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Morphological responses of *Datura ferox* L. seedlings to the presence of neighbours

Their relationships with canopy microclimate

C.L. Ballaré, R.A. Sánchez, Ana L. Scopel, and C.M. Ghersa

Cátedra de Fisiología Vegetal y Fitogeografía, Facultad de Agronomía (UBA), Av. San Martín 4453, (1417) Buenos Aires, Argentina

Summary. We studied the effects of density on the dynamics of seedling growth and canopy microclimate within experimental stands composed of *Datura ferox* L. seedlings grown in individual pots. Interception of photosynthetically active radiation (PAR) by seedlings was evaluated either indirectly, by measuring leaf area, proportion of leaf area shaded by neighbouring individuals and laminar orientation with respect to sunlight, or directly, by measuring PAR at individual leaves at their natural angle of display. An integrating cylinder, with a geometry approximating that of a stem, was used within the canopies to measure the red:far-red (R:FR) ratio of the light flux from all compass points parallel to the soil surface. Seedlings responded rapidly (i.e. 1–2 weeks) to increased density by producing longer internodes and partitioning more dry matter to stems relative to leaves. These responses were observed before either PAR interception or growth rate were reduced by the presence of neighbours. Conversely, morphogenetic adjustment was preceded by a consistent effect of plant density on the R:FR ratio of the light received by the integrating cylinder. Air and soil temperature were not affected by density in these experiments. Differences in wind velocity within the canopy associated with plant density were avoided by the experimental procedure. The results support the idea that the drop in R:FR ratio of the light flux parallel to the ground – e.g. reflected sunlight – is an early signal that allows rapid adjustment of plant form to changes in canopy structure.

Key words: *Datura ferox* – Plant density – Neighbour detection – Canopy microclimate – Light quality

Plants growing in a canopy differ in many aspects from those grown in isolation. In addition to the differences in size (i.e. total biomass) there are conspicuous changes in form. Some of these changes are the result of an altered pattern of assimilate partitioning between different plant structures (e.g. Harper 1977, p. 196). This capacity for morphogenetic adjustment appears to have adaptative value; for example an increased internode elongation in response to shade would result in young leaves reaching a better lit stratum within the canopy (for a general discussion, see Grime 1979). Previous studies suggested that plants may detect the presence of neighbours before being shaded by them and respond with morphological changes accordingly (Casal et al. 1986; Ballaré et al. 1987). One way of achieving this early detection would be through the perception of the low red:far-red (R:FR) ratio of the light reflected from the leaves of neighbouring plants (Ballaré et al. 1987). However, we know of no published report of concurrent measurements of the effects of density on canopy microenvironment and the concomitant effects of neighbours' proximity on plant growth (biomass and form). Such an approach is particularly relevant since it would allow: (1) to determine whether or not the morphological changes triggered by the presence of neighbours precede the reduction in light availability that the plant meets in a growing canopy, and (2), to find out which changes in canopy microenvironment may play a significant role in the production of these responses. In this paper we report on the effects of density on the dynamics of seedling growth and canopy microclimate within experimental stands composed of *Datura ferox* seedlings grown in individual pots.

Materials and methods

Species description

Datura ferox L. (Solanaceae) – chamico, chinese thornapple – is a summer annual. It is found as a weed of waste places and rotation crops in many agricultural areas of South America (Marzoca 1979). In the field, germination takes place in spring or summer and seedlings produce a main stem of 6–9 internodes before flowering. Afterwards plants branch dichotomously, each ramification – consisting of a single internode – is terminated in a flower. The growth cycle ends with the first frosts in autumn.

Plant culture

Seeds of *D. ferox* were collected from soybean fields in Rojas (Buenos Aires) in 1986. Seeds were germinated following the procedure described by De Miguel and Soriano (1974). Seedlings were planted in sand in individual (500 cm^3) pots. One week after planting (leaf area $= 1.1 \pm 0.06$ cm^2 $plant^{-1}$) the pots were arranged at 3 densities: 32, 100, and 240 pots m^{-2} in $0.5 \times 0.5 \times 0.15$ m deep wooden containers; the space between pots was filled with sand. Fertilizer (NPK 15:15:15) was added twice, before planting and 17 days later, at a rate of 2.5 g per pot. In one of the trials the experimental area (ca. 2×15 m) was surrounded with 1 m-high transparent-polyethylene-film fence

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Offprint requests to: C.L. Ballaré

in order to minimize differences in wind velocity between density treatments. All the experiments were conducted in the fields of the Faculty of Agronomy (UBA), Buenos Aires, 34° 35′ S; 58° 29′ W.

Growth and solar tracking measurements

Leaf area (A) was estimated using the equation: A (cm^2) = 0.86 × length (cm) × width (cm) (Ballaré et al. 1987). Total dry weight of the seedlings (DW) was obtained after drying the seedlings for 48 h at 72° C. The following relationships were derived: LSR (Morgan and Smith 1978), the leaf dry weight: stem (+ petioles) dry weight ratio; SRR, the shoot:root dry weight ratio; and RGR, the mean relative growth rate (Hunt 1982).

Leaf orientation measurements were taken at various times of the day for the cotyledons and the first two true-leaves; the efficiency of solar tracking was determined by calculating the cosine of the angle of incidence (Travis and Reed 1983).

Canopy microenvironment

Air temperature within the canopy was measured with a tele-thermometer (Yellow Springs Instrument Co., Inc., USA). Thermistors were placed in miniature white-painted louvered boxes in order to shield them from radiation and allow natural ventilation. Soil temperature, at a depth of 5 cm, was measured using integrated circuit sensors (type LM 335, National Semiconductor Co., USA). Photosynthetically active radiation (400–700 nm, PAR) was measured with a LI-188 B radiometer and a LI-190 SB sensor (Lambda Instruments, Inc., USA). PAR at specific leaves was measured for 4–5 tagged plants located at the centre of each container following the method described by Constable (1986). The quantum sensor was held at the same angle of display as the leaves. PAR intercepted per plant was calculated as follows:

$$\mathrm{PAR}\,(\mu\mathrm{mol\ plant}^{-1}\,\mathrm{s}^{-1}) = \sum_{l=1}^{n} \mathrm{PAR}_l(\mu\mathrm{mol\ m}^{-2}\,\mathrm{s}^{-1}) \cdot S_l\,(\mathrm{cm}^2) \cdot 10^{-4}\,(\mathrm{m}^2\,\mathrm{cm}^{-2}) \qquad (1)$$

where: n = number of leaves per plant; PAR_l = PAR received at leaf l at its natural angle of display; S_l = average area of leaf l.

Determinations of R:FR quantum flux ratio (650:725 nm, half-bandwidth 15 nm) were performed with an ISCO SR spectroradiometer calibrated against an ISCO calibrator. The R:FR ratio of light flux from all compass points parallel to the soil surface was measured by means of an integrating cylinder (Ballaré et al. 1987). The device has a geometry approximating that of a stem and can detect slight changes in light quality resulting from increased FR reflected by neighbouring plants. There is good evidence that these changes may affect internode elongation (Ballaré et al. 1987). To do these measurements, the central seedling (= pot) was momentarily removed from the canopy (= container) and the integrating cylinder was positioned in the place of the seedling at canopy height. All light measurements were taken near solar noon under clear sky. The proportion of the leaf area per plant which was shaded by neighbouring seedlings was calculated by measuring individual shade spots, as described in Ballaré et al. (1987). Estimated figures for R:FR ratio and proportion of shaded area per plant were derived from relationships between these variables and the leaf area index (LAI) which were obtained using the same experimental setting (Table 1).

Statistics

The experiment was carried out twice during the spring and summer of 1986–7. In both cases there were at least four *true*-replicates (i.e. containers) of each density treatment. Measurements of plant responses were made usually on 4–5 tagged individuals per container, but a single datum (mean of the samples) for each replicate was derived to be used for testing for treatment effects, as suggested by Hurlbert (1984). Both experiments yielded very similar results, therefore, only those from the first experiment are represented unless otherwise stated.

Weather conditions during the experiment

The range of air temperature recorded at a nearby meterological station spanned from a minimum of 11.6° C, with a relative humidity of 89% to a maximum of 32.4° C, with a relative humidity of 41%. Near solar noon PAR was 2030 μmol m^{-2} s^{-1} under clear sky. Rain was recorded on seven days.

Results

The effects of neighbours on seedling growth and canopy microclimate

PAR interception by seedlings was not affected by the presence of neighbours during the first half of these experiments (ca. first 12–14 days). This is supported by the following observations. (1) The leaf area per plant was not affected by density during this period (Fig. 1a). (2) Leaves of *D. ferox* showed solar tracking activity, as shown by the frequency histograms for leaf angle and leaf azimuth (Fig. 2). This solar tracking activity, as evaluated by the average cosine of incidence, declined with seedling age, but there was not any noticeable relationship between seedling density and tracking ability (Fig. 1b). (3) Even at the highest density, mutual shading among seedlings during the central hours of the photoperiod was negligible (Fig. 1c). (4) PAR interception per plant, as derived from light measurements at individual leaves at their natural angle of display, did not reveal any consistent effect of plant density (Fig. 3a). Notice that this estimate integrates the effects of leaf area, leaf angle and shading. (5) Accumulation of dry matter was not affected by the density treatments (Fig. 3b – 12 days –).

Shading among seedlings increased during the second two weeks. Near solar noon, plants at the highest density intercepted 30% less PAR than those growing at the lowest density (Fig. 3a – 20 days –). During the fourth week the leaf area of the plants at the highest density increased at a lower rate and, by day 23, these plants had a significantly smaller leaf area than those grown at the lowest density (Fig. 1a). This was a consequence of: (1) the early onset of senescence of older main stem leaves (Fig. 4a); (2) the reduced growth rate of the leaves in the middle region of the main stem since day 20 (Fig. 4b, c) and (3), the delayed

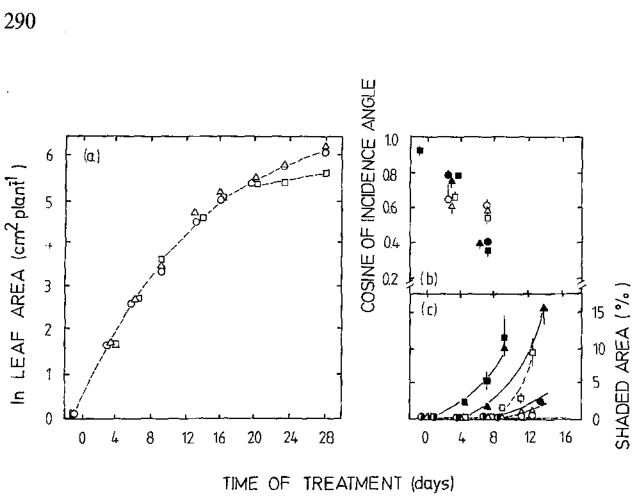

Fig. 1a–c. The effects of density on leaf size, leaf display and shading. Symbols: (○) 32, (△) 100, and (□) 240 seedlings m^{-2}. **a** Mean leaf area per plant; different lines indicate significant differences between means ($P<0.05$). On day 16 the first flower bud was visible in more than 80% of the plants; **b** The efficiency of solar tracking as a function of seedling age and seedling density measured at midday – solar angle >60° (open symbols) or late afternoon – solar angle <30° (closed symbols). Measurements were taken for at least 12 leaves in each of four replicate containers. Vertical bars represent ±1 s.e.m. – if≥0.01 – ($n=4$); **c** The proportion of leaf area per plant (±1 s.e.m. if ≥1%, $n=4$) which was shaded by neighbouring seedlings. At the time of the measurements solar angle was >60° (open symbols) or <30° (closed symbols). Lines indicate predicted values according to the LAI of the population (Regression equations in Table 1)

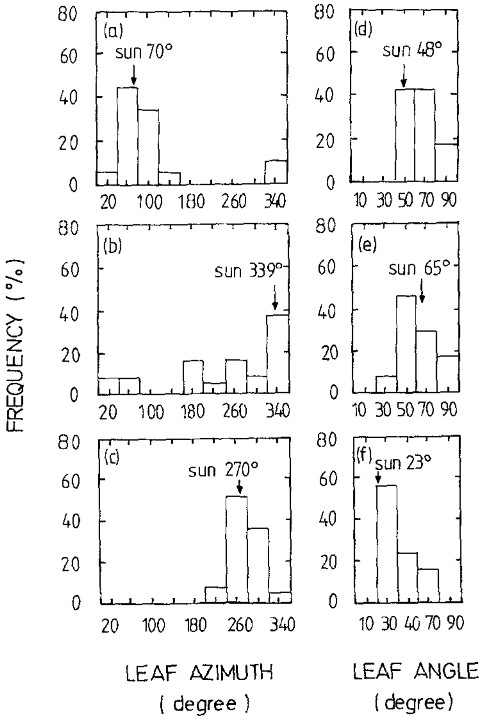

Fig. 2a–f. Frequency histograms for leaf azimuth (**a**, **b**, **c**) and leaf angle (**d**, **e**, **f**). Leaf angle is the angle between a perpendicular line originating at the leaf surface and the horizontal axis; leaf azimuth is the compass direction of that line with the magnetic north as 0°. Measurements were taken on day 3 at (**a**, **d**) 1000; (**b**, **e**) 1330 and (**c**, **f**) 1800 h local time. Solar angle and solar azimuth at the time of measurements are noted. Each histogram is derived from 24 cotyledons belonging to 12 seedlings randomly selected from those grown at the lowest density

Table 1. Regression equations used to predict the R:FR ratio of light flux from all compass points parallel to the soil at the height of maximum leaf density, and the proportion of the leaf area per plant (SHA) which is shaded by neighbouring seedlings

Equation[a]	F_{model}	R^2	Conditions of validity
R:FR = 0.405 – 0.231 log LAI	146.2 d.f. = 1;16 $P<0.001$	0.90 $P<0.01$	$0.01 \leq \text{LAI} \leq 1.2$ solar angle ≥ 60° clear sky
SHA (%) = $0.98\ e^{16.8 \log \text{LAI}}$	112.6 d.f. = 1;12 $P<0.001$	0.90 $P<0.01$	$0.01 \leq \text{LAI} \leq 1.2$ solar angle ≥ 60°
SHA (%) = $13.1\ e^{2.96 \log \text{LAI}}$	14.2 d.f. = 1;10 $P<0.01$	0.59 $P<0.01$	$0.01 \leq \text{LAI} \leq 1.2$ solar angle < 31°

[a] Equations were fitted by least squares regression to the original data (R:FR Fig. 3c and SHA Fig. 2 in Ballaré et al. 1987)

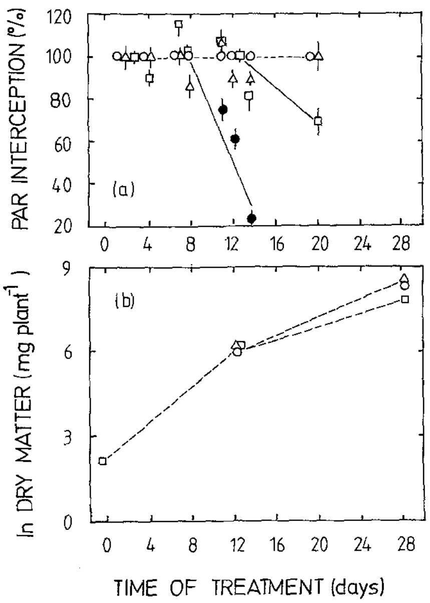

Fig. 3a, b. The effect of density on PAR interception and dry matter accumulation. Symbols: (○) 32, (△) 100, and (□) 240 seedlings m^{-2}. **a** PAR interception by whole seedlings. Results are expressed as percentage of PAR interception by seedlings grown at the lowest density. (●) indicates PAR interception by seedlings grown at the lowest density when they were placed (without altering their compass orientation) at the centre of a canopy of 240 seedlings m^{-2}. Vertical bars represent ±1 s.e.m. ($n=4$); **b** Mean dry weight of the whole seedlings. Different lines indicate significant differences between means ($P \leq 0.05$)

development of axillar branches after flowering, which resulted in a lower number of leaves at harvest (Table 2). The low RGR observed during the last two weeks in plants grown at the highest density (Table 3) was reflected in a significantly lower plant weight at the end of the experiment (Fig. 3b). Plants grown at the intermediate density never showed consistent differences in PAR interception (Fig. 3a) and RGR (Table 3) when compared to those grown at the lowest density.

Density treatments had strong effects on internode elongation (Fig. 5a) and assimilate partitioning between leaves

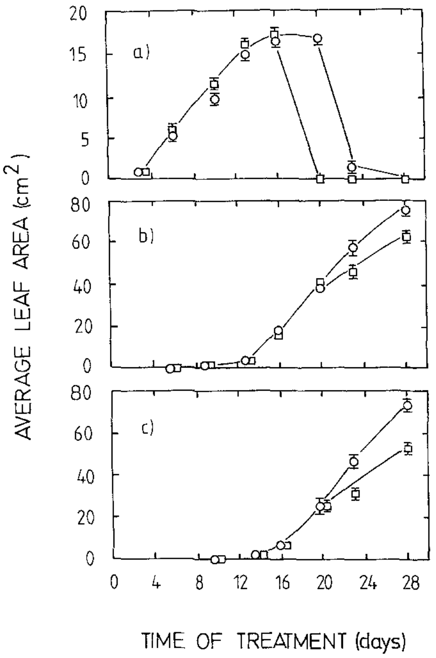

Fig. 4a–c. Average area of specific main stem leaves. **a** First, **b** fifth and **c** sixth true leaf. (o) 32 and (□) 240 plants m^{-2}. Vertical bars represent ±1 s.e.m. ($n = 4$). There was not abscission of leaves fifth and sixth during the period of observation

Table 2. The effect of density on the number of leaves at the end of the experiment

	Density (plants m^{-2})		
	32	100	240
No. of leaves on the main stem (plant^{-1})	8	8	8
No. of leaves on axillar branches (plant^{-1})[a]	8.5 (1.1)	8.5 (1.3)	3.1 (0.2)

[a] Includes leaves ≥0.5 cm^2. S.e.m. ($n = 4$) is given between brackets

Table 3. Mean relative growth rates of the seedlings (RGR) and leaf:stem (+ petioles) dry weight ratio (LSR)

Parameter	Days of treatment	Density (plants m^{-2})		
		32	100	240
RGR (day^{-1})	between 0 and 12	0.30 a	0.32 a	0.32 a
	between 12 and 28	0.14 a	0.14 a	0.10 b
LSR (g g^{-1})	0	1.80 a	1.80 a	1.80 a
	12	4.16 a	3.59 a	2.23 b
	28	2.47 a	1.49 b	1.19 b

Values within a row with the same letter are not significantly different at the 0.05 level

and stem (Table 3). The shoot : root dry weight ratio was not affected by density ($P > 0.05$, data not shown).

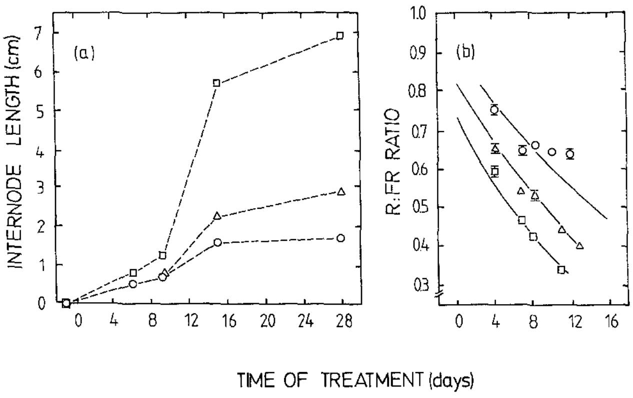

Fig. 5a, b. Time courses of stem elongation and light quality changes in canopies of different densities: (o) 32, (△) 100, and (□) 240 seedlings m^{-2}. **a** Mean length of the first internode; different lines indicate significant differences between means ($P < 0.05$). **b** The R:FR ratio (±1 s.e.m. – if ≥0.01 –, $n = 4$) of the light flux parallel to the soil surface. Measurements were taken with the integrating cylinder placed at the height of maximum leaf density in the centre of the canopies. Lines indicate the expected values according to the LAI of the population (regression equation in Table 1)

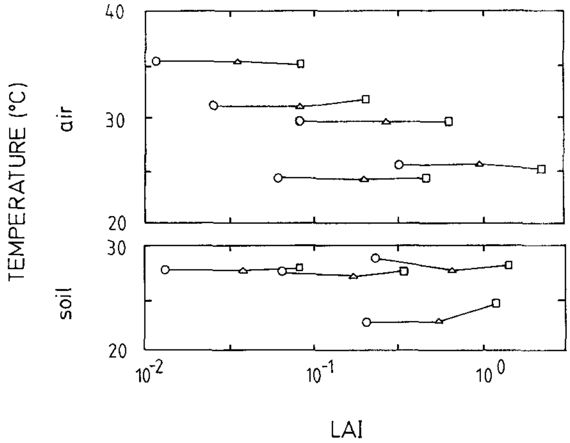

Fig. 6. The relationship between LAI and air temperature at the height of the first internode or soil temperature at −5 cm (local time: 1230 h). Symbols: (o) 32, (△) 100 and (□) 240 seedlings m^{-2}. Lines connect figures obtained on a same recording date. Measurements of air and soil temperature belong to different experiments. S.e.m. were usually less than 0.5%

Measurements with the integrating cylinder placed at the centre of the canopies showed a large effect of plant density on the R:FR ratio of the light flux parallel to the soil surface (Fig. 5b). Differences between density treatments were detected very early and there was a close agreement between actual values of R:FR and predictions based on the LAI of the canopy. Conversely, there was no relationship linking LAI with either air or soil temperature; rather, there was a large variation between data from different recording dates (Fig. 6).

Surrounding the experimental area with a 1 m-high transparent-polyethylene-film fence, a treatment to minimize differences in wind velocity between densities, did not alter the general pattern of responses presented in Figs. 1, 3 and 5 (data not shown).

The effect of morphogenetic adjustment on PAR interception

An attempt was made to quantify the impact of morphogenetic adjustment on the ability of the seedlings to intercept PAR.

We compared PAR interception by seedlings previously grown at low density and included in a high density canopy with that of seedlings continuously at high density. For this purpose a plant (=pot) from the centre of the high-density container was replaced by a plant grown in a low-density container. After the measurements of PAR both plants were returned to their positions. The seedlings that had adapted their form to low density canopies showed, in the presence of an increased number of neighbours, a significantly lower PAR interception than those grown at the higher density from the beginning of the experiment (Fig. 3a, cf. ● vs □). This difference in PAR interception was first detected on day 11, when the main morphological difference between high-density and low-density seedlings was the length of the internodes (Fig. 5a, cf. Fig. 1a).

Discussion

Seedlings of *D. ferox* responded rapidly to increased plant density by producing longer internodes (Fig. 5a) and partitioning more dry matter to stem relative to leaves (Table 3). In a previous paper (Ballaré et al. 1987) we reported that high densities stimulated stem elongation in *D. ferox* before the LAI of the canopy was large enough to cause a significant degree of mutual shading. Plant light interception depends not only on the proportion of sunlit leaf area, but also on the size of the photosynthetic apparatus and its orientation respect to the direction of solar beams. Therefore, the possible effects of neighbours' proximity on these two aspects should be considered to find out wether the increase in elongation rate occurs before there is a reduction in the amount of light intercepted per plant. Present experiments, which incorporated leaf area (Fig. 1a) and leaf orientation measurements (Fig. 1b) along with independent records of PAR receipt (Fig. 3a), indicated lack of interference between plants for light energy capture before day 12. By that time, plants at the highest density had significantly longer internodes (Fig. 5a), and lower LSR (Table 3) compared to those grown at the lowest density. Moreover, PAR interception measurements showed no differences between intermediate and low density treatments during the first three weeks (Fig. 3a); however internodes of plants grown at intermediate density were longer from day 15 onwards (Fig. 5a) and LSR was smaller on day 28 (Table 3). We concluded from these results that morphogenetic adjustment to the presence of neighbours was a response that preceded the decrease in PAR availability and was not a consequence of it. This conclusion stands also if the accumulation of dry matter – instead of PAR interception – is taken as an index of light availability (cf. Figs. 3b and 5a).

A second question is which was the environmental trigger of the events that culminated in the observed morphological responses. Harper (1977, p. 348), and Morgan and Smith (1981) have emphasized the difficulties for solving this kind of problems based on data from field experiments alone. Temperature, humidity (McIntyre and Boyer 1984), wind speed (Neel and Harris 1971) and light quality and quantity (e.g. Mohr 1972) may affect stem elongation and other physiological processes. All these variables may be affected by canopy density.

Differences in air temperature associated with plant density were not detected in our experiments during the period in which the density treatments had a major effect on morphological development (Fig. 6). That the initial responses to density had been a consequence of differences in wind velocity can be ruled out since (1) seedlings were small and containers had a high edge:area ratio, and (2), fencing the area with polyethylene film did not alter the general pattern of response.

We have no measurements of fluence rate at stem level but it was noted that the first internode was shaded at *all* densities by leaves belonging to the same plant during most of the photoperiod. Only during brief periods at the end of the day, and from the second week of treatment onwards, it was noted that the proportion of seedlings having their internodes shaded by neighbouring plants was greater at the higher density (data not shown). Therefore, we cannot reject the possibility that this transient difference in fluence rate had contributed to determine some of the changes in plant morphology associated with plant density.

The effect of vegetation canopies in reducing the R:FR ratio of sunlight is well documented (Kasperbauer 1971; Holmes and Smith 1977a; Deregibus et al. 1985). In the present case, there are two reasons to propose that most leaves were continuously exposed to direct sunlight. First, leaves of *D. ferox* track the sun during the day (Fig. 2), and second, between-plant shading was found to be negligible at all densities (Fig. 1c; Fig. 3a). Therefore, it is very unlikely that density treatments have had early effects on the R:FR ratio of the light reaching the leaf surface. In contrast the quality of the light reaching the stem surface could have been significantly altered, even at low LAI values. Our data show that the number of neighbours affected the R:FR ratio of the light flux from all compass points parallel to the ground (Fig. 5b). This effect was entirely consistent with previous observations (Table 1) showing that, within seedling canopies, increasing LAI above 0.01 causes a progressive reduction in the R:FR ratio of the light received by an integrating cylinder. At high solar elevations (e.g. near solar noon) this reduction of R:FR may be completely accounted for by the increased FR reflected by leaves of neighbouring plants; at low solar angles and LAI values close to 1, the reduction of R:FR ratio is caused by the drop in R due to selective absorption by leaves (Ballaré et al. 1987). Low R:FR ratios, acting through the phytochrome system, stimulate shoot extension rate (Holmes and Smith 1977b; Morgan and Smith 1978; Casal et al. 1987), and reduce LSR (Morgan and Smith 1978–9). Internode extension can be regulated by the light environment of the stem itself (Lecharny 1979; Morgan et al. 1980). An extreme sensitivity to a small reduction in R:FR ratio from typical values of sunlight has been demonstrated for plants grown in controlled environments (Morgan et al. 1981) and in field experiments where the light microenvironment of fully sunlit plants was modified by means of selective mirrors (Ballaré et al. 1987). These observations and the fact that the effects of density on light quality preceded its effect on plant morphology (Fig. 5) suggest that seedlings, by perceiving the low R:FR ratio of the light parallel to the ground, detected and responded to the presence of neighbours before being subjected to a drop in PAR availability. An early response to density, triggered by low R:FR ratios, has been also reported in the case of tillering in forage grasses (Casal et al. 1986).

Smith (1982) argued that R:FR ratio, being largely unaffected by weather, may be a good index of surrounding vegetation density. Light quantity, temperature, and other variables subjected to large unpredictable fluctuations should be perceived and integrated over a relatively long period of time in order to be an unambiguous index. This requirement would preclude rapid response to changes in canopy structure. Our data (Fig. 3a) emphasize the importance of continuous re-arrangement of form. In rapidly-growing canopies, delaying morphogenetic adjustment for a few days resulted in a sharp decrease in PAR availability.

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