

EFFECTS OF RED TO FAR-RED RATIO AND PLANT DENSITY ON BIOMASS ALLOCATION AND GAS EXCHANGE IN *IMPATIENS CAPENSIS*

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Phytochrome-mediated stem elongation in response to crowding in dense stands has been shown to be a form of adaptive phenotypic plasticity. However, increased stem elongation could affect the patterns of allocation to leaves and roots and so affect the water relations of the plants. We tested this hypothesis by measuring biomass allocation, light-saturated photosynthetic rates, and stomatal conductance of elongated and nonelongated *Impatiens capensis* plants in two experiments. In the first experiment, we compared elongated plants grown in high-density stands under neutral shade, which elicited normal stem elongation in response to crowding, with nonelongated plants grown in high-density stands receiving a high ratio of red : far-red (R : FR) light that suppressed the elongation response. In the second experiment, we compared elongated plants grown in high-density stands with nonelongated plants grown at low density. As expected, elongated plants had a higher allocation to stem biomass in both experiments. In addition, elongated plants had a lower proportion of root biomass to leaf area. In the light quality cue experiment, elongated plants had significantly lower photosynthetic rates and stomatal conductance and higher water use efficiency compared with non-elongated plants, but specific leaf area did not change. This result indicates that, as either a direct or indirect response to higher R : FR, stomatal conductance and therefore photosynthetic rate were increased. However, in the density experiment, we found no significant difference in photosynthetic rates between high-density and low-density plants. The high-density plants had higher stomatal conductance and higher specific leaf area. These results indicate that the lower specific leaf weight of low-density plants is more important than the light quality effects on stomatal conductance in determining the effects of density on gas exchange.

Keywords: *Impatiens capensis*, red : far-red ratio, plant density, light quality, stem elongation, biomass allocation, photosynthesis, stomatal conductance, water use efficiency, ecology, phenotypic plasticity.

Introduction

Phytochrome-mediated stem elongation in response to crowding and vegetation shade is hypothesized to be a form of adaptive phenotypic plasticity. The increased stem elongation is thought to allow the plants to place their leaves above their neighbors, increasing light interception. Light that has passed through a canopy of leaves has a reduced red to far-red ratio (R : FR) (Smith 1982). Via the phytochrome family of photoreceptors, plants are able to detect this change in light quality and respond morphologically (Smith 1982). A typical shade avoidance response is characterized by dramatic stem elongation, reduced branching, and a redistribution of leaves to the top of the canopy (Smith 1982; Geber 1989; Weiner et al. 1990; Ballaré et al. 1991; Weiner and Thomas 1992; Schmitt and Wulff 1993). Even before plants are directly shaded, light reflected off neighboring plants in a developing

dense canopy is sufficiently lowered in R : FR to elicit an elongation response (Ballaré et al. 1987, 1990); thus, important functions of phytochrome may be to sense future competition for light and to trigger morphological and physiological responses to avoid future shading (Casal and Smith 1989; Schmitt and Wulff 1993). Recent studies have demonstrated that elongated plants have higher fitness in high-density conditions and nonelongated plants have higher fitness in low-density conditions, as predicted by the shade avoidance hypothesis (Schmitt et al. 1995; Dudley and Schmitt 1996). But while such studies provided strong support for the shade avoidance hypothesis, they did not explicitly test hypotheses about the costs and benefits of the stem elongation response that cause the fitness differences.

Phytochrome-mediated stem elongation may incur such costs as susceptibility to breakage (Schmitt and Wulff 1993; Casal et al. 1994; Niklas 1994) and reduced allocation to resource acquisition structures such as roots and leaves (Givnish 1982; Schmitt and Wulff 1993). In the absence of competition for light, these costs should result in selection against the shade avoidance phenotype (Schmitt and Wulff 1993). Dudley and Schmitt (1996) found that the elongated *Impatiens capensis* transplanted into a natural population at high density had higher fitness than nonelongated plants because of direct

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selection for increased height. At low density, elongated plants had lower relative fitness as expected, but this fitness disadvantage could not be explained by direct selection on height. Though this study supports the shade avoidance hypothesis, the disadvantage of elongated plants at low density indicates that the apparent fitness cost of elongation results from another unmeasured component of the shade avoidance response.

Explicit attempts to test for such a cost are rare. An intriguing study by Ballaré et al. (1991) used R : FR manipulation to compare the growth and biomass allocation of elongated and nonelongated *Amaranthus quitensis* at both high and low density. At both densities, elongated plants were taller and had greater biomass from increased allocation to stems, but the average biomass of leaves and roots was unaffected by R : FR treatment. From these results, Ballaré et al. (1991) concluded that the opportunity costs of allocating resources to stem elongation were minimal and suggested that the faster growth of elongated plants could result either from more efficient light capture or from more efficient conversion of light into biomass. However, little is known about the comparative photosynthetic performance of elongated and nonelongated plants. It is, therefore, of interest to ask whether stem elongation is associated with increased photosynthetic rate, as Ballaré et al. (1991) predicted. It is also important to determine whether shade avoidance responses to neighbors affect stomatal conductance or water use efficiency (WUE). Although Ballaré et al. (1991) did not detect a cost of elongation in their greenhouse experiments, their observation of a reduced root : shoot ratio in elongated plants may indicate that the shade avoidance response affects water relations, a potential physiological cost. Because carbon fixation is in part dependent on stomatal conductance (Farquhar and Sharkey 1982; Schulze 1986), the predicted increase in photosynthetic rate in elongated plants might exacerbate this water stress through increased transpirational water loss.

Here we examine the effects of the shade avoidance response on biomass allocation, photosynthetic capacity, and water use efficiency in the annual North American herb *I. capensis* Meerb. (Balsaminaceae). This species grows in both open and woodland habitats in a wide range of densities and displays a dramatic elongation response to crowding and reduced R : FR (Schmitt et al. 1987; Dudley and Schmitt 1995, 1996). We compared the biomass allocation and gas exchange traits of elongated plants with nonelongated plants in two greenhouse experiments. To compare elongated and nonelongated plants in similar environments, in the first experiment we grew plants at high density at different light qualities. To compare elongated and nonelongated plants in their natural environments, in the second experiment we grew plants in natural light at high and low density. In both experiments we measured biomass allocation, leaf area, maximal photosynthetic rates, stomatal conductance, and water use efficiency. We asked in each experiment: (1) What are the patterns of biomass accumulation and allocation in elongated compared with nonelongated plants? and (2) What are the patterns of gas exchange traits in elongated compared with nonelongated plants? In comparing these results between experiments, we asked, (3) How do the responses to manipulated R : FR differ from the responses to high density?

Material and Methods

Experimental Design

Light quality experiment. In the light quality experiment, plants were grown in similar high-density stands. We altered only the light quality cue to produce both elongated and suppressed plants in high density. To suppress elongation, the plants received light that had been filtered through a copper sulfate solution, which filtered out far-red light, so that even beneath the canopy the R : FR was high enough so as not to induce an elongation response (Ballaré et al. 1991; Dudley and Schmitt 1996). Thus, plants were blocked from responding appropriately to competition. The control treatment was matched in light level above the canopy but had normal R : FR, so the plants were able to respond normally to their neighbors.

On May 26, 1994, we planted seeds in plug trays filled with sand on a misting bench from a stratified sample of greenhouse-maintained inbred lines derived from an oak-hickory woodland population of *Impatiens capensis* at Brown's Haffenreffer Reserve in Bristol, Rhode Island (Schmitt and Gamble 1990; Argyres and Schmitt 1991; Dudley and Schmitt 1995, 1996). These seeds had been sprayed with Olympic Triathlon fungicide and were then stratified in distilled water at 4°C for ca. 5 mo in plastic microtiter trays. Many seeds had radicles protruding when planted. The majority of seedlings emerged within 1 wk, and dates of emergence were recorded for all plants. On June 1, we began transplanting 108 seedlings shortly after they emerged into 16.5 × 2.75 cm plastic pine cells filled with Terra Green Soil Conditioner (Oil/Dry Corporation of America, Chicago), an inert, sterile, calcined mineral, with a piece of capillary cloth at the bottom. We finished transplanting on June 7. The pine cells eliminated all root competition so that all competition was aboveground.

On June 10, ca. 2 wk after most seeds had germinated, plants were randomly assigned to two treatments. They were arranged in racks in a ca. 7 × 8 array at a density of 1076 plants m⁻² and placed under two different light treatments. In the "suppressed" treatment, a stand of plants was placed under 12 L of a 15 g/L copper sulfate solution in Ziploc gallon-size bags inside a 0.5 m × 0.8 m rectangular Plexiglas tray. This treatment, by raising the R : FR within the stand, suppressed the normal elongation response to neighbors (e.g., Ballaré et al. 1990, 1991; Schmitt et al. 1995; Dudley and Schmitt 1996). In the "elongated" treatment, the array of plants was placed under 12 L of a 0.044 g/L nigrosin dye solution, in Ziploc bags inside a 0.5 m × 0.8 m Plexiglas tray. Nigrosin, a black dye, was used to match the light level experienced under the copper sulfate without altering R : FR. Plants in this treatment were thus able to detect their neighbors and respond with stem elongation. Aluminum foil was placed around both trays to block diffuse light from the side, as well as reflecting light back onto the plants, minimizing edge effects for the border plants. Both light treatments reduced overall irradiance ca. 60%. After 20 d in the treatments, the average R : FR measured with a LI-COR LI-1800 portable Spectroradiometer underneath the copper sulfate cuvette but above the canopy was 7.06. Below the canopy at soil level, the average dropped to ca. 1.63, higher than what plants would experience in full sun. Under the ni-

grosin cuvette but above the canopy, the average R : FR was ca. 1.12, very similar to full sunlight. Below the canopy, the average dropped to 0.50.

The positions of the treatments and all plants within each treatment were randomized once a week. Plants were bottom watered twice a day and treated with 50 mg/L of NPK 20 : 10 : 20 fertilizer every other day during bottom watering. They were grown under these treatments for 3 wk and harvested on July 1, 1994. The plants at this time had four to eight leaves and were still undergoing rapid vegetative growth. A few plants were producing cleistogamous flowers.

Density experiment. In the density experiment, plants were grown in high and low density under full sun. This experiment was designed to compare elongated and nonelongated plants in their appropriate contexts. In this experiment, both light level and light quality naturally differed between treatments because of shading by other plants in high density. Other associated effects of density on microclimate, such as humidity, also naturally varied between high and low density. However, as in the light quality experiment, by growing plants in pine cells, we prevented root competition for resources.

This experiment used seeds from greenhouse-maintained inbred lines of *I. capensis* plants collected from a high-density population in a clearing on the margin of a deciduous woodland at the Haffenreffer Reserve in Bristol, Rhode Island (Dudley and Schmitt 1995). On November 11, 1994, seeds treated and stratified as described earlier were planted in plug trays filled with sand and then transplanted into Terra Green under the same culture conditions as for the light quality experiment. However, instead of capillary cloth, wire mesh was used at the bottoms of the pine cells to prevent loss of Terra Green. On November 22, plants were randomly assigned to two treatments in pine cell trays. The high-density treatment consisted of two stands of 36 plants, each in a 6 × 6 array, to give a total of 72 plants. Two rows of border plants were placed around these plants to reduce edge effects within the experimental stand. Density in these trays was 1076 plants m⁻², as in the previous experiment. The low-density treatment consisted of four trays of 15 plants to give a total of 60 plants, equally spaced apart. Density in these trays was 80 plants m⁻². All replicates were randomized with respect to their position on the bench ca. once a week. They were bottom watered twice a day and treated with 50 ppm of NPK 20 : 10 : 20 fertilizer every day during bottom watering. All plants were randomized within the treatments ca. once a week. Plants were randomized between stands in high density and between trays in low density to eliminate differences among stands and among trays. Plants were harvested on January 11 and 13, 1995. The plants at this time had six to 12 leaves and were undergoing vegetative growth and producing some cleistogamous flowers.

Photosynthesis Measurements

In both experiments, we sampled the most recently fully expanded leaf on each plant. Parameters estimated were the leaf area of the most recently expanded leaf (cm²), net photosynthetic rate (assimilation of CO₂ in micromoles CO₂ m⁻² s⁻¹), and stomatal conductance (moles H₂O m⁻² s⁻¹). Instantaneous water use efficiency was then calculated as the ratio of photosynthetic rate to stomatal conductance. The gas

exchange rates of 84 plants in the light quality experiment were measured on July 1, 1994. The gas exchange rates of 50 plants in the density experiment were measured on January 13, 1995. In both experiments gas exchange measurement took place immediately before harvesting for biomass measurements.

Gas exchange was measured with an LCA-3 portable photosynthesis system (Analytical Development Co., Hoddeson, England). In the late morning and early afternoon on clear days, the measurements were taken on attached leaves in a random order. A 250-W halogen lamp was directed at the cuvette to ensure that a constant level of light (700 μmol m⁻² s⁻¹) was received by each leaf as the measurements were taken. To reduce heating of the chamber, a closed Plexiglas water bath was placed between the lamp and the cuvette. The pine cells in which the plants were growing were removed from the treatments and placed in a holder so that the attached leaf could be placed in the chamber. After measurement, the measured leaf was divided with a razor blade into the section within the chamber and the remainder. Area of both sections was measured for each leaf, and photosynthetic and conductance rates were corrected for leaf area within the chamber. The procedures used for estimation of leaf temperatures in the chamber, measurement of boundary layer resistance for leaves, calculation of photosynthetic rates and stomatal conductance, and statistical adjustment through covariate analysis for effects of time and temperature are described in Dudley (1996).

Morphological Measurements

Light quality experiment. On June 16 and 24 and July 1, 1994, internode lengths and total heights were measured for all plants. On July 1, all plants were harvested. First internode diameter was measured, plants were stripped of leaves, and plants were cut at ground level. Roots were washed to remove the Terra Green. The leaves, first internode, roots, and the rest of the plant (stem and petioles) were dried at 50°C for at least 1 wk and then weighed. Leaves were photocopied and scanned into Adobe Photoshop, and their area was calculated using NIH Image.

Density experiment. At 7–10-d intervals, internode lengths and total heights were determined for all plants. Plants were harvested on January 11 and 13, 1995. Plants were harvested and leaf areas were obtained in the same manner as described in the light quality experiment.

Light Measurements

At midday of June 30, 1994, we measured PAR (400–700 nm) and the red (655–665 nm) to far-red (725–735 nm) ratio of light received in a transect of each light quality treatment, with five different heights, including one above the canopy, and five different horizontal positions. The heights taken were adjusted for the average total height of the stand. For the suppressed treatment, the heights were 0, 3, 6, 9, and 12 cm, and for the elongated treatment, the heights were 0, 8, 16, 24, and 26 cm. The measurements were taken with a LI-COR LI-1800 portable spectroradiometer. We also measured levels of ambient PAR with a LI-COR LI-190SA light sensor. On the day of measurements the weather was overcast, with an average ambient PAR of 323 μmol m⁻² s⁻¹. At midday of January

9, 1995, light intensity was measured at the top of 10 randomly selected plants in both high- and low-density treatments using a LI-COR LI-190SA light sensor. On this day the sky was clear with occasional clouds, and the average light level above the canopy of plants was $575 \mu\text{mol m}^{-2} \text{s}^{-1}$. Light measurements were calculated as a proportion of ambient light at the time of measurement.

Statistical Analysis

All tests were performed with SAS for Windows 3.10 (SAS Institute 1992). ANOVA (PROC GLM) was used to determine the effects of treatment on plant morphological and physiological traits. The light quality experiment had treatment as a main effect. The density experiment had treatment and harvest date and their interaction as effects.

ANCOVAs were performed with PROC GLM to determine treatment differences in the linear relationship between total biomass and total height, between root weight and shoot weight, and between root weight and leaf area. Each ANCOVA included effects of the treatment, the covariate, and the interaction between treatment and covariate. Because the interaction term was significant or large in all analyses, indicating that slopes differed between treatments, the *t*-tests for treatment differences in means corrected for the effects of the covariate that were obtained from the LSMEANS option of GLM were used to test for overall treatment effects in the ANCOVA. PROC CORR was used to determine correlations between A (net photosynthetic rate), *g* (stomatal conductance), WUE, total height, and leaf size within and across treatments.

To deal with the question of multiple tests, we performed sequential Bonferroni tests (Rice 1989) to obtain tablewise significance for tests on a group of related traits within an experiment (e.g., treatment effects on biomass traits in the light quality experiment). In all but one case, individual tests were also significant at the 0.05 level after the sequential Bonferroni correction.

In both experiments the treatments were not replicated because of logistical constraints. As a consequence, it is possible that differences attributed to treatment may have resulted from other unmeasured differences between experimental units. However, the direction and magnitude of differences between treatments are consistent with expectations from the literature and indicate that the experimental treatments were the main cause of these differences.

Results

Light Quality Experiment

Reduction of far-red light by copper sulfate effectively suppressed the elongation response to density in the light quality experiment. We were thus able to test for differences in biomass allocation and physiological traits between a stand of plants that did not elongate in response to their neighbors in high density and a stand that did elongate as expected. The hypocotyl length, first internode length, and total height were increased significantly in the neutral shade treatment relative to the high R : FR treatment (fig. 1*a*). This difference was not due to an increase in overall growth; the ANCOVA demon-

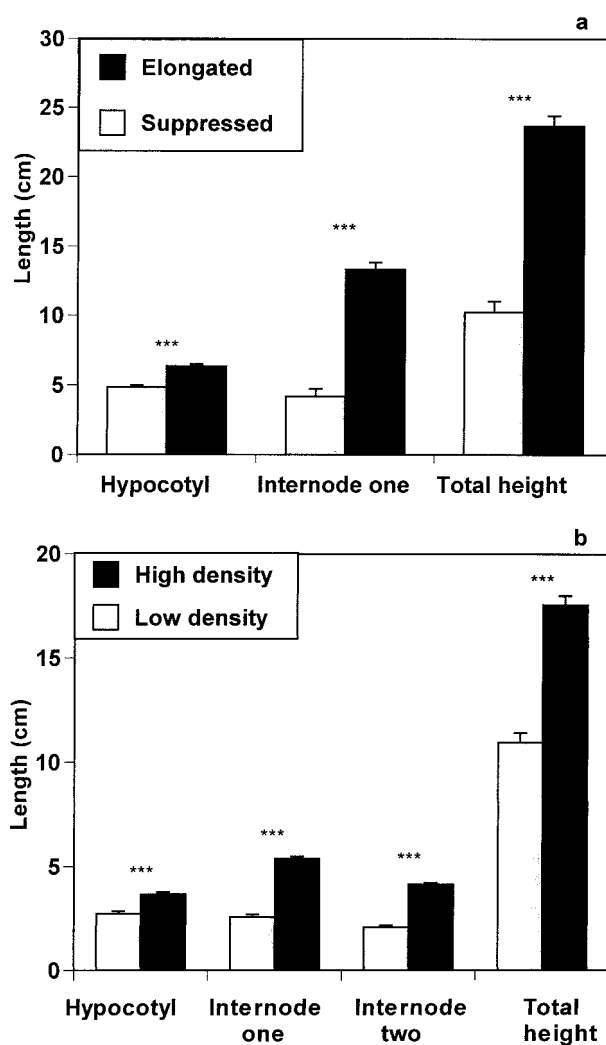


Fig. 1 The internode lengths and plant height for (a) the light quality experiment and (b) the density experiment. For each trait, the significance level for the treatment difference is given. ***, $P < 0.001$.

strated that the elongated plants were taller for their biomass than the suppressed plants (table 1).

The elongated plants had slightly, though not significantly, more total biomass than the suppressed plants (fig. 2*a*). The greatest change in biomass resulted from significantly higher stem mass of the elongated plants, with much of this difference attributable to the first internode; the mass of roots and leaves did not differ significantly between treatments (fig. 2*a*). However, the biomass allocation patterns were significantly different in these two treatments. Elongated plants had a significantly lower root mass for their shoot mass than suppressed plants (fig. 3*a*; table 1). Elongated plants also had significantly less root mass to support a given leaf area than suppressed plants (fig. 3*b*; table 1).

Elongated plants had significantly lower maximal photosynthetic rates and stomatal conductance and higher water use efficiency than the suppressed plants (table 2). Photosynthetic

Table 1
Effects of Treatments on Morphological Traits

Trait	Covariate	Light quality experiment			Density experiment		
		Corrected means		<i>t</i> value	Corrected means		<i>t</i> value
		Elongated	Suppressed		High density	Low density	
Shoot mass	Root mass	0.02801	0.00967	-15.4***	0.0795	0.0432	8.2***
Total leaf area	Root mass	23.13	18.87	-4.6***	78.760	60.495	4.9***
Plant height	Plant biomass	22.76	10.59	-20.1***	19.222	10.816	17.9***

Note. *t* values and means corrected for the variance in the covariate are taken from analyses of covariance fitting the effects of treatment, covariate, and the interaction between treatment and covariate on the trait. Light quality experiment: error degrees of freedom = 78. Density experiment: error degrees of freedom = 125.

*** $P < 0.001$.

rate was significantly correlated with stomatal conductance in both the elongated treatment ($r = 0.519$, $P < 0.01$) and the suppressed treatment ($r = 0.480$, $P < 0.001$) (fig. 4a). There was no correlation between leaf size and photosynthetic rate in either the elongated treatment ($r = 0.095$, $P > 0.5$) or the suppressed treatment ($r = -0.134$, $P > 0.4$) (fig. 5a). There was a significant positive correlation between photosynthetic rate and plant height in the elongated treatment ($r = 0.524$, $P < 0.001$) but not in the suppressed treatment ($r = 0.270$, $P > 0.1$) (fig. 5b).

In both the elongated and the suppressed treatments, light level increased with height within the canopy (fig. 6). The frequency distributions of plant heights were significantly different between the two treatments (fig. 7; Kolmogorov-Smirnov two-sample test, $P < 0.001$). The height distribution was skewed toward taller plants in the elongated treatment, where plants were elongating in response to competition (skewness = -0.30). In contrast, the distribution was more normal in the suppressed treatment (skewness = 0.06). Because more plants reached the high-light zone in the neutral shade treatment than in the high R : FR treatment, we tested to see whether there was a significant difference in estimated light interception by top leaves of individual plants between the two treatments. We regressed height in canopy on proportion of light for each treatment and found a positive curvilinear relationship (high R : FR treatment, $y = -0.0127x + 0.00239x^2 + 0.0274$, $R^2 = 0.867$, $P < 0.0001$; neutral treatment, $y = -0.00795x + 0.000569x^2 + 0.0401$, $R^2 = 0.619$, $P < 0.01$). We used these regression equations to estimate the light interception for the top leaves on all plants in both treatments, by predicting the light level they would be experiencing, using their known height. The average proportion of light received was higher in the neutral treatment (0.20) than in the high R : FR treatment (0.15), but this difference was not significant with the sample size available (Kruskal-Wallis test, $P > 0.2$).

Density Experiment

The plants grown in high density were significantly more elongated than the plants grown in low density. The hypocotyl length, first internode length, second internode length, and total height were significantly increased in high density relative to low density (fig. 1b). This difference occurred despite the

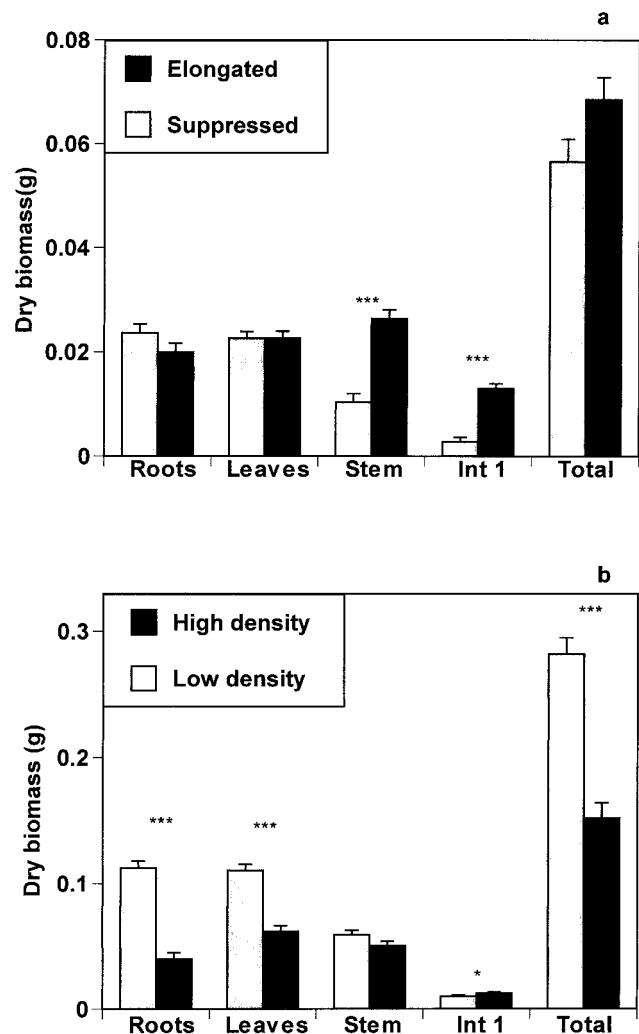


Fig. 2 Dry biomass of roots, leaves, stem, internode 1, and the total biomass of the plant for (a) the light quality experiment and (b) the density experiment. For each trait, the significance level for the treatment difference is given. *, $P < 0.05$; ***, $P < 0.001$.

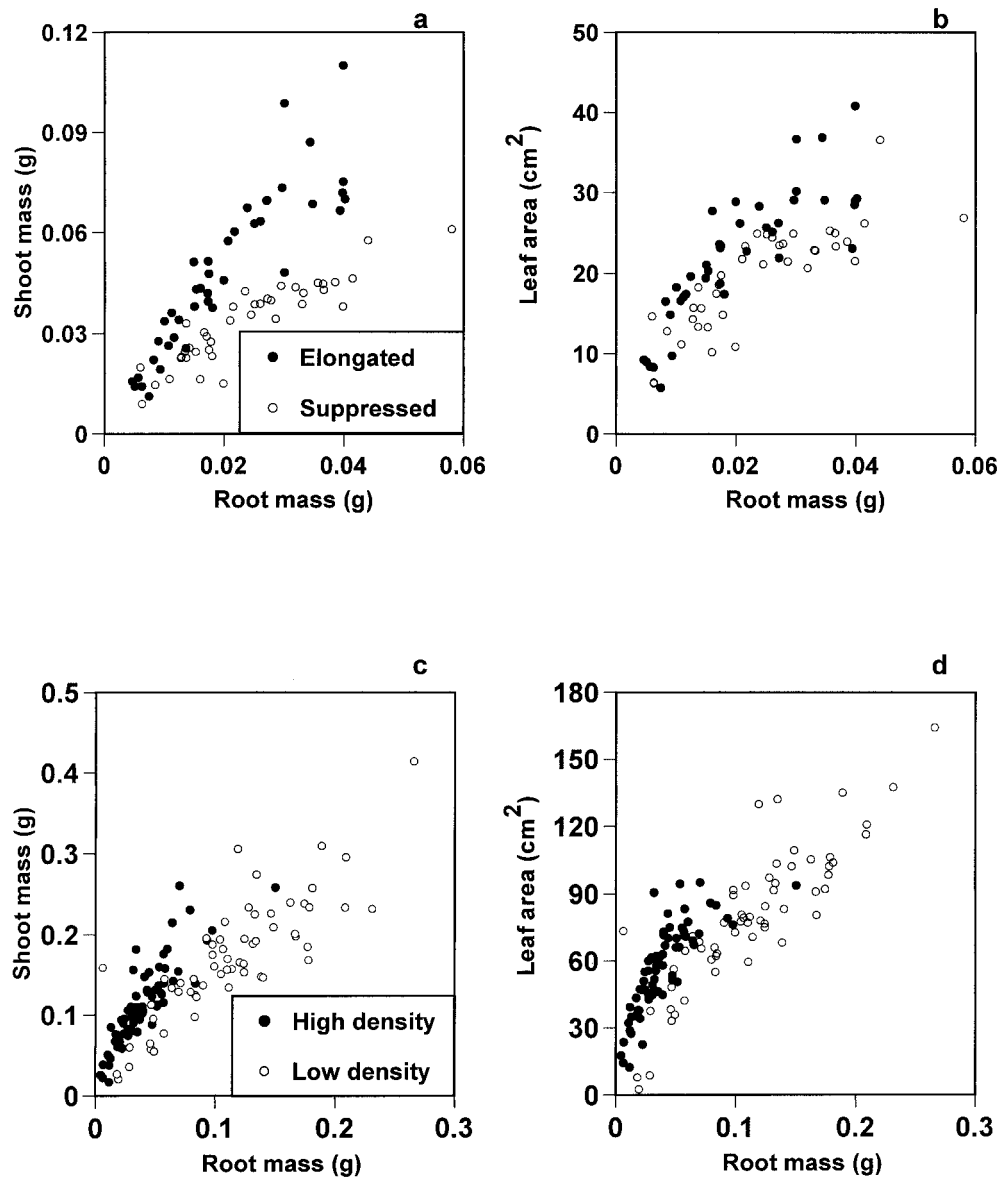


Fig. 3 Relationships of shoot dry biomass to root dry biomass, and plant leaf area (cm²) to root dry biomass (g), for both experiments. *a*, *b*, Results from the light quality experiment. *c*, *d*, Results from the density experiment.

overall lower biomass in high-density plants (fig. 2*b*), and the ANCOVA demonstrated that the elongated plants were taller for their biomass than the suppressed plants (table 1).

The low-density plants accumulated significantly more biomass (fig. 2*b*), indicating that growth was limited by above-ground competition in the high-density treatment. Biomass of roots and leaves was significantly higher in the low-density treatment; however, the total stem and first internode biomass did not differ significantly between the two treatments (fig. 2*b*). The patterns of biomass allocation differed between densities, with the high-density plants clearly allocating a much greater proportion of their biomass into stems. High-density plants had a significantly lower proportion of roots to support

a given shoot mass than did low-density plants (fig. 3*c*). High-density plants also had a significantly lower proportion of root mass to support a given leaf area than did low-density plants (fig. 3*d*).

There was no difference between density treatments in photosynthetic rates (table 2). The high-density plants had significantly higher stomatal conductance and significantly lower water use efficiency (table 2). Photosynthetic rate and stomatal conductance were significantly correlated in low density ($r = 0.642$, $P < 0.001$) but not in high density ($r = 0.355$, $P < 0.08$) (fig. 4*b*). There was a positive correlation between photosynthetic rate and plant height in the high-density treatment ($r = 0.420$, $P < 0.05$), though this was not

Table 2
Effects of Treatments on Gas Exchange Traits

Trait	Light quality experiment			Density experiment		
	Treatment mean (standard error)		<i>F</i> -ratio for difference between treatments	Treatment mean (standard error)		<i>F</i> -ratio for difference between treatments
	Elongated	Suppressed		High	Low	
Photosynthetic rate	5.39 (0.213)	7.06 (0.216)	30.25***	7.62 (0.222)	7.04 (0.222)	3.37
Stomatal conductance	0.40 (0.029)	0.64 (0.030)	32.88***	0.25 (0.013)	0.18 (0.013)	11.81**
Water use efficiency	14.10 (0.613)	11.85 (0.622)	6.63*	33.3 (1.99)	41.9 (1.99)	9.43**
Specific leaf area	853.01 (24.3)	913.48 (25.0)	3.10	925.14 (35.0)	645.32 (37.7)	29.63***

Note. *F*-ratios and probabilities for the difference between treatment means within experiments are taken from analyses of variance for each experiment. Light quality experiment: degrees of freedom = 70. Density experiment: degrees of freedom = 49.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

significant after the sequential Bonferroni correction, and a slightly negative correlation in low density ($r = -0.298$, $P > 0.1$) (fig. 5d). We found a significant negative correlation between leaf size and photosynthetic rate in the low-density treatment ($r = -0.566$, $P < 0.01$) but not in high density ($r = 0.034$, $P > 0.8$) (fig. 5c).

Light measurements revealed that taller plants received more light only in the high-density treatment. Light level was significantly positively correlated with height in the high-density treatment ($r = 0.74$, $P < 0.01$, $n = 10$), but there was no significant correlation for the low-density treatment ($r = 0.33$, $P = 0.35$, $n = 10$).

Discussion

As expected, we observed dramatic stem elongation in *Impatiens capensis* at high density; this response was suppressed when phytochrome-mediated perception of neighbors was blocked by raising the R : FR in dense stands, which is consistent with results from other studies (Ballaré et al. 1990, 1991; Schmitt et al. 1995; Dudley and Schmitt 1996). In both the light quality and the density experiments, the treatment that induced high stem elongation also caused a reduced root to shoot ratio and a lowered ratio of root biomass to leaf area, indicating that whole-plant allocation is responding to R : FR. In contrast, there was no consistent association between stem elongation and gas exchange rates. In light quality experiment, in which all factors except the light quality cue were held equal, the elongated plants had lower maximal photosynthetic rates, lower stomatal conductance, and higher water use efficiency compared to the suppressed plants. These results indicate that lowered R : FR either directly or indirectly induces a change in the gas exchange rates. However, in the density experiment, we found no significant difference in photosynthetic rates between treatments, and the elongated plants had higher stomatal conductance and lower water use efficiency. This difference between the experiments indicates that gas exchange rates are affected not only by the R : FR differences between high- and low-density stands but also by other variables that are affected by plant density such as light intensity, leaf temperature, and

humidity. Within elongated stands we found, as expected, that light interception increased with height in the canopy, as did maximal photosynthetic rates of the most recent fully expanded leaf for a plant. Thus, in elongated dense stands, there is evidence for a plastic “sun shade” response to the light that individual plants received.

Several studies have suggested that elongated plants have increased allocation to stem mass (McClaren and Smith 1978; Hoddinott and Hall 1982; Ballaré et al. 1991; Methy and Roy 1993). In the light quality experiment, we found, as others did in a similar experiment using *Amaranthus quitensis* (Ballaré et al. 1991), that the greater stem mass does not appear to have a cost; elongation increased average stem mass but did not reduce average root or leaf mass. Total plant mass was slightly though not significantly greater for elongated plants in the present experiment and was significantly greater for elongated plants in the results of Ballaré et al. (1991). Ballaré et al. (1991) offered two hypotheses that could explain the greater biomass accumulation of the elongated plants: (1) the elongated plants were more efficient at capturing light or (2) elongated plants had a greater light conversion into biomass. Our results indicated a tendency for elongated plants to receive more light on the topmost leaves, though this was not significant. However, in *Impatiens pallida*, a close relative of *I. capensis*, Weiner et al. (1990) and Berntson and Weiner (1991) found that crowded plants responding to competition by elongating had most of their leaf area at the top of the main stem, whereas the leaf area of the uncrowded plants was distributed more evenly throughout the main stem. Thus, it is possible that the elongated plants not only were more likely to reach the high-light zone but also had their leaf area concentrated in this high-light zone. We also observed that leaves appeared to overlap to a greater extent in the suppressed treatment, potentially reducing light interception in the suppressed plants.

Our results do not support the hypothesis of Ballaré et al. (1991) that elongated plants will have greater light conversion into biomass; contrary to this prediction, elongated plants in the light quality experiment had overall lower maximal photosynthetic rates at the time of measurement and thus were not more efficient per unit leaf area than suppressed plants at

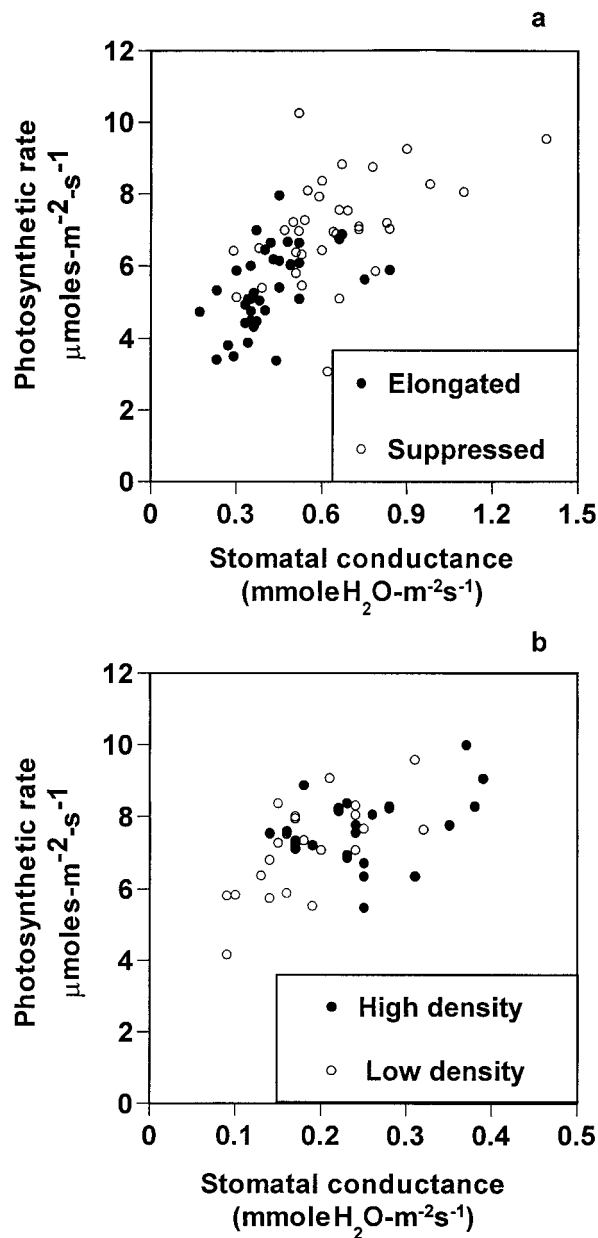


Fig. 4 Relationship between photosynthetic rate and stomatal conductance for (a) the light quality experiment and (b) the density experiment.

converting light into biomass. Because gas exchange traits were measured at the time of harvest, it is not appropriate to assume a cause-and-effect relationship between photosynthetic rates and measured biomass. It is possible, for example, that in younger seedlings the elongated plants had higher gas exchange rates. We chose to take gas exchange and biomass measurements at a time when the plants still show primarily vegetative growth. At this time the juvenile plants appeared to have a well-established size hierarchy but were before the major period of flowering. Our results indicate that at this im-

portant growth phase, plants in the treatments differed in gas exchange traits.

In both experiments, there were significant differences in biomass allocation between the treatments. As expected, elongated plants had a greater proportion of biomass allocated to stems. However, the ANCOVAs clearly indicated that root mass is significantly reduced relative to leaf area for the elongated plants compared to suppressed and low-density plants. These results demonstrate that elongation in *I. capensis* is associated not only with greater biomass allocation to stem tissue but also with a shift in the relative allocation between root and leaf tissue. Moreover, the concordance between the density manipulation and the light quality manipulation supports the hypothesis that the changes in allocation of root relative to leaf are cued by R : FR.

However, this study cannot determine whether this change in allocation is evidence of a cost of elongation or is itself adaptive. The proportion of roots to leaves will interact with the rates of water loss to determine the leaf water potential and therefore the whole-plant carbon gain (Givnish 1986). However, it is possible that rates of water loss are reduced by the increased humidity and reduced light in high-density stands (Jones 1983). Roots also provide mechanical stability, but the need for root anchorage could be lessened in high-density stands because plants mutually support each other. Increasing proportional investment in photosynthetic tissue has been shown to increase whole-plant carbon gain (Körner 1991). Therefore, increased proportional investment in leaves is another hypothesis for the lack of a cost in whole-plant carbon gain of elongation seen in this article and in the work of Ballaré et al. (1991).

The association between gas exchange traits and elongation differed between the experiments. In the light quality experiment, we found that elongated plants had lower stomatal conductance and lower photosynthetic rates than did nonelongated plants. Thus, the elongated plants had gas exchange characteristics typical of drought-stressed conditions. The lowered photosynthetic rates associated with the lower stomatal conductance in elongated plants, the lack of any difference between treatments in specific leaf area, and the significant correlations of stomatal conductance and photosynthetic rate within treatments are consistent with stomatal limitation on photosynthesis (Wong et al. 1979; Geber and Dawson 1990). Three hypotheses that could explain the lowered stomatal conductance of elongated neutral shade plants despite the well-watered conditions are that (1) the stand microclimate was altered by elongation, and the difference in the leaf gas exchange traits was a response to stand microclimate; (2) the reduced root biomass to leaf area results in lowered hydraulic conductance in the root, limiting the transpirational stream and so resulting in an effective drought-stressed state in the elongated plants compared to the suppressed plants; and (3) the low R : FR signal more directly affects stomatal conductance. One candidate as a potential mechanism for a direct effect is abscisic acid, which is well known to decrease stomatal conductance (Giraudat et al. 1994).

In the light quality experiment, the elongated plants had gas exchange characters typical of plants in dry environments. However, in the density experiment elongated plants had gas exchange characters indicating that they were less drought

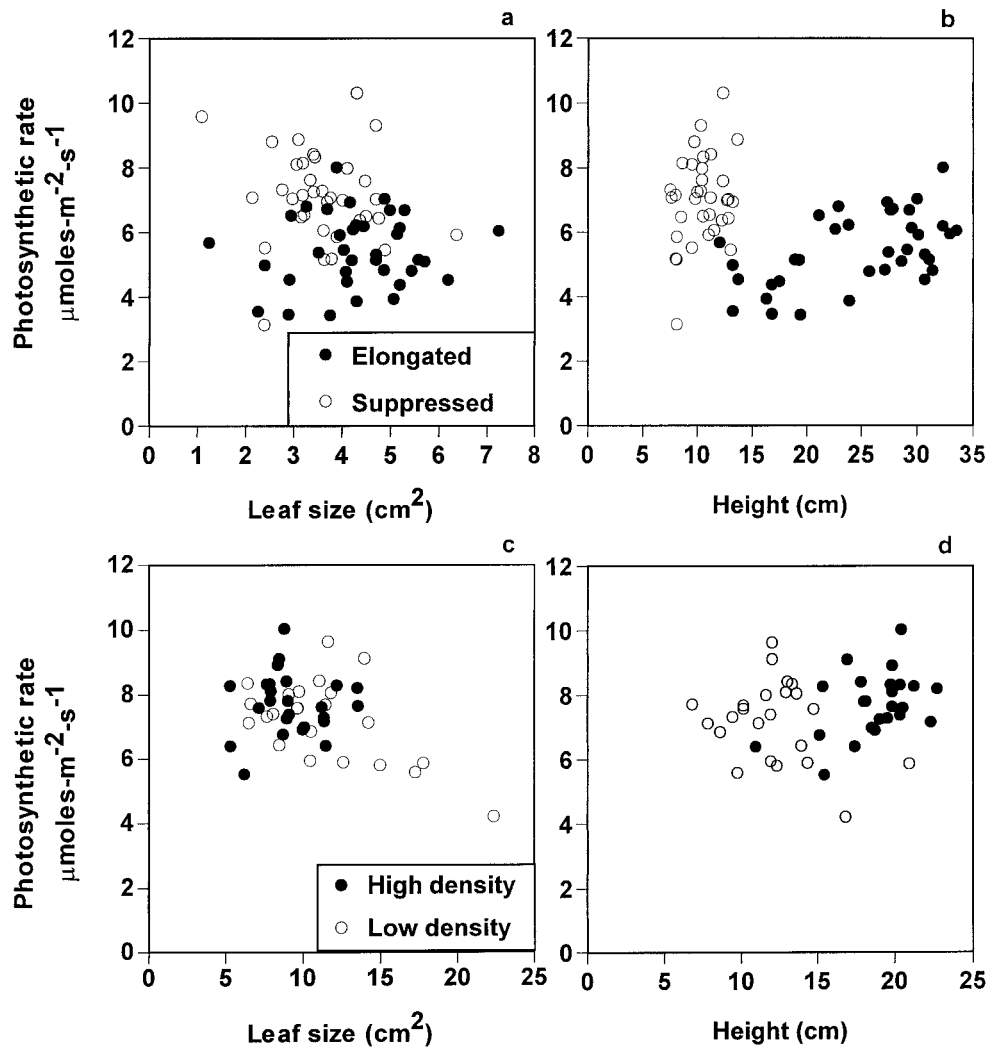
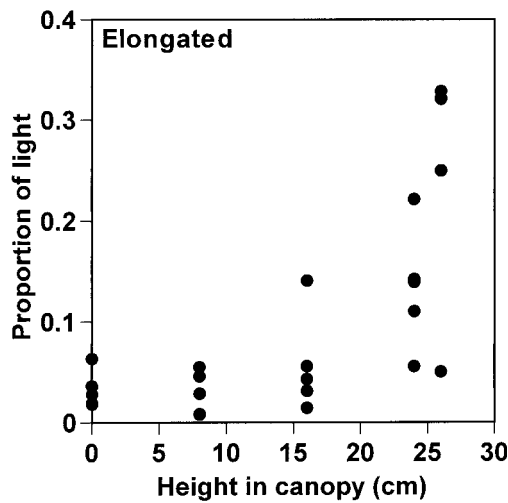
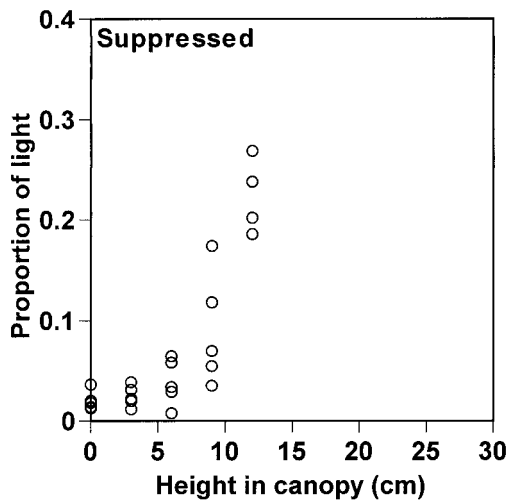


Fig. 5 Relationships between photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and morphology for the light quality experiment (a, b) and the density experiment (c, d).

stressed than the nonelongated plants. Elongated high-density plants had higher specific leaf area, higher stomatal conductance, lower water use efficiency, but similar photosynthetic rates compared to nonelongated low-density plants. The change in specific leaf area is particularly interesting; it indicates that the low-density plants had more photosynthetic tissue per unit leaf area compared to high-density plants. That change in morphology could explain why low-density plants had a lower stomatal conductance compared to high-density plants but still achieved similar photosynthetic rates. Microclimatic changes associated with low density is an important environmental factor in determining morphology and gas exchange rates. The high atmospheric humidity in dense stands because of the increased boundary layer, reduced wind speed, and transpiration by the plants (Jones 1983) can be expected to reduce the transpirational water demand on the plants within the stand. Light levels are reduced within plant canopies (Jones 1983), which may lower the maximal photosynthetic

rate and reduce the heat load on the leaves. It is striking that the effect of density on gas exchange traits was to lower stomatal conductance in nonelongated plants, a change in the opposite direction to that induced by light quality alone.

The results of these experiments indicate that density and water relations are linked because of the effects of elongation on root allocation and stomatal conductance and the effects of density on microclimate. A component of the water relations we did not examine is belowground competition for water. The well-watered conditions and the lack of root competition in these experiments may have prevented effects occurring in nature from being observed. Because the root mass of the low-density plants was considerably higher than in any of the other treatments, it is possible that these plants were pot bound to a greater extent and had a lessened ability to acquire water and mineral nutrients. In addition, because the light quality and density experiments were carried out at different times of the year, using different populations, and in different condi-



effects on physiological traits. It is commonly found that within a species, plants grown in full sun have higher maximal photosynthetic rates than plants grown in the shade (Boardman 1977). In the density experiment, the low-density plants experienced higher irradiance on average; however, since the most recently fully expanded leaf is at the top of the plant, the tallest of the high-density plants may have had those leaves in virtually full sun. Thus, a positive correlation between plant height and photosynthetic rate is expected. In both the light quality and the density experiment, we found a significant positive correlation between total height and photosynthetic rate in the elongated treatments: the high-density treatment of the density experiment and the neutral shade treatment of the light quality experiment. This correlation was not observed in the low-density treatment of the density experiment, because regardless of their height, all of these plants experienced full

Fig. 6 Relationship between proportion of light received (measured as the fraction of ambient light at the time of each measurement) and height in canopy for the light quality experiment.

tions, the possibility that other factors have affected the results cannot be excluded.

Leaf size has been shown to be correlated with photosynthetic rate in many agricultural species, such that larger leaves have lower maximal photosynthetic rates per unit area (Bhagsari and Brown 1986). In the low-density treatment of the density experiment, leaf size and photosynthetic rate were significantly negatively correlated, but this correlation did not occur in any other treatment of either experiment. In low density, there was more variation in leaf size, and leaves were generally larger than in any other treatment of either experiment, which could strengthen the effects of leaf size in this treatment. Thus, the larger leaves in low density may in part be the cause of the lower photosynthetic rates in the low-density treatment.

Position within the canopy in high density had significant

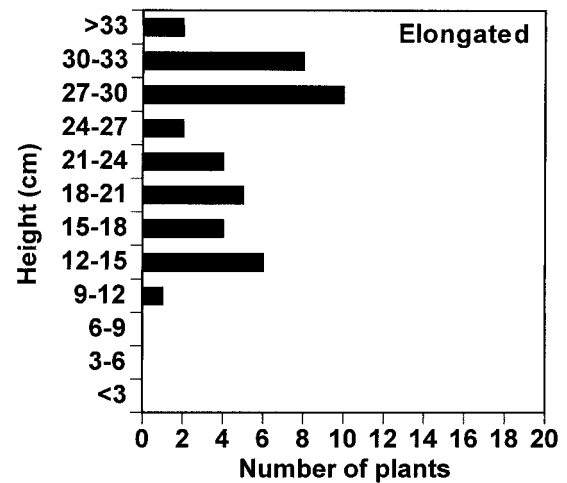
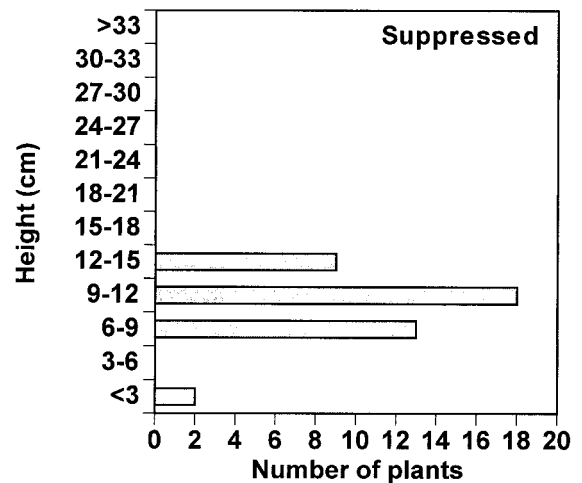


Fig. 7 Frequency distribution of plant heights for the light quality experiment.

sun. We have also observed a negative correlation between plant height and chlorophyll content in high density, which is in accord with classic sun shade predictions (K. McDonnell, S. K. Maliakal, S. A. Dudley, and J. Schmitt, unpublished data). Although there is evidence for microclimatic variation in light within dense stands (e.g., Jurik 1991), little is known about the plasticity of the physiological response to microclimate. We have found evidence for plastic “sun shade” responses to the light availability in dense stands.

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