

Does resource availability modulate shade avoidance responses to the ratio of red to far-red irradiation? An assessment of radiation quantity and soil volume

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SUMMARY

We conducted two experiments to investigate the expression of shade avoidance in response to low ratios of red to far-red irradiation (R:FR) in the C₄ perennial grass *Schizachyrium scoparium* at two levels of above-ground (photosynthetic photon flux density (PPFD) 400–700 nm) and below-ground (soil volume) resource availability and in plants of two ages. Young plants showed greater sheath and ramet height in response to low R:FR and old plants showed reduced ramet initiation in experiments one and two, respectively, but both responses were not expressed simultaneously in either group. Growth of all ramet variables, including ramet initiation, was suppressed in small as opposed to large soil volumes. By contrast, architectural variables, but not ramet initiation, were greater for plants grown in low as opposed to ambient PPFD. However, expression of shade avoidance to low R:FR was not significantly affected by either level of PPFD or soil volume. We must conclude that the levels of resource availability provided do not modulate shade avoidance in this perennial grass. These results demonstrate that *S. scoparium* is capable of expressing shade avoidance in response to low R:FR, but inconsistent juvenile ramet initiation and architectural responses in plants of different ages and phenological stages of development indicate that the shade avoidance response might not be expressed consistently throughout the life of plants.

Key words: *Schizachyrium scoparium* (little bluestem), red:far-red ratio, ramet initiation, radiation quality, shade avoidance response, photon flux density, C₄ grass.

INTRODUCTION

A low ratio of red to far-red irradiation (R:FR) is known to function as an environmental signal capable of modulating a suite of architectural responses often described as the shade avoidance syndrome (Morgan & Smith, 1979; Smith, 1982; Schmitt & Wulff, 1993). This signal is modified from that of ambient solar radiation by the absorption of red radiation (600–700 nm) and the reflection and transmission of far-red (700–800 nm) within plant canopies. Perception of the low R:FR by the phytochrome system enables many plants to detect the proximity of neighbours and the presence of impending light competition before a reduction in actual photosynthetic photon flux density (PPFD; 400–700 nm) (Casal *et al.*, 1986; Ballaré *et al.*, 1987,

1988). The shade avoidance syndrome is characterized by an increase in plant height, a reduction in branch number and a decrease in time to flowering, and it is considered to be an expression of adaptive plasticity (Casal & Smith, 1989; Ballaré *et al.*, 1994; Dudley & Schmitt, 1995, 1996).

The expression and ecological significance of the shade avoidance response in perennial grasses is less conclusive than for the large number of herbaceous dicots that have been investigated. The limited number of field investigations conducted with perennial grasses have produced inconsistent expressions of shade avoidance among species and investigations (Deregibus *et al.*, 1985; Casal *et al.*, 1986; Skálová & Krahulec, 1992; Murphy & Briske, 1994; Skálová *et al.*, 1997). These inconsistencies might reflect the following: (1) plant canopies modify numerous interrelated variables within the microclimate in addition to the R:FR (Casal *et al.*, 1986, 1990; Ballaré *et al.*, 1994), (2) the range of intra-

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specific and interspecific variation in response to the R:FR is not well known (Dudley & Schmitt, 1995; Skálová *et al.*, 1997; Wulff, 1998), and (3) considerable variation exists in the experimental procedures used to investigate the shade avoidance syndrome, including source of R:FR, far-red flux density and associated PFD.

Plants' expression of shade avoidance responses to the R:FR is further confounded by the effect of resource availability and competition within grassland canopies (Kays & Harper, 1974; Casal *et al.*, 1986; Jurik, 1991; Weiner & Thomas, 1992). For example, PFD decreases exponentially with canopy depth and low PFD is known to reduce ramet initiation and survival (Langer, 1963; Kays & Harper, 1974; Holmes & Smith, 1977; Davies & Thomas, 1983). Similarly, both intraspecific and interspecific competition have been shown to reduce ramet initiation and growth (Briske & Butler, 1989; Hartnett, 1989). Resource availability might interact with the R:FR to affect various physiological processes, including the sink strength of various organs and whole-plant resource allocation patterns (Keiller & Smith, 1989; Skinner & Nelson, 1994; Yanovsky *et al.*, 1995). Whole-plant allocation patterns and resource requirements might also vary with plant age and phenological development to influence plant response to the R:FR (Casal, 1988; Novoplansky, 1991).

Investigations of the expression of shade avoidance in plants have often been conducted under near-optimal growth conditions or during periods of rapid vegetative growth (i.e. young plants grown in chambers and glasshouses). Would the R:FR have similar adaptive value under conditions of sub-optimal resource availability? Could the adaptive value of shade avoidance be enhanced by suboptimal growth conditions? Resource availability might potentially modulate shade avoidance responses because branch initiation and leaf growth are known to respond positively to nutrient availability (Corré, 1983; Marriott & Zuazua, 1996), but negatively to reduced PFD (Solangaarachchi & Harper, 1987; Methy *et al.*, 1990). Potential interactions between the R:FR and resource availability, including PFD and soil volume, have not received much attention, especially in grasses (but see Casal *et al.* (1986) and Novoplansky (1991)).

Two experiments were conducted to investigate shade avoidance responses in the C₄ perennial grass *Schizachyrium scoparium* to two levels of above-ground (PFD) and below-ground (soil volume) resource availability. Three specific hypotheses were tested: (1) ramet initiation and architecture would be more responsive to low R:FR when plants were grown under reduced PFD, (2) ramet initiation and architecture would be more responsive to low R:FR when plants were grown with reduced soil volume, and (3) ramet initiation and architecture would be

more responsive to low R:FR in young plants than in old plants. In the first experiment, plants in containers were subjected to two levels of soil volume and PFD, and half of the plants in each treatment were exposed to supplemental far-red light to reduce the R:FR below that of ambient. The first experiment was designed to evaluate the short-term developmental responses in young (60 d) plants during a period of optimal growth conditions known to coincide with maximum ramet initiation rate in field populations (Briske & Butler, 1989; Murphy & Briske, 1994). In the second experiment, older (120 d) plants in large soil volumes were exposed to supplemental far-red light during midsummer when environmental conditions were less conducive to vegetative growth. An investigation of plant response to R:FR under conditions of varying above-ground and below-ground resource availability might provide additional insight into the inconsistent expression of shade avoidance among perennial grasses.

MATERIALS AND METHODS

Caryopses of *Schizachyrium scoparium* (Michx.) Nash var. *frequens* (Hubb.) were planted in PVC tubes 5 cm in diameter and 76 cm in length (1.5 l) and 10 cm in diameter and 76 cm in length (6 l) filled with a mixture of humus-rich black soil and sand (ratio 3:1, v/v) on 27 March 1997. The base of each tube was covered with fibreglass mesh to prevent soil loss and allow water drainage. Tubes were secured on a wood platform in a field plot within the Texas A&M University Native Plant and Animal Conservancy (lat. 30° 38' N, long. 96°21' W). Plants developed in an ambient environment, were provided with 200 ml of water per tube each day, and NPK fertilizer (granular; 20–20–20; 1 g l⁻¹) was added once a week during watering. Precipitation in April, May and June provided additional water for plants (100 mm, 90 mm and 170 mm per month, respectively). On 13 June 1997, 32 plants (each possessing 5–10 ramets) within each tube size were selected for placement into a 20 m × 20 m field plot. Tubes containing plants were placed into 0.9 m holes so that plant bases were level with the soil. Holes were spaced 1.5 m apart and the bottom was filled with sand to enhance water drainage from the tubes.

Eight plants from each tube size were randomly assigned to the four combinations of low and high levels of PFD and R:FR. The spectral flux densities of ambient and shaded microenvironments were measured at midday under cloudless conditions (June 1997) with a spectroradiometer (LI-COR 1800, LI-COR, Lincoln, NE, USA) equipped with a remote cosine sensor. The sensor was oriented horizontally to the ground in full view of the sun for direct radiation measurements (Fig. 1a) and then vertically, towards the north away from direct sun, to measure diffuse radiation (Fig. 1b). The relative

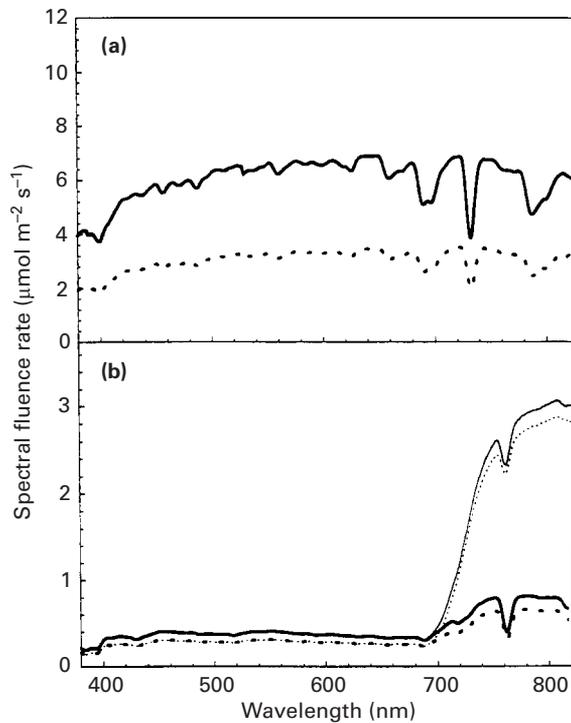


Fig. 1. Spectral flux density of the four radiation treatments used to evaluate the response of *Schizachyrium scoparium* plants to red:far-red ratio (R:FR) at two levels of PFD (400–700 nm) and soil volume in experiment 1. (a) Direct radiation within ambient (solid line; 1783, 1.19) and shade (broken line; 890, 1.17) treatments and (b) diffuse radiation within ambient R:FR (thick solid line; 109, 0.53), shade R:FR (broken line; 83, 0.51), low R:FR (thin solid line; 110, 0.19) and shade+low R:FR (dotted line; 84, 0.15) treatments. The values after each line type are mean ($n = 12$) PFD and R:FR within a treatment.

proportion of these two forms of R:FR might have important ecological implications because low R:FR below grassland canopies originates from both the direct attenuation of red light within the canopy and reflected diffuse far-red light from neighbouring plants. The low PFD treatment ($890 \pm 5 \mu\text{mol m}^{-2} \text{s}^{-1}$) was produced by placing a single layer of neutral-density fibreglass window screen (1 mm \times 1 mm) over a wire frame (45 cm \times 91 cm) shaped into an arch with an east–west orientation above individual plants. These filters uniformly shaded plants throughout the photoperiod and effectively reduced PFD by 50% compared with ambient ($1783 \pm 5 \mu\text{mol m}^{-2} \text{s}^{-1}$). Air temperatures below filters were unaffected, although leaf temperatures were 2–3°C lower than those of unshaded plants.

The low-R:FR treatment was produced by filtering radiation from a 90 W halogen (PAR38, 30°; Sylvania) flood light through a 15.25 cm \times 15.25 cm section of Perspex (Plexiglass) (FR filter; Westlake Plastics Company, Lenni, PA, USA) that transmitted only wavelengths > 700 nm (FR). Perspex filters were attached to each lamp 15 cm from the fixture and lamps were positioned 30 cm from the north periphery of selected plants. Far-red irra-

diation did not modify PFD, but it significantly reduced diffuse R:FR (0.19 ± 0.03) (Fig. 1b). The corresponding direct R:FR was (0.65 ± 0.02). To ensure equal radiation output between the 32 lamps, three 4-A circuits provided electricity to a similar number of lamps, and each lamp was adapted with a dimming device to adjust the radiation output.

For experiment 1, initial measurements (20 June 1997) of blade length per ramet and sheath height were taken from two uniformly sized ramets possessing three to six leaves, lacking previously initiated juvenile ramets, and located on the north periphery of experimental plants (60 d old). These ramets were then marked with wire loops and monitored weekly for cumulative juvenile ramet initiation, blade length per ramet, sheath length and ramet height for 8 successive weeks. The number of juvenile ramets reflects only those initiated because no ramet mortality was observed during the experiment. Sheath and ramet heights were measured from the soil surface to the highest leaf collar and the tip of the longest leaf, respectively. A newly initiated juvenile ramet was recorded when the first leaf emerged from the subtending sheath of the parental ramet. Each plant was harvested after 8 wk and all ramets were dissected by removing blades, sheaths, buds and initiated ramets. The dry mass of each ramet component was determined after drying for 48 h in a convective oven at 60°C.

For experiment 2, 60 *S. scoparium* plants were grown in the same 10-cm tubes as in experiment one for 120 d under ambient radiation; each tube was provided with 200 ml water d^{-1} and fertilized weekly with NPK. Tubes containing individual plants were placed into the field plot as described previously. Plants possessed 50–100 ramets; a small number of these exhibited culm elongation and inflorescences. All elongated culms (with or without inflorescences; $< 10\%$ of total ramets per plant) were removed at the position of the lowest visible node to minimize associated carbon allocation to this carbon sink. On 10 September, 30 plants were assigned to both an ambient radiation treatment and a supplemental far-red light treatment without shading. Lamps were positioned as described previously, but elevated 7 cm higher from the soil surface to ensure the irradiation of the upper portion of these larger plants. One ramet from each plant was marked with a wire loop and ramet variables were monitored weekly for 9 successive weeks as in experiment 1. The dry mass of ramet components was collected from experimental plants as described previously.

All variables of experiment one were analysed by repeated-measures ANOVA (SAS Institute Inc., 1989). The experiment was analysed as a complete factorial in a completely randomized design with soil volume, PFD and R:FR as the main effects. Tukey's 'honestly significant difference' (HSD) procedure was used to determine the significance between all

treatment means for all ramet variables. End-of-season dry mass was analysed with a one-way ANOVA for each ramet variable. Repeated-measures ANOVA was also used to analyse data from experiment 2 as a completely randomized design. Tukey's HSD was used to determine differences between treatments for all ramet variables. Student's *t* test was used to analyse the end-of-season dry mass.

RESULTS

Repeated-measures ANOVA in experiment 1 revealed a significant interaction between soil volume, PFD and R:FR for all ramet variables except height (Table 1). However, none of the two-factor interactions were significant. Investigation of the three-way interaction indicated that this situation resulted from a geometric interaction (Winer, 1971) between PFD and R:FR means in the large and small soil volumes (i.e. the main effect response slopes were not parallel, yet responses did not intersect; see Figs 2, 4 and 5). Consequently, all ramet variables were interpreted independently for soil volume, PFD and R:FR treatments.

All variables for the growth of ramets, including juvenile ramet initiation, were significantly ($P < 0.05$) lower in plants grown in small compared with large soil volumes (Fig. 2). Significant differences between plants in the two soil volumes were detectable at week 2 for blade and sheath length, week 3 for ramet initiation, and week 4 for ramet height. The end-of-experiment blade length per ramet, sheath length, ramet height and ramet number were, respectively, 62%, 51%, 49% and 45% greater for plants in the large soil volume compared with those in the low soil volume. End-of-experiment masses of all parental ramet variables also showed a significant ($P < 0.05$) response to soil volume (Fig. 3). Plants in the large soil volume had significantly ($P < 0.05$) greater whole

plant mass (7.2 g vs 34.9 g) and parental ramet mass (0.3 g vs 1.8 g) compared with plants in the small soil volume. Significantly ($P < 0.05$) greater mass was also observed for juvenile ramet blades (0.08 g vs 0.50 g), sheaths (0.06 g vs 0.38 g) and crowns (0.02 g vs 0.18 g), as well as blade (7.4 cm vs 34.2 cm) and sheath length (3.9 cm vs 17.2 cm), in the large compared with the small soil volume.

Plants grown in low PFD had a significantly ($P < 0.05$) greater blade length per ramet, sheath length and ramet height of parental ramets compared with those grown in ambient PFD (Fig. 4). However, ramet initiation did not differ significantly between levels of PFD. The positive growth response in low PFD compared with ambient PFD was significant ($P < 0.05$) from week 2 to week 8 for blade length per ramet and for week 4 to week 8 for ramet height. Blade length per ramet, sheath length, ramet height and ramet initiation were, respectively, 36%, 31% and 40% greater and 9% less in low PFD compared with ambient PFD at the end of the experiment. The blade and sheath masses of parental ramets were significantly ($P < 0.05$) greater in plants grown in low PFD compared with ambient PFD, but the effect on mass of parental ramet crowns and whole juvenile ramets was not significant (Fig. 3). Masses and lengths of juvenile ramet blades, sheaths and crowns were not significantly different between levels of PFD.

Parental ramet sheath length and ramet height were significantly ($P < 0.05$) greater when treated with low R:FR than with ambient R:FR (Fig. 5). These variables differed significantly on weeks 2, 3 and 8 for sheath length, and on weeks 4, 6, 7 and 8 for ramet height. However, the blade length per ramet of plants grown in low R:FR was not significantly greater than for those grown in ambient R:FR. Ramet height and sheath length were 15% and 28% greater, respectively, for plants grown with low R:FR than with ambient R:FR on week 8.

Table 1. Repeated-measures ANOVA for the effects of soil volume, PFD and R:FR and their interactions on blade length per ramet, sheath length, ramet height and juvenile ramet initiation for *Schizachyrium scoparium* plants in experiment 1 ($x = 56$ for blade length, $x = 54$ for sheath length, $x = 50$ for ramet height, and $x = 56$ for ramet initiation)

Source of variation	df	<i>F</i> -values for each dependent variable			
		Blade length per ramet	Sheath length	Ramet height	Ramet initiation
Soil volume	1, <i>x</i>	150.55***	58.98***	72.69***	27.19***
PFD	1, <i>x</i>	22.92***	30.92***	65.69***	0.76 ns
R:FR	1, <i>x</i>	1.88 ns	5.43*	9.73**	0.04 ns
Soil volume × PFD	1, <i>x</i>	0.51 ns	0.26 ns	1.93 ns	0.13 ns
Soil volume × R:FR	1, <i>x</i>	3.17 ns	1.32 ns	1.04 ns	0.07 ns
PFD × R:FR	1, <i>x</i>	0.35 ns	0.37 ns	0.73 ns	0.00 ns
Soil volume × PFD × R:FR	1, <i>x</i>	4.68*	6.16*	1.18 ns	5.15*

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

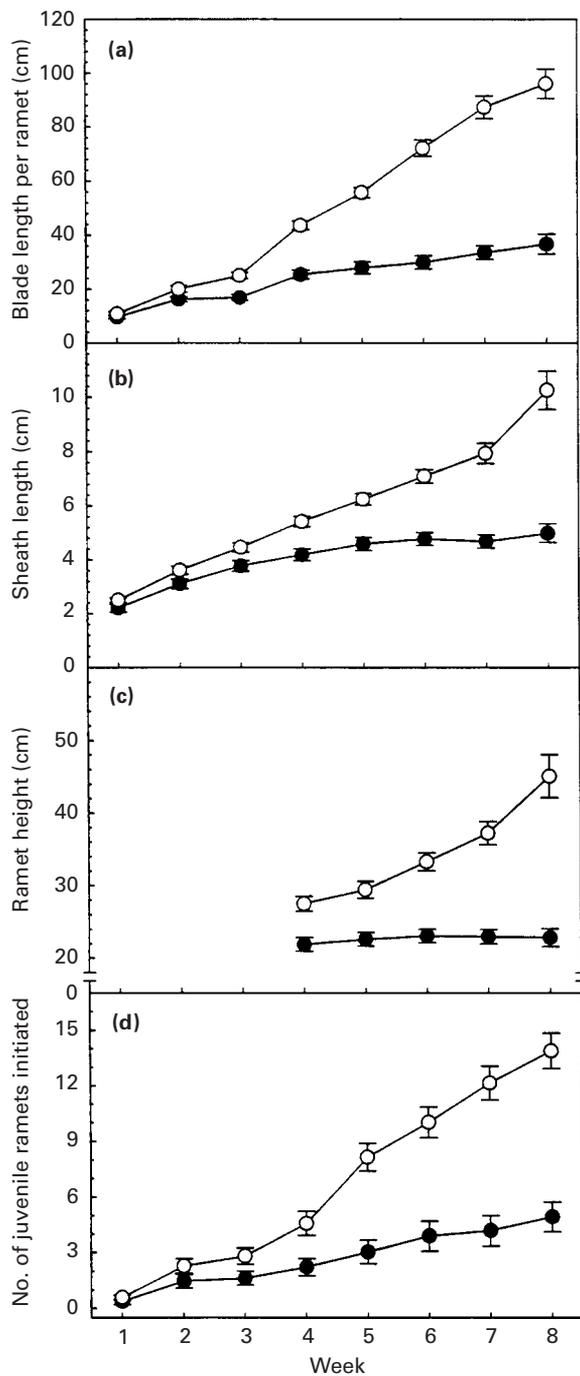


Fig. 2. Mean (\pm SE, $n = 32$) (a) blade length per ramet; (b) sheath length, (c) ramet height and (d) juvenile ramet initiation for *Schizachyrium scoparium* plants grown in small (1.5 l; closed circles) and large (6 l; open circles) soil volumes in experiment 1. There were no two-way interactions between soil volume and PFD or R:FR, so results were averaged across levels of the main effects. Significant differences ($P < 0.05$) between soil volumes were observed in weeks 2–8 for blade and sheath length, weeks 3–8 for juvenile ramet initiation, and weeks 4–8 for ramet height.

Blade length per ramet and sheath length, and ramet height, under conditions of low PFD and large soil volume, were, respectively, 26%, 36% and 16% greater when treated with low R:FR than with

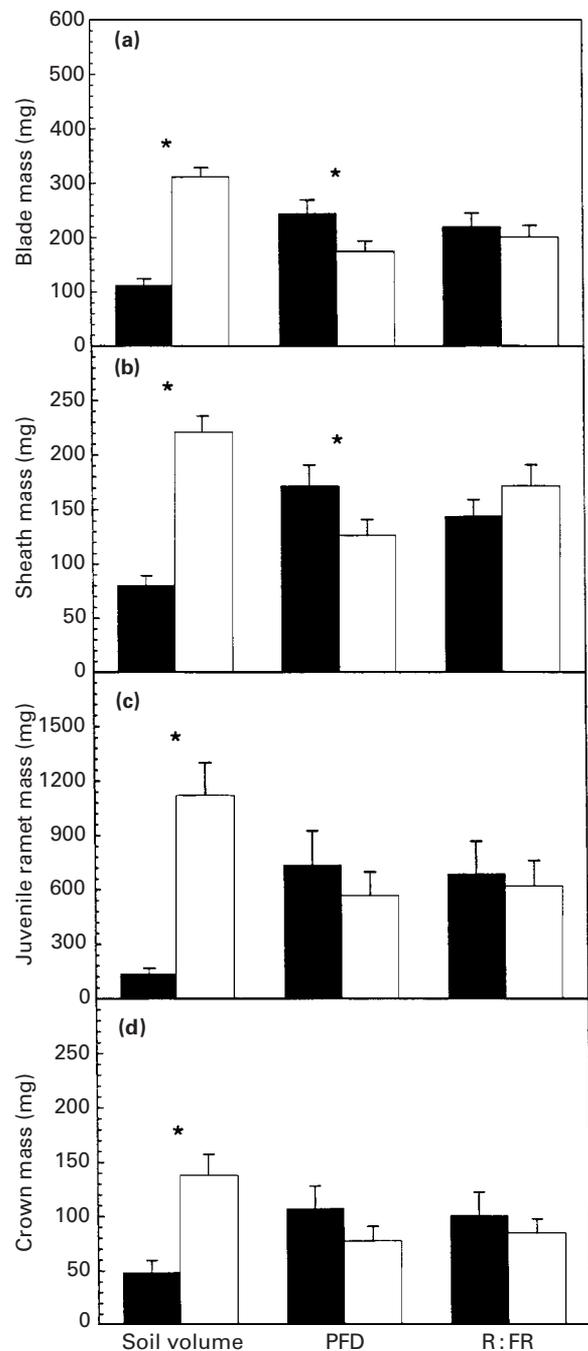


Fig. 3. Mean (\pm SE, $n = 32$) (a) blade mass, (b) sheath mass, (c) juvenile ramet mass and (d) crown mass of *Schizachyrium scoparium* plants grown with low (50% ambient) and high (ambient) PFD (400–700 nm) and small (1.5 l) and large (6 l) soil volumes to evaluate plant response to low and high R:FR in experiment 1. Closed bars indicate low levels; open bars indicate high levels. There were no two-way interactions between soil volume and PFD or R : FR, so results were averaged across levels of the main effects. Asterisks indicate significant differences between treatments ($P < 0.05$).

ambient R:FR. In contrast, low R:FR did not have a significant effect on ramet initiation compared with ambient R:FR. Low R:FR did not significantly affect the mass of any parental or juvenile ramet variables compared with ambient R:FR (Fig. 3).

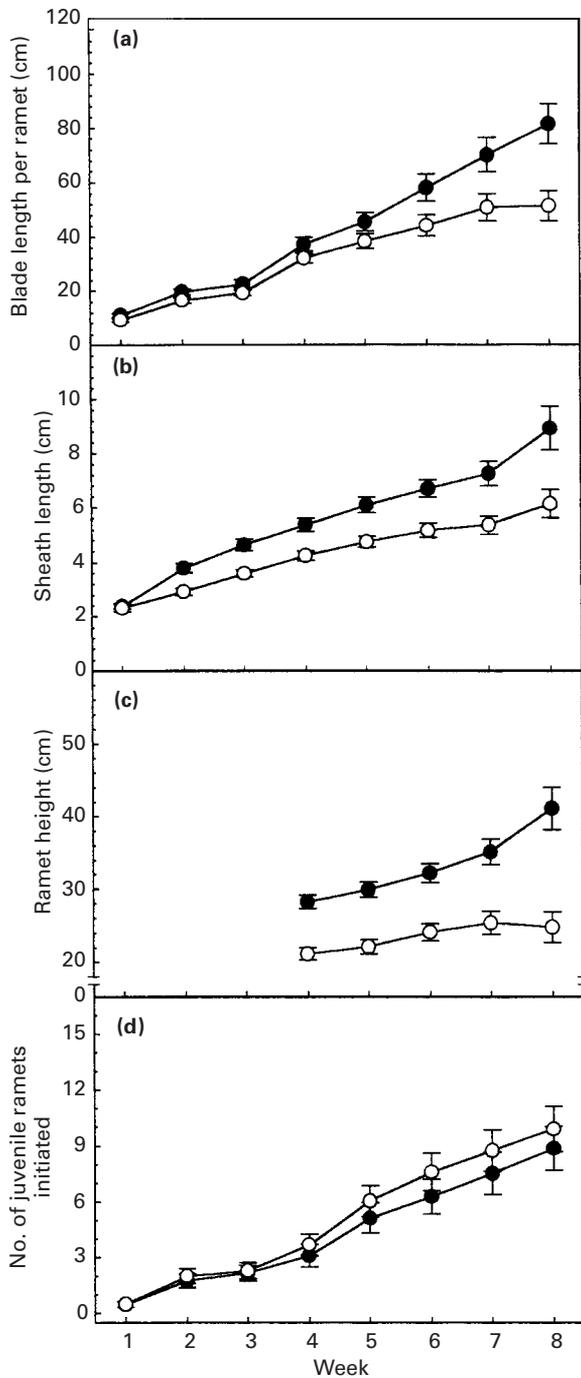


Fig. 4. Mean (\pm SE, $n = 32$) (a) blade length per ramet, (b) sheath length, (c) ramet height and (d) juvenile ramet initiation for *Schizachyrium scoparium* plants grown with low (50% ambient; closed circles) and high (ambient; open circles) photon flux density (400–700 nm) in experiment 1. There were no two-way interactions between soil volume and PFD or R:FR, so results were averaged across levels of the main effects. Significant differences ($P < 0.05$) between levels of PFD were observed in weeks 2–8 for blade length per ramet, and weeks 4–8 for ramet height.

Minimal vegetative growth occurred for parental ramets during the 8-wk experiment in midsummer and late summer in experiment 2 (Fig. 6). Blade mass collected at the end of the experiment was 19% greater for plants grown in low R:FR than in

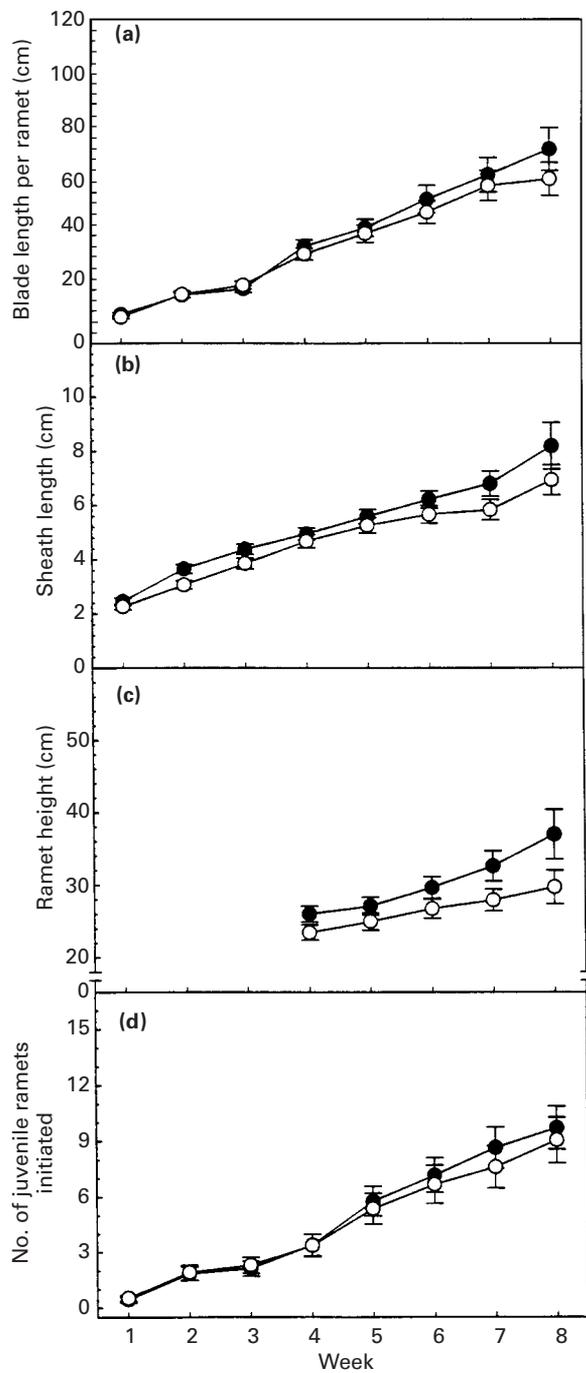


Fig. 5. Mean (\pm SE, $n = 32$) (a) blade length per ramet, (b) sheath length, (c) ramet height and (d) juvenile ramet initiation of *Schizachyrium scoparium* plants grown with low (closed circles) and high (open circles) R:FR in experiment 1. There were no two-way interactions between soil volume and PFD or R:FR, so results were averaged across levels of the main effects. Significant differences ($P < 0.05$) between levels of R:FR were observed in weeks 2, 3 and 8 for sheath length and weeks 4 and 6–8 for ramet height.

ambient R:FR ($P = 0.051$; Fig. 7). No discernible increase occurred in sheath length or ramet height during the experiment regardless of R:FR treatment. In contrast, juvenile ramets were rapidly initiated during the experiment, and plants grown

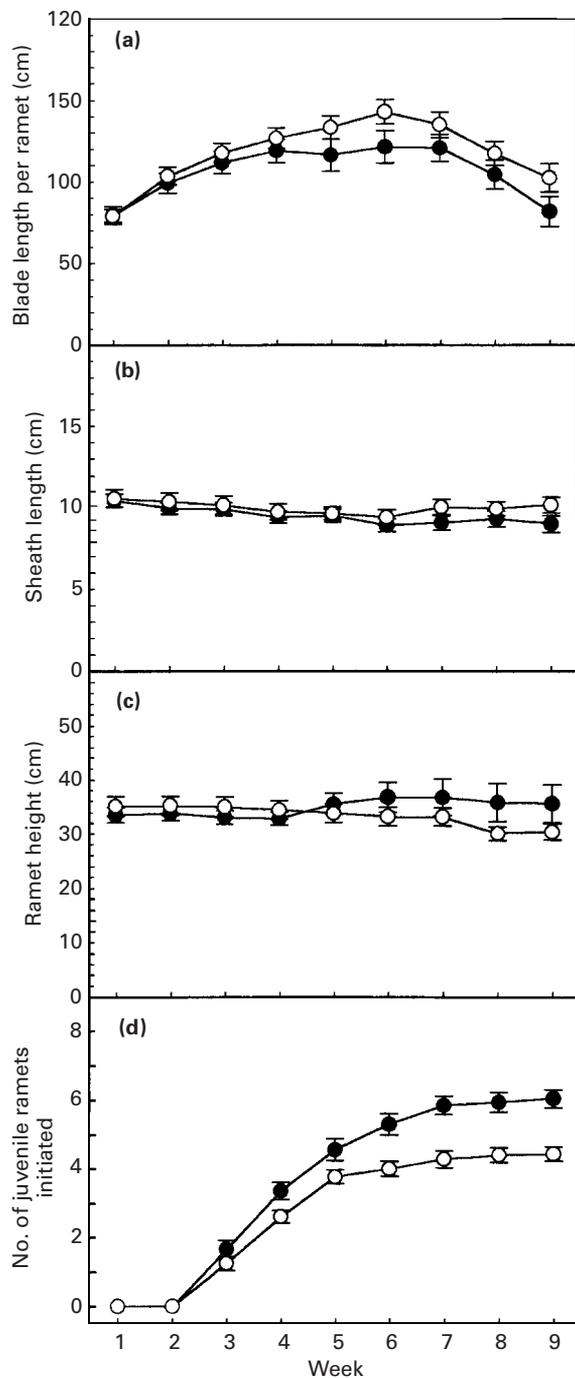


Fig. 6. Mean (\pm SE, $n = 32$) (a) blade length per ramet, (b) sheath length, (c) ramet height and (d) juvenile ramet initiation for *Schizachyrium scoparium* plants grown with low (open circles) and high (closed circles) R:FR ratios in experiment 2. Significant differences ($P < 0.05$) between ratios of R:FR were observed in weeks 4–9 for juvenile ramet initiation.

with low R:FR initiated significantly ($P < 0.05$) fewer juvenile ramets than those grown with ambient R:FR (Fig. 6). Although plants grown with ambient R:FR initiated more ramets than did plants grown with low R:FR, no significant differences occurred for the mass of any component of the juvenile ramets (Fig. 7).

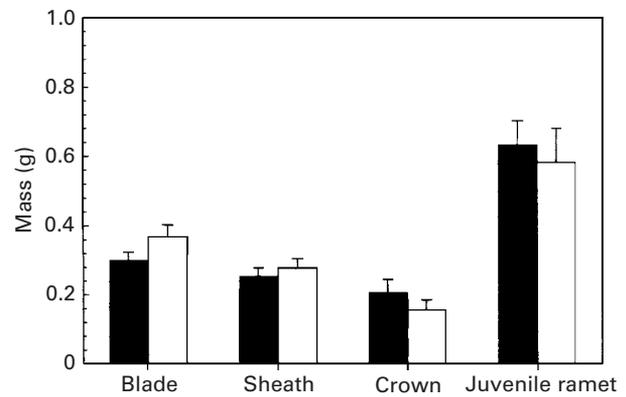


Fig. 7. Mean (\pm SE, $n = 30$) blade, sheath, crown and juvenile ramet dry masses for *Schizachyrium scoparium* plants grown with low (open bars) and high (closed bars) R:FR in experiment 2. No significant differences between levels of R:FR were observed for any of the ramet variables.

DISCUSSION

Schizachyrium scoparium expressed a partial shade avoidance response to low R:FR by enhancing leaf growth and suppressing ramet initiation in experiments 1 and 2, respectively, but both responses were not expressed simultaneously. The growth of all ramet variables, including ramet initiation, was suppressed in small compared with large soil volumes, but only architectural variables were significantly greater in low PFD compared with ambient PFD. However, the expression of shade avoidance to low R:FR was not significantly affected by either the PFD or the soil volume (no two-way interactions). Consequently, the first two hypotheses proposing that plants would exhibit greater shade avoidance to low R:FR when levels of PFD and soil volume were reduced were rejected because plant responses to R:FR were not significantly influenced by resource availability. The third hypothesis, indicating that greater shade avoidance would be expressed in response to low R:FR in younger than in older plants, was also rejected because low R:FR enhanced leaf growth but did not suppress ramet initiation in young (60 d) rapidly growing plants; however, low R:FR suppressed ramet initiation but did not enhance leaf growth in older (120 d), less rapidly growing, plants. We must conclude that resource availability does not modulate plant response to low R:FR within the context of these experimental conditions.

These results demonstrate that both ramet architecture and juvenile ramet initiation of *S. scoparium* are potentially responsive to low R:FR under specific conditions. The expression of a shade avoidance response by this species is inconsistent with a previous investigation indicating that ramet initiation was unresponsive to low R:FR (Murphy & Briske, 1994). However, these experiments are not directly comparable, because plants in the previous

investigation were much older, grown in the field without containers, and showed more rapid vegetative growth than plants in experiment 2 of this study. In the present study, plants were exposed to a similar R:FR to that in the previous investigation by providing supplemental far-red light to the side of plants to mimic the reflection of horizontal far-red light from neighbouring plants (Ballaré *et al.*, 1987; Smith *et al.*, 1990). However, an important distinction might be that the flux density of far-red light was greater in the present study than in the previous investigation because the lamps and filters were located closer to the plants. The flux density of FR has previously been suggested to enhance the expression of shade avoidance (Morgan *et al.*, 1980; Morgan & Smith, 1981; Ballaré *et al.*, 1992a) and it might even function independently of the R:FR (Ballaré *et al.*, 1992b).

The expression of a partial and unique shade avoidance response between young and old plants in experiments 1 and 2, respectively, was unexpected and is difficult to interpret. The expression of shade avoidance most often involves both an enhancement of leaf growth and a suppression of branch development (Morgan & Smith, 1978; Smith, 1982; Casal *et al.*, 1990). In experiment 2, unfavourable growth conditions limited the opportunity for enhanced leaf growth in response to low R:FR. Consequently, the more intriguing question is why ramet initiation was suppressed by low R:FR in experiment 2, but not in experiment 1. These contrasting intraspecific responses to R:FR suggest that plant age and/or phenological stage might have modified plant response to low R:FR. However, environmental variables, including temperature regimes, vapour pressure deficits and solar inclination, might also have contributed to the observed differences between these two experiments because they were conducted at different times of the season. Plant and tiller age have previously been recognized to influence the expression of shade avoidance, but a mechanism for this response has yet to be determined (Casal, 1988; Novoplansky, 1991).

It has previously been speculated that low R:FR might suppress ramet initiation by diverting carbon from axillary buds to rapidly growing leaves (Murphy & Briske, 1994), rather than by reducing the number or viability of axillary buds capable of growing out to form ramets (Casal *et al.*, 1985; Davis & Simmons, 1994). In the rapidly growing plants (experiment 1), carbon might have been allocated to leaves at the expense of axillary buds, but when vegetative growth was slowed by environmental constraints carbon might have been available to support axillary bud outgrowth. This interpretation implicitly assumes that the R:FR affects the expression of apical dominance to regulate bud growth. However, the mechanism by which the R:FR might interact with apical dominance has yet to be established.

Competition for water between parental ramets and axillary buds has gained considerable attention as a process involved in the regulation of bud outgrowth (McIntyre & Cessna, 1991, 1998). However, in both this and a related investigation with *S. scoparium* (Derner & Briske, 1999), water seemed to influence leaf and ramet growth to a greater extent than bud outgrowth and the initiation of juvenile ramets. Greater ramet height and leaf growth with low PFD than with ambient PFD indicates that neutral-density shade might have alleviated plant water stress by reducing leaf temperature and transpiration rate (Derner & Briske, 1999; Maliakal *et al.*, 1999). This interpretation is supported by the occurrence of greater blade and sheath mass in both small and large soil volumes treated with neutral-density shade.

Greater ramet initiation in plants grown in the large compared with the small soil volumes supports the generalization that ramet initiation increases as environmental variables become more conducive to plant growth (Langer, 1963; Murphy & Briske, 1992; Derner & Briske, 1999). However, this response should not be interpreted as indicating that resource availability regulates ramet initiation from axillary buds (Rubinstein & Nagao, 1976). In this investigation the number of juvenile ramets initiated per plant was 70% greater in plants grown in the large than in the small soil volumes and ramet number increased, rather than decreased, in response to a reduction in PFD. It can be inferred from these contrasting responses that juvenile ramet initiation was more responsive to below-ground than above-ground resource availability at the levels at which they were imposed in this investigation. These results are consistent with previous conclusions that juvenile ramet initiation in established *S. scoparium* plants was more responsive to a fourfold increase in soil volume than to a 50% reduction in PFD (Derner & Briske, 1999). Below-ground resource availability as influenced by intraspecific and interspecific competition and nitrogen fertilization has also been shown to influence ramet initiation in several perennial grasses (Olson & Richards, 1988; Briske & Butler, 1989; Hartnett, 1989). Unfortunately, the specific below-ground resource(s) promoting ramet initiation from axillary buds remain unknown (Cline, 1991; Murphy & Briske, 1992; Hendrickson & Briske, 1997).

These results demonstrate that the C₄ perennial grass *S. scoparium* is capable of expressing shade avoidance in response to low R:FR, but inconsistent juvenile ramet initiation and architectural responses in plants of various ages and phenological stages of development indicate that plant response to the R:FR might be more variable than previously recognized. The partial and inconsistent expression of shade avoidance between experiments in this investigation corroborates previous investigations

demonstrating that the R:FR does not consistently modulate shade avoidance in perennial grasses grown in field settings (Casal *et al.*, 1986; Skálová & Krahulec, 1992; Murphy & Briske, 1994). Investigations conducted to define further the role of the R:FR on whole plants grown in the field should consider the influence of plant age, phenological stage of development and associated growth conditions on the expression of the shade avoidance syndrome.

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