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TESTING THE ADAPTIVE PLASTICITY HYPOTHESIS:  
DENSITY-DEPENDENT SELECTION ON MANIPULATED STEM  
LENGTH IN *IMPATIENS CAPENSIS*

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**Abstract.**—In plants, stem elongation at high density in response to vegetation shade is hypothesized to be an example of adaptive phenotypic plasticity. Elongated stems may increase the light capture for plants in dense stands, while nonelongated stems may be favored for plants in low density. We tested the adaptive value of plastic stem elongation in *Impatiens capensis* by manipulating the controlling light cue, red to far red ratio, to produce elongated and nonelongated plants. These plants were then transplanted into high and low densities in a natural population. The results supported the adaptive plasticity hypothesis; elongated plants were more fit at high density, and suppressed plants were more fit at low density. Phenotypic selection analysis revealed selection for increased height in high density and for decreased height relative to leaf length in low density. Elongated plants showed less growth of the second internode at 2 wk after transplantation in both densities, which suggests a cost of elongation. Direct selection on height explained the fitness differences between suppressed and elongated plants at high density, but it did not completely explain the lower fitness of elongated plants at low density, which implies an intrinsic cost of elongation independent of selection on morphology.

A fundamental hypothesis about the evolution of phenotypic plasticity is that it provides a mechanism for adaptation to spatially or temporally variable environments. Given genetic variation for plasticity, reaction norms should thus evolve toward the optimal phenotype in response to differing selection in each environment (Via and Lande 1985). Functional arguments have often been used to suggest that an observed response to the environment increases fitness. However, very few studies have experimentally tested the hypothesis that the phenotype evoked by each environment results in higher relative fitness than the alternative phenotype (Cook and Johnson 1968; Kingsolver 1995*b*, 1995*c*; Schmitt et al. 1995), as is necessary to support the hypothesis of adaptive plasticity (Thompson 1991). The measurement of natural selection in differing environments (Lande and Arnold 1983; Wade and Kalisz 1990) may demonstrate that the adaptive value of a trait changes with environment (see, e.g., Dudley 1996; Kingsolver 1995*a*), but a determination of the fitness of the alternative (“wrong”) phenotype in an environment is prevented because the wrong phenotype is not expressed under

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natural conditions. Extending the range of variation of a trait by artificially manipulating the phenotype has become an increasingly important technique in studying natural selection (see, e.g., Andersson 1982; Nilsson 1988; Sinervo and Huey 1990; Anholt 1991; Sinervo and Licht 1991; Campbell et al. 1994; Kingsolver 1995*b*, 1995*c*). Phenotypic manipulation that results in the expression of the wrong phenotype in each environment offers a method for testing the hypothesis that phenotypic plasticity is adaptive.

For sessile plants, the physical environment is strongly determined by the presence of both interspecific and intraspecific competitors. Many plant species display characteristic stem elongation responses to crowding (Schmitt et al. 1987*b*; Geber 1989; Weiner et al. 1990; Ballaré et al. 1991; Weiner and Thomas 1992; Schmitt and Wulff 1993). Such elongation responses are elicited by a reduction in the red to far red ratio (R:FR) of incident light (Smith 1982). Vegetation shade alters spectral light quality, reducing R:FR, because chlorophyll absorbs more light in the red than in the far red wavelengths (Smith 1982). Consequently, R:FR provides a cue of the presence of competitors that is independent of irradiance (Smith 1982; Casal and Smith 1989; Ballaré et al. 1990; Smith et al. 1990). Other traits, such as branching and apical dominance, may also be affected by light quality (Morgan and Smith 1979; Smith 1982; Casal and Smith 1989). These plastic responses, referred to as the "shade avoidance syndrome" by plant physiologists, are thought to be mediated by light stable phytochromes, such as *Arabidopsis* phytochrome B, which are photoreceptors that convert reversibly between R- and FR-absorbing forms (Smith and Whitelam 1991; McCormac et al. 1992, 1993; Reed et al. 1994).

Because the environmental cue eliciting the response to density is known, stem elongation can be readily manipulated. The R:FR can be altered independently of plant density both to cue plants to elongate in the absence of competitors (see, e.g., Fitter and Ashmore 1974; Morgan and Smith 1979; Smith 1982; Solangarachchi and Harper 1987; Lee 1988; Ballaré et al. 1991; Schmitt and Wulff 1993; Dudley and Schmitt 1996) and to suppress the cue of elongation in the presence of competitors (Ballaré et al. 1990, 1991; Schmitt et al. 1995).

Functional arguments for the adaptive value of density-dependent stem elongation are based on the physiological ecology of resource acquisition and allocation in plants. At high density, stem elongation is hypothesized to permit plants to increase light interception under competitive conditions (Casal and Smith 1989; Ballaré et al. 1990; Schmitt and Wulff 1993). At low density stem elongation is hypothesized to be maladaptive (Casal and Smith 1989; Schmitt and Wulff 1993) because of the cost of allocating carbon to stems (Givnish 1982; Casal and Smith 1989) and because of the decreased mechanical strength of the elongated stem (Niklas 1992; Casal et al. 1994). In a greenhouse study using mutant *Brassica* and transgenic tobacco lines that lack plasticity (Schmitt et al. 1995), constitutively elongated plants had reduced fitness relative to plastic wild types at low density, whereas plants lacking the elongation response had reduced fitness at high density. However, the hypothesis that plasticity for stem elongation is adaptive has never been tested in the natural environment.

*Impatiens capensis* Meerb. (Balsaminaceae) offers an excellent system for test-

ing the adaptive value of the stem elongation response to density. *Impatiens capensis*, an annual, grows in a wide range of densities in woodland and open habitats. Asymmetric competition for light has been shown to result in density-dependent mortality and reproduction in natural populations (Schmitt et al. 1987a, 1987b). Elongation responses to crowding have been shown in *I. capensis* (Schmitt et al. 1987b; Schmitt and Wulff 1993) and its close relative *Impatiens pallida* (Weiner et al. 1990; Weiner and Thomas 1992). Elongation responses to simulated foliage shade have been observed in *I. capensis* (Wulff 1989; Schmitt and Wulff 1993; Dudley and Schmitt 1996) and in the closely related *Impatiens parviflora* (Whitelam and Johnson 1982; Young 1981). In *I. capensis*, this elongation response is stronger in genotypes from an open site than from woodland populations, which suggests adaptive genetic differentiation in response to selection in different light environments (Dudley and Schmitt 1996).

In this study, we manipulated the phenotype of *I. capensis* seedlings of 20 families descended from a natural population by either inducing or suppressing stem elongation. All plants were grown in high-density stands. In the elongated treatment, the stands received normal R:FR, which was reduced by the plant canopy to a level that induced elongation. In the suppressed treatment, the stands received high R:FR, which, though still reduced by the plant canopy, remained higher than the R:FR that induces strong elongation response (Smith 1982; Ballaré et al. 1991). The manipulated seedlings were transplanted into the natural environment at high and low densities, and lifetime reproduction was measured. We asked, How does the light quality manipulation affect the plant phenotype in each density? Are elongated plants more fit than suppressed plants at high density and less fit at low density, as the adaptive hypothesis predicts? If so, is this due to stronger selection for increased height at high density compared to low density?

#### MATERIAL AND METHODS

On May 6–8, 1992, we collected *Impatiens capensis* seedlings from a permanent 40 × 40 m grid within a large, continuous, highly selfing population in the understory of an oak-hickory forest at Brown University's Haffenreffer Reserve, Bristol, Rhode Island (Schmitt and Gamble 1990; Argyres and Schmitt 1991), to start a collection of inbred lines (Dudley and Schmitt 1996). From December 1993 to January 1994, third-generation selfed seeds from cleistogamous flowers were collected from three to five parent plants from each of 20 inbred lines and stratified in distilled water in individual wells of plastic microtiter trays at 4°C.

On April 16, 1994, approximately 600 seeds, most with emerging radicles, were planted in Metromix 350 in plug trays in 7 × 14 arrays 3.6 cm apart and placed in a cold frame outside the Brown University greenhouse. Seedlings started emerging after 4 d, and the date of emergence was scored for each individual.

#### *Experimental Design*

Seedlings with either suppressed (nonelongated) or elongated phenotypes were created by manipulating the light quality the seedlings received during their first 2 wk as follows. On May 3, 1994, 12–24 individuals from each of the 20 families

were randomly assigned to the four phenotype and density treatment combinations, which gave three to six individuals per family in each treatment combination. The seedlings were transplanted in Metromix 350 into six plug trays in arrays of  $5 \times 12$  plants 3.6 cm apart. Each plug tray was placed 0.2 m under a  $0.5 \times 0.8$  m Plexiglas tray containing either 12 L of a 15.0-g/L copper sulfate solution or 12 L of a 4.4-mg/L nigrosin solution contained in clear plastic bags. A screen of aluminum foil suspended from the Plexiglas tray blocked diffuse light from the side and reflected light back on plants. We also placed hardware cloth screens with aluminum foil around the plug trays immediately adjacent to the plants to support plants, block diffuse light from the side, and reflect light passed through the stand onto the border plants, reducing edge effects. Irradiance was reduced approximately 50% by the treatments; in the elongated (nigrosin) treatment, the R:FR above the plants was 1.11, slightly lower than the 1.24 of full sun, while in the suppressed (copper sulfate) treatment, the R:FR above the plants was 6.9 (J. Schmitt and S. A. Dudley, unpublished data), well above values normally found in nature. There were no treatment differences in the blue wavelengths. However, it is the R:FR beneath the plant canopy that determines plant morphogenesis. In a comparable experiment, these treatments resulted in R:FR at ground level underneath the plant stand of 0.29 in the elongated treatment and 0.91 in the suppressed treatment (J. Schmitt and S. A. Dudley, unpublished data). Studies in other plant species have shown that R:FR within a stand ranges from 1.1 to 0.3 or lower, decreasing with increasing density (Ballaré et al. 1990) or with increasing proximity to plants (Smith et al. 1990). For *I. capensis* in the field, one measure found R:FR at the base of a high-density stand to be 0.23 (J. Dudley and S. A. Schmitt, unpublished data).

On May 17–19, 1994, 240 elongated and 240 suppressed plants were ringed with numbered bird bands and planted out into two blocks in the same site as the source population. Each block contained a low-density plot and a high-density plot. Within each plot, suppressed and elongated plants were planted in a checkerboard array, with elongated and suppressed plants alternated within each row and column so that for each individual the adjacent four neighbors were of the opposite treatment and the diagonal neighbors of the same treatment. The position within the array was random with respect to family. The low-density plots consisted of two  $5 \times 12$  arrays of plants 20 cm apart, separated by a 1-m aisle. One end of the aisle contained a high-density plot, a  $10 \times 12$  array of plants 3 cm apart, surrounded by two border rows of transplanted local seedlings. All other plants and leaf litter were removed from the blocks. All plants were watered at the time of planting and two to three times thereafter in the first week to reduce transplant shock. After 1 wk, leaf litter was replaced in the low-density plot to retard soil moisture loss.

### *Measurements*

At the time of transplanting into the field, node heights, total height, and longest leaf length were measured on each plant. At a second census on June 3–4, 1994, 2 wk after transplanting, node heights, total height, and longest leaf length were measured, and flowers, immature fruits, mature fruits, and pedicels from dehisced

fruits were counted on each plant. At the second census 15 plants from each light treatment and density combination were harvested for dry biomass measures. At subsequent censuses at 7- to 10-d intervals, mortality was recorded, height and longest leaf length were measured, and flowers, immature fruits, mature fruits, and pedicels were counted. Censuses continued until all plants had died in late September.

Node heights were used to calculate internode lengths. Lifetime fitness was calculated for each individual as the number of reproductive structures (flowers, fruits, and pedicels) produced over the lifetime of the plant. For intact plants, lifetime cumulative reproduction was the sum of flowers, fruits, and pedicels at the census immediately prior to death. If a plant was damaged so that previous reproductive structures were lost, lifetime reproduction was estimated by summing the flowers and fruits at censuses subsequent to the damage with the estimate of cumulative reproduction at the last census when the plant was intact.

### *Data Analysis*

Plants that died between transplantation and the next census were assumed to have died of transplant shock and therefore were omitted from all analyses.

Statistical analyses were done on PC-SAS 6.08 for Windows (SAS 1989). A mixed-model ANOVA (see, e.g., Miller and Fowler 1993) was used to test for the fixed effects of light quality treatment, density, and light  $\times$  density interaction on height at the second census, longest leaf length at the second census, log(cumulative reproduction), and hypocotyl, internode 1, internode 2, and internode 3 lengths (PROC MIXED with REML, restricted maximum-likelihood estimation; SAS 1992). Random effects in the model were block, family, block  $\times$  density, family  $\times$  light, family  $\times$  density, and family  $\times$  light  $\times$  density. This approach corresponds to a split-plot design, with density effects tested over the block  $\times$  density interaction. The decision was made to omit interactions between block and light treatment, since the light treatments were imposed before the plants were placed in the blocks, and all interactions involving block and family, because they were expected to be small and unimportant for the hypotheses tested here. A check of these assumptions (not shown) found that the second-order interactions block  $\times$  light and block  $\times$  family were very small or zero. The random effects in PROC MIXED are estimated by restricted maximum likelihood. When any of these terms were estimated as zero, the model was rerun without them. The significance of the fixed effects, light treatment, density, and light  $\times$  density interaction was tested from Type III estimable functions, with denominator degrees of freedom taken from a containment method (SAS 1992). The significance of the random effects was computed from a *Z* value (the variance parameter divided by its approximate standard error), which was then tested for a difference from zero (SAS 1992).

For each density treatment, we used PROC LIFETEST to test the hypothesis that the survival rate curves differed between light treatments.

To test the adaptive hypotheses about direct selection on stem elongation in high and low density, we carried out two phenotypic selection analyses following Lande and Arnold (1983). The first selection analysis included the emergence

date and height and leaf length at the time of transplantation. Selection on elongation, which is height relative to size, is measured by the selection on height when the plant size, measured in this analysis by leaf length and emergence date, is included in the selection analysis. This selection analysis tested for the role of initial stem elongation, which was strongly determined by the light treatments, in determining fitness.

The second selection analysis included height and leaf length at the second census, 2 wk after transplantation. Leaf length at the second census was included as a measure of plant size. Height at the second census measures relative position in the competitive hierarchy arising from both the initial light treatment and the subsequent plastic responses to density. An examination of heights across all the censuses (not shown) suggested that relative height ranking changed considerably between the first and second census but relatively little thereafter. Height was not bimodally distributed at the second census, and so this selection analysis more closely resembles selection in natural populations.

Directional standardized selection gradients were obtained from a linear regression of relative fitness on the standardized traits, and quadratic selection gradients were obtained from then regressing relative fitness on linear and quadratic terms (PROC GLM in SAS 1989). Because the residual variance was nonnormal, significance values for the selection gradients were estimated from a jackknife analysis (FreeStat; Mitchell-Olds 1989). Differences in selection gradients between densities were tested by constructing *t* statistics to test the hypothesis that the differences between corresponding selection gradients from the two densities were zero. The difference between the selection gradients was divided by the standard error for the difference of the selection gradients (Sokal and Rohlf 1981), using the standard errors for each selection gradient from the jackknife analyses. None of the nonlinear selection gradients were significant, and so these results are not presented.

Family means were estimated for each trait and fitness. Family mean selection analyses (Rausher 1992) were calculated for each selection analysis above. Results tended to be similar, though less significant because of the lower sample size (20 families vs. approximately 200 individuals in each density treatment), and are therefore not presented.

To differentiate between treatment effects on height due to stem elongation and effects due to changes in overall size, we used an ANCOVA with height as the dependent variable and leaf length as a covariate (PROC GLM, TYPE III Sums of Squares). Significant differences in the mean for stem length adjusted for leaf size (tested by the TDIFF option in the LSMEANS option of PROC GLM) due to either covariate or covariate  $\times$  leaf interactions would indicate that the treatment had affected elongation, changing stem length relative to leaf size.

To test the post hoc hypothesis that effects of light treatments on internode 3 length at the second census could be explained by greater overall height, we carried out an ANCOVA for the effect of light treatment on internode 3 in each density, with height at the second census as a covariate (PROC GLM). Differences in the adjusted mean were tested using option TDIFF, as above.

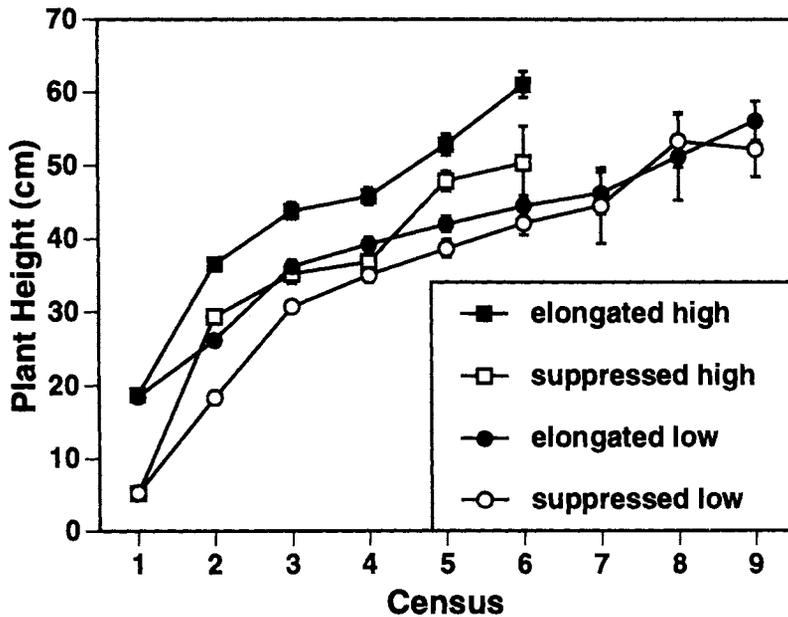


FIG. 1.—Average plant heights for each combination of light and density treatment from census 1 to census 9. After census 9, only low-density suppressed plants were alive. Bars indicate 1 SE and may be smaller than the symbol.

To test the hypothesis that light treatments had effects on fitness independent of direct selection on leaf length and height at the second census, we used an ANCOVA at each density with height and leaf length as covariates (PROC GLM, TYPE III Sums of Squares) and fitness as the dependent variable. Significant covariate or covariate  $\times$  light interactions would indicate that elongation had intrinsic effects on fitness that were not due specifically to light treatment effects on height and leaf length. No such analysis was done for the early height characters, because at this time height and light treatment were strongly collinear.

## RESULTS

Increasing R:FR in dense seedling stands dramatically suppressed stem elongation (fig. 1). At the time of planting, plants grown under neutral shade were over three times taller than plants grown in high R:FR (fig. 1). Plant height also responded to subsequent planting density, with height at the second census in high density 10 cm taller than height at low density for both light treatments (table 1; fig. 1). However, significant height differences between initial light treatments were still found at the second census (table 1) and were maintained throughout the experiment in the high-density treatment (fig. 1). There was no significant interaction between light and density treatment effects on height at the second census (table 1). Longest leaf length was significantly greater in elongated plants at the second census, but it did not differ significantly between density treatments

TABLE 1

MIXED-MODEL ANOVA OF EFFECTS OF R:FR LIGHT AND PLANTING DENSITY ON HEIGHT AND LEAF LENGTH AT 2 WK AFTER TRANSPLANTATION TO THE FIELD AND LOG (CUMULATIVE REPRODUCTION)

SOURCE	HEIGHT AT SECOND CENSUS			LEAF LENGTH AT SECOND CENSUS			LOG (CUMULATIVE REPRODUCTION)		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Light	19	95.1	.0000	57	6.1	.0164	19	.0	.9925
Density	38	218.2	.0000	1	10.0	.1953	2	17.2	.0536
Light × density	38	.4	.5172	57	.0	.8770	19	5.6	.0291

NOTE.—Results from likelihood-ratio Type III *F*-tests for fixed effects are shown; *N* = 396. Numerator degrees of freedom were one for all fixed effects. Denominator degrees of freedom are shown in the table. They may differ between variables because when random effects were estimated as zero (see table 3), they were omitted from the model.

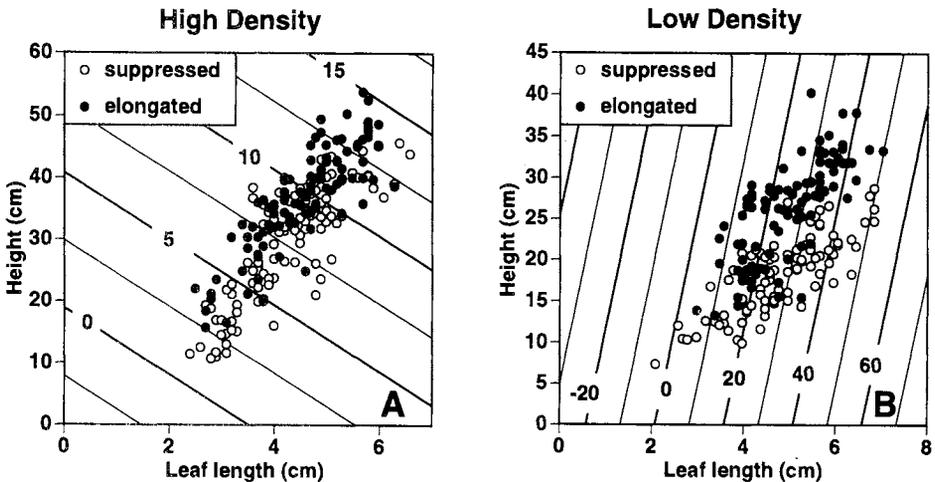


FIG. 2.—Relationship of height to leaf length at the second census for elongated and suppressed plants at (A) high density and (B) low density. Selection surfaces are superimposed over this plot. Contour lines are of estimated cumulative reproduction at each height and leaf length at the second census. Note that scales differ between high and low density.

at the second census (table 1). The changes in the relationship between height and leaf length caused by the light and density treatments were revealed by ANCOVA. Elongated plants had significantly longer stems relative to their leaf length than did suppressed plants at the second census in both density treatments (GLM, LSMEANS option TDIF, high-density  $t = 8.28$ ,  $P = .0001$ ; low-density  $t = 9.87$ ,  $P = .0001$ ) (fig. 2). Height relative to leaf length was significantly greater in the high-density treatment than in the low-density treatment (GLM, LSMEANS option TDIF,  $t = 12.8$ ,  $P = .0001$ ).

At the time of planting, the stem was primarily composed of the hypocotyl, internode 1, and internode 2, which were all significantly longer in plants from

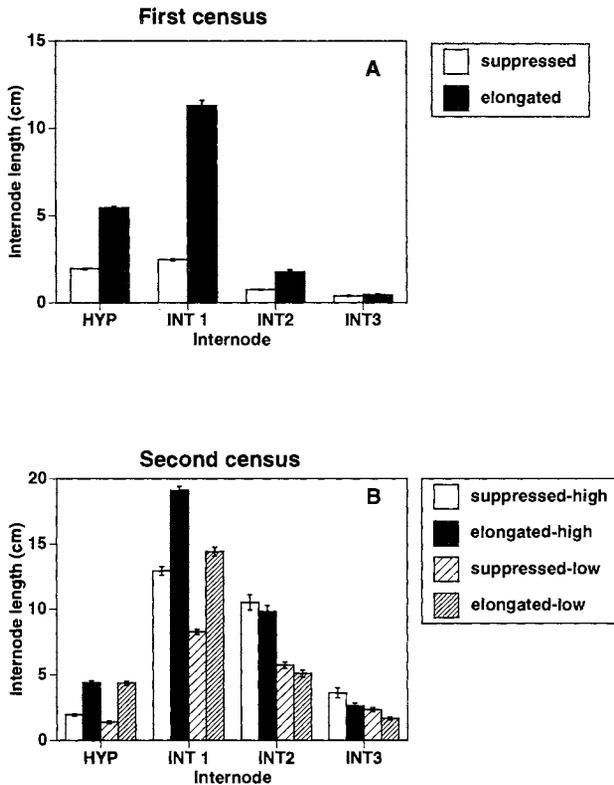


FIG. 3.—Average internode lengths at (A) the time of transplantation and (B) 2 wk after transplantation for each light treatment and density. Bars indicate 1 SE.

the elongated treatment (fig. 3). At the second census, 2 wk later, the hypocotyl and internode 1 were still significantly longer for plants from the elongated treatment, but there was no significant effect of the initial phenotype manipulation on internode 2, which had continued to expand actively after transplantation (table 2). Internode 3, which had begun expansion after the time of transplantation, was significantly *shorter* for plants from the elongated treatment in both densities (fig. 3; table 2). An ANCOVA for each planting density revealed that taller plants had more internode 3 growth within each light treatment; when the effects of plant height were controlled, the difference in adjusted means between light treatments remained significant (GLM, LSMEANS option TDIF, at high density,  $t = 7.06$ ,  $P < .0007$ ; at low density,  $t = 17.17$ ,  $P < .0001$ ). These results suggest that in both densities new stem growth was slower in elongated plants, which thus may indicate an intrinsic cost of elongation.

The hypocotyl, which had completed expansion at the time of transplantation, showed no significant response to density treatment at the second census (table 2). However, internodes 1, 2, and 3 all were significantly longer in the high-density treatment, which indicates a plastic elongation response to neighbors (table 2;

TABLE 2

MIXED-MODEL ANOVA OF EFFECTS OF R:FR LIGHT AND PLANTING DENSITY ON HYPOCOTYL, INTERNODE 1, INTERNODE 2, AND INTERNODE 3 AT 2 WK AFTER TRANSPLANTATION TO THE FIELD

SOURCE	HYPOCOTYL			INTERNODE 1			INTERNODE 2			INTERNODE 3		
	df	F	P	df	F	P	df	F	P	df	F	P
Light	19	303.4	.0000	19	245.9	.0000	19	2.5	.1291	19	11.8	.0028
Density	2	.8	.4678	2	77.3	.0127	38	114.4	.0000	19	16.2	.0007
Light × density	334	3.4	.0672	19	.0	.9354	38	.3	.6136	19	.6	.4381

NOTE.—Results from likelihood-ratio Type III *F*-tests for fixed effects are shown; *N* = 396. Numerator degrees of freedom were one for all fixed effects. Denominator degrees of freedom may differ because when random effects were estimated as zero (see table 4), they were omitted from the model.

TABLE 3

VARIANCE COMPONENTS FOR HEIGHT AND LEAF LENGTH AT 2 WK AFTER TRANSPLANTATION TO THE FIELD AND FOR LOGARITHM OF CUMULATIVE REPRODUCTION, FROM THE MIXED-MODEL ANOVA FOR RANDOM EFFECTS, USING REML

SOURCE	HEIGHT AT SECOND CENSUS		LEAF LENGTH AT SECOND CENSUS		LOG (CUMULATIVE REPRODUCTION)	
	Component	SE	Component	SE	Component	SE
Block	.000	...	.002	.02	.000	.012
Block × density	.000	...	.013	.03	.012	.02
Family	10.9*	4.72	.211*	.09	.006	.00
Family × light	.424	2.61	.000	...	.000	.00
Family × density	.000	...	.000	...	.002	.00
Family × light × density	2.45	2.75	.059	.04	.003	.00
Residual	41.4***	3.28	.600***	.05	.053***	.00

NOTE.—Significance of variance components was tested by determining whether the *Z*-values (component divided by the SE) differed from zero.

\* *P* < .05.

\*\*\* *P* < .001.

fig. 3). There were no significant light × density treatment interactions for any internode (table 2).

Mixed-model analysis revealed significant variation among families for all traits except internode 1 at the second census and cumulative reproduction (tables 3, 4). However, no significant family × light treatment or family × density effects were detected. There was thus no evidence for family variation in plastic response to initial R:FR treatment or subsequent neighbor density.

An ANCOVA for the dry aboveground biomass of the sample of plants harvested at the second census, with emergence date as a covariate, revealed that plants from the elongated treatment had greater aboveground biomass averaged over both densities (table 5; fig. 4). However, there was a significant light treatment × density effect (table 5), with the plants from the suppressed treatment having greater biomass in low density than high, and plants from the elongated treatment having greater biomass in high density than in low (fig. 5). This interaction is in the direction predicted by the adaptive plasticity hypothesis.

TABLE 4

VARIANCE COMPONENTS FOR HYPOCOTYL, INTERNODE 1, INTERNODE 2, AND INTERNODE 3 AT 2 WK AFTER TRANSPLANTATION TO THE FIELD, FROM THE MIXED-MODEL ANOVA FOR RANDOM EFFECTS, USING REML

SOURCE	HYPOCOTYL		INTERNODE 1		INTERNODE 2		INTERNODE 3	
	Component	SE	Component	SE	Component	SE	Component	SE
Block	.000	...	.000	...	.000	...	.000	...
Block × density	.153	.16	.102	.17	.000	...	.000	...
Family	.346*	.16	.643	.73	3.77*	1.63	1.06*	.49
Family × light	.137	.08	.492	.61	.037	.92	.027	.23
Family × density	.028	.05	.850	.71	.000	...	.197	.26
Family × light × density	.000	...	.656	.69	1.24	1.01	.163	.32
Residual	1.06***	.08	6.93***	.55	13.5***	1.08	4.05***	.32

NOTE.—Significance of variance components was tested by determining whether the *Z*-values (component divided by the SE) differed from zero.

\* *P* < .05.

\*\*\* *P* < .001.

TABLE 5

ANCOVA FOR THE DRY BIOMASS OF THE 58 PLANTS HARVESTED AT THE SECOND CENSUS, 2 WK AFTER TRANSPLANTATION TO THE DENSITY TREATMENTS

Source	df	MS	<i>F</i>
Light	1	.04464	11.30**
Density	1	.00488	1.23
Light × density	1	.01754	4.44*
Block	1	.00331	.84
Emergence date	1	.19746	49.98***
Error	56	.00395	...

\* *P* < .05.

\*\* *P* < .01.

\*\*\* *P* < .001.

Log-transformed cumulative reproduction, our measure of lifetime fitness, was marginally greater in low-density plants, but it did not differ overall between light treatments (table 1) and did not vary among families (table 3). There was, however, a significant light treatment × density interaction for log-transformed cumulative reproduction (table 1). As predicted, suppressed plants had higher cumulative reproduction than did elongated plants at low density, but elongated plants had higher cumulative reproduction than suppressed plants at high density (fig. 5), which strongly supports the adaptive plasticity hypothesis. Survival rate within a density treatment did not significantly differ between light treatments (PROC LIFETEST log-rank test, high-density,  $\chi^2 = 0.57$ , *P* = .45; low-density,  $\chi^2 = 3.10$ , *P* = .08), which implies that the differences in fitness resulted from effects of the light treatment on growth rather than mortality.

The adaptive plasticity hypothesis further predicts that the observed light treatment × density interaction effect on fitness is caused by differing selection on plant height between high and low density. A phenotypic selection analysis of

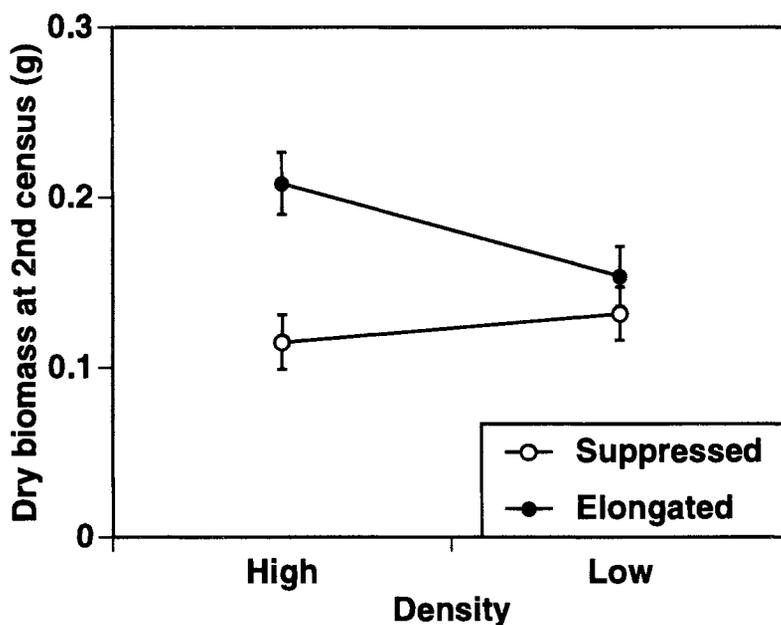


FIG. 4.—Dry biomass adjusted for emergence date by ANCOVA of 58 plants harvested after 2 wk in the density treatments. Bars indicate 1 SE.

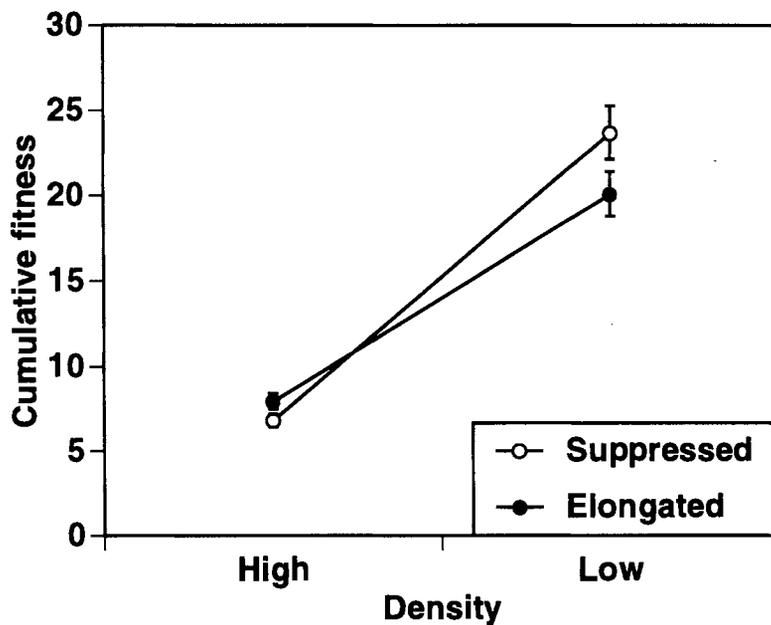


FIG. 5.—Average cumulative reproduction for each light treatment at high and low density. Means and SEs were obtained on log-transformed data and have been back transformed for this figure. Bars indicate 1 SE.

TABLE 6

STANDARDIZED PHENOTYPIC SELECTION GRADIENTS ( $\beta'$ ) AT EACH DENSITY FOR  
(A) EMERGENCE DATE, AND LEAF LENGTH AND HEIGHT AT THE TIME OF  
TRANSPLANTATION, AND FOR (B) LEAF LENGTH AND HEIGHT 2 WK  
AFTER TRANSPLANTATION TO THE FIELD

TRAIT	$\beta'$ AT EACH DENSITY		<i>t</i>
	High	Low	
A:			
Emergence date	-.139**	-.078	-.81
Leaf length at first census	.223***	.250**	-.27
Height at first census	.082 <sup>+</sup>	-.153*	2.65**
B:			
Leaf length at second census	.129*	.468***	4.48***
Height at second census	.252***	-.119*	-3.18***

NOTE.—Individuals from both light treatments are included in each selection analysis. Low density,  $n = 193$ ; high density,  $n = 203$ . Probabilities associated with each  $\beta'$  are for difference from zero, from a drop-one jackknife of the regression coefficient. The  $t$  value is for the significance of differences of  $\beta'$ 's between densities, using a pooled SE from the jackknife analyses.

<sup>+</sup>  $P < .10$ .

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

traits at the time of transplantation showed selection favoring early emergence date, significant in high density, and large leaves, significant in both densities (table 6). However, the selection gradients for height at first census differed significantly from one another. Selection tended toward increased height at high density and was marginally significant, and it significantly favored decreased height at low density. A second phenotypic selection analysis was done on height and leaf length traits after plants had responded to the density treatments and the height hierarchy had been established. This second analysis better represents selection in a natural stand because height was not bimodally distributed. It showed that direct selection on height and leaf size at the second census differed between high and low densities (table 6; fig. 2). At low density, longer leaves were strongly favored, and there was significant selection for lower height. At high density, selection on leaf length, though still positive, was significantly weaker than in low density, and there was strong selection for increased height. The results of both selection analyses support the hypothesis that stem elongation is adaptive in high density, and they suggest that it may be maladaptive when plants are at low density.

An ANCOVA showed that in high density, fitness differences between suppressed and elongated phenotypes were completely explained by the induced changes in height and leaf length at the second census; there was no independent light treatment effect (table 7). At low density, however, elongated plants had lower fitness than suppressed plants, controlling for the effects of height and leaf length at the second census; no significant selection on height was detected when the light treatment effect was included (table 7). This result suggests an intrinsic cost to elongation at low density independent of direct selection on height.

TABLE 7

ANCOVA FOR LIGHT QUALITY TREATMENT EFFECTS ON CUMULATIVE REPRODUCTION IN EACH DENSITY, WITH LEAF LENGTH AND HEIGHT AT 2 WK AFTER TRANSPLANTATION INCLUDED AS COVARIATES

TRAIT	HIGH DENSITY			LOW DENSITY		
	df	MS	F	df	MS	F
Leaf length at second census	1	.65	3.3 <sup>+</sup>	1	9.28	20.5***
Height at second census	1	4.33	21.7***	1	.35	.8
Light	1	.22	1.1	1	3.14	6.9**
Light × leaf	1	.03	.2	1	.15	.3
Light × height	1	.22	1.1	1	.25	.5
Error	202	.20	...	192	.45	...

<sup>+</sup>  $P < .10$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

## DISCUSSION

The adaptive plasticity hypothesis for the shade avoidance response in plants predicts that the fitness consequence of stem elongation will be density-dependent and specifically that selection for increased stem height will be greater in high density. We were able to test these predictions by manipulating the R:FR light cue controlling stem elongation, successfully extending the range of phenotypes in both density environments. As the shade avoidance hypothesis predicts, elongated plants had higher fitness than suppressed plants at high density and lower fitness at low density in a natural population. This result supports the hypothesis that phytochrome-mediated plastic response to crowding is adaptive. The observed differences between density treatments in phenotypic selection gradients support the hypothesis that plastic stem elongation, specifically, is adaptive; at high density selection favored taller plants, but at low density selection favored shorter plants. Direct selection on height explained the fitness differences between suppressed and elongated plants at high density but did not completely explain the lower fitness of elongated plants at low density, which suggests an intrinsic cost of elongation independent of selection on morphology.

The shade avoidance hypothesis for phytochrome-mediated adaptive plasticity in response to crowding has been widely discussed in the physiological literature (see, e.g., Smith 1982; Ballaré et al. 1987, 1990; Casal and Smith 1989). However, until recently, this hypothesis has never been explicitly tested by examining the relative fitness of elongated and nonelongated phenotypes at high and low densities, although a few studies have examined the impact of shade avoidance on yields from a stand perspective (Ballaré et al. 1991; Smith 1992). In a greenhouse study that extended the range of the phenotype through using mutant *Brassica* and transgenic tobacco plants (Schmitt et al. 1995), elongated plants were found to have higher relative fitness at high densities than low, and nonelongated plants to have higher relative fitness at low densities than high, which supports the shade avoidance hypothesis. However, to our knowledge, the present study is

the first test of the hypothesis in a natural plant population. The strength of this study lies in the opportunity to use R:FR manipulation to extend the range of the phenotype and in the measurement of lifetime fitness consequences in the natural environment.

In our experiment, an increase in the R:FR received by plants in dense stands dramatically suppressed the stem elongation response to crowding, as previously reported in other species (Ballaré et al. 1990, 1991; Schmitt et al. 1995). Plants in the high R:FR treatment were shorter and had longer leaves relative to their height than plants receiving reduced R:FR as a cue of neighbor proximity. This result provides strong evidence that previous observations of density-dependent stem elongation in *Impatiens* (Schmitt et al. 1987b; Weiner et al. 1990; Weiner and Thomas 1992) are phytochrome-mediated R:FR responses (Smith 1982). Since the treatments did not differ in the blue wavelengths, the observed response cannot be attributed to the blue light receptor (Ahmad and Cashmore 1993). The effects of the initial phenotype manipulation on plant height persisted over time, although the plants also responded to the planting densities that were subsequently imposed. The effects of initial elongation persisted most strongly in the hypocotyl and internode 1, which were the earliest to complete expansion relative to the initiation of the density treatments. Thus, the initial light quality treatment successfully extended the range of variation in both density treatments, and the plastic response to density could not completely compensate for initial morphology. Consequently, we were able to test the predictions of the shade avoidance hypothesis for adaptive plasticity by examining selection on alternative phenotypes within each density. It seems likely that the similar morphological responses to density often observed in other species (Geber 1989; Weiner and Thomas 1992) are also at least partially phytochrome mediated. If so, R:FR manipulation may be generally useful as a noninvasive tool for phenotype manipulation in plant population biology.

The general prediction of the adaptive plasticity hypothesis is that the effect on fitness of the R:FR-induced shade avoidance response should depend on density (Casal and Smith 1989; Schmitt and Wulff 1993; Schmitt et al. 1995). The results supported this prediction. The biomass of elongated plants 2 wk after transplant was higher relative to that of suppressed plants at high density than at low density. More important, at high density, the elongated plants had greater lifetime fitness. At low density, the suppressed plants had greater fitness. This result supports the hypothesis that R:FR-mediated phenotypic changes induced in response to the density environment are adaptive.

A specific prediction of the adaptive plasticity hypothesis is that selection for increased height should be greater in high density than in low density (Casal and Smith 1989; Schmitt and Wulff 1993). This prediction was also supported by the results of this experiment. In the phenotypic selection analyses, longest leaf length was also included as a measure of plant size and of ability to capture light. Selection depended on density for both traits. At high density, height at the first census was marginally selected to increase and at the second census was significantly selected to increase, but, at low density, selection significantly favored shorter plants height at both the first and second census. In contrast, leaf

length at both censuses was selected to increase in both densities, and leaf length at the second census was more strongly selected to increase at low density than at high density. Thus, in high density, height, which determines the placement of the light capture surface in the foliage canopy, best predicted fitness. In low density, longest leaf length, a measure of surface for light capture, best predicted fitness. Taken together, these results provide strong support to the hypothesis that under natural conditions stem elongation at high density, and lack of elongation at low density, are adaptive.

Although we observed a direct benefit to height at high density, these results do not necessarily indicate a direct cost of height itself at low density. In high density, when the effects of height and leaf length on fitness were included in an ANCOVA, phenotypic manipulation had no direct effect on fitness, which indicates that the fitness impact of the treatment was entirely due to selection on these morphological traits. But in low density the plants from the elongated treatment had lower fitness even after adjustment for the effects of leaf size and height, which suggests that these traits per se cannot account for the cost of the shade avoidance response at low density. This result suggests that an unmeasured phenotypic response accompanying stem elongation caused the cost of elongation in the low-density environment.

Additional evidence for an intrinsic cost of the elongation response was found in examining internode lengths at the second census. Internode 3 was longer in plants in high density, as expected. However, within each density the length of internode 3 was shorter in plants from the elongated treatment. Internode 3 was growing at the time of measurement, so that its length depended on the elongation and on the rate of growth. Thus, this result implies that internode 3 grew more slowly in plants from the elongated treatment in both planting densities. It is unlikely to be a shift in growth pattern, since greater apical dominance, and so greater vertical growth, is commonly observed in elongated plants. Thus, the observed reduction in internode 3 growth implies that an intrinsic cost of the elongation response may be later growth, independent of density. However, at high density, this intrinsic cost is counterbalanced by strong selection on early stem height.

The elongation response has been suggested to be costly because of the biomass allocated to stem tissue (Givnish 1982; Casal and Smith 1989) and the mechanical fragility of the longer stem (Niklas 1992; Casal et al. 1994). For both of these explanations the costs would be expected to be correlated with height, contrary to the results of our ANCOVA. However, the effects of R:FR are not confined to stem elongation. Other studies have shown that branching and flowering are affected by R:FR (Schmitt and Wulff 1993; Ballaré 1994), though a study in *Impatiens capensis* found no effects of light quality on branching under low-irradiance conditions (Dudley and Schmitt 1996). Opportunity costs of suppressed branching (Geber 1990) could account for the lowered fitness of elongated plants at low density. Another study of *I. capensis* plants grown under similar light treatments (S. Maliakal, S. A. Dudley, and J. Schmitt, unpublished data) found that, compared to elongated plants, suppressed plants had greater allocation to roots relative to leaves. In that study, though all plants received similar watering

and roots were not competing, suppressed plants had greater stomatal conductance and higher photosynthetic rates. Thus, suppressed plants may be more drought-tolerant and acquire carbon more quickly for a given leaf area, traits that might have conferred an advantage in the field experiment reported here.

For adaptive plasticity to evolve in response to heterogeneous selection, there must be within-population variation in reaction norms, that is, genotype  $\times$  environment interaction (Via and Lande 1985; Gomulkiewicz and Kirkpatrick 1992). We were unable to detect such variation among families in plastic response to either initial R:FR treatment or density, although there was a significant main effect of family across the four experimental treatments for most of the morphological traits measured. Possibly this experiment did not have the power to detect significant family  $\times$  environment interactions in stem length, given the sample size and the sequential imposition of light quality and density treatments. However, the lack of any family  $\times$  environment interaction together with the significant main effect of family may also suggest that strong positive genetic correlations across treatments (Fry 1992) could constrain the evolution of the plastic elongation response in this population (see, e.g., Via and Lande 1985). Nevertheless, the observation of apparently adaptive population differentiation in the stem elongation response between this and nearby populations (Dudley and Schmitt 1996) suggests that genetic variation in plasticity was available to selection in the past. It is also important to note that maternal effects acting through seed size (which was unmeasured in this experiment) may be included in the observed family effects. There was no evidence for variation among families in reaction norms of fitness to the experimental treatments.

Relatively few other studies have examined the fitness consequences of phenotypic plasticity in any plant trait, especially in natural populations. In a recent study (Dudley 1996), *Cakile edentula* var. *lacustris* plants grown in a dry environment were found to have smaller leaves and lower rates of water use efficiency than did wet-grown plants. Measurement of natural selection in the field demonstrated that natural selection favored smaller leaves and higher rates of water use efficiency in the dry environment compared to the wet environment, which suggests that the plasticity in leaf size was adaptive, but the plasticity in water use efficiency was not (Dudley 1996). Another approach has been to examine the fitness of genotypes that vary in plasticity (see, e.g., Van Tienderen 1991). For example, in *Ranunculus flammula*, heterophyllous genotypes display greater ecological amplitude and greater tolerance of changes in water level than nonheterophyllous genotypes (Cook and Johnson 1968). In a greenhouse experiment with inbred lines of *I. capensis*, the plastic response of flowering time to irradiance was positively correlated with fitness (Schmitt 1993). Tests of adaptive plasticity in plants using phenotype manipulation have been surprisingly rare (but see Kingsolver 1995a, 1995b, 1995c, for an important example in animals). One exception is a greenhouse study in which *Abutilon theophrasti* plants grown in high and low irradiance were reciprocally switched between light environments (Rice and Bazzaz 1989). The shade-grown phenotype had a higher growth rate than the sun-grown phenotype in both environments, an observation inconsistent with the hypothesis that plastic response to irradiance is adaptive in this species, although

Rice and Bazzaz (1989) suggest that light-induced plasticity may still be advantageous because the high-light phenotype has higher reproductive allocation at high irradiance.

Phenotypic manipulation has been demonstrated to be a valuable tool in studying selection (see, e.g., Andersson 1982; Nilsson 1988; Sinervo and Huey 1990; Anholt 1991; Sinervo and Licht 1991; Campbell et al. 1994; Kingsolver 1995*b*, 1995*c*). In this study, we used phenotypic manipulation together with a comparison of natural selection in differing environments (Wade and Kalisz 1990) to test for the adaptive value of the stem elongation response to density. We suggest that this method may offer a paradigm for testing adaptive plasticity. Because plant phenotypes are difficult to manipulate directly, the phenotype was altered during early growth by changing the light quality cue, which permits plants to sense the presence of neighbors. Consequently, the entire suite of traits associated with the shade avoidance response was likely to be altered. Moreover, because the light treatments could only be applied before transplantation into a mixed stand, the traits responded to the planting density. Nonetheless, the light treatments did result in extension of stem height phenotype and decoupled stem height from growth and biomass. Our results demonstrated that the suite of phenotypic responses cued by the change in light quality is adaptive. We furthermore confirmed the hypothesis from the literature that stem elongation in response to neighbor proximity is adaptive because selection on height differs between densities. However, we also observed a cost to the elongated phenotype in low density that could not be explained by direct selection on height. The mechanism underlying this cost, most likely a plastic response to R:FR in other unmeasured traits, could not be determined by this study. Further physiological and selection studies will be necessary to find out why stem elongation is costly at low densities.

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