areas may germinate as soon as abiotic conditions permit. However, velvetleaf in crop fields must emerge when their competitors do; individuals that germinate extremely early would emerge prior to crop sowing and would be eliminated during cultivation. As a result, competitive success in cultivated fields should depend largely on elongation. A number of other studies have suggested that differences in seed dormancy and germination

timing should affect the evolution of postgermination traits (Templeton and Levin 1979; Brown and Venable 1986; Venable 1989; Evans and Cabin 1995), such as stem elongation.

Population differences observed at later internodes are also likely to reflect adaptive responses to the competitive environment. Selection favors decreased late elongation in cornfields, because individuals that elongate at later life-history stages experience the carbon cost of elongation, but fail to increase leaf exposure (Weinig 2000). The present study detected that average elongation at later internodes was significantly reduced among individuals from a field undergoing continuous corn cultivation relative to individuals from weedy areas. Populations from corn-soy fields exhibited levels of elongation intermediate to those observed in populations from cornfields and weedy areas. This intermediate level may have evolved in response to alternating years of selection to increase elongation in soybean fields and to decrease elongation in cornfields.

Evolved differences in elongation are unlikely to result as a correlated response to selection acting on plant size because biomass levels failed to account for differences in length of both early and later internodes. Interpopulation differences observed at later stages are also unlikely to occur as a simple consequence of early responses and ensuing resource depletion, because early elongation did not appear to involve an allocation trade-off, that is, genetically based differences in seedling elongation did not affect proportional allocation to stem tissue. Seedling elongation is therefore unlikely to have had a detrimental affect on later elongation. Finally, populations did not differ in average time to flower-bud appearance, suggesting that differences in developmental rate are insufficient to explain differences in elongation.

FIG. 4. Effects of light quality and population on time to bud appearance. Means (± 1 SE) are shown.

Phenotypic Plasticity and Evolutionary Responses

Phenotypic plasticity may be evolutionarily favored over specialization, depending on the scale and frequency of environmental variation (Levins 1962, 1963, 1968; Lively 1986). When the environment has a high frequency of stressful, competitive patches, the direction of selection remains fairly constant. This may favor specialization and the evolution of a more fixed, competitive phenotype (Levene 1953; Waddington 1957). However, selection favors plasticity over a wide range of patch frequencies when individuals can adaptively modify their phenotype in response to reliable environmental cues and if the costs of stress-tolerant (e.g., competitive) phenotypes are high (Levins 1963; Lively 1986). Plastic individuals experience the fitness advantage of expressing the competitive phenotype under crowded condi-

tions, while avoiding the costs of expressing that phenotype under noncompetitive conditions.

The results of this study are consistent with the theoretical prediction that selection to avoid the costs of a fixed phenotype favors the evolution of plasticity and limits genetic differentiation, that is, specialization. Populations from the homogeneous cornfield environment were 18–35% taller, on average, at the seedling stage than populations from weedy areas. These differences are probably large enough to affect competitive ability, but they were not associated with increased allocation to stems. Light quality had a much larger effect on elongation than did population origin. In comparison to neutral shade, simulated foliar shade resulted in a 101% increase in hypocotyl length and a 60% increase in average seedling height. As other studies have shown (Morgan and Smith 1978; Robson et al. 1996), the comparatively high levels of elongation mediated by light quality were associated with increases in proportional allocation of biomass to stems. Under natural conditions, velvetleaf probably rely on light-quality cues to initiate competitive responses. This plasticity enables them to adopt costly, elongated phenotypes when such responses are explicitly adaptive, that is, under high-density conditions, and to avoid paying the cost of that phenotype in noncompetitive patches.

Population differences in plasticity to light-quality cues were observed at both early and later internodes. Differential plasticity might have evolved as a by-product of differences in average elongation or as an independent response to selection. Velvetleaf populations diverged with respect to average elongation in full-spectrum light, such that the cornfield population exhibited greater elongation at the seedling stage and diminished elongation at later internodes relative to the other populations. Cellular processes underlying elongation may be more active in early internodes and less active in later internodes. Other studies have shown that responsiveness to light quality is greatest in young, actively elongating internodes (Bain and Attridge 1988; Dudley and Schmitt 1996a). Thus, differences in average elongation and cell-level processes could explain why stem elongation was both enhanced among seedlings and reduced in older plants from the cornfield population.

The observed differences in plasticity could, alternatively, be adaptive responses to the selective environment. One cornfield population exhibited significantly enhanced plasticity relative to the other populations. Selection in cornfields may favor enhanced sensitivity to light quality at the seedling stage because of the wide, 30-in spacing of corn plants. The ability to detect neighbors may rely upon enhanced sensitivity to shifts in light conditions. At later stages, populations experiencing competition with corn showed diminished responsiveness to light quality relative to populations from weedy sites. As described above, individuals in cornfields that elongate at later internodes incur the costs of allocation to stem tissue, but fail to increase light capture. Decreased sensitivity to light quality is favored when elongation affects fitness detrimentally (Morgan and Smith 1979; Young 1981). Studies in *Impatiens* have detected analogous differences in plasticity between woodland and field populations (Dudley and Schmitt 1996b). Elongation is expected to be maladaptive in woodland sites because *Impatiens* individuals are clearly

incapable of overtopping the neighboring trees. Internode responsiveness to light cues is in fact lower in woodland relative to field populations. The results of both studies are consistent with evolutionary predictions that plasticity diminishes when environmental cues are unreliable and fail to provide useful information regarding environmental conditions (Levins 1963, 1968; Lloyd 1984; Lively 1986, 1998).

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