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Photomodulation of Axis Extension in Sparse Canopies[1]

Role of the Stem in the Perception of Light-Quality Signals of Stand Density

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ABSTRACT

A fiber optic probe inserted into plant tissues was used to investigate the effects of canopy density on the light environment in different organs. The red:far-red ratio inside the stem of *Datura ferox* L. seedlings and the estimated phytochrome photoequilibrium were strongly reduced by the presence of neighbors forming canopies too sparse to cause any mutual shading at the level of the leaves. In such canopies, changes in plant density had little effects on the light regime inside the leaves of the succulent *Aeonium haworthii* (S.D.) Webb et Berth., particularly when the lamina was kept nearly normal to the direct rays of the sun. In field experiments using *D. ferox* and *Sinapis alba* L. seedlings, the elongation of the internodes responded to various types of localized light-quality treatments that simulated different plant densities in sparse canopies. The responses were quantitatively similar to those elicited by changes in plant density. The evidence supports the hypothesis that, in stands formed by plants of similar size, the red:far-red ratio of the light that impinges laterally on the stems is among the earliest environmental cues that allow plants to detect local canopy density and adjust axis extension accordingly.

Stem elongation is markedly affected by the presence of neighboring plants, and changes in light quality are currently viewed as an important factor in the perception of canopy density (2, 5, 14, 20). It has recently been shown (1, 2) that in stands formed by individuals of similar size, relatively small density increments in the LAI[2] range of 0 to 1 stimulate stem elongation without involving a significant reduction in PAR interception per plant. In these conditions, elongation rate is well correlated with the R:FR ratio of the light parallel to the ground collected by an integrating-cylinder probe standing vertically in the canopy (1, 2). In contrast, the quality of the light received on a horizontal, cosine-corrected receptor changes little with density at low LAI values, and consequently, is not correlated with elongation (1). Field experiments with selective mirrors showed that the FR reflected by neighboring individuals may be sufficient to stimulate stem elongation in fully sunlit plants (1). This suggests that the spectral quality of the light scattered by adjacent plants is involved in the mechanism of density detection. An important question is where this spectral signal might be perceived by the plant. Internode extension may be influenced by the light conditions prevailing at various parts of the shoot (*e.g.* leaves: 3, 6, 16, 21, and stem; 4, 7, 8, 10, 13, 16, 21). In an open canopy, leaves and stems are, to some degree, exposed to direct sunlight and to the light scattered by neighbors but, because of the complicated optics of plant tissues (9, 30), the effects of canopy density on the light conditions within the organs are difficult to predict. Rich *et al.* (23) found that the amount of light inside internodes of intact seedlings increases markedly when the source of light is moved from above to the side. Thus, the light scattered by adjacent plants might make a greater contribution to the light regime inside the stem than that expected from its low relative contribution to global radiation. If this were the case, a shift in the spectral composition of the light impinging laterally on the axis might affect phytochrome status in the stem, which would be the major site of density perception in sparse canopies. The experiments reported here were carried out to test this hypothesis.

In the first part of this paper, we address the influence of canopy density on the light environment of stems and leaves, as evaluated with a fiber optic probe inserted into the plant tissues. In the second part, we present results of field experiments showing the elongation responses to localized light treatments that simulated different densities in sparse canopies.

MATERIALS AND METHODS

Seeds of the arable weed *Datura ferox* L. were obtained from plants invading soybean fields in Rojas (Buenos Aires) in 1986. In order to decrease primary dormancy, seeds were kept in an atmosphere in equilibrium with distilled water for 2 weeks (19) and given a saturating R pulse (24). Seeds were germinated in darkness on cottonwool saturated with tap water. Seedlings were planted in individual pots (0.5 L, greenhouse experiments, or 2.5 L, field experiments), filled with a light-textured soil fertilized with 2.5 g of 15:15:15 NPK mixture. Seeds of *Sinapis alba* L. (Compañía Fanacoa, Argentina) were sown directly in this substrate in 2.5-L pots. Leaves of the succulent *Aeonium haworthii* (S.D.) Webb et Berth. were

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[2] Abbreviations: LAI, leaf area index (m^2 leaf · m^{-2} soil); R, red light; FR, far-red light; P, total phytochrome; WL, white light; IA, incidence angles.

obtained from plants growing at the Botanical Garden of the Faculty of Agronomy, UBA. All the experiments were carried out at the Faculty of Agronomy, UBA, Buenos Aires, 34°35′ S and 58°29′ W.

The spectral regime within leaves and stems was sampled using 0.5-mm fiber optic (Poly-Optics Inc., USA) probes attached to a LI-COR 1800 spectroradiometer (Lambda Instruments Co., USA). The fiber was covered with black paint (No. 125, Deka SA, Argentina) and the fiber tips were cut using a glass knife. The half acceptance angle of the resulting probe was about 17° in air. The fiber was attached to the spectroradiometer by means of a special mount constructed following the design of Vogelmann and Björn (29). Each probe was calibrated against a standard lamp (ISCO, USA) from 600 to 800 nm at 2 nm intervals.

For measurements of spectral photon distribution within the stem, the probes were carefully inserted into the internodes of intact seedlings of *D. ferox* growing under natural radiation (Fig. 1A). Dimensions of the internodes varied between 1.6 and 3.0 mm (diameter) and between 4 and 13 mm (length). Collimated light is strongly scattered by the initial millimeter of plant tissue (29, 30); thus, since our fiber probes had narrow acceptance angles, they would measure scattered light when inserted into the stem in the mode shown in Figure 1A. The fiber probe could not be used on *D. ferox* leaves because they are thinner than the probe itself, so the possible effects of canopy density on the internal light regime were investigated using the leaves of the succulent *A. haworthii* as a test system. These leaves are thick and have a homogeneous internal structure. The leaves were mounted on a special arm that allowed selection of IA of direct sunlight between 0° and 90° (Fig. 1B). The probe was then driven into the lamina from one of the margins, perpendicularly to the long axis of the leaf, and halfway between the adaxial and abaxial surfaces.

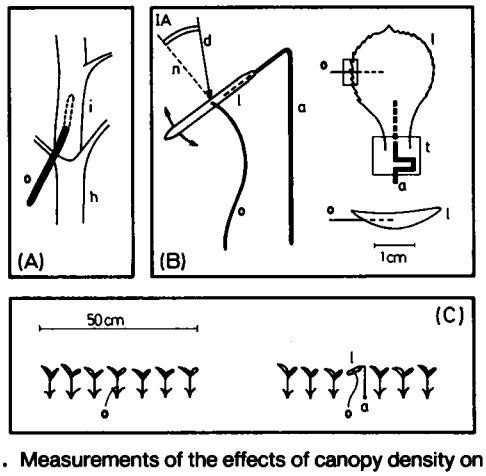

Figure 1. Measurements of the effects of canopy density on the light environment inside leaves and stems. A, Diagram showing how the fiber optic probe was inserted into the internodes of intact seedlings of *D. ferox*; B,mount for *Aeonium* leaves and mode of insertion of the fiber optic probe; C, mode in which the seedlings and the leaves were set at the center of canopies of *D. ferox* seedlings. Abbreviations: a, arm; d, direct light vector; h, hypocotyl; i, first internode; IA, angle of incidence of direct rays; l, leaf of *Aeonium*; n, perpendicular line originating at the leaf surface; o, optical fiber; t, clamps of transparent tape.

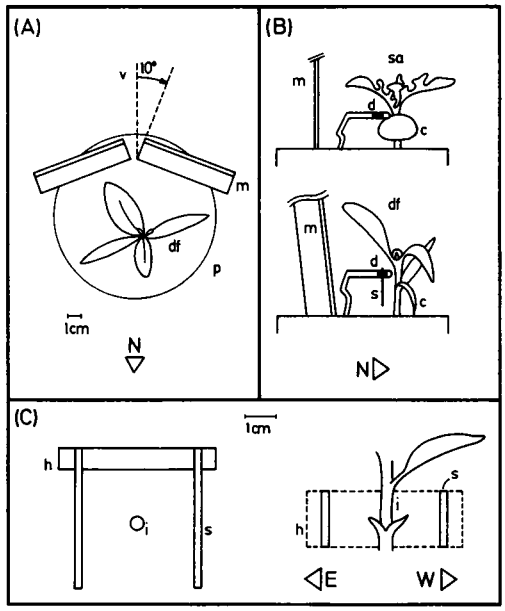

Figure 2. Modification of light quality at selected portions of the seedlings in the field. A, Disposition of mirrors in the experiments with *D. ferox*; B, disposition of diodes and screens in the experiments with *S. alba* (above) or with *D. ferox* (below); C, disposition of lateral screens: top (left) and front (right) views. Abbreviations: c, cotyledons; d, light emitting diode (λ_{max} = 660 nm); df, seedling of *D. ferox*; E, east; h, black holder; i, first internode; m, mirror; N, north; p, pot; s, screen; sa, seedling of *S. alba*; v, normal vector originating at the soil surface; W, west.

Table I. *Definition of Treatments with Mirrors and Effects on the R:FR Ratio of the Diffuse Light Measured Parallel to the Ground at the Level of the First Internode*

Treatment Designation	Description	R:FR[a]
Experiments with *S. alba* (winter and spring)		
R1 + A	1 R1 mirror + clear acrylic bar	1.05
R1 + D	1 R1 mirror + diode	1.17
FrM + A	1 FrM mirror + clear acrylic bar	0.51
FrM + D	1 FrM mirror + diode	0.82
Experiments with *D. ferox* (spring and summer)		
R1 + A	2 R1 mirrors + clear acrylic bar	0.78
R1 + D	2 R1 mirrors + diode + red screen	0.88
FrM + A	2 FrM mirrors + clear acrylic bar	0.50
FrM + D	2 FrM mirrors + diode + red screen	0.70

[a] 650:725 nm photon flux ratio. Measurements were obtained at midday. An integrating-cylinder probe (1) was used attached to an ISCO SR spectroradiometer (ISCO, USA). The SE of the R:FR ratios were ≤4%, n = 4. Treatments had negligible effects on the R:FR ratio of the light received by a horizontal sensor placed in the position of the seedlings (1).

With this sampling method, IA could be varied while maintaining the long axis of the probe perpendicular to the direct light vector.

The effects of canopy density on the spectral distribution of light within the tissues were investigated by positioning the seedlings of *D. ferox* or the succulent leaves at the center of 50 × 50-cm canopies (Fig. 1C). The canopies consisted of a

Table II. *Definition of Treatments with Lateral Screens and Effects on the Light Flux Measured Parallel to the Ground at the Level of the First Internode*

Treatment Designation	Description	Relative Photon Fluence Rate at		R:FR[a]
		650	725	
		nm		
Midday				
CL	Transparent-acrylic screen	1.00	1.33	0.75
NSH	Black-acrylic screen + red acetate	0.68	0.81	0.84
FRSH	Blue-acrylic screen + red acetate	0.66	1.35	0.49
Late afternoon				
CL		1.00[b]	0.86	1.16
NSH		0.21	0.19	1.08
FRSH		0.31	0.89	0.35

[a] Measurements were taken between the screen with the integrating cylinder probe attached to an ISCO spectroradiometer. SE <6%, $n = 3$. [b] Absolute photon fluence rate at 650 nm was 1.95 times greater at late afternoon than at midday.

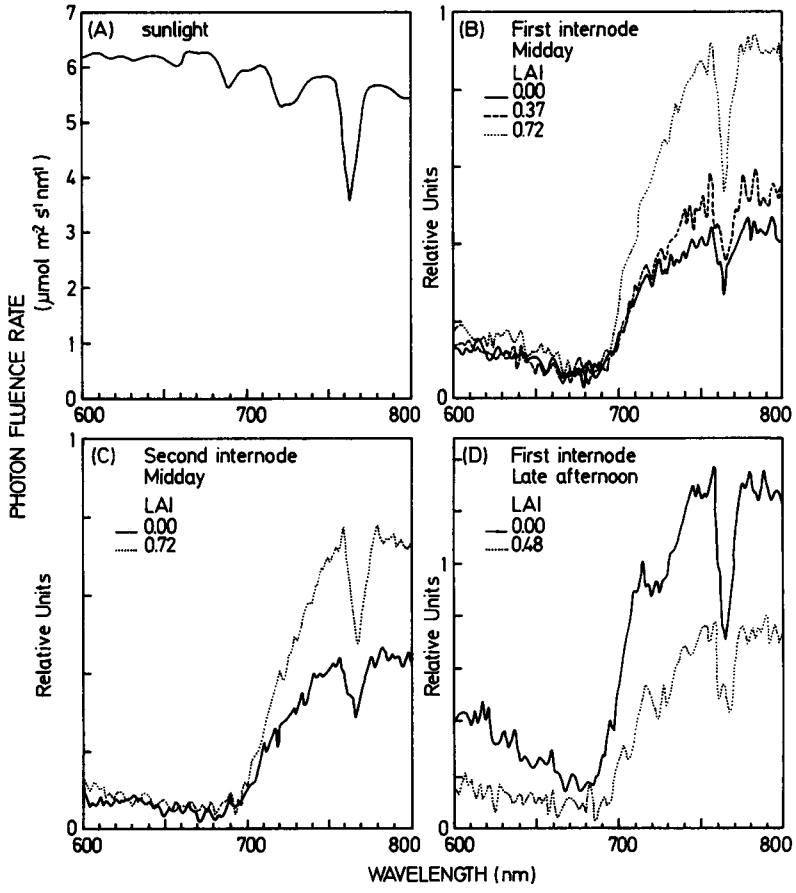

Figure 3. Effects of canopy density on the light regime within the internodes of *D. ferox* seedlings. A, Sunlight spectrum: cosine-corrected horizontal receiver, clear sky, PAR = 1600 μmol m^{-2} s^{-1} (347 W m^{-2}), calculated Pfr/P = 0.56. B and C, Measurements at midday: solar elevation $\geq 68°$, clear sky; plants with six visible true-leaves; first internode = 2 × 12 mm, second internode 1.8 × 4.0 mm. (D), Measurements in the afternoon: solar elevation $\leq 35°$, clear sky; first internode = 2 × 10 mm. Each curve is the average of 18 to 40 scans. A value of 1 in the ordinate (panels B, C, and D) corresponds to a measured photon fluence rate of 0.2 μmol m^{-2} s^{-1} nm^{-1}.

group of *D. ferox* seedlings growing in individual pots; the different LAI values were obtained by changing seedling density between 0 and 200 plants m^{-2}. To avoid oscillations of plants due to wind, spectral measurements were taken on the northern (sunlit) bench of a greenhouse. The spectrum was scanned between 600 and 800 nm at 2 nm intervals; each scan took about 20 s to complete. The longest measurements, involving various replicate scans for each density treatment, lasted 2 h or less. The R:FR ratios were computed according to Smith (26) except when otherwise stated. Phytochrome photoequilibria (Pfr/P) were calculated using the coefficients of *in vivo* phytochrome photoconversion obtained by Seyfried and Schäfer (25) with etiolated *Cucurbita* cotyledons. Because there is considerable variation among the spectral properties of phytochrome published by different authors (18), we have repeated these calculations using two additional sets of pho-

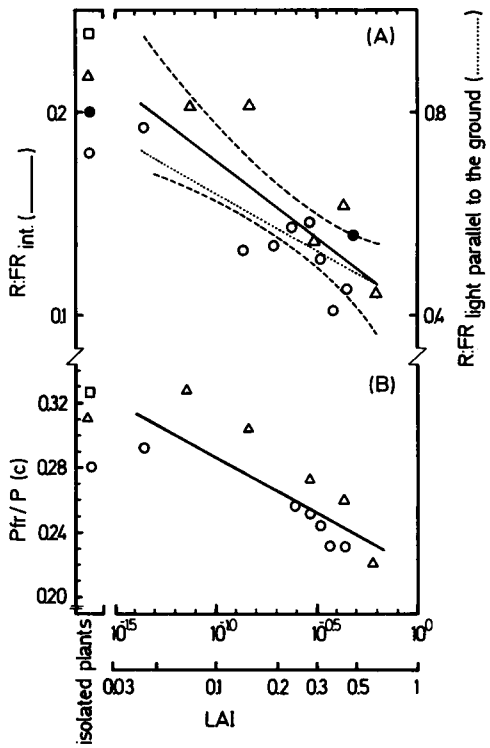

Figure 4. Effect of increasing LAI on the light regime within the first internode of *D. ferox* seedlings. Different symbols indicate different sets of measurements; open symbols, midday; closed symbols, afternoon; each point is the average of 10 to 25 scans. A, Effects on the internal R:FR ratio. Solid line, regression fitted by least squares; dashed line, 95% confidence band; dotted line, relationship between the R:FR ratio of the light measured parallel to the ground and canopy LAI (after [1]). B, Effects on the calculated phytochrome photoequilibrium inside the stem. The slope of the fitted regression is significant at $P < 0.01$.

toconversion coefficients: that derived by Mancinelli (18, Figs. 2–4) from the work of Kelly and Lagarias (15), and that reported by Gardner and Graceffo (Table 4 in ref. 11).

Selective mirrors (10 × 13 cm) were used to vary the spectral composition of the light received by fully sunlit seedlings in the field (1). In the experiments with *S. alba* (winter and spring) one mirror per pot was placed 6 cm to the south of the seedlings; in the experiments with *D. ferox* (spring and summer) there were two mirrors per pot (Fig. 2A). Two types of mirrors were used: FrM (high reflectance for FR, low reflectance for R) and R1 (low reflectance for both R and FR). In order to modify the spectral regime at localized portions of the stem, a light emitting diode (λ_{max} = 660 nm) (5) or a diode plus a black screen covered with red acetate were positioned between the mirrors and the first internode (Fig. 2B). The effect of diodes and screens was twofold: they reduced the amount of reflected light (R and FR) impinging on the first internode and added a low amount of R light. Diodes turned on and off automatically 20 min after sunrise and before sunset, respectively. Small bars (5 mm, diameter; 7 mm, length) of clear acrylic placed in the same position as the diodes were used as controls. In this way, four different R:FR ratios at the level of the first internode were obtained (Table I).

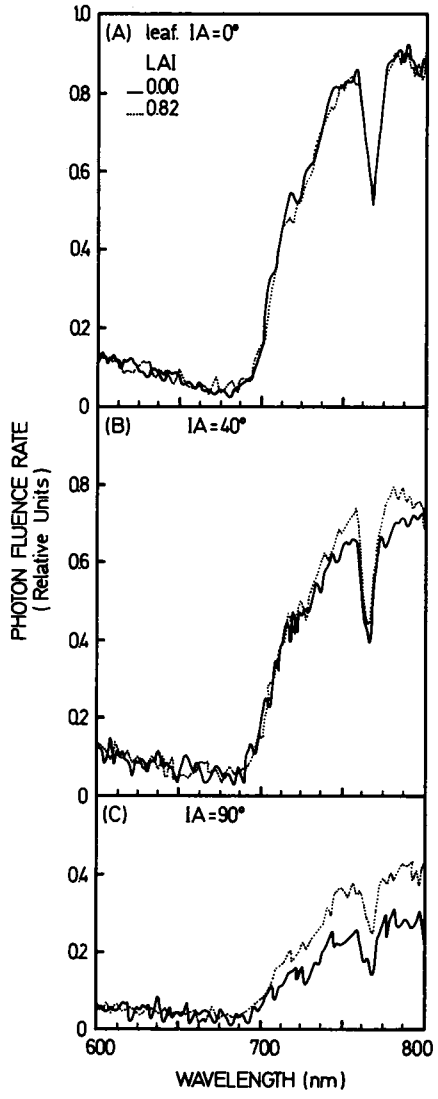

Figure 5. Effects of leaf orientation and canopy density on the light regime inside *Aeonium* leaves. Incidence angle = 0° (A), 40° (B), or 90° (C). (——), isolated leaves; (·····), leaves included in a seedling canopy (LAI = 0.82). All measurements were at midday, solar elevation ⩾ 66°; each curve is the average of 20 scans. A value of 1 in the ordinate corresponds to a measured photon fluence rate of 0.45 μmol m^{-2} s^{-1} nm^{-1}.

In order to shade localized portions of the stem, small screens were placed on the east and west sides of the first internode of *D. ferox* seedlings growing in the field (Fig. 2C). Three types of screens were used: CL, consisting of a sheet of transparent acrylic; NSH (opaque to visible and FR light), constructed with a sheet of black acrylic and covered in their internal side with red acetate, and FRSH (low transmittance for visible light and high transmittance for FR), constructed with a sheet of blue acrylic (No. 2031, Paolini SA, Argentina) and covered in their internal side with red acetate. The screens were 2 cm high, 5 cm long, and 0.25 cm thick; the distance between screens was 4.5 cm. NSH screens had similar effects on the R and FR components of the light flux measured parallel to the ground; the FRSH screens reduced the R flux

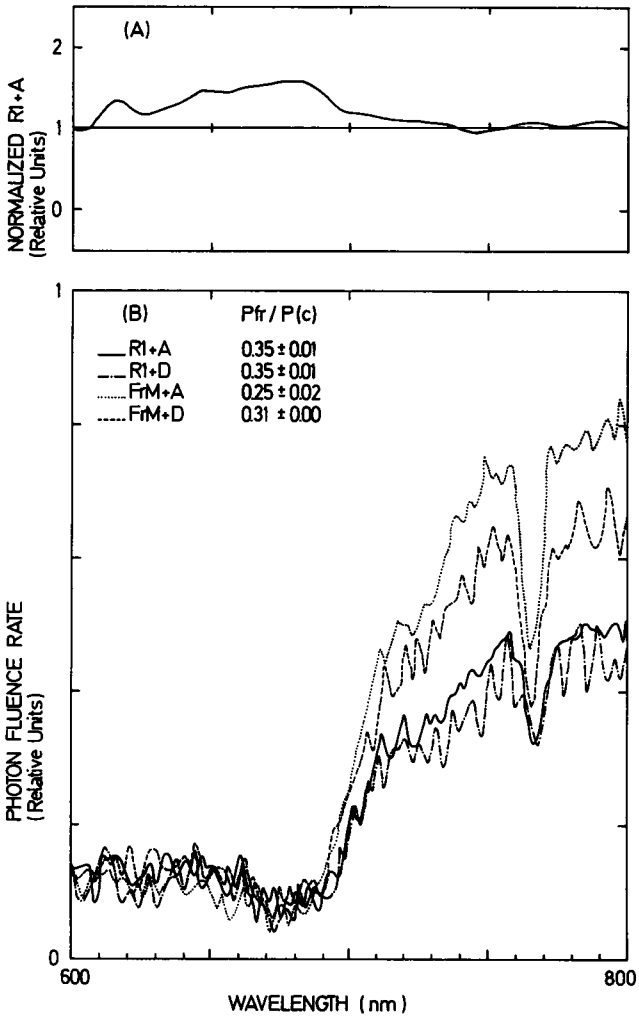

Figure 6. Effects of treatments with mirrors and diodes (Table I) on the light environment inside the first internode of *D. ferox* seedlings. A, Quotient between the spectrum produced by treatment R1+A and that corresponding to the untreated seedling placed at the same position; B, spectral photon distribution inside the internode for each treatment. Measurements were at midday, clear sky; seedlings had three visible leaves; first internode = 1.6 × 8.5 mm. Each curve is the average of 12 to 24 scans.

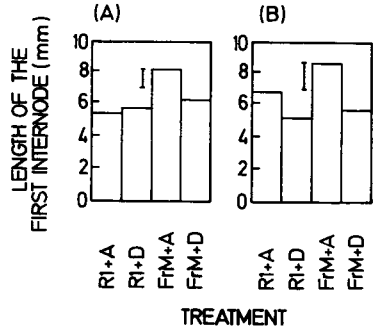

Figure 7. Effects of modifications of the R:FR ratio (Table I) on the final length of the first internode of *S. alba* seedlings grown in the field. A, Winter experiment; B, spring experiment. Thin bars indicate LSD ($P = 0.05$), $n = 12$ to 20. The length of the internode at the beginning of the experiments was 1 mm.

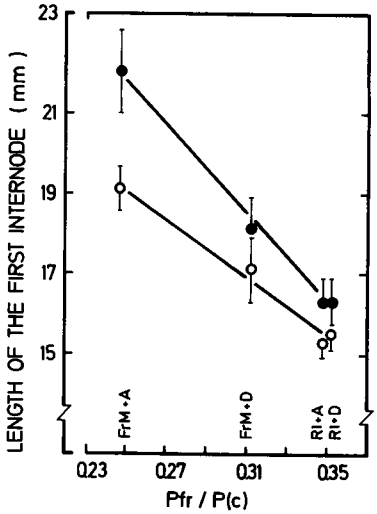

Figure 8. Relationship between final length of the first internode of *D. ferox* seedlings and the calculated phytochrome photoequilibrium inside the internode (Fig. 6). (●), Spring experiment; (○), summer experiment. Bars indicate ±1 SE. The length of the internode at the beginning of the experiments was 1 to 2 mm.

to the same extent but did not modify the amount of FR (Table II). Due to the position of the screens relative to the stem, they had a larger effect at low solar elevations, when filtering direct sunlight.

RESULTS

The spectral photon distribution within the stems was profoundly affected by canopy density (Fig. 3). Near solar noon, the light reflected by neighboring plants doubled the amount of FR scattered inside the internodes without having appreciable effects on the internal level of R light (Fig. 3, B and C). At low solar elevations, the internodes of isolated seedlings received direct sunlight; the presence of neighboring plants (LAI ~ 0.5) reduced both the amount of light inside the stem and the R:FR ratio (Fig. 3D). Within the LAI range of 0 to 1, we found a strong negative relationship between the R:FR ratio inside the axis and the LAI of the canopy (Fig. 4A). The slope of the fitted model did not depart significantly from that of the line describing the drop in the R:FR ratio of the light measured parallel to the ground with the increase in canopy LAI; the ordinates differed by a factor of about 4. The effects of canopy density on the internal R:FR ratio were quantitatively similar at the different solar angles. Phytochrome photoequilibrium inside the stem, as calculated from our spectral data and the photoconversion coefficients obtained by Seyfried and Schäfer (25), was also affected by canopy density (Fig. 4B). The use of photochemical parameters of phytochrome published by others (see "Materials and Methods") led to predictions about the state of the photoreceptor that differed from those presented in Figure 4B; however, the relationships between Pfr/P and LAI were always negative ($P < 0.01$; data not shown).

In order to determine possible effects of canopy density on the light environment of the leaves, we used a succulent as a

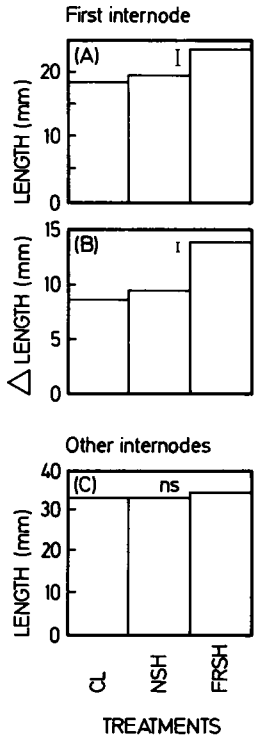

Figure 9. Effects of shading the first internode on stem elongation in *D. ferox* seedlings grown in the field. A, Final length of the first internode; B, internode elongation during the experiment; C, length of the epicotyl minus first internode. CL, Control; NSH, neutral shading; FRSH, shading simulating vegetation (for details, see Table II). Thin bars indicate LSD ($P = 0.05$, $n = 14$). The length of the first internode at the beginning of the experiments was 9.6 (± SD 3.2) mm.

test system (Fig. 1, B and C). The spectral structure of the light scattered within the leaves was similar to that found inside the internodes, but the effects of canopy density depended strongly on leaf orientation (Fig. 5). When the lamina was kept normal to the direct light vector the presence of neighbors did not affect the shape of the spectra (Fig. 5A). Indeed, a clear differentiation between the spectra corresponding to the isolated leaf and to the leaf placed at the center of a canopy of seedlings was observed only when the lamina was parallel to the direct sunlight (*i.e.* IA = 90°; Fig. 5C).

The spectral composition of the diffuse light flux measured parallel to the ground was varied by means of selective mirrors (Table I). FrM mirrors (high reflectance for FR) produced an increase in the amount of FR scattered within the stem that closely resembled the effect of neighboring seedlings (Fig. 6B, FrM+A; *cf.* Fig. 3, B and C and Fig. 4B). Plants exposed to additional FR developed longer internodes (Figs. 7 and 8) than did those grown in front of R1 mirrors, which had small effects on the spectral regime inside the axis (Fig. 6A). Interposing a light emitting diode (experiments with *S. alba*) or a diode plus a screen (experiments with *D. ferox*) between the FrM mirrors and the first internode allowed a local increase in the R:FR and Pfr/P ratios (Table I; Fig. 6B, FrM+D), which resulted in shorter internodes (Figs. 7 and 8). In the experiments with *D. ferox* for which measurements of the spectral regime within the stem were taken, we found a negative linear relationship between the final length of the internodes and the estimated Pfr/P inside them (Fig. 8).

Shading the stem at localized portions was achieved by means of small screens placed at the east and west sides of the first internode of isolated *D. ferox* plants (Fig. 2C). In this way we obtained a neutral shade (=NSH) and a selective shade (=FRSH) where R light fluence rate was lowered without modifying the amount of FR (Table II). NSH did not promote internode elongation, which did occur when both the photon fluence rate and the R:FR ratio were reduced (Fig. 9, A and B). These localized treatments had no effects on the elongation of stem portions above the first internode (Fig. 9C).

DISCUSSION

The results presented in this paper indicate that in open canopies formed by plants of similar size, the spectral distribution of the light scattered inside the internodes is affected by canopy density throughout the photoperiod (Fig. 3). The observed parallel between the effects of density on the spectral readings within the stem and those obtained with an integrating cylinder placed at the center of the canopy (Fig. 4A) suggests that the light inpinging laterally on the stems makes an important contribution to the internal light regime, even in the younger internodes of small seedlings (Fig. 3C). The spectral distribution of the light measured parallel to the soil surface is influenced strongly by the presence of surrounding vegetation (1, 2, 14); thus, even a small change in canopy density may bring about a significant spectral shift inside the stem. In fact, a reduction of the internal R:FR and Pfr/P ratios with increasing plant density was detected for LAI values that were well below those required to decrease PAR interception per plant, but high enough to cause a detectable increase in stem elongation rate (Fig. 4; *cf.* refs. 1, 2). This makes plausible the proposal that the growing internodes play an important role in the perception of canopy density in stands formed by plants of similar size. Furthermore, though the distribution of phytochrome in the stem is unknown (13, 27), our spectral measurements show that the above contention could be maintained even if the photoreceptor is not located at the outer surface of the organ. Strong support for the hypothesis postulating a role for the stem in the detection of neighborhood density comes from the experiments involving manipulations of the light conditions of the axis. In agreement with most of the information derived from experiments in controlled environments (4, 7, 8, 10, 13, 16, 21), we found that the elongation of the internodes was affected by localized light-quality treatments (Fig. 7–9). An important feature of our results is that the observed changes in elongation rate were triggered by treatments producing alterations of the light regime inside the stem that were essentially identical to those produced by the presence of neighbors in canopies of low LAI (Fig. 6; *cf.* Figs. 3 and 4). Moreover, the elongation responses were very similar in magnitude to those elicited by changes in plant density in such canopies (1, 2).

Two other factors that may be modified by canopy density with potential consequences on internode elongation are: the photon fluence rate received by the stem and the spectral

regime at leaf level. Changes in WL fluence rate modify epicotyl elongation in many species (12, 17, 22, 28), and these changes may be perceived by the stem itself (17). Opposite results have also been reported: Child and Smith (7) did not find effects of WL fluence rate on internode elongation in *S. alba*. In our field experiment, shading the stem with neutral screens had no effect on internode elongation (Fig. 9, A and B). Thus, similar drops in WL fluence rate caused by the presence of neighbors at low solar angles (*e.g.* Fig. 3D) are unlikely to play a key role in the elongation reactions in sparse canopies, at least in *D. ferox*.

The involvement of the leaves in the control of internode elongation has already been demonstrated (3, 6, 16, 21). However, their possible contribution to the perception of density in sparse canopies is still difficult to evaluate. This is due to the lack of a suitable method for measuring the spectral regime in thin laminas at their natural position in the canopy. Based on our results with *Aeonium* (Fig. 5), however, it seems very unlikely that the spectral photon distribution within leaves exposed to direct sunlight may be affected by changes in stand structure. A more prominent role for the leaves might be expected in the lower strata of dense canopies or in the case of plants with more erect foliage (Fig. 5C).

The maintenance of some degree of autonomy in the internode responses to light quality may have substantial implications for the adaptation of the plant to changes in canopy structure. On the one hand, it would enable the seedling to detect neighboring vegetation in the earlier phases of canopy development (Figs. 3 and 4) and to adjust elongation rate accordingly (Figs. 7–9). This capacity may be a valuable trait in rapidly growing canopies, where relatively small lags in stem extension imply a sharp reduction in PAR availability (2). On the other hand, the internodes growing at the outer strata of established crops would be able to probe the canopy and to respond to the local conditions of density before the leaves are shaded by neighboring plants.

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