

Christine C. Muth · F. A. Bazzaz

Tree seedling canopy responses to conflicting photosensory cues

Received: 1 October 2001 / Accepted: 9 April 2002 / Published online: 14 June 2002
© Springer-Verlag 2002

Abstract Light with decreased red:far-red (R:FR) ratios may signal neighbor presence and trigger plant developmental responses. There is some evidence that plant canopies forage towards increased R:FR ratios, but it is unclear to what extent R:FR versus the total amount of photosynthetically active radiation (PAR) influences canopy foraging responses among forest trees. The objective of this study was to examine the relative importance of PAR and R:FR as photosensory cues leading to tree canopy foraging responses. Seedlings of *Betula papyrifera* Marshall (paper birch) were grown in an experimental garden. Each seedling was germinated and grown in its own shading structure and exposed to two spatially separated light environments, in a factorial design of PAR and R:FR. Plant canopy foraging was evaluated at the end of one growing season in terms of canopy displacement, canopy area, leaf number, direction of stem lean, petiole aspect, and lamina aspect with respect to experimental light treatments. Leaf number and canopy area were greater on the high PAR sides of plants, irrespective of the R:FR treatment. Seedling canopies were displaced towards the direction of high PAR, but this relationship was not significant across all treatments. Petiole aspect was random and showed no significant directedness towards any of the light treatments. Lamina aspect and the direction of stem lean were distributed towards the direction of high PAR, irrespective of the R:FR treatment. Overall, first-year *B. papyrifera* seedlings used PAR, rather than R:FR ratio, as a photosensory cue for canopy light foraging.

Keywords *Betula papyrifera* Marshall · Canopy displacement · Light foraging · Light quality · Red:far-red ratio

Introduction

Plants growing in competitive stands must capture resources efficiently to survive. In order to capture resources efficiently, plants must obtain information on local resource availability and position their foraging organs towards high resource patches and away from neighbors (Bazzaz 1991, 1996). In ecosystems with high primary productivity, light is a particularly critical resource (Wales 1972; Hutchinson and Matt 1977) that is heterogeneous and may be disproportionately available to different regions within an individual plant canopy (Baldocchi and Collineau 1994). Plants that are able to detect such gradients in light availability and position their canopies in a way that maximizes light interception should have increased competitive success.

For plants, light is both a resource and a carrier of information about the external environment (Jennings et al. 1996). The quantity of light available to a plant is generally expressed as the total amount of photosynthetically active radiation (PAR). Light varies not only in total quantity but also in quality, or range of wavelengths present (Haupt 1996). The ratio of red light (660 nm) to far-red light (730 nm) (R:FR ratio) is a widely used measure of light quality (Holmes and McCartney 1976; Holmes and Smith 1977). R:FR ratio is reduced under plant canopies due to the absorption of red radiation and the reflection and transmission of far-red radiation (Holmes and McCartney 1976; Holmes and Smith 1977; Schmitt and Wulff 1993). Plants are able to detect changes in the R:FR ratio of intercepted light through phytochrome (Smith 1982; Ballaré et al. 1992). By detecting the FR-rich light reflected by neighbors, plants may actually be able to sense the presence of potential competitors before being shaded by them (Ballaré et al. 1987, 1988; Novoplansky et al. 1990; Schmitt and Wulff 1993; Ballaré 1999).

C.C. Muth (✉) · F.A. Bazzaz
Department of Organismic and Evolutionary Biology,
Harvard University, Cambridge, MA 02138, USA

Present address:

C.C. Muth, American Museum of Natural History, New York,
NY 10024, USA, e-mail: cmuth@amnh.org,
Tel.: +1-212-4963523, Fax: +1-212-7695329

Decreased R:FR ratio is an environmental signal that leads to a suite of architectural responses often described as shade avoidance syndrome (Schmitt and Wulff 1993). Shade avoidance syndrome is characterized by increased shoot extension rate, internode elongation, decreased branching, and decreased leaf dry weight:stem ratio (Morgan and Smith 1979; Smith 1982). In addition to these well-documented responses to uniform decreases in R:FR ratio, there is some evidence of plant responses to directional R:FR gradients. For example, *Portulaca oleracea* L., an annual weed, produced fewer branches on the sides of plants facing decreased R:FR ratios (Novoplansky 1991), and Scots pine (*Pinus sylvestris* L.) seedlings produced fewer needles on the sides of plants facing decreased R:FR ratios (Galinski 1994).

In a natural forest stand, we previously demonstrated that tree canopies were displaced away from neighbors and towards gaps in a way that appeared to increase canopy light interception (Muth and Bazzaz 2002). We wanted to determine if the kind of directional canopy light foraging that we had observed was in response to a light quantity gradient or a light quality gradient. Thus, our objective in this study was to examine the relative importance of PAR and R:FR ratio as photosensory cues leading to tree canopy foraging responses. We hypothesized that tree canopies forage towards high R:FR ratios and towards PAR values close to their light saturation points.

Materials and methods

Study plants and growing conditions

This study was conducted from June to October 2000 in an experimental garden located at the Harvard Forest Long Term Ecological Research (LTER) site in central Massachusetts, USA (42°30' N, 72°15' W). Because this site is located at a temperate latitude in the northern hemisphere, sunlight is inherently asymmetrical and comes primarily from the south. The garden was situated in a large, open field with a slight (<5°) slope towards the south.

We used *Betula papyrifera* Marshall (paper birch) as a model species for understanding tree canopy responses to photosensory cues. *B. papyrifera* is a fast-growing, shade-intolerant tree (Baker 1949; Burns and Honkala 1990). It is an important component of the natural vegetation of the region, which is classified as transition hemlock-white pine-northern hardwoods forest (Westveld 1956). In an earlier study on canopy displacement of mature trees (Muth and Bazzaz 2002), we found that *B. papyrifera* had high levels of canopy light foraging towards forest gaps, in terms of both magnitude and precision (sensu Campbell et al. 1991).

In the experimental garden, we dug 40 holes that were 40 cm deep, 20 cm in diameter, and 60 cm apart from one another. We lined the holes with sonotubes, cylindrical tubes made of thick cardboard, and filled the holes with nutrient-rich "pro-mix" potting soil (Premier Company, Red Hill, Pa., USA). Above each hole, we placed a shading structure (described below). We germinated and grew one *B. papyrifera* seedling inside each shading structure. The sonotubes prevented the study plants from experiencing root competition from weeds or other study plants, while still allowing ample below-ground space for root foraging. When we harvested the roots at the end of the study period, we found no evidence of spatial constraints on root foraging. Seedlings were watered to field capacity three times per week. They were fertilized once during the study period, using Osmocote slow release fertilizer (Scotts, Marysville, Ohio, USA). The entire garden area was weeded regularly to prevent weeds from altering light treatments.

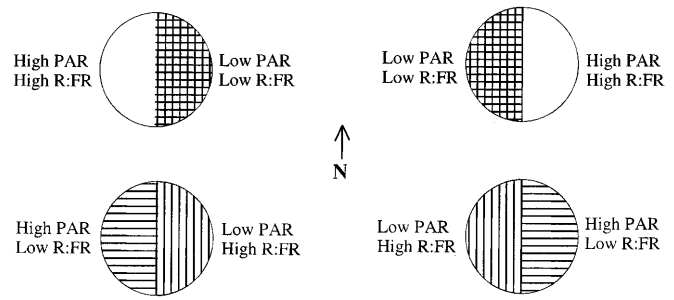


Fig. 1 The four light environments to which individual *Betula papyrifera* seedlings were exposed. The control treatments (*top*) had one side with high PAR and high R:FR and the other side with low PAR and low R:FR. The experimental treatments (*bottom*) had one side with high PAR and low R:FR and the other side with low PAR and high R:FR. Each combination of light treatments was replicated east-west, as shown, to control for aspect

Light treatments and experimental procedures

There were four different light treatments in which *B. papyrifera* seedlings were germinated and grown (Fig. 1). Each seedling was exposed to two contrasting light environments, one on the east side of the plant and one on the west side of the plant. The control treatments had one side with high PAR and high R:FR and the other side with low PAR and low R:FR. These treatments were considered controls because PAR and R:FR are typically positively correlated in natural ecosystems. The experimental treatments had one side with high PAR and low R:FR and the other side with low PAR and high R:FR. These treatments allowed us to determine the relative importance of PAR versus R:FR ratio. Resources and controllers vary temporally, so resource congruency, and ultimately plant response, might have depended on the time of day that light passed through the treatments. Each combination of light treatments was replicated east-west in case plant responses differed based on the direction that a treatment was oriented. We grew 20 control plants and 20 experimental plants, for a total of 40 study plants.

Each *B. papyrifera* seedling was germinated and grown in its own shading structure (Fig. 2), which was placed over 1 of the 40 holes described above. The shading structures were constructed from cylindrical metal frames covered with a combination of neutral shade cloth (to reduce PAR levels) and filter plastic (to reduce R:FR ratios). Shading structures were 60 cm tall and 30 cm in diameter, with metal anchors for structural support and a south-facing, tilted roof that allowed for air circulation. Shading structures of the four light treatments were assigned randomly to the 40 holes.

For the high PAR, high R:FR sides of control treatments, we used 50% neutral shade cloth and no filter plastic, resulting in PAR levels 50% below full sun levels and R:FR levels at full sun levels. For the low PAR, low R:FR sides of control treatments, we used 90% neutral shade cloth layered over a filter plastic (Roscolux 97, light gray, Rosco Laboratories, Stamford, Conn., USA) that reduced PAR levels by 50% and reduced R:FR ratios to 0.4. The overall result of these two layers was PAR levels 95% below full sun levels and R:FR ratios of 0.4. For the high PAR, low R:FR sides of experimental treatments, we used no shade cloth and a filter plastic (Roscolux 97, light gray) that reduced PAR levels by 50% and reduced R:FR ratios to 0.4. For the low PAR, high R:FR sides of the experimental treatments, we used 95% neutral shade cloth and no filter plastic, which resulted in PAR levels 95% below full sun and R:FR ratios at full sun levels. Thus, each plant received the same total amount of PAR and received the same R:FR ratios, but the spatial arrangement and congruency of these resources and controllers were different across treatments. Typical values for high PAR and high R:FR were 1,600 $\mu\text{mol}/\text{m}^2$ per second and 1.2 respectively, but these values varied considerably based on cloud cover and other meteorological factors. These PAR and R:FR levels were chosen to reflect typical values for understore-

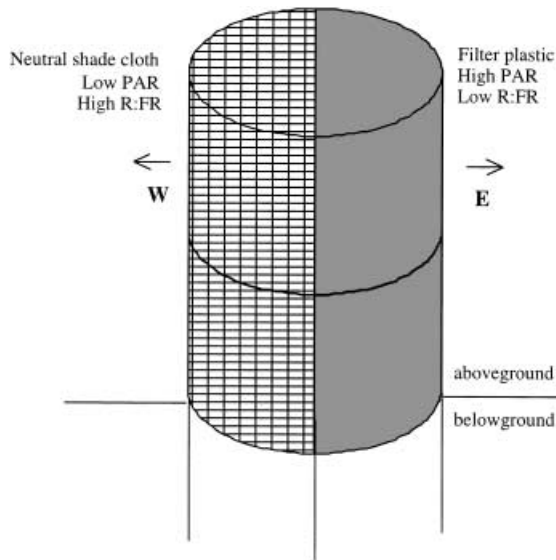


Fig. 2 Each plant was germinated and grown in its own shading structure. Shading structures were constructed from cylindrical frames covered with a combination of neutral shade cloth (to reduce PAR levels) and filter plastic (to reduce R:FR ratios). The above shading structure is for the experimental treatment, with high PAR facing east

ry shade (low PAR and low R:FR levels) and canopy gaps (high PAR and high R:FR levels) (Holmes and McCartney 1976; Holmes and Smith 1977; Smith and Morgan 1981; Lee 1987; Sipe 1990; Smith 1994; Muth and Bazzaz, unpublished data). The seedlings never grew taller than the shading structures, and all direct light received by the study plants passed through the shade cloth and filter plastic. We measured light quantities and qualities in the shading structures with a quantum sensor (Li-Cor, Lincoln, Neb., USA) and a fiber optic spectroradiometer (Ocean Optics, Dunedin, Fla., USA) respectively to verify that our intended light treatments had been successfully imposed. We also measured temperature and humidity inside the shading structures and found no microclimatic differences among treatments.

At the end of the 130-day study period, we evaluated plant responses to the light treatments in terms of canopy displacement, canopy area, leaf number, lean direction, petiole aspect, and lamina aspect with respect to experimental light treatments. In order to determine the magnitude and direction of canopy displacement, we measured the distance from the stem base of each seedling to the edge of its canopy in eight sub-cardinal directions (Young and Hubbell 1991). From these measurements, we calculated the magnitude and direction of canopy displacement, as well as canopy area on each side of each plant. Calculations are described in detail below. For all plants with stems leaning at least 10° from the vertical, we recorded the direction of stem lean to the nearest sub-cardinal direction. We counted the number of leaves on each side of each plant, and we measured petiole aspect and lamina aspect for each leaf to the nearest sub-cardinal direction. Petiole aspect was defined as the compass direction at which a leaf petiole was attached to the main stem. Lamina aspect was defined as the compass direction towards which the top of a leaf blade was facing. Finally, we harvested, washed, dried, and weighed the root systems on each half of each plant in order to determine whether or not the below-ground portions of the plants were evenly distributed.

Data analysis

For each plant, we calculated the magnitude and direction of canopy displacement. First, canopy center of mass was calculated based on the eight canopy edge points of each seedling (Batschelet

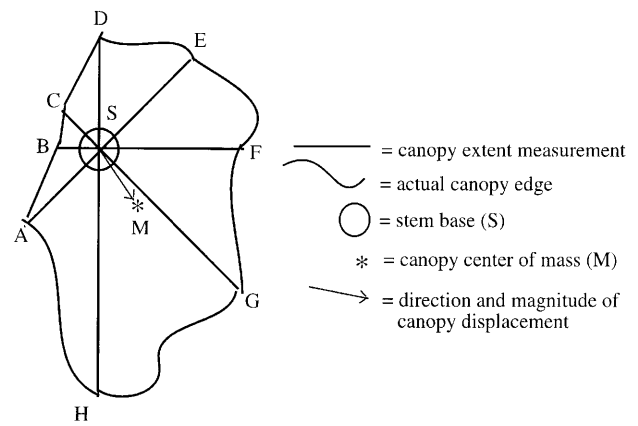


Fig. 3 We calculated canopy center of mass (M) based on the eight canopy edge points (A, B, C, D, E, F, G, H) and created a vector from the stem base (S) to the canopy center of mass (M). The direction of canopy displacement was defined as the direction of the vector, and the magnitude of canopy displacement was defined as the length of the vector. In order to compare the magnitude of canopy displacement across trees with a range of sizes, we calculated relative canopy displacement. This parameter was defined as the magnitude of canopy displacement divided by the mean of the eight canopy extent measurements

1981). The magnitude and direction of canopy displacement were defined as the length and direction of the vector pointing from stem base to canopy center of mass (Franco 1986; Brisson and Reynolds 1994; Umeki 1995a, b, 1997; Rouvinen and Kuuluvainen 1997; Muth and Bazzaz 2002) (Fig. 3). In order to compare canopy displacement across seedlings with a range of sizes, we calculated a relative canopy displacement value for each seedling. Relative canopy displacement was defined as the distance between the stem position and the canopy center of mass divided by the mean of the eight canopy extent measurements (Muth and Bazzaz 2002). Thus, relative canopy displacement is a unit-less measure, and a value of zero represents a plant with its canopy placed directly above its stem base. A value greater than one represents a situation in which the canopy is displaced entirely from the stem base. For the majority of forest trees, relative canopy displacement values tend to range between zero and one, indicating that the canopy is displaced but that the stem base is still positioned at some location beneath the canopy.

Canopy area was calculated by dividing the canopy into eight pie-shaped sections, each one centered on a sub-cardinal direction. We then estimated the area of each section by assuming that the canopy radius at the sub-cardinal direction was equal to the radius throughout that section. The area of a given section was defined as $(\Pi r^2)/8$, where Π was equal to the constant pi and r was equal to the canopy extent measurement for that sub-cardinal direction. To determine the canopy area on the east side of each plant, we added up the canopy areas of the 45° , 90° , and 135° sections, as well as one half of the areas of the 0° and 180° sections. Likewise, to determine the canopy area on the west side of each plant, we added up the canopy areas of the 225° , 270° , and 315° sections, as well as one half of the areas of the 180° and 0° sections.

We determined the canopy area, leaf number, and root dry mass on each side of each plant. In order to quantitatively compare the asymmetry of these traits on opposite sides of the plants relative to the PAR and R:FR treatments, we calculated trait asymmetry ratios. There were two different kinds of trait asymmetry ratios: PAR trait asymmetry ratios and R:FR trait asymmetry ratios. The trait asymmetry ratios were defined as follows. A PAR trait asymmetry ratio was defined as the difference in a trait value between the high PAR side of the plant and the low PAR side of the plant divided by the total trait value for the whole plant. A R:FR

trait asymmetry ratio was similarly defined as the difference in a trait value between the high R:FR side of the plant and the low R:FR side of the plant divided by the total trait value for the whole plant. For example, leaf number PAR asymmetry ratio was defined as the difference in leaf number between the high PAR side of the plant and the low PAR side of the plant divided by the total leaf number for the whole plant. Thus, a trait asymmetry ratio of zero would be achieved if the trait was not asymmetrical but was present in equal amounts on both sides of the plant. A positive PAR trait asymmetry ratio represents the situation where the trait is greater on the high PAR side of the plant, and a negative PAR trait asymmetry ratio represents the situation where the trait is greater on the low PAR side of the plant. Likewise, a positive R:FR trait asymmetry ratio represents the situation where the trait is greater on the high R:FR side of the plant, and a negative R:FR trait asymmetry ratio represents the situation where the trait is greater on the low R:FR side of the plant. For example, if a plant has 35 leaves on the high PAR side and 20 leaves on the low PAR side, then the plant's leaf number PAR asymmetry ratio is $(35-20)/55=0.27$. This value is positive, indicating that leaf number is asymmetrical towards the high PAR side of the plant. PAR and R:FR trait asymmetry ratios were calculated for each plant for canopy area, leaf number, and root mass.

Relative canopy displacement was used to assess the magnitude of canopy displacement. Contrasts in canopy area, leaf number, and root mass on opposite sides of plants were assessed with PAR and R:FR trait asymmetry ratios. For relative canopy displacement and for each of the trait asymmetry ratios, an analysis of variance (ANOVA) (Sokal and Rohlf 1995) was used to evaluate the significance of variation across treatments and aspects (Data Desk version 4.2, Data Description, Ithaca, New York, USA). In each of these ANOVAs, the factors were treatment and aspect, with aspect nested within treatment. The treatments were control and experimental, and the aspects were east-facing and west-facing. We then calculated means and 95% confidence intervals for each of the parameters in order to determine if they were different from zero.

The direction of canopy displacement, the direction of stem lean, petiole aspect, and lamina aspect were evaluated with circular statistics. For each of these parameters, we calculated a mean and 95% confidence interval for each treatment and then used the Rayleigh test to determine whether or not there was significant directness towards the mean (Batschelet 1981). For petiole aspect and lamina aspect, we found very similar means and 95% confidence intervals whether we calculated the means based on individual plants or on individual leaves. By treating individual leaves as separate data points, we had a large enough sample size to meet the assumptions for a chi-squared test (Batschelet 1981). Thus, for petiole aspect and lamina aspect we also used chi-squared tests to determine which of the treatment means differed significantly from one another.

Results

ANOVAs for relative canopy displacement and the trait asymmetry ratios (Table 1) were originally set up with treatment and aspect as the two factors. Since none of the ANOVAs revealed significant effects of aspect, we ran each ANOVA a second time without including aspect as a factor. This allowed more degrees of freedom to separate the effects of treatment, the factor that we predicted to be most important. The ANOVA for relative canopy displacement revealed no differences between control and experimental treatments. None of the PAR trait asymmetry ratios (canopy area PAR asymmetry ratio, leaf number PAR asymmetry ratio, and root mass PAR asymmetry ratio) differed between control and experimental treatments. In contrast, two of the R:FR trait asymmetry ratios (canopy area R:FR asymmetry ratio

Table 1 ANOVA results for relative canopy displacement and for the trait asymmetry ratios. ANOVAs were originally set up with aspect nested within treatment. The treatments were control and experimental. The aspects were east-facing and west-facing. Since none of the ANOVAs revealed significant effects of aspect, we ran each ANOVA a second time without including aspect as a factor

Source of variation	<i>df</i>	MS	<i>F</i>	<i>P</i>
Relative canopy displacement				
Treatment	1	0.000	0.00	0.983
Error	33	0.011		
Canopy area PAR asymmetry ratio				
Treatment	1	0.071	2.48	0.125
Error	33	0.029		
Leaf number PAR asymmetry ratio				
Treatment	1	0.071	0.78	0.383
Error	33	0.090		
Root mass PAR asymmetry ratio				
Treatment	1	0.022	0.27	0.607
Error	33	0.081		
Canopy area R:FR asymmetry ratio				
Treatment	1	0.390	13.60	0.001
Error	33	0.029		
Leaf number R:FR asymmetry ratio				
Treatment	1	1.907	21.12	<0.001
Error	33	0.090		
Root mass R:FR asymmetry ratio				
Treatment	1	0.149	1.84	0.184
Error	33	0.081		

Table 2 Means and 95% confidence intervals for relative canopy displacement and trait asymmetry ratios. ANOVA results (Table 1) demonstrated that canopy area R:FR asymmetry ratio and leaf

number R:FR asymmetry ratio differed between treatments. For these two asymmetry ratios, we present separate means and 95% confidence intervals for the control and experimental treatments

Plant trait and treatment	Mean	95% CI	Result	Interpretation
Relative canopy displacement				
All treatments	0.171	(0.137, 0.206)	>0	Canopies displaced from stem bases
Canopy area asymmetry ratios				
PAR, all treatments	0.104	(0.047, 0.162)	>0	Greater canopy area on high PAR side
R:FR, control treatment	0.171	(0.124, 0.219)	>0	Greater canopy area on high R:FR side (high PAR side)
R:FR, experimental treatment	-0.151	(-0.233, -0.068)	<0	Greater canopy area on low R:FR side (high PAR side)
Leaf number asymmetry ratios				
PAR, all treatments	0.232	(0.133, 0.331)	>0	Greater leaf number on high PAR side
R:FR, control treatment	0.061	(-0.016, 0.137)	=0	Same leaf number on high and low R:FR sides
R:FR, experimental treatment	-0.278	(-0.421, -0.136)	<0	Greater leaf number on low R:FR side (high PAR side)
Root mass asymmetry ratios				
PAR, all treatments	0.159	(-0.027, 0.093)	=0	Same root mass on high and low PAR sides
R:FR, all treatments	0.027	(-0.069, 0.122)	=0	Same root mass on high and low R:FR sides

and leaf number R:FR asymmetry ratio) differed significantly between control and experimental treatments ($P<0.001$). Root mass R:FR asymmetry ratio did not differ between treatments. Thus, of all the trait asymmetry ratios, only canopy area R:FR asymmetry ratio and leaf number R:FR asymmetry ratio differed between the experimental and control treatments.

Means and 95% confidence intervals for relative canopy displacement and the trait asymmetry ratios are shown in Table 2. Because ANOVA results (Table 1) demonstrated that canopy area R:FR asymmetry ratio and leaf number R:FR asymmetry ratio differed between control and experimental treatments, we calculated separate means and 95% confidence intervals for the control and experimental treatments for these two trait asymmetry ratios. Relative canopy displacement was greater than zero but less than one, indicating that canopies were displaced from the main stem but that stem bases were still positioned at some point beneath the canopy. Canopy area PAR asymmetry ratio and canopy area R:FR asymmetry ratio (control treatment) were greater than zero, indicating that canopy area was greater on the high PAR, high R:FR sides of control plants and on the high PAR, low R:FR sides of experimental plants. Canopy area R:FR asymmetry ratio (experimental treatment) was less than zero, indicating again that canopy area was greater on the high PAR, low R:FR sides of experimental plants. Leaf number PAR asymmetry ratio was greater than zero, indicating that leaf number was greater on the high PAR sides of plants. Leaf number R:FR asymmetry ratio (experimental treatment) was less than zero, indicating that leaf number was greater on the high PAR, low R:FR sides of experimental plants. Leaf number R:FR asymmetry ratio (control treatment) was not different from zero. Thus, we were unable to detect a difference in leaf number on opposite sides of control plants based on this parameter. The 95% confidence intervals for root mass PAR asymmetry ratio and for root mass R:FR asymmetry

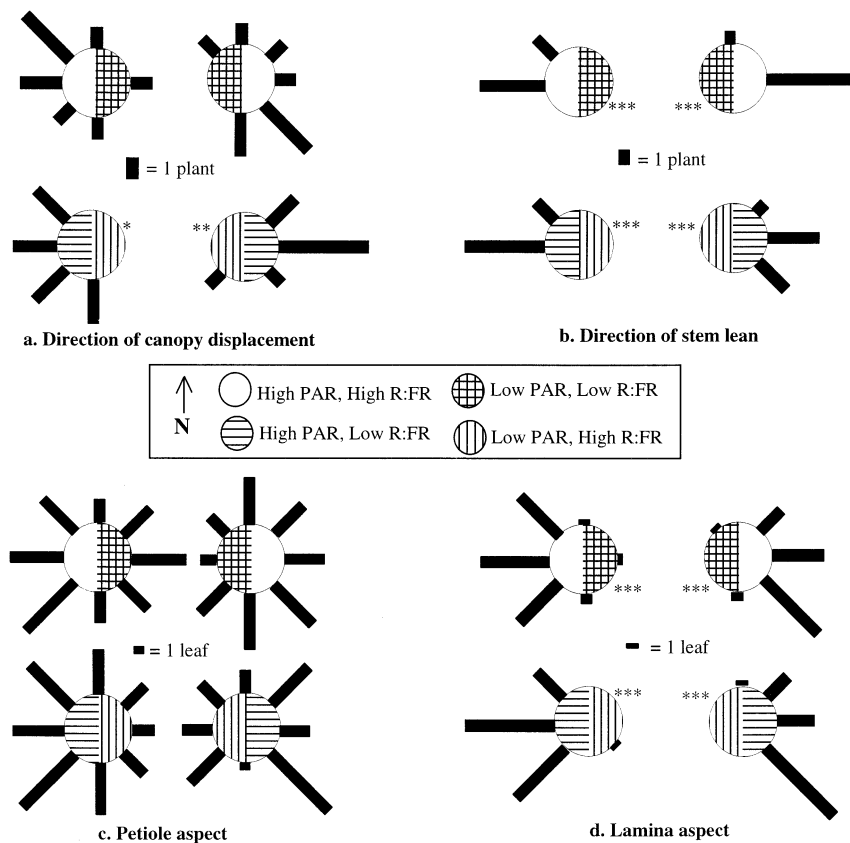
ratio included zero, indicating that root mass did not differ on opposite sides of the plants. In sum, canopies were displaced from their stem bases, and canopy area and leaf number were greater on high PAR sides of plants, irrespective of R:FR ratios. There was no effect of light treatment on root mass distribution.

B. papyrifera seedling canopies had significant directedness towards high PAR in the experimental treatments (Fig. 4a). In the experimental treatment with high PAR to the east, canopies were displaced towards the east (95% confidence interval $94^{\circ}\pm 37^{\circ}$) ($P<0.001$, Rayleigh test). In the experimental treatment with high PAR to the west, canopies were displaced towards the west (95% confidence interval $243^{\circ}\pm 43^{\circ}$) ($P<0.05$, Rayleigh test). Despite a general trend of canopy displacement towards high PAR in the control treatments, canopy displacement showed no significant directedness for these treatments (95% confidence intervals $123^{\circ}\pm 115^{\circ}$ and $280^{\circ}\pm 150^{\circ}$ for control treatments with high PAR to the east and high PAR to the west respectively). In general, seedling canopies were displaced towards the direction of high PAR, but this relationship was not significant across all treatments.

Within each treatment, the direction of stem lean was not random, but showed significant directedness towards high PAR ($P<0.001$, Rayleigh test) (Fig. 4b). The control and experimental treatments with high PAR to the east had mean stem lean directions and 95% confidence intervals of $82^{\circ}\pm 27^{\circ}$ and $102^{\circ}\pm 28^{\circ}$ respectively. The control and experimental treatments with high PAR to the west had mean stem lean directions and 95% confidence intervals of $282^{\circ}\pm 20^{\circ}$ and $281^{\circ}\pm 19^{\circ}$ respectively. It is striking that not a single stem leaned away from the direction of high PAR. Overall, stems leaned towards the direction of high PAR, irrespective of the R:FR treatment.

Despite average values approximating the direction of high PAR, petiole aspect was random and showed no significant directedness towards any of the light treatments

Fig. 4 Direction of **a** canopy displacement, **b** stem lean, **c** petiole aspect, and **d** lamina aspect for *B. papyrifera* seedlings grown in four light environments. *Hatch marks* represent seedling light environments, as shown in legend. *Bar lengths* represent the number of plants (**a, b**) or leaves (**c, d**) oriented in a given direction. *Stars* represent statistically significant directedness, according to the Rayleigh test (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)



(Rayleigh test) (Fig. 4c). When we treated each leaf as an individual sample and employed a chi-squared test to examine differences among plant light treatments, we found that none of the means for petiole aspect were significantly different from one another. The control and experimental treatments with high PAR to the east had mean petiole aspects and 95% confidence intervals of $123^\circ \pm 120^\circ$ and $112^\circ \pm 150^\circ$ respectively. The control and experimental treatments with high PAR to the west had mean petiole aspects and 95% confidence intervals of $229^\circ \pm 150^\circ$ and $258^\circ \pm 55^\circ$ respectively. Petiole aspect thus showed no clear preference for any of the imposed light treatments.

Within each treatment, lamina aspect was not random, but showed significant directedness towards high PAR ($P < 0.001$, Rayleigh test) (Fig. 4d). A chi-squared test revealed that treatments with high PAR to the east differed from treatments with high PAR to the west ($P < 0.001$). We found no difference in lamina aspect between the control treatment with high PAR to the east (mean and 95% confidence interval $107^\circ \pm 14^\circ$) and the experimental treatment with high PAR to the east ($109^\circ \pm 12^\circ$). We likewise found no difference in lamina aspect between the control treatment with high PAR to the west ($268^\circ \pm 13^\circ$) and the experimental treatment with high PAR to the west ($261^\circ \pm 10^\circ$). When we calculated a mean lamina aspect for all leaves across all treatments, we found that, overall, leaves had significant directedness towards the south (mean and 95% confidence interval $207^\circ \pm 40^\circ$) ($P < 0.01$, Rayleigh test). In sum, lamina aspect was con-

sistently distributed towards the direction of high PAR, even when high PAR was coupled with low R:FR.

Discussion

We wished to determine the relative importance of PAR and R:FR as photosensory cues leading to tree canopy foraging responses. We found clear evidence of tree canopy foraging towards high PAR. Across all treatments, canopy area was greater on the high PAR sides of plants, stems leaned towards the direction of high PAR, and lamina aspect was towards high PAR. In contrast, we found no evidence of foraging in response to experimental R:FR gradients among the traits that we measured. These results demonstrate that, among *B. papyrifera* seedlings, PAR is a more important photosensory cue for canopy light foraging than is R:FR.

The kinds of light foraging responses that we observed are typical of trees exposed to contrasting light environments (Young and Hubbell 1991; Holmes 1995; Umeki 1995b; Muth and Bazzaz 2002). In the field, it is not possible to decouple the effects of PAR and R:FR on these light foraging responses, but our experimental approach allowed us to attribute the canopy foraging responses that we observed to PAR gradients. In addition, the relatively small stature of our study plants allowed the inclusion of more detailed measurements (e.g., leaf number and lamina aspect) than are possible with mature trees. We observed

that certain traits (e.g., petiole aspect) appeared largely unresponsive to spatial variation in light availability, while other traits (e.g., lamina aspect and direction of stem lean) showed strong responses. This is likely because some traits are developmentally predetermined, while others are quite flexible and can respond easily to environmental stimuli. For example, it appears that, in this study, leaves were produced along the stem in a predetermined manner, but once leaves were formed, they were able to alter their orientation to maximize light interception.

The few previous studies that have investigated directional canopy foraging in response to R:FR gradients (Novoplansky 1991; Ballaré et al. 1992; Galinski 1994) exposed plants to decreased R:FR on one side while maintaining high PAR levels on both sides. In contrast to our results, these studies found that plants foraged away from low R:FR. High PAR was maintained in these studies since the goal of experimental R:FR treatments was to simulate non-shading neighbors. Because we were interested in tree canopy foraging in response to the contrasts in light availability between a gap and a forest understory, we grew control plants in simulated gap edges, with high PAR and high R:FR on one side and low PAR and low R:FR on the other side. Experimental plants were exposed to conflicting photosensory cues, with high PAR and low R:FR on one side and low PAR and high R:FR on the other side. In order to grow towards high R:FR levels, our experimental plants would have had to grow towards low PAR levels. Our experimental treatments allowed us to examine the relative importance of PAR versus R:FR but may have reduced the likelihood of obtaining a plant response to R:FR compared to studies that maintained high PAR on both sides of plants.

Most work on plant R:FR responses has focused on annuals of open habitats. Relatively little is known about the R:FR responses of forest plants, and our study is relatively unique in its focus on a tree species as a study organism. Species vary in their responses to R:FR gradients (Morgan and Smith 1979; Smith 1994; Dudley and Schmitt 1995), and there are likely to be substantial differences in selective pressures among plants of contrasting habitats and life history strategies. Plants of open habitats would strongly benefit from detecting and avoiding potential neighbors, which are likely to be of comparable size to the target plant (Morgan and Smith 1979; Novoplansky et al. 1990; Ballaré 1999). In contrast, it is impossible to quickly overtop the forest canopy. For forest plants, shade avoidance responses like stem elongation would be inefficient and potentially costly, in terms of both decreased investment in leaf tissue and increased risk of mechanical failure (Morgan and Smith 1979; Dudley and Schmitt 1995). Dudley and Schmitt (1995) compared the R:FR responses of plants from open habitats with those from forested habitats and found that the forest plants were less responsive to experimentally imposed decreases in R:FR. It is not surprising, then, that forest trees like *B. papyrifera* might be less responsive to R:FR gradients than annual herbs of open habitats. Aphalo and Lehto (1997) exposed seedlings of *Betula pendula* Roth to decreased R:FR and found little

effect of R:FR on plant assimilation and allocation. These results, coupled with our findings, suggest that birches in general may have relatively little responsiveness to variation in R:FR. If light-demanding, early successional trees like birches do not use R:FR as a photosensory cue for canopy foraging, then shade-tolerant, later successional trees are even less likely to be responsive to R:FR gradients (Smith 1994).

Despite the strong effects of canopy foraging towards high PAR and the lack of response to R:FR gradients that we observed, we cannot completely rule out light quality as a potential photosensory cue for *B. papyrifera* foraging responses. Our experimental treatments exposed plants to large contrasts in PAR and R:FR; however, R:FR may serve as a photosensory cue in situations with limited variation in PAR. Plant detection of and response to blue light might also play a role in tree canopy light foraging. Furthermore, although R:FR responses were not observed among first-year tree seedlings in this study, processes and traits appearing later in development (e.g., bud development or branch production) may be influenced by R:FR cues. Additional studies investigating these issues would greatly enhance our understanding of R:FR as a potential photosensory cue for tree canopy light foraging.

Conclusions

Tree canopies forage for light by positioning their canopies towards high light areas and away from neighbors (Young and Hubbell 1991; Holmes 1995; Umeki 1995b; Muth and Bazzaz 2002). We conducted an experiment to determine the relative importance of PAR and R:FR as photosensory cues leading to tree canopy light foraging. Our results demonstrate clear evidence of canopy foraging towards high PAR among *B. papyrifera* seedlings and no foraging responses to R:FR gradients, suggesting that PAR is more important than R:FR as a photosensory cue for tree canopy light foraging.

Acknowledgements We thank A. Wilczek, K. Lewis, G. Bauer, S. Catovsky, R. Stomberg, N. Holbrook, D. Foster, N. Pierce, the Harvard Forest staff, members of the Bazzaz laboratory, R. Pearcy, and two anonymous reviewers for valuable feedback on the research and the manuscript. K. Capecelatro, T. Collazo, and R. Anderson provided valuable assistance in the experimental garden. This work was funded by grants from the National Science Foundation and the Mellon foundation to the Harvard Forest LTER site and by fellowships from the National Science Foundation and Harvard University (Department of Organismic & Evolutionary Biology) to C. Muth.

References

- Aphalo PJ, Lehto T (1997) Effects of light quality on growth and N accumulation in birch seedlings. *Tree Physiol* 17:125–132
- Baker FS (1949) A revised tolerance table. *J For* 47:179–181
- Baldocchi D, Collineau S (1994) The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. In: Caldwell MM, Pearcy RW (eds) *Exploitation of environmental heterogeneity by plants*. Academic Press, London, pp 21–71

- Ballaré CL (1999) Keeping up with the neighbours: Phytochrome sensing and other signalling mechanisms. *Trends Plant Sci* 4: 97–102
- Ballaré CL, Sánchez RA, Scopel AL, Casal JJ, Ghersa CM (1987) Early detection of neighbor plants by phytochrome perception of spectral changes in reflected sunlight. *Plant Cell Environ* 10:551–557
- Ballaré CL, Sánchez RA, Scopel AL, Ghersa CM (1988) Morphological responses of *Datura ferox* L. seedlings to the presence of neighbors: their relationships with canopy microclimate. *Oecologia* 76:288–293
- Ballaré CL, Scopel AL, Radosevich SR, Kendrick RE (1992) Phytochrome-mediated phototropism in de-etiolated seedlings. *Plant Physiol* 100:170–177
- Batschelet E (1981) *Circular statistics in biology*. Academic Press, London
- Bazzaz FA (1991) Habitat selection in plants. *Am Nat* 137:S116–S130
- Bazzaz FA (1996) *Plants in changing environments*. Cambridge University Press, Cambridge
- Brisson J, Reynolds JF (1994) The effects of neighbors on root distribution in a creosote bush (*Larrea tridentata*) population. *Ecology* 75:1693–1702
- Burns RM, Honkala BH (1990) *Silvics of North America*, vol 2. Hardwoods. United States Department of Agriculture, Washington, D.C.
- Campbell BD, Grime JP, Mackey JML (1991) A trade-off between scale and precision in resource foraging. *Oecologia* 87: 532–538
- Dudley SA, Schmitt J (1995) Genetic differentiation in morphological responses to simulated foliage shade between populations of *Impatiens capensis* from open and woodland sites. *Funct Ecol* 9:655–666
- Franco M (1986) The influence of neighbors on the growth of modular organisms with an example from trees. *Philos Trans R Soc Lond B* 313:209–225
- Galinski W (1994) Non-random needle orientation in 1-year-old Scots pine (*Pinus sylvestris* L.) seedlings when adjacent to non-shading vegetation. *Trees* 8:160–164
- Haupt W (1996) Overview of photosensing in plant physiology. In: Jennings RC, Zucchelli G, Ghetti F, Colombetti G (eds) *Light as an energy source and information carrier in plant physiology*. Plenum, New York, pp 169–183
- Holmes MG, McCartney HA (1976) Spectral energy distribution in the natural environment and its implications for phytochrome function. In: Smith H (ed) *Light and plant development*. Butterworth, London, pp 467–476
- Holmes MG, Smith H (1977) The function of phytochrome in the natural environment. I. Characterisation of daylight for studies in photomorphogenesis and photoperiodism. *Photochem Photobiol* 25:533–538
- Holmes TH (1995) Woodland canopy structure and the light response of juvenile *Quercus lobata* (Fagaceae). *Am J Bot* 82:1432–1442
- Hutchinson BA, Matt DR (1977) The distribution of solar radiation within a deciduous forest. *Ecol Monogr* 47:185–207
- Jennings RC, Zucchelli G, Ghetti F, Colombetti G (eds) (1996) *Light as an energy source and information carrier in plant physiology*. Plenum, New York
- Lee DW (1987) The spectral distribution of radiation in two neotropical rainforests. *Biotropica* 19:161–166
- Morgan DC, Smith H (1979) Function of phytochrome in the natural-environment: systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* 145:253–258
- Muth CC, Bazzaz FA (2002) Tree canopy displacement at forest gap edges. *Can J For Res* 32:247–254
- Novoplansky A (1991) Developmental responses of portulaca seedlings to conflicting spectral signals. *Oecologia* 88:138–140
- Novoplansky A, Cohen D, Sachs T (1990) How portulaca seedlings avoid their neighbors. *Oecologia* 82:490–493
- Rouvinen S, Kuuluvainen T (1997) Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. *Can J For Res* 27:890–902
- Schmitt J, Wulff RD (1993) Light spectral quality, phytochrome and plant competition. *Trends Ecol Evol* 8:47–51
- Sipe TW (1990) Gap partitioning among maples (*Acer*) in the forests of central New England. PhD thesis, Harvard University
- Smith H (1982) Light quality, photoreception, and plant strategy. *Annu Rev Plant Physiol* 33:481–518
- Smith H (1994) Sensing the light environment: the functions of the phytochrome family. In: Kendrick RE, Kronenberg GHM (eds) *Photomorphogenesis in plants*, 2nd edn. Kluwer Academic, Dordrecht, pp 377–416
- Smith H, Morgan DC (1981) The spectral characteristics of the visible radiation incident upon the surface of the earth. In: Smith H (ed) *Plants and the daylight spectrum*. Academic Press, London, pp 3–20
- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. Freeman, New York
- Umeki K (1995a) Importance of crown position and morphological plasticity in competitive interactions in a population of *Xanthium canadense*. *Ann Bot* 75:259–265
- Umeki K (1995b) A comparison of crown asymmetry between *Picea abies* and *Betula maximowicziana*. *Can J For Res* 25:1876–1880
- Umeki K (1997) Effect of crown asymmetry on size-structure dynamics of plant populations. *Ann Bot* 79:631–641
- Wales BA (1972) Vegetation analysis of north and south edges in a mature, oak-hickory forest. *Ecol Monogr* 42:451–471
- Westveld M (1956) Natural forest vegetation zones of New England. *J For* 54:332–338
- Young TP, Hubbell SJ (1991) Crown asymmetry, treefalls, and repeat disturbance of broadleaved forest gaps. *Ecology* 72:1464–1471