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Density-dependent regulation of ramet recruitment by the red:far-red ratio of solar radiation: a field evaluation with the bunchgrass *Schizachyrium scoparium*

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Abstract Depressions in the red to far-red ratio (R:FR) of solar radiation arising from the selective absorption of R (600–700 nm) and scattering of FR (700–800 nm) by chlorophyll within plant canopies may function as an environmental signal directly regulating axillary bud growth and subsequent ramet recruitment in clonal plants. We tested this hypothesis in the field within a single cohort of parental ramets in established clones of the perennial bunchgrass, *Schizachyrium scoparium*. The R:FR was modified near leaf sheaths and axillary buds at the bases of individual ramets throughout the photoperiod without increasing photosynthetic photon flux density (PPFD) by either (1) supplementing R beneath canopies to raise the naturally low R:FR or (2) supplementing FR beneath partially defoliated canopies to suppress the natural R:FR increase following defoliation. Treatment responses were assessed by simultaneously monitoring ramet recruitment, PPFD and the R:FR beneath individual clone canopies at biweekly intervals over a 12-week period. Neither supplemental R nor FR influenced the rate or magnitude of ramet recruitment despite the occurrence of ramet recruitment in all experimental clones. In contrast, defoliation with or without supplemental FR beneath clone canopies reduced ramet recruitment 88% by the end of the experiment. The hypothesis stating that the R:FR signal directly regulates ramet recruitment is further weakened by evidence demonstrating that (1) the low R:FR-induced suppression of ramet recruitment is only one component of several architectural modifications exhibited by ramets in response to the R:FR signal (2) immature leaf blades, rather than leaf sheaths or buds, function as sites of R:FR perception on individual ramets, and (3) increases in the R:FR at clone bases following partial canopy removal are relatively transient and do not override the associated constraints on ramet recruitment resulting from defoliation. A depressed R:FR is probably of greater ecological significance as a signal of competition for light in vegetation canopies than as a density-dependent signal which directly regulates bud growth and ramet recruitment.

Key words Population regulation
Schizachyrium scoparium · Ramet recruitment
Phytochrome · Red:far-red ratio

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Introduction

Clonal plants are characterized by the frequent recruitment and rapid turnover of potentially free-living ramets to maintain genet existence. Ramet recruitment is particularly important in clonal plant demography because it provides genets with a mechanism for clone expansion and resource acquisition while simultaneously reducing the risk of genet extinction (Harper 1985; Ericksson and Jerling 1990). Consequently, the mechanism(s) potentially capable of regulating ramet recruitment has received considerable attention (see Hutchings 1979; Pitelka 1984; Hutchings and Mogie 1990; Murphy and Briske 1992 for reviews).

Ramet recruitment appears to be regulated in a density-dependent manner minimizing the overproduction of ramets within clones (Pitelka 1984; Hutchings and Bradbury 1986; Hutchings and Mogie 1990). Physiological integration among interconnected ramets was initially proposed as a potential mechanism regulating ramet recruitment within the entire clone (Hutchings 1979; Hutchings and Bradbury 1986). However, recent information indicates that ramet recruitment is regulated at a scale finer than that of the entire clone (i.e. individual ramets and/or axillary buds; Briske and Butler 1989; de Kroon and Kwant 1991). Similarly, apical

dominance has frequently been proposed as a mechanism controlling ramet recruitment in grasses, but the supporting evidence is less than conclusive (Murphy and Briske 1992). Consequently, a mechanistic understanding of density-dependent regulation of ramet recruitment in clonal plants has not yet been achieved.

Depressions in the red:far-red ratio (R:FR, 660 ± 5 nm:730 ± 5 nm) of solar radiation from values typical of sunlight have been proposed as yet a third potential mechanism capable of regulating ramet recruitment within perennial grass clones (Deregibus et al. 1985; Butler and Briske 1989; de Kroon and Kwant 1991). The R:FR beneath plant canopies can be reduced either by (1) the selective absorption of visible (400–700 nm) and transmission of far-red (FR, 700–800 nm) wavelengths by chlorophyll as solar radiation penetrates the canopy (Holmes and Smith 1977; Holmes 1981) or (2) FR scattered within the canopy or reflected from leaves of neighbors (Ballaré et al. 1987, 1990; Novoplansky et al. 1990). Plants continuously monitor the R:FR through the pigment phytochrome which provides a sensitive mechanism for detecting shade before reductions in photosynthetic photon flux density (PPFD) actually occur (Smith 1982; Casal and Smith 1989; Smith and Whitelam 1990).

The hypothesized regulatory influence of the R:FR on ramet recruitment is attractive for at least three reasons. First, depressions in the R:FR provide plants with a reliable signal of incipient competition for light (Smith 1982; Casal and Smith 1989). Second, ramet recruitment can be delayed or stopped by reductions in the R:FR (Casal et al. 1985, 1987b, 1990) and these reductions appear to result from direct influences of the R:FR signal on axillary bud growth (Corré 1983; Casal et al. 1985). Third, reductions in ramet recruitment are induced by depressions in the R:FR before measurable decreases in PPFD occur (Casal et al. 1985; Ballaré et al. 1987, 1990). Therefore, it is conceivable that perception of the R:FR signal by axillary buds and/or leaf sheaths at the bases of individual ramets (Casal et al. 1985, 1987b; Deregibus et al. 1985; Skálová and Krahulec 1992) initiates physiological processes capable of delaying or halting bud growth and the subsequent recruitment of juvenile ramets, thereby avoiding intense intraclonal competition for light.

This experiment evaluated the ecological significance of the R:FR as an environmental signal capable of directly regulating ramet recruitment from existing buds on parental ramets in established clones of the perennial bunchgrass, *Schizachyrium scoparium* var. *frequens* (Hubb) Gould. *S. scoparium* a late-seral, shade-intolerant, C_4 species widely distributed throughout North America (Gould and Shaw 1983). We tested the specific hypotheses that (1) supplemental R (600–700 nm) beneath *S. scoparium* canopies overrides the relatively low R:FR to increase ramet recruitment and (2) supplemental FR beneath partially defoliated *S. scoparium* clones overrides the natural increase in the R:FR produced by defoliation to inhibit ramet recruitment. The R:FR was modified continuously throughout the photoperiod at the base of established clones in the field without significantly increasing PPFD by passing supplemental radiation from halogen light sources through selective radiation filters. The responses of a single cohort of parental ramets to supplemental R or FR were assessed by simultaneously monitoring ramet recruitment, PPFD and the R:FR beneath individual clones at biweekly intervals during the period of maximum ramet recruitment in spring.

Methods

Study area

The experiment was conducted in an abandoned field recolonized by *S. scoparium* clones within the Texas A&M University Native Plant and Animal Conservancy 2 km west of College Station, Texas, United States of America. The native perennial grasses *S. scoparium* and *Paspalum plicatulum* often dominate herbaceous plant communities in this region of east-central Texas (Gould 1975). The soil on the experimental plot was a Lufkin fine sandy loam (fine, montmorillonitic, thermic Veric Albaaqualf), an upland series formed from alluvium deposited over coastal plains sediments commonly ≤ 20 cm deep to a dense layer of clay (Hallmark et al. 1986). Rainfall was above normal between January and June 1992 which included the winter preceding and the spring during the experiment. Precipitation was evenly distributed within this 6-month period ranging from 87 to 198% of the 30-year monthly means, except for February when rainfall was almost 400% above the 30-year mean.

Experiments

Twenty *S. scoparium* clones comparable in basal area (40–60 cm^2), ramet number (60–90 ramets/clone) and distance (≥ 1 m) from the nearest conspecific neighbor were selected 1 month prior to beginning the experiment. Aboveground vegetation, consisting primarily of annual grasses and herbaceous dicotyledons, was cleared within a 60-cm radius around each clone 1 month prior to the experiment and as needed thereafter with a gasoline-powered weed trimmer. This minimized the potentially confounding influences of differences in background competition (Briske and Butler 1989; Hartnett 1989; Olson and Richards 1989) and reflected FR from neighbors (Ballaré et al. 1987, 1990) on ramet recruitment.

Five replicate clones were randomly assigned to each of four groups: (1) undisturbed clones (control), (2) undisturbed clones supplemented with R beneath each canopy, (3) clones defoliated to a 15-cm height at the beginning of the experiment (9 April) and again 6 weeks later (20 May), and (4) clones defoliated as above and supplemented with FR beneath the remaining canopy of each plant. Immediately before these treatments were imposed, four vegetative ramets on the northern periphery of each clone were marked by attaching color-coded wire loops around the ramet base. All marked ramets were of uniform size with four or five leaves and no visible juvenile ramets. Ramet recruitment was assessed by counting the number of juvenile ramets recruited from each of the marked parental ramets on all clones. A juvenile ramet was counted as a new recruit when it was visible above the subtending leaf sheath on the parental tiller. Counts of juvenile ramets were conducted on six dates separated by 2-week intervals during the period beginning on 21 April and ending on 1 July.

Supplemental R or FR was directed toward the bases of the four marked parental ramets beneath the canopy of each clone using a single outdoor floodlight fixture (Fig. 1). Each fixture contained a 300 W tubular quartz halogen bulb and was attached to a 45-cm long metal pipe inserted into the ground. All fixtures were wired to a single electrical power source and an automatic timer

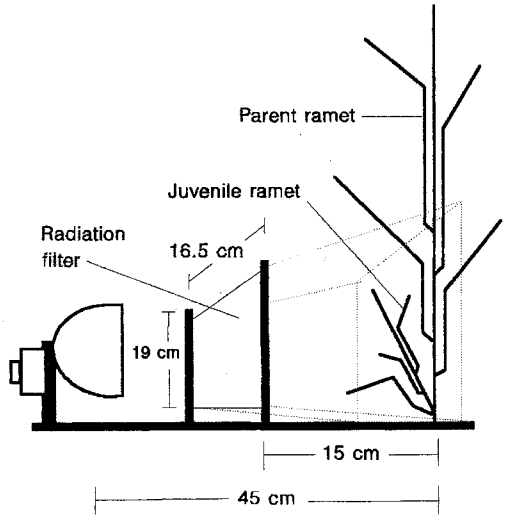

Fig. 1 Schematic depicting the application of supplemental radiation to individual clones of the bunchgrass *Schizachyrium scoparium*. Either R or FR radiation was supplemented at the bases of individual clones by passing radiation from a halogen light source through either a visible- (400–700 nm) or FR-transmitting (> 700 nm) filter. *Dashed lines* illustrate the approximate region of parental ramets irradiated. For clarity, only a single parental and juvenile ramet within the clone are illustrated

maintained continuous irradiation from sunrise to sunset each day during the 12-week experiment.

Supplemental radiation from each fixture was directed through either a visible-transmitting (< 700 nm) detector trimmer filter (Optical Instrument Laboratory, Houston, TX) or FR-transmitting (> 700 nm) plexiglass (Westlake Plastics Co, Lenni, PA) to obtain the desired wavelength bands (Fig. 1). Each filter was anchored at ground level directly between the fixture and marked parental ramets. Supplemental R or FR irradiated an area of approximately 16.5 × 19 cm beneath each clone canopy which covered at least the lower half of all four parental ramets (Fig. 1). Periodic measurements with a thermocouple probe (Omega Engineering, Inc., Stamford, CT) shielded from radiant energy confirmed that supplemental radiation elevated temperatures near clone bases < 1.5 °C.

PPFD and the R:FR, calculated as the ratio of spectral photon fluxes at 660 ± 5 nm and 730 ± 5 nm (Smith 1982), were measured beneath canopies of all clones on the same dates that juvenile ramets were counted. Reported PPFD and R:FR values obtained from each clone are means of two scans made between 12:30 and 13:30 h with an LI-1800 portable spectroradiometer (calibrated at LI-COR, Inc., Lincoln NE) equipped with a small, remote cosine-corrected probe. In addition, PPFD and the R:FR were measured at the bases of clones assigned to defoliation treatments immediately before and after partial canopy removal. During all radiation measurements, the probe was placed against the clone base with the receptor facing the light fixture at a 45° angle to the soil surface. PPFD and the R:FR were also monitored throughout the photoperiod away from the influence of overtopping vegetation near the beginning and ending dates of the experiment. Scans of spectral irradiance on each of these two days were made every 10 min during the initial and final hours of daylight and at 1 h intervals during the remaining daylight hours.

Analysis

Ramet recruitment data were initially analyzed using analysis of variance (ANOVA) in a balanced split-split plot design with treatments as the whole plot factor, marked parental ramets as the first split factor and sampling date as the second split factor. However, variances within and between factors were extremely heterogenous and residuals were not normally distributed. Several data transformations were performed, but all failed to significantly reduce heteroscedasticity and normalize residuals. Therefore, the derived-variables alternative to using time as a split unit factor in ANOVA was used for data analysis as recommended and outlined by Mead (1988).

Interpretations of the data were based on four variables each analyzed by ANOVA in a completely randomized design with subsampling: (1) total number of juvenile ramets recruited per treatment by the end of the 12-week experiment, (2) linear rate of increase in juvenile ramet numbers per treatment over the experiment duration, (3) number of juvenile ramets recruited per treatment within the 6-week period following the initial defoliation and (4) number of juvenile ramets recruited per treatment within the 6-week period following the second defoliation. The same orthogonal set of linear contrasts was used in all four analyses to test for significant differences between treatment means: (1) undisturbed clones (control) versus undisturbed clones supplemented with R (+R), (2) defoliated clones (defoliated) versus defoliated clones supplemented with FR (+FR), and (3) treatments without defoliation (control and +R) versus treatments with defoliation (defoliated and +FR). A $\log(x+1)$ transformation was performed prior to each analysis to stabilize variances and normalize residuals; means and confidence intervals are reported after back-transformation.

Results

Radiation measurements

Measurements of the natural radiation environment made near the beginning (14 April) and end (7 July) of the experiment demonstrate that the R:FR exceeded 1.1 and was relatively stable throughout the photoperiod (solar elevation > 10°), but rapidly increased during sunrise and decreased during sunset (Fig. 2). In comparison, substantial depressions in PPFD and the R:FR were measured beneath *S. scoparium* canopies. Mean PPFD and mean R:FR beneath canopies of undisturbed clones over the 12-week experiment were reduced relative to values measured in sunlight by approximately 95% (1975 to 97 μmol m^{-2} s^{-1}) and 63% (1.21 to 0.45), respectively (Fig. 3).

Supplemental R and FR treatments effectively altered the R:FR beneath clone canopies without significantly raising PPFD (Fig. 3). Supplemental R increased the mean R:FR by 56% in comparison with undisturbed clones throughout the duration of the experiment (0.70 and 0.45, respectively). Supplemental FR reduced the mean R:FR by 27% in comparison with defoliated clones without supplemental FR throughout the duration of the experiment (0.45 and 0.62, respectively). Mean PPFD measured beneath *S. scoparium* canopies differed by a maximum of 23% between treatments (85–110 μmol m^{-2} s^{-1}) at the start of the experiment (before defoliation on 9 April) and remained similar between the control and +R treatments and between the defoliated and defoliated +FR treatments at each sampling date (Fig. 3A).

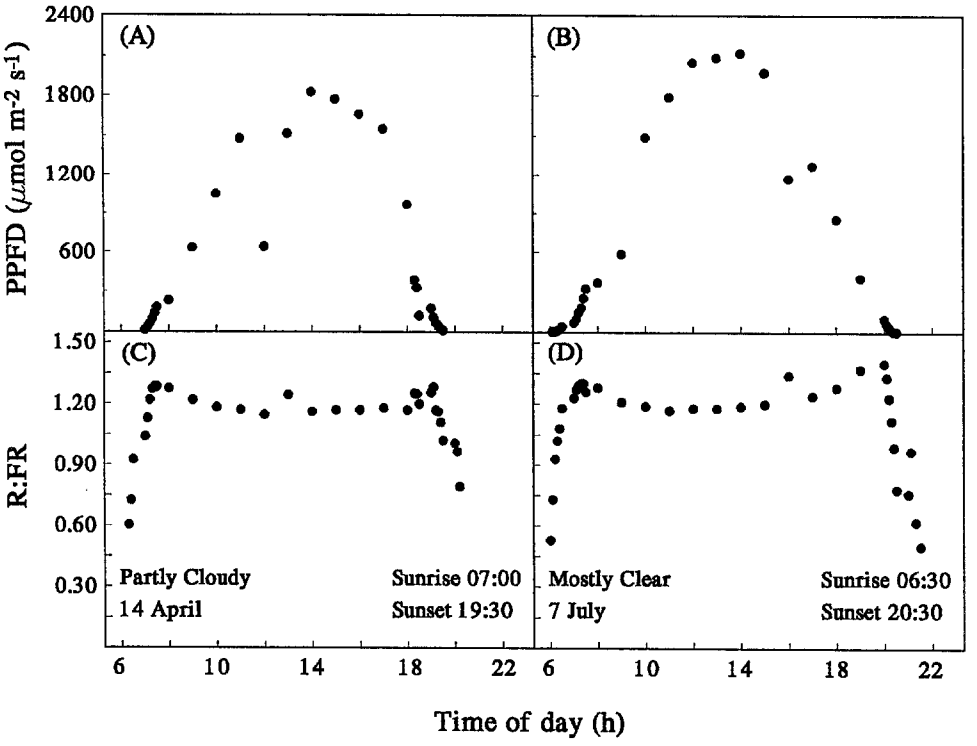

Fig. 2 **A, B** Daily patterns of PPFD and **C, D** the R:FR measured away from the influence of vegetation near the beginning (14 April) and end (7 July) of the experiment. Spectroradiometer scans were made every 10 min during the first and last hours of daylight and at 1-h intervals during the remaining daylight hours. Each *data point* represents the mean of two scans

Partial canopy removal on 9 April and 20 May increased both PPFD and the R:FR at the bases of defoliated clones in comparison with PPFD and R:FR values measured beneath those same canopies immediately before defoliation (Fig. 3A, B; Table 1). The mean R:FR increase following the first defoliation was small relative to that following the second defoliation. However, the large R:FR increase following the second defoliation was also quite transient, lasting less than 2 weeks (Fig. 3B). The greater magnitude of the R:FR increase following the second defoliation probably resulted from the removal of the much denser canopies which had developed by 20 May while its limited persistence was attributable to rapid canopy regrowth. The lower pre- and postdefoliation PPFD beneath defoliated canopies supplemented with FR relative to defoliated canopies without supplemental FR was partly attributable to the black FR-transmitting filter which blocked a portion of diffuse solar radiation from reaching clone bases.

Tiller initiation

Newly recruited juvenile ramets were observed on *S. scoparium* clones within three of the four treatments at the first sampling date (21 April) 2 weeks after the defoliation and supplemental radiation treatments were first imposed (Fig. 3C). By the second sampling date (6 May), juvenile ramets were observed on clones within all treatments, although not all parental ramets from all clones had recruited juvenile ramets by that time. The spring period of ramet recruitment was completed by the fifth sampling date at week 10 (17 June) and no new juvenile ramets were observed in any of the treatments 2 weeks later on the last sampling date (Fig. 3C).

Ramet recruitment was affected more by partial canopy removal than supplemental R or FR (Figs. 3C and 4). Significant treatment differences ($P=0.08$) were found in the total number of juvenile ramets recruited/treatment by the end of the experiment and in the linear rate of increase in juvenile ramet number/treatment over the duration of the experiment (Fig. 4). However, linear contrasts indicated that significant treatment differences for both variables were attributable to significantly ($P=0.02$) greater ramet recruitment on undefoliated clones (control and +R) in comparison with recruitment from defoliated clones (defoliated and +FR). Contrasts of control with supplemental R ($P\geq 0.59$) and defoliation alone with defoliation plus supplemental FR ($P\geq 0.35$) were not significant for either the total number of juvenile ramets or the linear rate of increase in juvenile ramet number per treatment.

Because partial canopy removal had a greater effect on ramet recruitment than supplemental radiation, separate analyses were performed for each 6-week period following the two defoliation events (Fig. 4). No significant ($P=0.32$) differences in the total number of juvenile ramets/treatment were detected within the 6 weeks following the first defoliation. However, significant differences ($P=0.03$) were found between treatments in the 6-week period following the second defoliation. Comparisons of mean ramet recruitment following the second defoliation indicated that clones which were not defoliated had recruited significantly ($P=0.01$) more juvenile ramets than clones which were defoliated. No significant differences were found between means in the contrasts of control versus supplemental R ($P=0.27$) or defoliation versus defoliation plus supplemental FR ($P=0.81$).

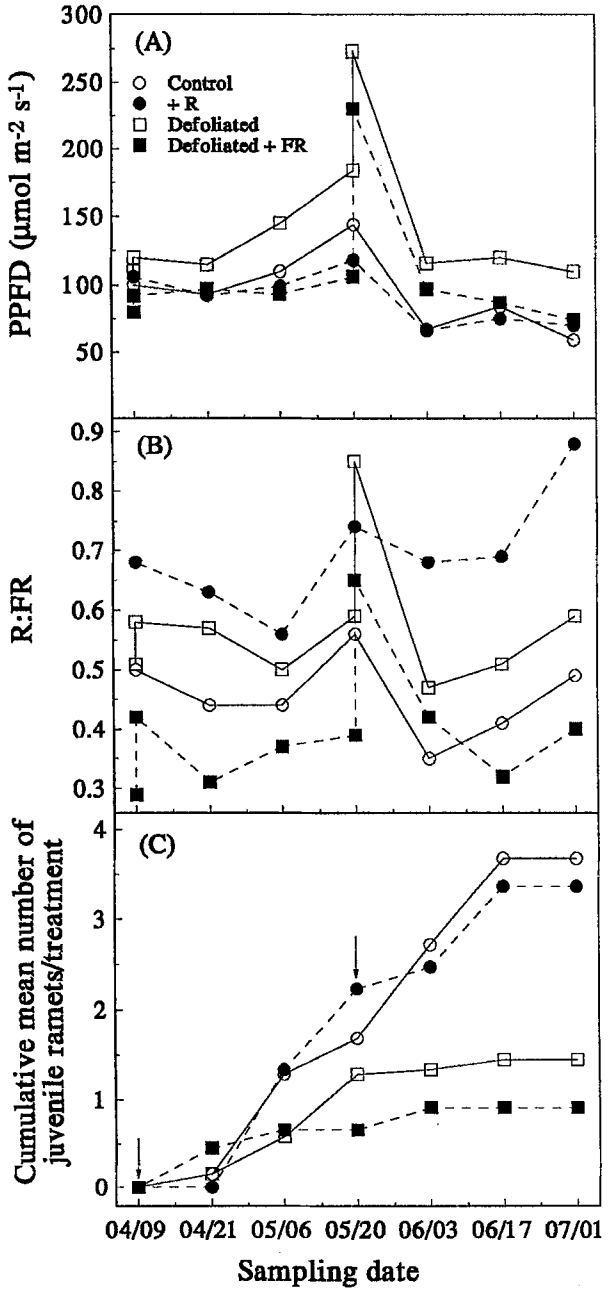

Fig. 3 **A** Mean PPFD beneath clone canopies of *S. scoparium*, **B** mean R:FR beneath clone canopies ($n=2$ for each variable at each date) and **C** cumulative mean number of juvenile ramets recruited per treatment ($n=20$). *Arrows* indicate the dates of partial canopy removal to a height of 15 cm on clones assigned to defoliation treatments. The two values shown for PPFD and the R:FR on 9 April and 20 May for defoliated and defoliated + FR treatments indicate PPFD and R:FR values measured immediately before and after partial canopy removal

Table 1. Mean (±SE) PPFD (μmol m^{-2} s^{-1}) and R:FR beneath *Schizachyrium scoparium* canopies before and immediately following partial canopy removal to a 15-cm height on 9 April (first defoliation) and 6 weeks later on 20 May. Treatments were clone defoliation and clone defoliation plus supplemental FR beneath the remaining canopy throughout the 12-week experiment ($n=10$ per treatment)

Treatment	First defoliation		Second defoliation	
	PPFD	R:FR	PPFD	R:FD
Defoliated				
Predefoliation	110±9.5	0.51±0.04	184±17.5	0.59±0.04
Postdefoliation	129±2.2	0.58±0.03	274±21.8	0.85±0.05
% Increase	16	14	49	44
Defoliated+FR				
Predefoliation	85±2.5	0.29±0.02	106±9.5	0.39±0.03
Postdefoliation	92±5.6	0.41±0.01	181±21.2	0.65±0.02
% Increase	8	45	72	67

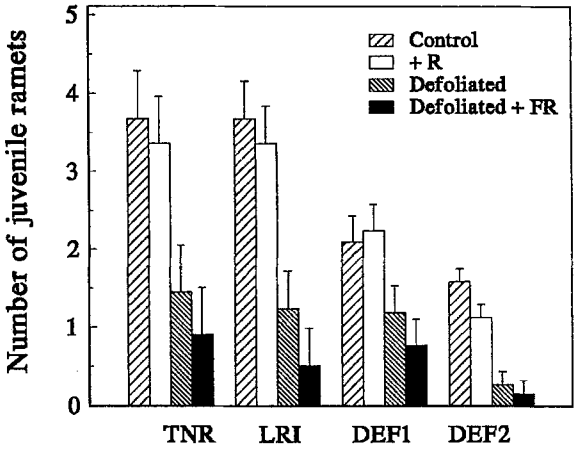

Fig. 4 Mean (±90% C.I.) numbers of juvenile ramets recruited from four parental ramets/clone in response to supplemental R beneath clone canopies, clone defoliation and clone defoliation plus supplemental FR beneath clone canopies in comparison with undisturbed clones ($n=5$ clones/treatment). Variables analyzed were: total number of juvenile ramets present at the end of the experiment (*TNR*, $P=0.08$), linear rate of increase in juvenile ramet numbers over the duration of the experiment (*LRI*, $P=0.08$) and total number of juvenile ramets recruited within the 6-week period following the first (*DEF1*, $P=0.32$) and second (*DEF2*, $P=0.03$) defoliation events. P is the probability from analysis of variance of significant differences between treatments for each variable

Discussion

Results from this field experiment do not support the hypothesis that alterations of the R:FR near leaf sheaths and axillary buds at ramet bases function as a density-dependent signal capable of regulating bud growth and subsequent ramet recruitment on parental ramets in clones of the bunchgrass *S. scoparium*. Experimentally induced modifications in the R:FR but not PPFD beneath clone canopies had no detectable influence on the magnitude of ramet recruitment (Figs. 3 and 4) even though: (1) supplemental R and FR effectively altered the R:FR near buds and leaf sheaths at the bases of parental ramets beneath *S. scoparium* canopies, (2) juvenile ramets were recruited from monitored parental ramets within all experimental clones during the study and no juvenile or parent ramet mortality was observed and (3) precipitation was above the long-term mean

during the 3 months prior to the experiment and during the 12-week investigation.

Small reductions in the R:FR below values typical of sunlight (1.2) have been demonstrated to induce substantial modifications in the morphology of annual and perennial grasses (Deregibus et al. 1983; Casal et al. 1987a, b; Barnes and Bugbee 1991). For example, the square root-transformed tillering rate of *Lolium multiflorum* exhibited a steep linear decline in response to small incremental reductions in the R:FR between 2.36 and 0.46 (Casal et al. 1987b). The magnitudes of artificially induced changes in the R:FR beneath *S. scoparium* clones (ranging from 0.29 to 0.89) in our field experiment were within the range of values typically measured in vegetation shade and previously demonstrated to affect ramet recruitment in numerous grass species. Therefore, artificially induced R:FR changes beneath clone canopies in our experiment should have affected ramet recruitment if this radiation signal was capable of regulating axillary bud growth and therefore ramet recruitment from parental ramets.

We have previously established that *S. scoparium* seedlings grown in controlled environments exhibit phytochrome-mediated reductions in ramet recruitment (Murphy and Briske, unpublished data). Phytochrome mediates architectural modifications by ramets of *S. scoparium* which increase ramet height and leaf area and simultaneously delay ramet recruitment by delaying bud growth (Murphy and Briske, unpublished data). Similar phytochrome-mediated architectural modifications have been reported for the grasses *L. perenne, L. multiflorum, Paspalum dilatatum, Sporobolis indicus, Triticum aestivum, Festuca rubra* and *Hordeum vulgare* grown in controlled environments (Deregibus et al. 1983; Casal et al. 1985, 1986, 1987a, b, 1990; Kasperbauer and Karlen 1986; Barnes and Bugbee 1991; Skálová and Krahulec 1992; Skinner and Simmons 1993). Therefore, the absence of detectable differences in ramet recruitment in response to supplemental R or FR in our field experiment did not originate from an inability of *S. scoparium* to respond to changes in the R:FR.

Given that changes in the R:FR were of sufficient magnitude to induce recruitment responses and that *S. scoparium* clones grown in controlled environments exhibit phytochrome-mediated reductions in ramet recruitment, then why didn't experimental alterations of the R:FR beneath *S. scoparium* canopies influence ramet recruitment in our field experiment? One plausible explanation is that leaf sheaths and/or axillary buds at the base of parental ramets are not important sites of perception for R:FR-induced alterations in ramet recruitment. Recent studies indicate that reductions in ramet recruitment can be induced in *H. vulgare* and *S. scoparium* following FR irradiation of the immature leaf blade which emerges from enveloping sheaths of older leaves immediately above the uppermost mature leaf on each ramet (Skinner and Simmons 1993; Murphy and Briske, unpublished data). Conversely, FR irradiation of individual ramet bases is either much less effective in *H. vulgare* (Skinner and Simmons 1993) or totally ineffective in *S. scoparium* (Murphy and Briske, unpublished data) in reducing ramet recruitment. Although the heights of parental ramets and their immature leaf blades were not measured during our experiment, we observed emerging blades of most established parental ramets to extend into the upper portions of the canopy. Consequently, supplemental R or FR may not have affected ramet recruitment because the immature leaf blades of parental ramets located in the upper canopy did not spatially coincide with artificially induced modifications of the R:FR at the clone bases (see Fig. 1).

Two other published field investigations have examined the influence of experimentally induced alterations in the R:FR beneath perennial grass canopies on ramet recruitment. Skálová and Krahulec (1992) placed green plastic cones around the bases of three morphologically distinct *F. rubra* clones to simulate canopy shade and reduce the R:FR by 69% relative to values measured in sunlight. The plastic cone treatments reduced tiller natality in two of the three *F. rubra* clones, but the plastic cones also reduced photon fluence rate by 56% making it difficult to unequivocally determine whether it was reductions in the R:FR or in radiation quantity that were responsible for reducing tiller natality. In seeming contradiction with our data, Deregibus et al. (1985) reported enhanced daily tiller appearance rates in *P. dilatatum* and *S. indicus* in response to supplemental R from light-emitting diodes placed at clone bases over a 9-month period. However, Deregibus et al. (1985) may have measured recruitment responses from several ramet generations comprising each clone as a consequence of the coarser scale of observation (entire clones versus individual parental ramets) and longer duration of experimental observation relative to our study. Therefore, the increases in ramet recruitment exhibited by *P. dilatatum* and *S. indicus* in response to increases in the R:FR may have been attributable to younger ramet generations initially present and/or recruited during the experiment. The sites of R:FR perception (i.e., emerging leaf blades) of these younger, shorter ramets would have been located well beneath the canopy at the base of each clone where the depression of the R:FR was greatest. If this supposition is correct, then our results and those of Deregibus et al. (1985) are in much closer agreement then they appear initially.

Simultaneous measurements of ramet recruitment, the R:FR and PPFD following partial canopy removal in our study do not support the hypothesis that an increase in the R:FR following defoliation functions as a signal to promote ramet recruitment from axillary buds (Deregibus et al. 1985; Deregibus and Trlica 1990). Although both the R:FR and PPFD at the base of the clones increased following partial canopy removal (Table 1; Fig. 3A, B), defoliation reduced ramet recruitment by 88% in comparison with undefoliated clones at the end of the experiment (Figs. 3C and 4). Partial canopy removal increased the R:FR at clone bases to a maximum of 71% (about 0.85) of the values measured in

direct sunlight, but the higher R:FR existed for only 2 weeks because defoliated canopies regrew rapidly (Fig 3A, B; Table 1). While the mechanism(s) responsible for lower ramet recruitment following defoliation was not investigated during our study, defoliation has been frequently documented to reduce ramet recruitment in numerous grass species (reviewed in Murphy and Briske 1992). Transient increases in the R:FR following partial canopy removal were clearly not sufficient to override the associated constraints imposed on ramet recruitment by defoliation.

In conclusion, results from our field experiment do not support the hypothesis that the R:FR perceived by leaf sheaths and/or axillary buds at the bases of individual ramets functions as a density-dependent signal capable of regulating ramet recruitment in clones of *S. scoparium*. However, two alternative hypotheses should be considered in relation to these data. First, the R:FR may function as a density-dependent signal capable of regulating ramet recruitment when a low R:FR occurs within the vicinity of the emerging leaves, rather than in the vicinity of leaf sheaths and/or buds of ramets. If this hypothesis is accurate, it minimizes the ecological significance of the R:FR as a density-dependent signal because the site of photoperception and a low R:FR would spatially coincide only in young, juvenile ramets and seedlings beneath or near clone canopies. The second alternative hypothesis is that documented reductions in ramet recruitment following exposure to a depressed R:FR are *indirect* responses induced by temporary increases in carbon allocation to leaf sheaths and blades at the expense of axillary bud growth and juvenile ramet initiation. If this hypothesis is correct, then phytochrome-mediated reductions in ramet recruitment may be most appropriately interpreted as but one component of an overall shade avoidance strategy increasing ramet survival in vegetation shade *after* the juvenile ramet is initiated from a bud. Therefore, the R:FR would have greater ecological significance as a signal of incipient competition for light in vegetation canopies than as a density-dependent signal capable of directly regulating axillary bud growth and subsequent ramet recruitment.

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References

Ballaré CL, Sánchez R, 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, Scopel AL, Sánchez R (1990) Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. Science 247:329–332

Barnes C, Bugbee B (1991) Morphological responses of wheat to changes in phytochrome photoequilibrium. Plant Physiol 97:359–365

Briske DD, Butler JL (1989) Density dependent regulation of ramet populations within the bunchgrass *Schizachyrium scoparium*: interclonal versus intraclonal interference. J Ecol 77:963–974

Casal JJ, Deregibus VA, Sánchez RA (1985) Variations in tiller dynamics and morphology in *Lolium multiflorum* Lam. vegetative and reproductive plants as affected by differences in red/far-red irradiation. Ann Bot 56:59–65

Casal JJ, Sánchez RA, Deregibus VA (1986) The effect of plant density on tillering: The involvement of R/FR ratio and the proportion of radiation intercepted per plant. Environ Exp Bot 26:365–371

Casal JJ, Sánchez RA, Deregibus VA (1987a) The effect of light quality on shoot extension growth in three species of grasses. Ann Bot 59:1–7

Casal JJ, Sánchez RA, Deregibus VA (1987b) Tillering responses of *Lolium multiflorum* plants to changes of red/far-red ratio typical of sparse canopies. J Exp Bot 38:1432–1439

Casal JJ, Sánchez RA, Gibson, D (1990) The significance of changes in the red/far-red ratio, associated with either neighbour plants or twilight, for tillering in *Lolium multiflorum* Lam. New Phytol 116:565–572

Casal JJ, Smith H (1989) The function, action and adaptive significance of phytochrome in light-grown plants. Plant Cell Environ 12:855–862

Corré WJ (1983) Growth and morphogenesis of sun and shade plants II. The influence of light quality. Acta Bot Neerl 33:185–202

Deregibus VA, Trlica MJ (1990) Influence of defoliation upon tiller structure and demography in two warm-season grasses. Acta Oecol 11:693–699

Deregibus VA, Sánchez RA, Casal JJ (1983) Effects of light quality on tiller production in *Lolium* spp. Plant Physiol 72:900–902

Deregibus VA, Sánchez RA, Casal JJ, Trlica MJ (1985) Tillering responses to enrichment of red light beneath the canopy in a humid natural grassland. J Appl Ecol 221:199–206

Ericksson O, Jerling L (1990) Hierarchical selection and risk spreading in clonal plants. In: Van Groenendael J, Kroon H de (eds) Clonal growth in plants: regulation and function. SPB Academic, The Hague, pp 79–94

Gould FW (1975) The grasses of Texas. Texas A&M University Press, College Station

Gould FW, Shaw RB (1983) Grass systematics, 2nd edn. Texas A&M Univ Press, College Station

Hallmark CT, West LT, Wilding LP, Dress LR (1986) Characterization data for selected Texas soils. Texas Agric Exp Sta MP-1583

Harper JL (1985) Modules, branches and the capture of resources. In: Jackson JBC, Buss LW, Cook RE (eds) Population biology and evolution of clonal organisms. Yale Univ Press, New Haven, pp 1–33

Hartnett DC (1989) Density- and growth stage-dependent responses to defoliation in two rhizomatous grasses. Oecologia 80:414–420

Holmes MG (1981) Spectral distribution of radiation within plant canopies. In: Smith H (ed) Plants and the daylight spectrum. Academic Press, London, pp 147–158

Holmes MG, Smith H (1977) The function of phytochrome in plants growing in natural environments–II. The influence of vegetation canopies on the spectral energy distribution of natural daylight. Photochem Photobiol 25:539–545

Hutchings MJ (1979) Weight-density relationships in ramet populations of clonal perennial herbs, with special reference to the −3/2 thinning law. J Ecol 67:21–33

Hutchings MJ, Bradbury IK (1986) Ecological perspectives on clonal perennial herbs. BioScience 36:178–182

Hutchings MJ, Mogie M (1990) The spacial structure of clonal plants: control and consequences. In: Van Groenendael J, Kroon H de (eds) Clonal growth in plants: regulation and function. SPB Academic, The Hague, pp 57–76

Kasperbauer MJ, Karlen DL (1986) Light-mediated bioregulation of tillering and photosynthate partitioning in wheat. Physiol Plant 66:159–163

Kroon H de, Kwant R (1991) Density-dependent growth responses in two perennial herbs: regulation of shoot density. Oecologia 86:298–304

Mead R (1988) The design of experiments: statistical principles for practical application. Cambridge University Press, Cambridge

Murphy JS, Briske DD (1992) Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. J Range Manage 45:419–430

Novoplansky A, Cohen D, Sachs T (1990) How portulaca seedlings avoid their neighbors. Oecologia 82:490–493

Olson BE, Richards JH (1989) Crested wheatgrass growth and replacement following fertilization, thinning and neighbor removal. J Range Manage 42:93–97

Pitelka LF (1984) Application of the $-3/2$ power law to clonal plants. Am Nat 123:442–449

Skálová H, Krahulec F (1992) The response of three *Festuca rubra* clones to changes in light quality and plant density. Funct Ecol 6:282–290

Skinner RH, Simmons SR (1993) Modulation of leaf elongation, tiller appearence and tiller senescence in spring barley by far-red light. Plant Cell Environ 16:555–562

Smith H (1982) Light quality, photoperception, and plant strategy. Annu Rev Plant Physiol 33:481–518

Smith H, Whitelam GC (1990) Phytochrome, a family of photoreceptors with multiple physiological roles. Plant Cell Environ 13:695–707