Contrasting shade avoidance responses in two perennial grasses: a field investigation in simulated sparse and dense canopies

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Abstract

We designed an experiment with potted plants grown outdoors to investigate the expression of shade avoidance in simulated sparse and dense canopies by two perennial grasses known to express contrasting responses to low red:far-red ratios (R:FR). Plants were grown in canopy microenvironments designed to lower the R:FR by reflection of horizontally propagated FR from neighbors and by direct attenuation of R by filters located above plants. Two specific hypotheses were tested: (1) *Paspalum dilatatum* will express greater shade avoidance than *Schizachyrium scoparium* to low R:FR in both sparse and dense canopies, and (2) low R:FR will produce greater expressions of shade avoidance in sparse than in dense canopies in both species. *P. dilatatum* was more responsive to low R:FR than *S. scoparium* in both the sparse and dense canopies and lower ramet number plant^{-1} was the only common shade avoidance response between species in sparse canopies. *P. dilatatum* also showed significant reductions in juvenile ramet initiation, juvenile ramet mass, total shoot mass, and shoot:root ratios in sparse canopies, but only juvenile ramet initiation was reduced in dense canopies. The suppression of juvenile ramet initiation in the dense canopy was at least partially modulated by the vertically propagated R:FR because a similar reduction in PFD and horizontally propagated R:FR showed 42% greater juvenile ramet initiation in the respective control. *S. scoparium* only showed a significant reduction in ramet number plant^{-1} and a significant increase in blade length in sparse canopies, but no significant responses occurred in dense canopies. Consequently, neither hypothesis was rejected. Variable shade avoidance responses between species and canopy densities indicate that both interspecific variation and various proportions of vertically and horizontally propagated low R:FR can influence the expression of shade avoidance responses of perennial grasses in field settings.

Introduction

The ability of plants to modify their phenotype in response to low red:far-red ratios (R:FR; 660 ± 5 nm:730 ± 5 nm) within vegetation canopies is well documented (Schmitt and Wulff 1993; Schmitt 1997; Smith and Whitelam 1997). The expression of increased height, reduced branch development, and reduced time to flowering in response to low R:FR is termed the shade avoidance syndrome and has been shown to be of adaptive value compared to alternative phenotypes (Smith 1982; Schmitt and Wulff 1993; Schmitt 1997; Alphalo et al. 1999). Similar phenotypic responses to low R:FR occur in both monocots and dicots, but the expression of shade avoidance in perennial grasses has been inconsistently expressed among species in actual and simulated canopies of varying density (Deregibus et al. 1985; Skálová and Krahulec 1992; Murphy and Briske 1994; Monaco and Briske 2000). Insight into mechanisms contributing to variable responses to R:FR among perennial grasses within canopies of varying foliage density is required to effectively scale shade avoidance responses from individual plants to canopies and communities (Ballaré et al. 1990, 1992b, 1997).

Shade avoidance responses were initially demonstrated in dense canopies of *Paspalum dilatatum* and *Sporobolus indicus* growing in the flooding Pampas of Argentina (Deregibus et al. 1985). However, a subsequent investigation with potted *P. dilatatum* plants conducted outdoors concluded that only plants grown in canopies with low LAI displayed shade avoidance responses, whereas neither isolated plants nor plants in canopies with high LAI responded to the R:FR (Casal et al. 1986). Genotypes originating from sparse, rather than dense canopies have been subsequently documented to exhibit greater expression of shade avoidance by several investigators since the initial report by Casal et al. (1986); Skálová and Krahulec (1992); Skálová et al. (1997). The limits for the expression of shade avoidance in response to canopy density are established by insufficient PFD in very dense canopies and by insufficiently low R:FR in very sparse canopies (Casal et al. 1986). Variable intraspecific responses to the R:FR over a range of canopy densities suggests that specific attributes of the radiation signal or associated variables within the canopy microenvironment may be involved in modulating species responses to low R:FR under field conditions (Skálová et al. 1999).

Canopy density may also modulate shade avoidance responses by affecting the manner in which the R:FR is reduced. The R:FR is primarily reduced by horizontally reflected FR from adjacent plant surfaces in canopies with low LAI (Casal et al. 1986; Ballaré et al. 1987; Skálová et al. 1999). The low R:FR produced by horizontally reflected FR functions as a proximity signal that allows plants to anticipate the presence of neighbors and express shade avoidance responses before a reduction in PFD occurs (Casal et al. 1986; Ballaré et al. 1987, 1988; Smith et al. 1990). In contrast, the R:FR is suppressed to an increasing extent by direct foliar absorption of R as LAI increases (Ballaré et al. 1987, 1988, 1989). Canopy absorption of R coincides with a reduction in PFD and has also been demonstrated to induce shade avoidance responses (Kasperbauer and Karlen 1986; Ballaré et al. 1987, 1989; Casal et al. 1987a, 1987b).

We designed a field experiment to investigate the relative expression of shade avoidance in simulated sparse and dense canopies with two perennial C_4 grasses known to show unique responses to low R:FR. *P. dilatatum* has shown a greater expression of shade avoidance to low R:FR (Deregibus et al. 1985; Casal et al. 1986) than has *Schizachyrium scoparium* (Murphy and Briske 1994; Monaco and Briske 2000).

We tested two specific hypotheses: (1) *P. dilatatum* will express greater shade avoidance than *S. scoparium* to low R:FR in both sparse and dense canopies, and (2) low R:FR will produce greater expressions of shade avoidance in sparse than in dense canopies in both species. Sparse canopies were simulated by placing potted plants within 15 cm of established plants in the field to lower the R:FR by horizontally reflected FR from these neighbors. Dense canopies were simulated by placing potted plants within 15 cm of established plants beneath acetate filters to lower the R:FR by direct absorption of R. The dense canopy was designed to mimic the radiation microenvironment associated with the initial demonstration of shade avoidance in perennial grasses in field settings (80% reduction in PFD; Deregibus et al. (1985)). Unique species responses to low R:FR in this investigation would indicate the occurrence of interspecific variation to low R:FR. However, similar species responses to low R:FR in sparse or dense canopies, but not both, would indicate that canopy density is an important variable modulating this response.

Materials and methods

Ramets of *P. dilatatum* and *S. scoparium* were collected from 10 established field grown plants within the Texas A&M Native Plant and Animal Conservatory, College Station, Texas (30° 38′N, 96° 21′W). We assumed that these plants were distinct genotypes because plants were separated by a distance of 2–5 m. Three connected ramets of each species possessing 5-cm lengths of adventitious roots were transplanted into 0.1-m (dia) × 0.36-m (depth) PVC tubes filled with sandy loam topsoil collected from the site on 15 April 1999. Ramets of each plant were randomly distributed across all treatments. Plants were placed under a neutral density shade canopy that reduced ambient PFD by 60% for the initial two weeks following transplanting and shade intensity was decreased to produce a 30% reduction in PFD for an additional two weeks to facilitate plant establishment. Plants were watered daily and fertilized with an NPK solution once a week. Following a one month establishment period, 32 potted plants of each species were placed into a common garden by inserting the pots into holes so that plant bases were level with the soil surface. Potted plants prevented the confounding of plant response to low R:FR with root competition

from neighbors. The watering regime continued, but fertilization ceased after the experiment began.

Sparse canopies were simulated by placing individual plants (n = 8) of each species between four mature *Andropogon gerardii* neighbors (0.15 m equidistant) that had been transplanted into the garden 2 years previously (Figure 1). The *A. gerardii* neighbors had a basal diameter of ~ 0.30 m and were periodically defoliated to maintain a uniform border height of 0.36 m to reflect FR toward experimental plants (Morgan and Smith 1981; Ballaré et al. 1987; Davis and Simmons 1994a, 1994b). In addition, eight plants of each species were grown without neighbors to minimize absorption of horizontally reflected FR and to serve as a control for the sparse canopy. Horizontally propagated radiation reflected from the four neighbors had a significantly lower R:FR compared to ambient radiation near control plants (0.73 ± 0.02 vs. 0.95 ± 0.02), but vertically propagated PFD was only minimally reduced compared to ambient (1744 ± 5 vs. $1746 \pm 5 \ \mu$mol m^{-2} s^{-1}). Plants in the sparse canopy likely experienced lower levels of PFD at low solar angles compared to control plants because of shading by *A. gerardii* neighbors. However, minimal shading was unavoidable in the sparse canopy because neighbor plants were required on all sides to reflect FR toward treatment plants.

Dense canopies were simulated by placing individual plants (n = 8) a distance of 0.15 m from neighbors and additionally reducing the vertically propagated R:FR (0.56 ± 0.02) and PFD ($319 \pm 7 \ \mu$mol m^{-2} s^{-1}) with gel acetate filters (electric blue, GAM, Hollywood CA) located above plants (Figure 1). The dense canopy provided experimental plants with both a horizontal and vertical low R:FR signal. A control for the dense canopy was produced by placing individual plants (n = 8) of each species between neighbors and reducing PFD ($317 \pm 4 \ \mu$mol m^{-2} s^{-1}) above experimental plants with neutral shade material that did not reduce the R:FR (1.12 ± 0.02). The neutral density shade and acetate materials were attached to a 45 × 90 cm curved wire frame to form an arch extending from the east to west periphery of plants to modify radiation at both high and low sun angles. Wire frames supporting the shade materials were elevated as necessary to prevent obstruction of vertical plant growth. Sparse and dense canopy treatments were not compared because PFD varied approximately 80% between them.

Spectral quality of the four radiation microenvironments was assessed by measuring the R (655–665
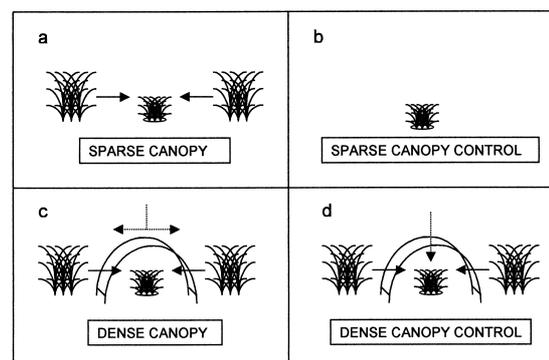

Figure 1. Schematic of the four radiation microenvironments used to investigate contrasting shade avoidance responses to low R:FR in simulated sparse and dense canopies. Solid arrows represent horizontally reflected far-red (FR) and dotted arrows represent vertically propagated red (R). Sparse canopies were simulated by placing plants between four *Andropogon gerardii* neighbors to reflect FR and create a low horizontally propagated R:FR (0.73 ± 0.02) with ambient PFD (a). Plants grown without neighbors under ambient radiation provided the control for the sparse canopy (b). Dense canopies were simulated by placing plants between *A. gerardii* neighbors and beneath gel acetate filters to reduce horizontally (0.73 ± 0.02) and vertically (0.56 ± 0.02) propagated R:FR and to reduce PFD 83% from ambient (c). Plants grown between neighbors and beneath neutral density shade to reduce horizontally propagated R:FR (0.73 ± 0.02) and PFD 83% from ambient provided the control for the dense canopy (d).

nm) and FR (725–735 nm) wavebands with a portable spectroradiometer (LI-1800, LICOR, Lincoln, NE) equipped with a remote cosine receptor. The receptor was positioned parallel to the soil surface just above individual plants to measure vertical radiation. Horizontal radiation was measured with the receptor positioned perpendicular to the soil surface at a height of 0.2 m on the plant periphery. Four scans were made per experimental plant, one in the direction of each adjacent neighbor or in similar directions for control plants and a mean value was calculated. PFD above plants and below the wire frames was measured with a quantum sensor (LI-COR model 190SA). All spectral quality and PFD measurements were made between 11:30 and 13:30 h on cloudless days.

Whole plant and ramet variables were monitored at two-week intervals for eight successive weeks. Ramet number plant^{-1} and maximum ramet height plant^{-1} were initially measured (May 6) prior to treatment installation and on each subsequent sampling date. Ramet height, sheath length, and blade length were measured for one randomly chosen ramet plant^{-1}. Selected ramets had not previously initiated juvenile ramets and were marked with a wire loop for subsequent inventory. Blade length was measured

from the youngest blade that possessed a ligule, which was usually the third youngest blade on a ramet. Ramet and sheath heights were measured from the soil surface to the tip of the longest leaf and to the highest leaf collar, respectively. Senesced portions of leaf tips were not included in length measurements. Aboveground biomass was harvested for all plants and shoot mass of juvenile ramets of the initially marked ramets was harvested separately at the end of the investigation (15 July). Root dry mass plant^{-1} was obtained by hand washing soil from roots in each container and weighing the dried biomass. An average shoot:root ratio was calculated for each radiation microenvironment by dividing total shoot dry mass by total root dry mass.

Plant and ramet variables were analyzed with PROC GLM using repeated measures ANOVA for treatment, species, and the species × treatment interaction (between subject effects) (SAS Institute Incorporated 1989). Variables collected at the end of the experiment were analyzed with one-way ANOVA for the same factors. Tukey's honestly significant difference procedure (HSD) was used to determine significance ($P < 0.05$) between treatment means for all plant and ramet variables. A significant interaction between treatments and species would indicate the occurrence of interspecific variation in the expression of shade avoidance (hypothesis 1). A significant difference between canopy treatments within a species would indicate a significant effect of canopy density on the expression of shade avoidance (hypothesis 2). The sparse and dense canopy treatments were compared to their respective controls. Plants grown in the sparse canopy (low horizontal R:FR) were compared to plants grown in the sparse canopy control (without neighbors, high horizontal R:FR), and plants grown in the dense canopy (low horizontal and vertical R:FR) were compared to plants grown in the dense canopy control (low horizontal R:FR only). Significantly greater ramet height, blade or sheath length, and lower ramet initiation in the sparse and dense canopy treatments compared to the respective controls would demonstrate the occurrence of a shade avoidance response.

Results

Both the repeated measures and one-way ANOVA models showed significant canopy treatment × species interactions for six of the nine ramet and plant

Table 1. Repeated measures and one-way ANOVA for ramet and plant variables. Values are the *F*-statistic for each dependent variable. The two statistical models tested the response of *Paspalum dilatatum* and *Schizachyrium scoparium* (SPP) to four different radiation microenvironments (TRT) to evaluate contrasting shade avoidance to low R:FR. A significant interaction term (TRT × SPP) indicates that the effect of low R:FR on the expression of shade avoidance differs between the species. $x = 55$ for ramets plant^{-1}, 33 for blade length, 54 for sheath length and ramet height.

repeated measures ANOVA	*F*-statistic for each dependent variable		
	TRT	SPP	TRT × SPP
df	3,x	1,x	3,x
ramets plant^{-1}	60.78***	1.63 *NS*	2.85*
blade length	15.34***	0.23 *NS*	1.85 *NS*
sheath length	22.82***	396.83***	4.70**
ramet height	14.62***	290.62***	4.05*
one-way ANOVA	TRT	SPP	TRT*SPP
df	3,56	3,56	3,56
juvenile ramets	4.32**	3.66 *NS*	2.00 *NS*
juvenile ramet dry mass	7.23***	39.24***	5.65***
shoot dry mass plant^{-1}	30.14***	79.67**	6.02***
root dry mass plant^{-1}	17.91***	8.05**	2.50 *NS*
shoot:root	5.73***	86.67***	4.93**

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; *NS* not significant

variables (Table 1). This interaction was used to test both hypotheses even though treatment and species were significant factors. We only interpreted canopy density to effects relative their respective controls to avoid confounding to PFD between canopy treatments.

Ramet number plant^{-1} was significantly lower in the sparse canopy compared to the respective control for both *P. dilatatum* and *S. scoparium* (41 and 47%, respectively) at the end of the experiment (Figure 2, Table 2). In contrast, ramet number plant^{-1} did not differ significantly between the dense canopy and the respective control for either species. Blade length was significantly greater in the sparse canopy compared to the respective control for *S. scoparium* (32%) at the end of the experiment, but blade length did not differ for *P. dilatatum* (Figure 2, Table 2). Blade length did not differ for either species in the dense canopy compared to the respective control. Sheath length did not differ significantly in either the sparse or dense canopy comparisons for either species (Figure 2, Table 2). Ramet height did not differ significantly within the sparse or dense canopy comparisons for either species (Figure 2, Table 2). Number of juvenile ramets initiated from parental ramets of *P. dilatatum*

was significantly lower in both the sparse (34%) and dense canopy (42%) compared to their respective controls (Table 2). In contrast, number of juvenile ramets initiated from parental ramets of *S. scoparium* was similar within the sparse and dense canopy comparisons.

Dry mass of initiated juvenile ramets was significantly lower (43%) for *P. dilatatum* in the sparse canopy compared to the respective control, but was similar in the dense canopy comparison (Table 2). In contrast, dry mass of initiated juvenile ramets for *S. scoparium* was similar for both the sparse and dense canopy comparisons. Shoot dry mass plant^{-1} was significantly lower (48%) for *P. dilatatum* in the sparse canopy compared to control, but was similar for the dense canopy comparison (Table 2). In contrast, shoot dry mass plant^{-1} for *S. scoparium* was similar for both the sparse and dense canopy comparisons. Root dry mass plant^{-1} was similar for both species in the sparse and dense canopy comparisons. Shoot:root ratio was significantly greater (52%) for *P. dilatatum* in the sparse canopy comparison, but was similar for the dense canopy comparison (Table 2). In contrast, shoot:root ratio for *S. scoparium* was similar for both the sparse and dense canopy comparisons.

Discussion

P. dilatatum was more responsive to low R:FR than *S. scoparium* in both the sparse and dense canopies and lower ramet number plant^{-1} in sparse canopies was the only common shade avoidance response between species. *P. dilatatum* also showed significant reductions in juvenile ramet initiation, juvenile ramet mass, total shoot mass, and shoot:root ratios in sparse canopies, but only juvenile ramet initiation was reduced in dense canopies. *S. scoparium* only showed a significant reduction in ramet number plant^{-1} and a significant increase in blade length in sparse canopies, but no significant responses occurred in dense canopies. Consequently, these data support both hypotheses: 1) *P. dilatatum* will express greater shade avoidance than *S. scoparium* to the low R:FR in both sparse and dense canopies, but *S. scoparium* did express a partial shade avoidance response in the sparse canopy and, 2) low R:FR will produce greater expressions of shade avoidance in sparse than in dense canopies in both species, but *P. dilatatum* did express a partial shade avoidance response in the dense canopy.

A reduction in the expression of shade avoidance in simulated dense compared to sparse canopies for both species corroborates previous investigations documenting greater perennial grass responsiveness to low R:FR in sparse, rather than in dense canopies (Casal et al. 1986; Skálová and Krahulec 1992; Skálová et al. 1997). However, greater expression of shade avoidance in sparse canopies is inconsistent with the expression of shade avoidance in the dense canopy microenvironment investigated by Deregibus et al. (1985). A potential explanation for the inconsistent response of *P. dilatatum* in the dense canopy invesigated by Deregibus et al. (1985) may have been associated with the addition of R to the base of selected plants to increase the R:FR. The supplemental R may have added a significant amount of PAR (25 μmol m^{-1} s^{-1}) to increase plant growth, including ramet initiation. The expression of shade avoidance in both perennial grasses in response to low R:FR in sparse canopies further contributes to the growing body of information documenting the role of the low R:FR as a proximity signal of impending canopy shade (Ballaré et al. 1987, 1990, 1997; Smith et al. 1990; Ballaré 1999).

Two potentially interactive mechanisms may explain the expression of greater shade avoidance to low R:FR in sparse than in dense canopies in *P. dilatatum*. The first mechanism involves the potential interaction between canopy density and numerous interrelated variables within the canopy microenvironment, including PFD (Casal et al. 1986, 1990; Ballaré et al. 1994). Our results indicate that the expression of shade avoidance in dense canopies was partially, but not entirely, negated when *P. dilatatum* plants were exposed to reduced PFD. This suggests that a threshold level of PFD may have been surpassed in the dense canopy to negate the shoot mass difference that occurred in the sparse canopy comparison, but juvenile ramet initiation was still suppressed by low R:FR in the dense canopy. The suppression of juvenile ramet initiation in the dense canopy was at least partially modulated by the vertically propagated R:FR because a similar reduction in PFD and horizontally propagated R:FR showed 42% greater juvenile ramet initiation in the respective control. A greater suppression of juvenile ramet initiation in the sparse than in the dense canopy treatment indicates that horizontally propagated low R:FR has a stronger effect than vertically propagated low R:FR. This supports the interpretation of the proximity signal (Ballaré et al. 1987, 1988; Ballaré 1999) and further suggests that the low
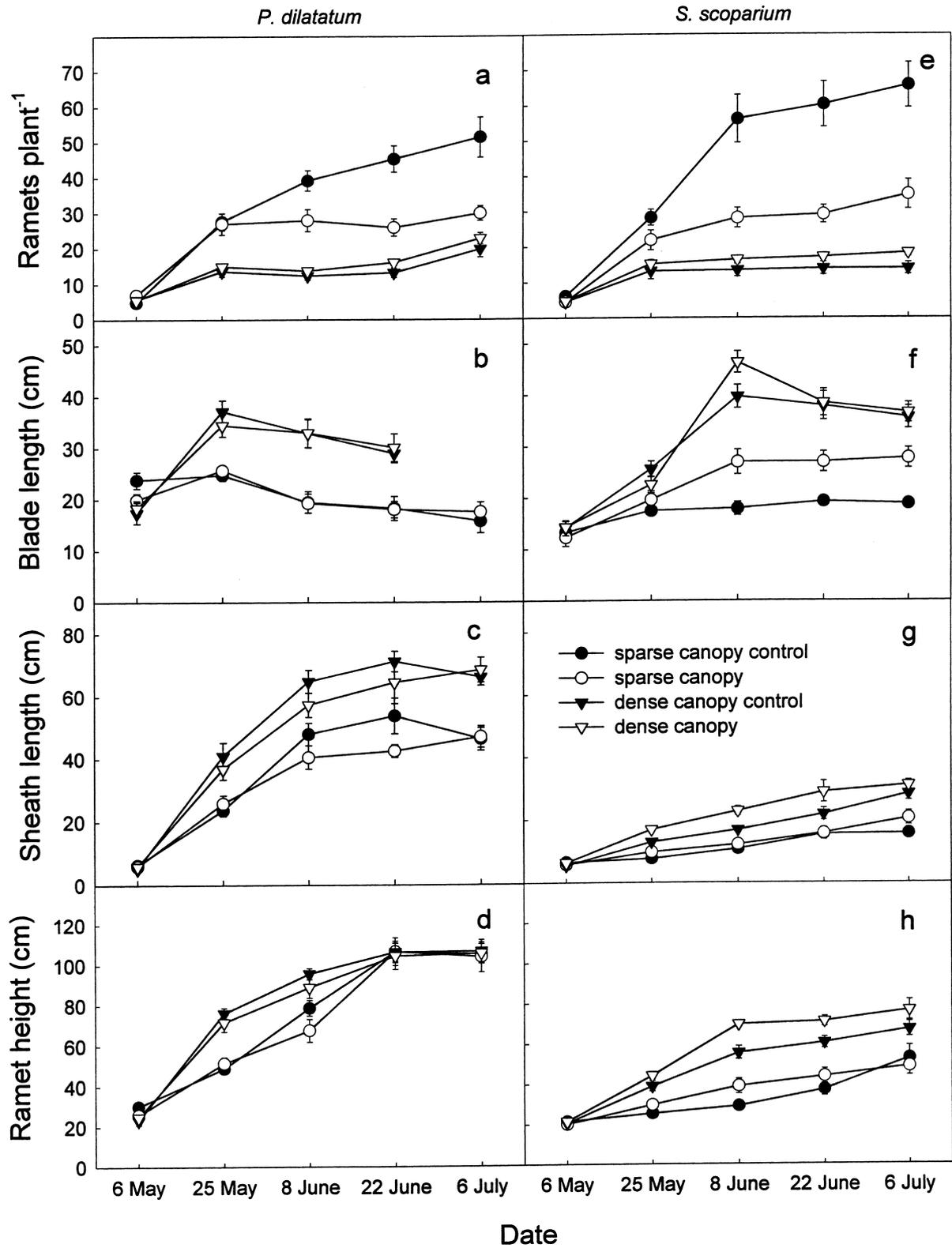
Figure 2. Mean (±SE, n = 8) ramets plant⁻¹, blade length, sheath length, and ramet height for *P. dilatatum* a–d and *S. scoparium* e–h plants grown for eight weeks in an experimental garden. Plants of each species were exposed to four radiation microenvironments to evaluate shade avoidance responses to low R:FR in simulated sparse and dense canopies compared to their respective controls.

Table 2. Repeated measures ANOVA of ramets plant^{-1}, blade length, sheath length, and ramet height for last date. One-way ANOVA of juvenile ramets, juvenile ramet dry mass, shoot dry mass plant^{-1}, root dry mass plant^{-1}, and shoot:root. Plants of *Paspalum dilatatum* and *Schizachyrium scoparium* were grown for eight weeks and subjected to four different radiation microenvironments to evaluate contrasting shade avoidance to low R:FR in simulated sparse and dense canopies versus their respective controls. Means within a variable and species proceeded by an asterisk indicate a significant difference between canopy comparisons with $P < 0.05$. See Figure 1 for complete treatment descriptions.

species	canopy density comparison	repeated measures ANOVA				one-way ANOVA				
		ramets plant^{-1}	blade length (cm)	sheath length (cm)	ramet height (cm)	juvenile ramets	juvenile ramet dry mass (g)	shoot dry mass plant^{-1} (g)	root dry mass plant^{-1} (g)	shoot:root
P. dilatatum	control	*51.0 ± 5.7	15.8 ± 2.3	46.4 ± 3.7	105.6 ± 4.8	*6.6 ± 0.2	*22.6 ± 2.9	*99.7 ± 7.4	11.7 ± 0.9	*9.3 ± 1.6
	sparse	30.0 ± 2.1	17.5 ± 1.9	47.1 ± 3.5	104.0 ± 7.5	4.3 ± 0.2	11.3 ± 2.4	52.0 ± 3.2	13.6 ± 2.7	4.5 ± 0.6
	control	19.8 ± 2.3	23.0 ± 8.5	66.2 ± 2.6	107.1 ± 5.6	*4.5 ± 0.4	9.2 ± 1.9	37.0 ± 2.8	6.5 ± 1.0	6.4 ± 0.8
	dense	22.9 ± 1.6	32.0 ± 1.0	68.6 ± 4.0	105.8 ± 4.9	2.6 ± 0.2	8.1 ± 1.9	44.5 ± 2.6	4.9 ± 0.7	9.9 ± 6.4
S. scoparium	control	*65.6 ± 6.3	*18.8 ± 0.9	15.6 ± 1.5	56.7 ± 6.3	6.3 ± 1.1	5.2 ± 1.6	41.5 ± 5.1	20.2 ± 2.3	2.1 ± 0.2
	sparse	34.8 ± 4.1	27.7 ± 1.9	20.5 ± 2.2	48.6 ± 4.4	6.1 ± 1.2	4.4 ± 1.4	28.3 ± 3.4	15.9 ± 2.2	2.0 ± 0.3
	control	13.9 ± 1.7	35.6 ± 2.2	28.2 ± 2.1	67.1 ± 3.7	4.4 ± 1.1	3.7 ± 1.1	16.0 ± 2.9	5.7 ± 0.9	2.9 ± 0.3
	dense	18.3 ± 1.0	36.5 ± 1.9	31.0 ± 1.5	76.6 ± 5.1	5.3 ± 0.6	4.8 ± 1.1	19.5 ± 2.2	8.7 ± 1.7	2.6 ± 0.4

R:FR may be less effective in modulating shade avoidance responses with increasing canopy density as the vertically propagated low R:FR replaces the horizontally propagated low R:FR.

The second mechanism that may partially explain the greater expression of shade avoidance in sparse than in dense canopies involves the flux density of FR necessary to alter the phytochrome equilibrium in plants (Morgan et al. 1980; Morgan and Smith 1981; Ballaré et al. 1992a). Shade avoidance responses at a particular R:FR and phytochrome equilibrium (i.e., Pfr:P) are often assumed to be independent of PFD, but directly proportional to the flux density of FR (Ballaré et al. 1992a). The flux density of horizontally propagated FR in sparse canopies will always be greater than in dense canopies regardless of R:FR because FR is reflected from neighboring plants. In dense canopies, the R:FR is reduced by the depletion of R and the flux density of FR is much lower than in sparse canopies because multiple reflections between adjacent leaves and stems attenuate radiation (Jones 1992). Horizontally propagated low R:FR may provide an energetically stronger signal (FR flux density) than vertically propagated low R:FR at comparable R:FR values. However, we acknowledge that increas-ing canopy density alters numerous interrelated variables other than R:FR and PFD, e.g., wind speed, leaf and air temperature, and vapor pressure density (Jones 1992). Plant architecture may even be modulated by other radiation signals within canopies, including blue light as perceived by the photoreceptor cryptochrome (Gautier and Varlet-Grancher 1996; Ballaré et al. 1997; Ballaré 1999).

However, we have observed that a high flux density of horizontal FR does not consistently modulate a shade avoidance response in perennial grasses. For example, horizontal FR emitted from lamps with a flux density nearly four times greater than those measured in the sparse and dense canopies in this experiment (11 vs 38 μmol m^{-2} s^{-1}) did not modulate the expression of shade avoidance in isolated plants of *S. scoparium* in the field (Murphy and Briske 1994; Monaco and Briske 2000). A high flux density of FR was required to lower the ambient R:FR in isolated plants exposed to ambient PFD (i.e., high R flux density). However, it has been suggested that a very high FR flux density may mitigate shade avoidance responses when plants are provided long-term supplemental FR (Morgan and Smith 1978; Morgan et al. 1980).

Plant architecture may potentially interact with the flux density of FR to modulate the expression of shade avoidance. Vertically oriented blades and sheaths of grasses may perceive horizontally reflected FR from neighboring plants to a greater extent than vertically propagated FR transmitted through overhead foliage (Ballaré et al. 1987, 1988, 1989; Davis and Simmons 1994a, 1994b; Ballaré 1999). Contrasting ramet architectures may provide a partial explanation for the greater expression of shade avoidance in *P. dilatatum* than *S. scoparium* in the simulated dense canopy that possessed both horizontal and vertical FR. Ramets of *P. dilatatum* generally grow with a more decumbent orientation (Gibson et al. 1992; Laterra et al. 1997) compared to the orientation of *S. scoparium* ramets which may have increased the flux density of vertically propagated FR incident on *P. dilatatum* compared to *S. scoparium* ramets.

The two species showed substantially different individual ramet responses to low R:FR even though ramet number plant^{-1} was reduced in sparse canopies for both perennial grasses. The most important interspecific difference was the reduction in juvenile ramet initiation from individual parental ramets of *P. dilatatum* that occurred in both sparse and dense canopies, but this variable was unaffected by either canopy density for *S. scoparium*. Distinct expression of ramet initiation between species appeared to have been largely a function of low R:FR because both species initiated similar numbers of juvenile ramets when grown with ambient R:FR. However, blade length was greater in the sparse canopy comparison for *S. scoparium* ramets, but it was unaffected by either canopy density for *P. dilatatum*. The partial expression of shade avoidance, involving enhanced leaf elongation without a corresponding reduction in ramet initiation has previously been recognized for *S. scoparium* (Monaco and Briske 2000). Unique ramet responses to low R:FR between these two C$_4$ perennial grasses demonstrates the occurrence of considerable interspecific variation that may partially explain the inconsistent expression of shade avoidance in this group of plants. The only recognized pattern of interspecific variation is a greater expression of shade avoidance by shade intolerant compared to shade tolerant species (Morgan and Smith 1979; Corré 1983; van Hinsberg and van Tienderen 1997; Wulff 1998).

Low R:FR in sparse canopies modified plant dry mass and biomass partitioning in *P. dilatatum*, but not *S. scoparium*, providing further evidence of interspecific variation in the expression of shade avoidance

between these two species. Low R:FR in sparse canopies reduced juvenile ramet dry mass and shoot dry mass plant^{-1} by nearly 50% which contributed to the reduction in the shoot:root ratio for *P. dilatatum* in low R:FR. These reductions in shoot mass were very likely a function of low R:FR suppression of juvenile ramet initiation and total ramets plant^{-1} in *P. dilatatum*. Although total shoot and ramet mass for *S. scoparium* was not significantly reduced in sparse canopies, the percentage reduction for shoot dry mass plant^{-1} in the treatment comparison was similar to that for *P. dilatatum*. The 39% greater standard error of the mean associated with shoot dry mass plant^{-1} for *S. scoparium* compared to *P. dilatatum* explains why this variable was not significantly different for *S. scoparium* in the sparse canopy. These patterns of biomass partitioning are inconsistent with the observed increase in shoot mass and decrease in root mass frequently associated with the expression of shade avoidance (Skálová et al. 1997; Maliakal et al. 1999; Pecháčková 1999). We are unable to explain these unique biomass responses in *P. dilatatum*. The absence of significant mass responses to low R:FR in *S. scoparium* reflects the minimal expression of shade avoidance in this species.

The observation that shade avoidance is expressed to a greater extent in sparse than in dense canopies has important ecological implication for grassland ecology. It suggests that the R:FR may not be of equal ecological importance at all stages of canopy development or in all grassland communities. The low R:FR produced by vertical attenuation of R in dense canopies may not illicit as great a shade avoidance expression as the horizontal reflection of FR from adjacent vegetation in a sparse canopy. This implies that the R:FR may have its greatest effect on asymmetric competition and the establishment of size hierarchies in less productive communities that maintain a relatively low LAI (Morgan and Smith 1979; Corré 1983; Skálová and Krahulec 1992; Wulff 1998). Alternatively, in productive communities with high LAI, low R:FR may exert its greatest effect early in the growing season or following disturbances that reduce canopy density and increase horizontal reflection of FR from adjacent vegetation i.e., proximity signal (Weiner 1990; Schmitt et al. 1999; Ballaré 1999). Variable shade avoidance responses between species and canopy densities indicate that both interspecific variation and vertically and horizontally propagated low R:FR may have contributed to the inconsistent shade avoidance responses of perennial grasses in field settings.

Both processes should be considered when scaling shade avoidance responses from individual plants to canopies and communities.

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