Signaling among neighboring plants and the development of size inequalities in plant populations

(plant canopies/plant competition/phytochrome/sensory ecology)

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ABSTRACT   Transgenic tobacco plants that express an oat phytochrome gene (*phyA*) under control of the cauliflower mosaic virus (CaMV) 35S promoter and display altered photophysiology were used to test the role of light as a vehicle of information in dominance relationships between neighboring plants. Compared with the isogenic wild type, *phyA*-overexpressing plants showed dramatically reduced morphological responsivity to changes in the red/far red ratio of the incident light and to the proximity of neighboring plants in spacing experiments. In transgenic canopies an increase in stand density caused the small plants of the population to be rapidly suppressed by their neighbors. In wild-type canopies, plants responded to increased density with large morphological changes, and there appeared to be an inverse relationship between the magnitude of this morphological response and the ranking of the individual plant in the population size hierarchy. In these wild-type populations, size inequality increased only moderately with density within the time frame of the experiments. Our results suggest that, in crowded stands, the ability of individual plants to acquire information about their light environment via phytochrome plays a central role in driving architectural changes that, at the population level, delay the development of size differences between neighbors.

Higher plants respond to the proximity of other plants with plastic morphological and physiological changes. Some of these responses are simple changes in growth rate caused by variation in the supply of environmental resources (e.g., light, nutrients) imposed by neighboring individuals (1). Others are triggered by systems that appear to have evolved specifically to acquire information about the nearness of other plants (2). One such system is driven by phytochrome, a family of photochromic plant photoreceptors (3) that are sensitive to the red (R)-to-far red (FR) ratio (R/FR) of the incident light (4, 5). By perceiving R/FR changes in the spectral composition of reflected (back-scattered) light via phytochrome, plants can remotely detect the proximity of other plants and respond with morphological changes before being shaded by their neighbors (2, 6, 7). Early proximity responses include: changes in branching rate (8), accelerated stem elongation (9, 10), stem bending away from neighbors, and other phototropic phenomena (11, 12). Because some of these responses would increase the ability of individual plants to capture photosynthetic light in a patchy canopy, R/FR-light signals are thought to convey critical information to plants that are competing with each other for colonizing the aerial environment (2, 5, 6). What is not clear is to what extent the hierarchical relationships among individuals in a plant population depend on the perception of light information.

Among the best characterized population responses to increased plant density (number of plants per unit area) are (13): (*i*) reduction in individual plant size (weight), (*ii*) increase in mortality rate, and (*iii*) development of size inequalities among neighbors (14–18). Reproductive output and size are often positively correlated within plant populations (e.g., refs. 16 and 19). Therefore, understanding the determinants of size variability is of fundamental importance, and the need of a mechanistic theory to explain the development of inequalities in plant stands has been repeatedly emphasized (17, 18).

Virtually nothing is known about how interfering with the normal traffic of light signals among neighboring plants or with the plants' information-acquiring systems would affect plant interactions over periods longer than a few hours or days, the development of size inequalities, and the dynamics of population structure (2, 20). It is interesting to note that, by contrast, sociologists and animal ecologists have traditionally paid attention to the role of information and visual clues in the development of dominance relationships among individuals in animal populations (21).

Ellison (22) and Geber (17) have suggested that morphological responses of individual plants to crowding (e.g., increased height:dry weight ratio) would reduce interference among neighbors and delay size-structuring and self-thinning in plant populations. Thus, it has been predicted (20) that populations of genotypes with reduced R/FR responsivity would show a marked tendency to develop strongly hierarchical size distributions. Implicit in this prediction are the following assumptions: (*i*) light signaling through phytochrome plays a critical and unique part in controlling plant morphogenesis in canopies, and (*ii*) morphological responses to R/FR do somehow favor small plants over large plants. Although the first assumption is gaining acceptance (2), the second assumption has not been thoroughly explored. Morphological changes induced by low R/FR may benefit small plants if they allow light to penetrate deeper into the canopy or if the extent of the responses triggered by R/FR is greater in the dominated (more shaded) plants than in the dominant individuals. None of these conditions has been verified, and the second one may be even counterintuitive, according to what is known from physiological experiments, about interactions between light intensity and R/FR responsivity (23, 24). The lack of information on the role of light signaling in the genesis of population structure may have far reaching consequences, as the idea of engineering photomorphogenically "blind" genotypes to "improve" crop plants is currently being actively debated (25).

Abbreviations: CV, coefficient of variation; FR, far-red radiation; LAI, leaf area index; PPFD, photosynthetic photon flux density; R, red radiation; wt, wild type.
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We have studied plant morphological development in canopies of wild-type (wt) tobacco (*Nicotiana tabacum* L., cv. Xanthi) and an isogenic transformed line (code 8-3) that expresses an introduced phytochrome gene (*phyA*) from oat under the control of the constitutively active cauliflower mosaic virus 35S promoter (26) and displays altered responses (see below) to changes in the R/FR ratio (27). The results we report here point to a critical role for information signals and proximity perception mechanisms in retarding the development of size inequalities among neighbors in plant populations.

MATERIALS AND METHODS

Plant Material. The construction of the 8-3 transgenic line of tobacco was described by Cherry *et al.* (26). Light-grown *phyA*-transformed tobacco lines are known from extensive previous work (27, 28) to be impaired in their ability to respond with increased stem elongation to treatments of continuous FR light, although they present elongation responses to brief FR pulses applied at the end of the photoperiod. In wt plants, the *phyA* gene is negatively regulated by light, and the gene product is rapidly degraded in light-grown tissue. Therefore, phytochrome A is normally present at very low levels in light-grown plants. One interpretation (27) of the transgenic photophysiology is that the abnormally high levels of phytochrome A might disturb R/FR perception by other phytochrome species (e.g., phytochrome B). It is not known to what extent the ectopic expression of the phyA cDNA in the transformed plants contributes to their abnormal photoresponses.

Controlled-Environment Experiments. The objective of this series of experiments was to confirm, in the 8-3 transgenic line, the impairment in responsivity to changes in the R/FR ratio that has been described for other *phyA* overexpressers (27). Seeds were germinated on moist filter paper at 22°C under white light in a walk-in growth room (11). Seedlings were transplanted to 2.8 × 20-cm-deep plastic cones filled with garden soil and grown for 6 weeks under the same conditions used for germination. Light treatments began when plants had six true leaves. Plants were kept under white light provided by a mixture of fluorescent and incandescent bulbs (photoperiod = 12 hr) and were exposed or not exposed to FR radiation provided during the whole photoperiod from one side as described by Ballaré *et al.* (11). The FR treatment reduced the R/FR ratio (to <0.2 in the horizontal flux) without altering the photosynthetic photon flux density (PPFD) received by the plants, which was held at 160 μmol/m^2 per s. Individual plants (= pots) were assigned at random to the light treatments, which were all carried out in the same growth room. There were three independent replicates, with 10 plants per replicate.

Competition Experiment. The objective of this experiment was to evaluate the effects of population density on plant morphology and inequality development in even-aged monocultures of wt and transgenic 8-3 tobacco. The experiment was conducted under natural radiation at the Oregon State University campus in Corvallis, during the summer of 1992. Seeds were germinated in peat pellets soaked with tap water. After germination the pellets were "planted" in plastic cones (see above, one per cone). When seedlings had 7 true leaves, the cones were assigned at random to the density treatments, which were obtained by changing the spacing between cones in plastic cone racks. The following monoculture densities were used: 71, 166, and 583 plants/m^2; these density treatments were replicated five times following a completely randomized block design, and the experiment was run for 30 days. Three blocks were grown in the field and two in a glasshouse without any supplemental lighting. Although the "block" term was significant in some analyses, no qualitative differences between field and glasshouse groups were apparent in the responses to plant density. Results averaged over the five blocks are reported except for one case (see Fig. 5 *Lower*) in which data are available for three blocks (two greenhouse) only. All observations were made on the central eight plants of each replicate canopy, which were bordered by at least two (low density) or three (medium density and high density) rows of plants at the same density to minimize edge effects. Leaf area development was faster in the wt than in the 8-3 transgenics. Therefore, to compare the two genotypes at equivalent levels of competition intensity, all results are plotted as a function of the leaf area index of the canopies (LAI = m^2 of leaf per m^2 of soil). Average LAI at the beginning of the experiment varied widely between low and high density—i.e., from 0.21 to 1.71 in wt monocultures and from 0.12 to 0.97 in the 8-3 canopies. There was virtually no seedling mortality during experiment.

Plant Measurements. Stem length and shoot height were measured as the distance between the soil surface and the apex or between the soil surface and the uppermost point of the tallest leaf at its normal angle of display, respectively. Specific leaf area is the ratio between whole-plant leaf area (measured with a Li-Cor area meter) and leaf dry weight (obtained after drying for 48 hr at 71°C). Specific shoot area is the ratio between whole-plant leaf area and shoot (leaves + stem) dry weight. In the competition experiment, initial LAI (LAI$_i$) was estimated nondestructively by using allometric functions relating width of the largest leaf to leaf area per seedling, which were derived for seedlings of the WT and 8-3 genotypes. Six seedlings per canopy were sampled at random to estimate LAI$_i$. Final LAI was obtained after leaf area measurements following destructive harvest; LAI at the middle of the experiment (15 days) was obtained by interpolation assuming exponential growth of leaf area. In the figures, LAI is plotted on a logarithmic scale because the decay of the R/FR ratio in the horizontal light flux (and often the increase in elongation rate) is linearly related to the exponent of LAI in open canopies (9, 10). The coefficient of variation (CV = SD/mean) of stem length and shoot dry weight was calculated for each replicate canopy (n = 8 plants per canopy) at the beginning of the experiment (stem length) and after 30 days of treatment (stem length and shoot dry weight). As another measure of size inequality among neighboring plants, we calculated the ratio of dry weight between "large" and "small" plant subgroups in the populations. Thus, in each replicate canopy, the two smallest and the two largest plants among the eight central individuals were tagged at the beginning of the experiment. These plants were identified by taking measurements of width of the largest leaf, a size metric that is very well correlated with shoot dry weight in tobacco seedlings of the sizes used. The allometric relationships ($R^2 \geq 0.92$) were constructed independently for wt and 8-3 populations. The estimated initial dry weights were used to calculate the initial size inequality ratio in each replicate canopy. The final size inequality ratio was calculated for each replicate canopy by using dry weight data from the final harvest.

Responses to FR irradiance and canopy density (i.e., LAI) were evaluated for each genotype by means of analysis of variance using SAS (Statistical Analysis System) algorithms (29), which were also used to test the assumptions of the analysis. Results given in figures are treatment means and SEMs calculated from error mean squares derived from analysis of variance. Probabilities given throughout the text indicate the significance of FR and density effects.

Phytochrome Extraction and Analysis. For phytochrome determinations, leaf tissue pooled from several individuals was rapidly frozen in liquid nitrogen and pulverized with mortar and pestle. Phytochrome extraction and determinations of phytochrome content [Δ(ΔA)] were carried out as described by Cherry *et al.* (30); [Δ(ΔA)] measures the change

in $(A_{730} - A_{800})$ caused by exposing R-irradiated tissue to actinic FR. Total protein was measured by the Bradford method (31) with ovalbumin as a standard after trichloroacetic acid precipitation of clarified crude extracts.

RESULTS

Morphological Responses to the R/FR Ratio. wt tobacco plants exposed to additional FR light in a controlled environment responded with a marked increase in stem elongation rate ($P = 0.024$) and specific leaf area ($P = 0.040$) (Fig. 1). Transgenic 8-3 plants showed little or no morphological response to reductions in R/FR (Fig. 1; $P = 0.980$, stem length; $P = 0.464$, specific leaf area), which confirms and extends previous observations on other *phyA*-overexpressing tobacco lines (27, 28). This transgenic line was used in our spacing experiment to explore the impact of altered photophysiology on (*i*) morphological responses to neighbor proximity and (*ii*) the genesis of size inequalities.

Elongation Responses to Population Density. Transgenic 8-3 plants grown under natural radiation had ≈7-fold more total phytochrome than did their wt counterparts {i.e., phytochrome content, which = $[\Delta(\Delta A)]/g$ of protein, was 0.00445 ± 0.00055 in WT and 0.03280 ± 0.00170 in 8-3 shoots; $n = 4$} and displayed reduced responses (promotion of stem elongation) to natural leaf shading when grown underneath established canopies (data from field experiments not shown). As expected in wt canopies (9, 10, 32, 33), an increase in population density (canopy LAI, see *Materials and Methods*) caused a rapid and marked increase in stem elongation rate ($P \leq 0.016$) and shoot height ($P < 0.001$) (Fig. 2). For comparable ranges of LAI (e.g., between $10^{-0.3}$ and $10^{0.3}$), the (relative) elongation response of the transgenic line was reduced by a factor between *ca.* 7 (shoot height) and 8 (stem length) (Fig. 2 *Right*). None of the apparent responses of the 8-3 transgenics were significant at $P = 0.05$. These results are consistent with the idea that the sensing of the R/FR ratio via phytochrome, which is affected in the transgenic line (Fig. 1), plays a central role in triggering plant elongation responses to crowding.

Development of Size Inequalities. Inspection of the coefficient of variation (CV) of plant height provided insight into a critical aspect of morphological plasticity (17, 33, 34): its relation with the ranking of the individual plant in the population size hierarchy. In wt populations, the CV of final stem length (Fig. 3) and shoot height (not shown) decreased by a factor of 2 with increased plant density ($P = 0.028$), indicating that, on a relative basis, the heights of neighboring plants tended to become more similar with time as the density of the canopy was increased. That is, as plant density was
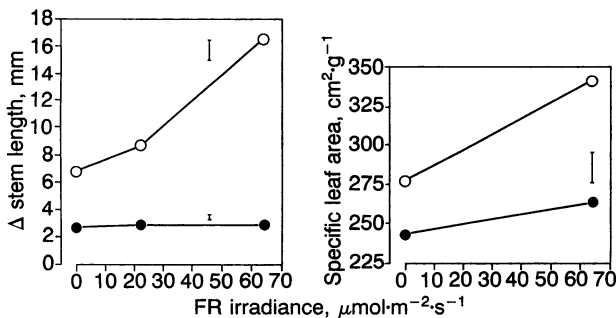

FIG. 2. Elongation responses of wt (○) and 8-3 transgenic (●) tobacco plants to increased plant population density (canopy LAI) in even-aged monocultures measured 2 (*Left*) or 30 (*Right*) days after the beginning of treatments and plotted against the initial LAI (LAI$_i$) or the LAI estimated for day 15 of the experiment, respectively. Each point is the average of five canopy means; bars indicate 1 SEM. - - -, Shoot; ——, stem.

increased in wt populations, the shorter plants appeared to elongate (relatively) more than the larger individuals. In contrast, in 8-3 transgenic populations, the CV of plant height appeared to increase with plant density ($P = 0.164$) (Fig. 3).

The groups of plants classed as "small" (according to their estimated dry weights at the beginning of the experiment) in the WT populations responded to increased canopy density with a 65% increase in specific shoot area (leaf area per unit of shoot weight) ($P = 0.001$) (Fig. 4). In contrast, the specific shoot area of the "large" plants remained constant across canopy densities (size × density interaction significant at $P = 0.013$). In the 8-3 transgenics there was only a slight increase in specific shoot area with canopy density (between 23% and 30%) ($P = 0.013$), and the patterns of response of "small" and "large" plant groups were similar (size × density interaction not significant; $P = 0.785$). Thus, in WT (but not in 8-3 transgenic) canopies, morphological responses to canopy density appeared to be inversely correlated with initial size (Figs. 3 and 4).

Increases in stem elongation (Figs. 2 and 3) and specific shoot area (Fig. 4) are likely to improve the competitive ability of small individuals, which otherwise would be suppressed by their taller neighbors, as discussed by Geber (ref. 17, p. 282–283). If this is correct, one would expect to see marked differences between WT and "R/FR-blind" plants in

FIG. 1. Morphological responses of wt (○) and 8-3 transgenic (●) tobacco plants to additional FR (reduced R/FR, simulating neighbor proximity). Data were obtained after 1 wk (*Left*) or 2 wk (*Right*) of treatment and are the average of the means of three independent experiments (*Left*) or 10 individual plants in a single experiment (*Right*). Bars denote 1 SEM.
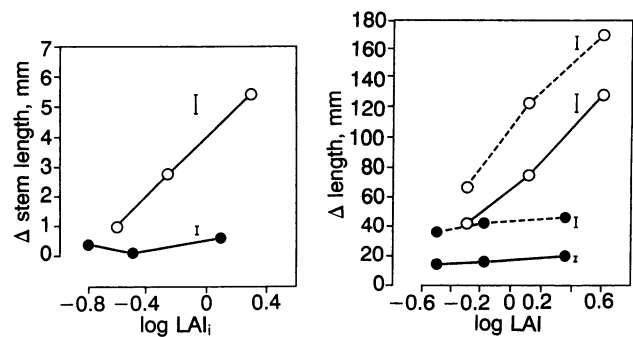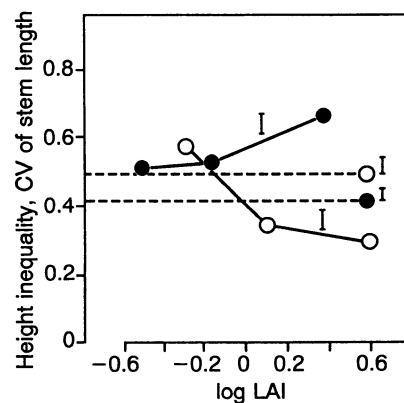

FIG. 3. Effects of increasing population density (canopy LAI) on height inequality in monocultures of wt (○) and 8-3 transgenic (●) tobacco plants. - - -, Average initial height inequality; ——, final height inequality. Each datum is the average CV; bars indicate 1 SEM; $n = 5$ (final) or $n = 15$ (initial) replicate canopies. Data are plotted against the LAI estimated for day 15. Initial inequality (i.e., the CV of stem length at the beginning of the experiment) was within ± 15% of the reported average (- - -) in all density treatments.
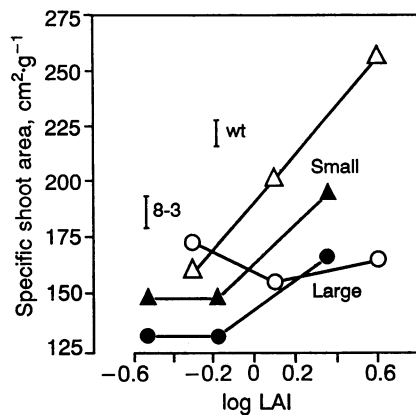
FIG. 4. Effects of increasing population density in monocultures of wt (○, △) and 8-3 transgenic (●, ▲) tobacco plants on leaf area produced per unit of shoot dry weight in the "small" (▲, △) and "large" (●, ○) plant groups. Bars indicate 1 SEM; *n* = 5 replicate canopies. Data are plotted against the LAI estimated for day 15.

the development of size (dry weight) inequalities at high population densities. Our results with the 8-3 *phyA* overexpressers are consistent with this expectation. In low density populations of *both* tobacco genotypes, size inequality tended to decrease during the course of the experiment, and by the final harvest, the "large" plants were roughly 3 times as heavy compared with the "small" plants (Fig. 5 *Upper*). This measure of inequality increased only 58% at the highest
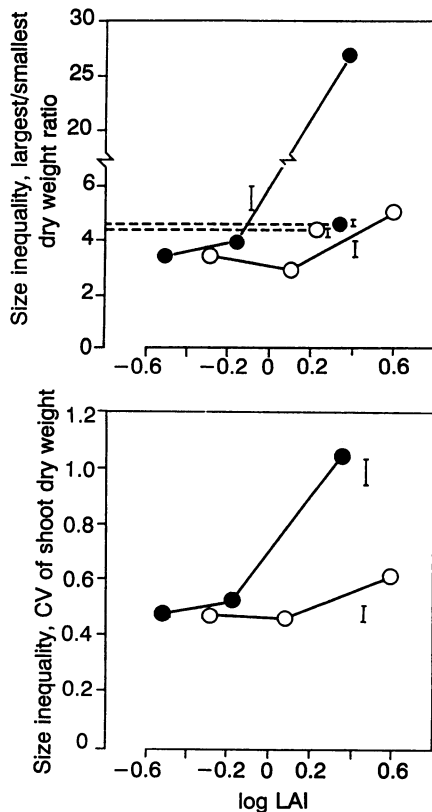

FIG. 5. Effects of increasing plant density on the development of size inequalities among neighbors in monocultures of wt (○) and 8-3 transgenic (●) tobacco plants. (*Upper*) Average dry weight ratio. - - -, Average initial ratio; ——, final ratio. Initial inequality was within ±15% of the plotted average (- - -) in all density treatments. (*Lower*) Average CV for each density treatment. Bars indicate 1 SEM; *n* = 5 (final) or *n* = 15 (initial) (*Upper*); *n* = 3 (*Lower*). Data are plotted against the LAI estimated for day 15.

density in WT populations (P = 0.089, density effect). In contrast, in transgenic canopies, an increase in plant density caused a dramatic (>8-fold) increase in the size inequality ratio ($P \ll 0.001$) (Fig. 5 *Upper*), even when the LAIs reached by these populations were considerably lower (ca. 50% less at each density) than in WT canopies. The mean CV of final shoot dry weight changed little with density in WT populations (P = 0.120), whereas it increased markedly in the 8-3 transgenics (P = 0.017) (Fig. 5 *Lower*). There was a significant difference between genotypes in the slopes of the lines describing the increase in CV with log LAI (P = 0.005), confirming that the density dependence of size inequality differed markedly between WT and transgenic canopies.

DISCUSSION

The results of our experiments show that transgenic tobacco plants that overexpress a *phyA* gene display (*i*) little or no morphological response to reduced R/FR ratio (Fig. 1), (*ii*) little or no morphological response to the proximity of neighboring plants in spacing experiments (Figs. 2 and 4), and (*iii*) a marked tendency to develop size hierarchies in dense monocultures (Figs. 3 and 5). The first observation is consistent with previous reports on other tobacco lines overexpressing oat *phyA* (27, 28). The second observation in our experiments (i.e., reduced morphological plasticity in canopies of the 8-3 line) supports the hypothesis that perception-of-proximity signals via phytochrome is a critical component in the elicitation of architectural responses to the nearness of neighboring plants (reviews in refs. 2, 5–7, and 20). This evidence is consistent with observations made on phytochrome B-deficient mutants (11, 35) and with results obtained in manipulative experiments involving canopies of wt plants (8, 10, 36). However, other interpretations of the 8-3 behavior are possible, as a complete picture of the 8-3 photophysiology is not yet available.

The third observation (i.e., differences between wt and 8-3 transgenic populations in size inequality development) is the most important result of our experiments. To begin with, the spacing experiment showed that, in wt populations, the CV of stem length (Fig. 3) and shoot height (not shown) decreased when canopy density was increased, suggesting that the relative elongation response to crowding was larger in the shortest plants. This result is remarkable for two reasons. First, in studies with several herbaceous species (33, 34), it was found that plants from crowded populations that ranked in the middle of their size (dry weight) distributions tended to be taller than uncrowded plants of the same dry weight, but the effect of "crowding" on morphology tended to disappear toward both ends of the size distribution. On the other hand, examination of morphological changes over time (in only one species) failed to detect any association between the size of the individual plant at the beginning of competition and the slope of the individual allometric trajectory (ref. 34, p. 653). Second, although the light environment sensed by short plants would be more affected by changes in LAI than the light environment of their taller neighbors, which might cause them to present a larger relative response to crowding, very little is known about how plant responsivity to a given signal of neighbor proximity (e.g., reduced R/FR) is affected by other environmental factors altered by canopy density (e.g., PPFD, blue light irradiance). Smith and Hayward (23) have shown that, under controlled conditions, the response to R/FR is reduced at very low PPFD in mustard seedlings, and Casal and Smith (24) reported little or no response to R/FR treatments given to the internodes in plants whose leaves received low levels of blue light. Thus, by scaling up from these physiological data, one might have expected the least relative response to canopy density in the shortest (more shaded) plants.

In addition to the elongation response, the changes of specific shoot area with density in wt canopies (Fig. 4) clearly demonstrate a morphological response that is inversely correlated with size in tobacco monocultures, and we have advanced the hypothesis that the rapid development of size inequalities in populations of R/FR-"blind" transgenic plants is primarily caused by the lack of this ranking-dependent photomorphogenic (Fig. 1) shape adjustment.

Alternative explanations for the greater size inequalities within crowded 8-3 transgenic populations compared with the wt populations include the following arguments. First, responses to R/FR ratio may result in a more efficient arrangement of canopy leaf area with respect to the distribution of light gaps. If these responses reduce shoot overlap, they might lessen competition for light between neighbors, provided that initial inequalities are small. However, it is unlikely that differences in leaf distribution alone may explain the differential size structuring in wt and 8-3 populations, since total leaf area was always much larger in wt than in 8-3 canopies, and total leaf area is normally the major determinant of light absorption by the canopy. Second, the 8-3 population might be inherently more variable than the wt. This explanation is not supported by the initial inequality data (Figs. 3 and 5) and does not account for the critical fact that inequality and the differences in inequality between the two genotypes were density dependent. Third, relative growth rate and size might be positively correlated within the 8-3 transgenics. A positive correlation between relative growth rate and initial dry weight would lead to increased inequality (as measured by CV or largest/smallest ratio) with time, even in the absence of competition (i.e., even at low densities) (discussed in ref. 17). This possibility is ruled out in our studies because dry-weight inequality actually appeared to decrease with time in populations of both genotypes at the lowest density (Fig. 5 *Upper*). Fourth, increased size inequality at high densities in 8-3 transgenics might result if these plants were more susceptible to low light than wt plants. Information on this issue is lacking, but gas exchange studies indicate that photosynthesis in other *phyA*-overexpressing tobacco lines is severely CO_2-limited at ambient CO_2 levels (37). This suggests that the photosynthesis–irradiance response curve would be (if anything) actually flatter (less affected by shading) in 8-3 transgenic than in wt plants.

We conclude that the weight of the evidence favors the hypothesis that the tendency of our 8-3 transgenic line to rapidly develop strong size hierarchies at high density (Figs. 3 and 5) is primarily caused by its reduced photomorphogenic responsivity (Fig. 1), which renders 8-3 plants, particularly the suppressed individuals, less capable of reacting morphologically to the proximity of other plants (Figs. 2–4). In fact, our data suggest that light plays a dual role in shaping the size structure of plant populations: (*i*) as a resource, because of its directional distribution, light would exacerbate size differences among neighbors (14, 38), and (*ii*) as an information vehicle, light acting via specific photoreceptors participates in the elicitation of morphological responses that, at the population level, reduce the inequalities produced by asymmetric competition. An unexpected corollary of this conclusion is that any factor (e.g., genetic or environmental) that alters the acquisition or interpretation of proximity signals by individual plants might result in increased inequalities in populations where competition for light is severe. This prediction adds a new axis to our understanding of inequality development, as it suggests that it is not merely the variation among neighbors in resource interception but also its interaction with the sensing and processing of information by individual plants that determines the dynamics of size-structuring.

1. Goldberg, D. E. (1990) in *Perspectives on Plant Competition*, eds. Grace, J. B. & Tilman, D. (Academic, San Diego), pp. 27–49.
2. Ballaré, C. L. (1994) in *Exploitation of Environmental Heterogeneity by Plants*, eds. Caldwell, M. M. & Pearcy, R. W. (Academic, San Diego), pp. 73–110.
3. Furuya, M. (1993) *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **44,** 617–645.
4. Morgan, D. C. & Smith, H. (1978) *Planta* **142,** 187–193.
5. Casal, J. J. & Smith, H. (1989) *Plant Cell Environ.* **12,** 855–862.
6. Ballaré, C. L., Scopel, A. L., Sánchez, R. A. & Radosevich, S. R. (1992) *Photochem. Photobiol.* **56,** 777–788.
7. Sánchez, R. A., Casal, J. J., Ballaré, C. L. & Scopel, A. L. (1993) in *International Crop Science I*, ed. Buxton, D. R. (Crop Sci. Soc. Am., Madison, WI), pp. 779–786.
8. Casal, J. J., Sánchez, R. A. & Deregibus, V. A. (1986) *Exp. Environ. Bot.* **26,** 365–371.
9. Ballaré, C. L., Sánchez, R. A., Scopel, A. L., Casal, J. J. & Ghersa, C. M. (1987) *Plant Cell Environ.* **10,** 551–557.
10. Ballaré, C. L., Scopel, A. L. & Sánchez, R. A. (1990) *Science* **247,** 329–332.
11. Ballaré, C. L., Scopel, A. L., Radosevich, S. R. & Kendrick, R. E. (1992) *Plant Physiol.* **100,** 170–177.
12. Novoplansky, A., Cohen, D. & Sachs, T. (1990) *Oecologia* **82,** 490–493.
13. Harper, J. L. (1977) *Population Biology of Plants* (Academic, London).
14. Weiner, J. (1985) *Ecology* **66,** 743–752.
15. Weiner, J. & Thomas, S. C. (1986) *Oikos* **46,** 211–222.
16. Schmitt, J., Eccleston, J. & Ehrhardt, D. W. (1987) *Oecologia* **72,** 341–347.
17. Geber, M. A. (1989) *Ecol. Monogr.* **59,** 267–288.
18. Weiner, J., Mallory, E. B. & Kennedy, C. (1990) *Ann. Bot.* **65,** 513–524.
19. Thompson, B. K., Weiner, J. & Warwick, S. I. (1991) *Can. J. Bot.* **69,** 442–446.
20. Schmitt, J. & Wulff, R. D. (1993) *Trends Ecol. Evol.* **8,** 46–51.
21. Ellis, L. (1993) in *Social Stratification and Socioeconomic Inequality: A Comparative Biosocial Analysis*, ed. Ellis, L. (Praeger, Westport, CT), Vol. 1, pp. 15–35.
22. Ellison, A. M. (1987) *Ecology* **68,** 737–741.
23. Smith, H. & Hayward, P. (1985) *Photochem. Photobiol.* **42,** 685–688.
24. Casal, J. J. & Smith, H. (1988) *Planta* **176,** 277–282.
25. Smith, H. (1992) *Photochem. Photobiol.* **56,** 815–822.
26. Cherry, J. R., Hondred, D., Walker, J. M. & Vierstra, R. D. (1992) *Proc. Natl. Acad. Sci. USA* **89,** 5039–5043.
27. McCormac, A. C., Cherry, J. R., Hershey, H. P., Vierstra, R. D. & Smith, H. (1991) *Planta* **185,** 162–170.
28. McCormac, A. C., Withelam, G. & Smith, H. (1992) *Planta* **188,** 173–181.
29. SAS Institute (1987) *SAS/STAT Guide for Personal Computers* (SAS Institute, Cary, NC).
30. Cherry, J. R., Hershey, H. P. & Vierstra, R. D. (1991) *Plant Physiol.* **100,** 775–785.
31. Bradford, M. M. (1976) *Anal. Biochem.* **72,** 248–254.
32. Ballaré, C. L., Sánchez, R. A., Scopel, A. L. & Ghersa, C. M. (1988) *Oecologia* **76,** 288–293.
33. Weiner, J., Berntson, G. M. & Thomas, S. C. (1990) *J. Ecol.* **78,** 459–469.
34. Weiner, J. & Thomas, S. C. (1992) *Ecology* **73,** 648–656.
35. Ballaré, C. L., Casal, J. J. & Kendrick, R. E. (1991) *Photochem. Photobiol.* **54,** 819–826.
36. Ballaré, C. L., Scopel, A. L. & Sánchez, R. A. (1991) *Oecologia* **86,** 561–567.
37. Sharkey, T. D., Vassey, T. L., Vanderveer, P. J. & Vierstra, R. D. (1991) *Planta* **185,** 287–296.
38. Schmitt, J., Ehrhardt, D. W. & Cheo, M. (1986) *Ecology* **67,** 1502–1507.