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Effects of Shading and Rhizome Isolation on Soluble Carbohydrate Levels in Blades and Rhizomes of the Seagrass *Syringodium filiforme*

JORGE R. REY AND F. CAROL STEPHENS

The effects of severe shading on soluble carbohydrate content of blades and rhizomes of *Syringodium filiforme* growing in the Indian River Lagoon, Florida, were investigated. We used plants that were connected to unshaded neighbors and plants that were isolated from neighbors by severing their rhizome connections. Before shading, mean soluble carbohydrate levels ranged from 29.2 to 26.5% dry weight (dw) in the rhizomes and from 19.5 to 18.4% dw in the blades. Both shading and isolation contributed to a significant decline in soluble carbohydrate levels of blades and rhizomes, with shading eliciting the greater response. However, after 40 days, shaded-connected plants appeared to maintain more stable carbohydrate levels than shaded isolated ones.

Seagrasses are important trophic and structural components of shallow marine and estuarine systems (Duarte, 1989), and are often good indicators of overall habitat quality (Stevenson et al., 1993). The importance of light as one of the primary factors affecting seagrass establishment and growth has been well documented at widely different geographic locations (Koch et al., 1974; Dennison and Alberte, 1985; Dennison, 1987; Williams, 1987; Buesa, 1990; Zimmerman et al., 1991; Dunton and Tomasko, 1994; Gordon et al., 1994; Onuf, 1994), including the Indian River Lagoon, Florida (Rice et al., 1983; Short et al., 1993).

As in most plant species, resource allocation is an important component of strategies for growth and survival of seagrasses. Allocation patterns of stored carbon reserves vary seasonally, both in entire plants and in individual organs (Dawes et al., 1979; Best and Visser, 1987; Madsen, 1991), and are often critical to survival and regrowth of seagrasses after unfavorable conditions such as periods of low light and temperature (Olesen and Sand-Jensen, 1993). For example, Dawes and Lawrence (1980) concluded that soluble carbohydrates, mobilized from storage sites in rhizomes, supported blade regeneration after artificial defoliation of the seagrass *Thalassia testudinum*. Likewise, Drew (1983) found that soluble sugars in *Thalassodendron ciliatum* rhizomes were rapidly depleted during several days in darkness. In an elegant experiment with *T. testudinum*, Tomasko and Dawes (1989) demonstrated that adjoining ramets of this species are physiologically integrated (*sensu* Hartnett and Bazzaz, 1983), and discussed the ecological ramifications of integration as they apply to seagrasses. These authors successfully demonstrated that shaded short shoots were supported, in terms of growth and proximate organic constituents, by unshaded older shoots that were connected to the shaded ones.

The Indian River Lagoon is a shallow barbuilt estuary located along the central east coast of Florida. In the lagoon, seagrass communities are dominated by *Halodule wrightii* Ascherson and *Syringodium filiforme* Kützing, with *Thalassia testudinum* Banks ex König and *Halophila* spp. usually accounting for less than 5% of the seagrass cover (Thompson, 1978; Virnstein and Carbonara, 1985).

Along the lagoon, light transmittance through the water column is typically low (Howard and Short, 1986), and short term (e.g., days, weeks) fluctuations caused by upland runoff, sediment suspension, ephemeral algal blooms, and shading by drift algae are superimposed on seasonal changes in the light field. As a result, conditions for seagrass growth are often marginal at best, and often severely limiting. Nevertheless, seagrasses persist in many such areas, which indicates that they can take advantage of periods of favorable illumination and store carbon for use when light conditions are such that photosynthesis is severely restricted.

Compared to other species such as *T. testudinum* and *Zostera marina* L., the ecology of *S. filiforme* has received little attention (Phillips, 1960; Short et al., 1985). The objective of this study was to investigate the effects of shading and ramet isolation on carbohydrate stores in blades and rhizomes of the latter species.

METHODS

Study site.—The study area is located on the barrier island side of the Indian River Lagoon,

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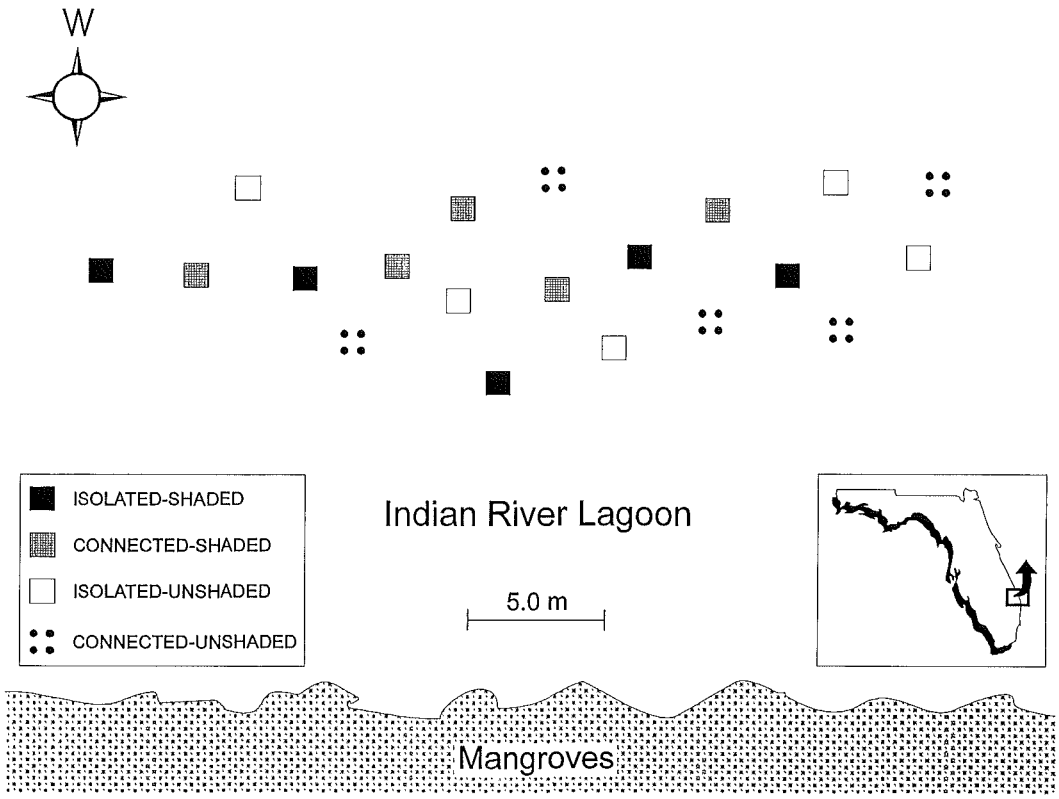

Fig. 1. Location of the study site and experimental quadrats.

approximately 5.8 km north of the St. Lucie Inlet (Fig. 1). The area supports seagrass beds dominated by *H. wrightii* in the shallow (<0.4 m) portions and by *S. filiforme* in the deeper areas. Scattered clumps of *Halophila decipiens* Ostenfield occur in areas deeper than 1.5 m. Data on relevant physical variables measured at the site during the study are presented in Table 1.

TABLE 1. Physical variables measured at the experimental site during the study.

Variable	n	Mean	SE
Air temperature (C)	10	26.40	0.78
Water temperature (C)	10	24.42	0.46
Salinity (ppt)	10	28.30	1.13
Dissolved oxygen (ppm)	10	3.58	0.40
pH	10	7.87	0.04
Color (Pt-Co units)	3	30.99	7.13
Turbidity (NTU)	3	15.60	1.20
Suspended solids (mg/liter)	3	21.45	1.92
Incident PAR (μmol/sec/m^2)	50	1,356.74	57.00
K (m^{-1})	50	2.46	0.02

Twenty plots (0.58 × 0.58 m) were selected at random within the *S. filiforme* bed. The maximum depth differential between plots was approximately 25 cm. Treatments were randomly assigned to the plots to yield five replicates each of the following four treatments: (1) isolated-shaded (IS), (2) isolated-unshaded (IU), (3) connected-shaded (CS), and (4) connected-unshaded (CU). Treatments are explained in more detail below.

Shading.—Plots were shaded using 58.4 × 58.4-cm black fiberglass screens supported by PVC frames (Fig. 2). The legs of the frame fit into PVC pipes that were "permanently" driven into the substrate and were secured to the latter with cotter pins so that the screen tops were approximately 0.2 m above the seagrass blades. The screens were attached to the frame with removable clips. The clips were pressure-fitted over the screens and frames and allowed easy removal of the screens. All screens were changed once per week to minimize fouling. Measurements made with with Li-Cor LI192 PAR sensors indicated that the screens reduced PAR intensity by approximately 69%. The un-

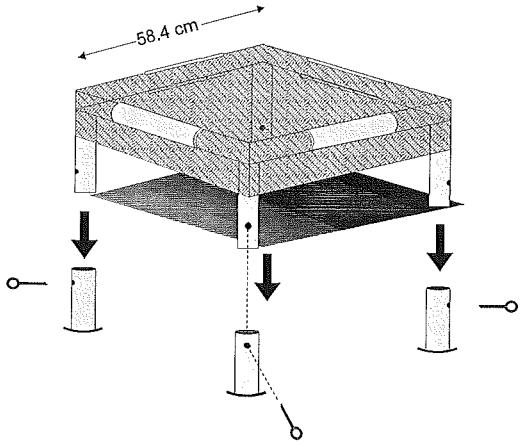

Fig. 2. Schematic diagram of the shading screens.

shaded stations were marked with PVC pipe with no screens installed.

Isolation.—The "isolated" treatment consisted of severing the rhizome connections between the experimental plots and the surrounding seagrasses. This was accomplished by using a long steel blade to cut around plot perimeters to a depth of 60 cm. Rhizomes were cut at the start of the study, and again after 30 d to prevent new growth from invading the plots.

Carbohydrate analysis.—Plot setup was completed on 15 Sep. 1993. Samples for carbohydrate analysis were collected with an 11-cm-diameter, 25-cm-long corer on 16 Sep. (day 0), 26 Oct. (day 40), and 22 Nov. (day 67). The samples were collected near the center of each plot to minimize edge effects, and core locations were marked to avoid resampling the same area. After extraction, the samples were placed in plastic bags and stored in a dark cooler. In the laboratory, blades and rhizomes were separated and roots were removed from the rhizomes and discarded. The blades were cleaned of epiphytes by briefly immersing them in 1.0 N HCl to remove calcareous material, rinsing in distilled water, and wiping clean with cheesecloth. Rhizomes were rinsed in distilled water and wiped with cheesecloth. Both blades and rhizomes were then dried to constant weight at 60 C and ground to a fine powder with a ceramic mortar and pestle. After thoroughly mixing each fraction, 6–7 mg was removed and soluble carbohydrates were extracted with 10 ml of 5% trichloroacetic acid in a water bath (80–90° C) for 3 h (Dawes and Kenworthy, 1990). Triplicate analyses (average precision = 0.824 SD) were performed except for some of the blade samples from the IS plots for which insufficient material for triplicate analyses was recovered during the latter samples due to blade loss from these plots (see below). Carbohydrate content was quantified using the phenol–sulfuric acid method (Kochert, 1978). The amount of soluble carbohydrate per mg dry weight (dw) in each sample was determined from absorbance measurements at 485 nm (Beckman DU640 spectrophotometer) fitted to least-squares regressions of glucose standard solutions (Kochert, 1978).

Physical data.—The following water quality variables were measured at irregular intervals during the study: water temperature (mercury thermometer), salinity (refractometer), dissolved oxygen (DO, YSI Model 57 meter), pH (HBI pH probe), suspended solids (measured gravimetrically), incident PAR (Li-Cor 192SA sensor), vertical attenuation coefficient (K_d, paired Li-Cor Li-192SA sensors), and color (measured spectrophotometrically by fitting measured sample absorption at 440 and 465 nm to curves generated from platinum cobalt standard solutions and measured at the same wavelengths). Means, standard errors, and sample sizes are shown in Table 1.

Statistical analysis.—Two-way ANOVAS were computed to examine effects of isolation and shading on changes in % dw carbohydrate of blades and rhizomes throughout the study. Additive models using the residual component for the denominator of the F statistic were utilized unless there was a significant interaction between factors, in which case an interactive model using the error component was applied. A posteriori comparison of means was performed using Duncan's Multiple Range Test (DMR). We also computed separate ANOVAS for changes between individual sampling dates. Separate ANOVAS were used instead of a single repeated-measures analysis because our interest was in absolute differences rather than in differences in rate of change between time periods. With only one repeated measure and the inherent variability of the data, the latter analysis would have carried little weight. ANOVAs were also used to compare the initial blade and carbohydrate content of the different treatment groups. An angular transformation was applied to all percent data prior to analysis.

RESULTS

Initial carbohydrate content.—Initial mean carbohydrate content of the rhizomes was 29.2,

TABLE 2. Results of two-way ANOVA for differences between treatment groups in initial carbohydrate content of *Syringodium filiforme* blades and rhizomes. Treatments are as follows: ISOL = isolated or connected; SHADE = shaded or unshaded.

Factor	df	r^2	F	$P \leq$
Rhizomes				
ISOL	1	0.031	0.547	0.470
SHADE	1	0.002	0.042	0.840
Interaction	1	0.059	1.031	0.325
Residual	17	0.966		
Blades				
ISOL	1	0.046	0.817	0.379
SHADE	1	0.004	0.080	0.781
Interaction	1	0.016	0.267	0.612
Residual	17	0.950		

27.9, 26.5, and 28.4% dw in the IS, IU, CS, and CU plots, respectively. Corresponding values for the blades were 18.9, 19.5, 18.6, and 18.4% dw. No significant differences were evident between the initial carbohydrate contents of the four treatment groups for either blades or rhizomes (Table 2).

Blades.—Carbohydrate content of the *S. filiforme* blades decreased during the experiment regardless of the treatment (Fig. 3A). Analysis of variance indicated a significant effect of shading ($P < 0.05$) on blade carbohydrate levels, but the overall effect was due mostly to decreases during the first time interval (0–40 d, Table 3). Likewise, cutting the rhizomes was significant ($P = 0.053$) for the first time interval (Table 3). No significant interactions between shading and isolation were evident for any of the time periods. Results of DMR tests indicated that from day 0 to day 40 and from day 0 to day 67, decreases in carbohydrate content were significantly greater in the shaded plots than in the unshaded plots ($P < 0.05$).

Considerable blade loss was observed in the IS plots during the second and third samplings. Two of the five IS plots were completely devoid of blades by the end of the experiment, and considerable thinning ocurred at the other three. Quantitative standing crop data were not collected in order to avoid disturbing the experimental plots, but the decrease in blade density was strikingly obvious. Maps of percent seagrass cover of the site that were compiled during the previous year indicated an average cover by *Syringodium* of about 50% (range 20–60%, Rey, unpubl. data) in the exact area were the quadrats were located.

Rhizomes.—In the unshaded plots, rhizome carbohydrate content remained at approximately the same level during the first 40 d, and then increased from day 40 to day 67 (Fig. 3B). In the shaded plots, there was a sharp decrease in % dw carbohydrate between days 0 and 40. The decline continued to day 67 in the IS plots, but leveled off after 40 days in the CS plots (Fig. 3B). ANOVA results indicated significant ($P < 0.05$) effects of shading and isolation for the duration of the experiment (days 0–67, Table 4). Shading was significant during all individual time intervals, whereas the overall effect of isolation was mostly due to changes during the second interval (Table 4). Significant isolation–shading interactions were evident for the days 40–67 and the days 0–67 comparisons (Table 4). DMR test results indicate that for all time intervals, there were highly significant ($P \leq 0.03$) decreases in rhizome carbohydrate content of shaded plots when compared to changes (or lack thereof) in the unshaded ones. Likewise, isolation caused a significant ($P \approx 0.05$) decrease in rhizome carbohydrate between the second and third and between the first and third samplings. However, examination of Figure 3B reveals that the overall significance of isolation is mainly a result of its effect on the shaded, and not on the unshaded, plots (hence the interaction effects).

DISCUSSION

Soluble carbohydrate content.—The initial blade carbohydrate levels recorded in this study are similar to those measured by Dawes and Lawrence (1980) in *S. filiforme* blades from the Gulf of Mexico, near Indian Bluff Island, Florida. However, rhizome carbohydrate levels at our site were lower than those measured by the above authors. The reasons for the differences are not known, but could include differences between the two sites in nutrient concentrations, currents, substrates, and bed structure, and also the fact that the Gulf of Mexico sites are located in clearer oceanic waters.

Shading and isolation effects.—The fact that during the first 40 days of the study both shading and isolation contributed to a decrease in carbohydrate content of blades but only shading contributed to a decrease in the rhizomes suggests that shading decreased carbohydrate production to a point where carbohydrate stores in the rhizomes were used up for maintenance faster than new production could replace them. Apparently, connected rhizomes could

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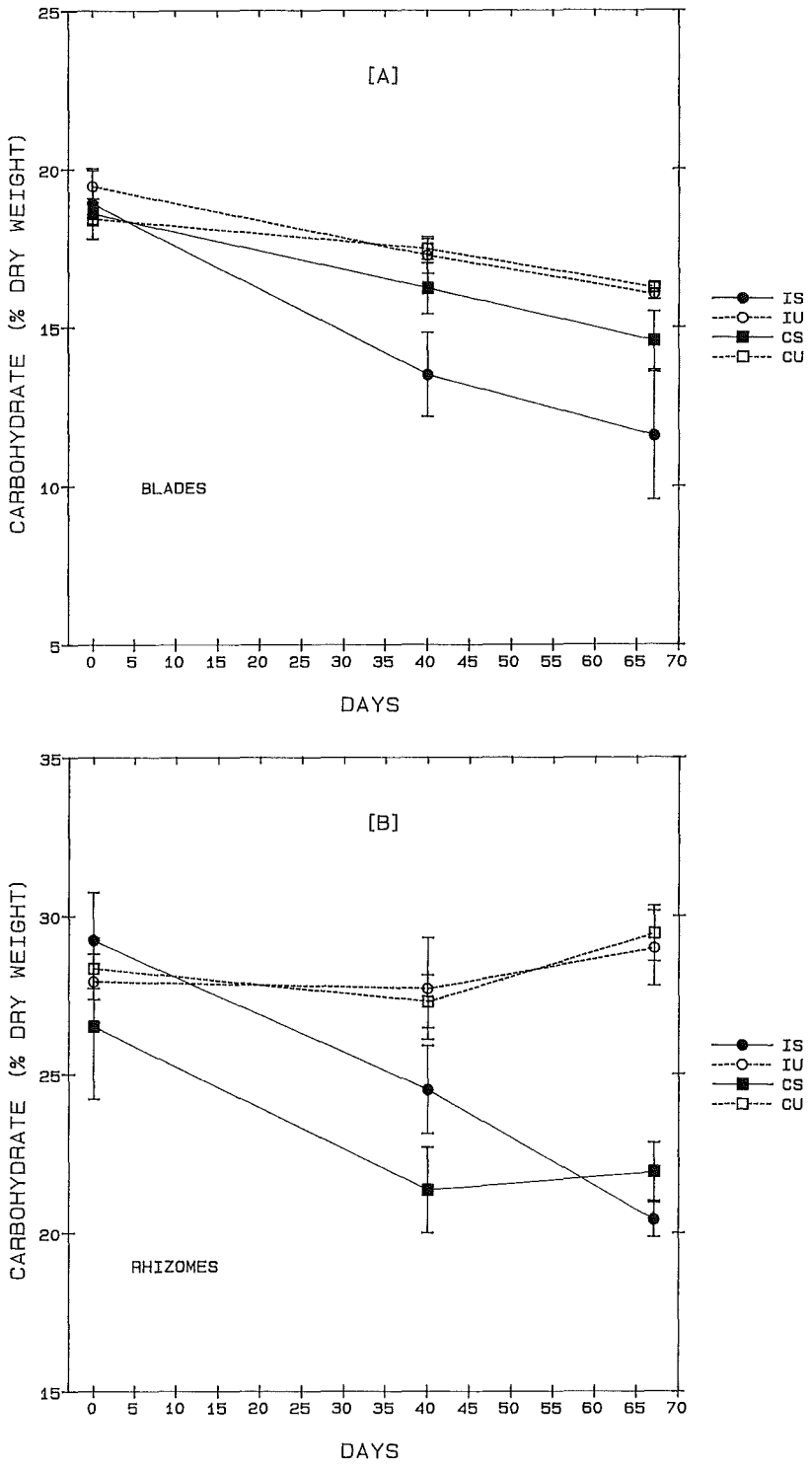

Fig. 3. Carbohydrate content (% dry weight) of (A) *S. filiforme* blades and (B) rhizomes.

TABLE 3. Results of two-way ANOVA for change in % dw carbohydrate of *Syringodium filiforme* blades. Treatments are as follows: ISOL = isolated or connected; SHADE = shaded or unshaded.

Factor	df	r^2	F	$P \leq$
Days 0–40				
ISOL	1	0.162	4.312	0.053
SHADE	1	0.201	5.346	0.034
Interaction	1	0.031	0.914	0.353
Residual	17	0.638		
Days 40–67				
ISOL	1	0.020	0.314	0.584
SHADE	1	0.071	1.093	0.314
Interaction	1	0.021	0.303	0.592
Residual	14	0.909		
Days 0–67				
ISOL	1	0.145	3.557	0.082
SHADE	1	0.283	6.940	0.020
Interaction	1	0.022	0.052	0.483
Residual	14	0.571		

TABLE 4. Results of two-way ANOVA for change in % dw carbohydrate of *Syringodium filiforme* rhizomes. Treatments are as follows: ISOL = isolated or connected; SHADE = shaded or unshaded.

Factor	df	r^2	F	$P \leq$
Days 0–40				
ISOL	1	0.006	0.142	0.711
SHADE	1	0.243	5.514	0.013
Interaction	1	0.001	0.003	0.961
Residual	17	0.750		
Days 40–67				
ISOL	1	0.194	4.494	0.050
SHADE	1	0.226	6.208	0.023
Interaction	1	0.198	4.501	0.050
Residual	16	0.382		
Days 0–67				
ISOL	1	0.162	12.741	0.003
SHADE	1	0.488	38.405	0.001
Interaction	1	0.159	12.538	0.003
Residual	16	0.191		

maintain a better supply to their blades than isolated ones (Table 3), suggesting translocation from outside the plots.

Between days 40 and 67, both shading and isolation significantly lowered the carbohydrate content of rhizomes but not that of blades. These effects, however, resulted mainly from a drop in the rhizomes at the shaded-isolated plots and not at the shaded-connected ones (interaction effect; Table 4, Fig. 3B). Thus, after 40 d, the shaded-connected plots were able to maintain stable carbohydrate levels relative to the unshaded ones in both blades and rhizomes. Conversely, at the shaded-isolated plots, rhizome carbohydrate levels continued to drop after 40 d and a considerable loss of blades occurred in response to shading. The lack of significant effects of shading on blade carbohydrate levels during the second interval may be a result of the fact that, due to blade loss, there were much fewer blades to support at the isolated plots than at the connected plots.

The loss of aboveground biomass during unfavorable conditions has been previously documented for other submerged macrophytes (Backman and Barilotti, 1976; Bulthuis, 1983; Howard and Short, 1986), and has been explained as a mechanism for conserving resources for growth under more favorable conditions, as a strategy for reducing self-shading under limiting light conditions, and as a way to eliminate epiphytes that block light (Backman and Barilotti, 1976; Barko et al., 1982; Duarte and Kalff, 1987; Gordon et al., 1994). The results presented here, although only qualitative, suggest a similar response by *S. filiforme* to artifically induced shading.

Physiological integration is an important strategy of clonal plants that allows a more "fine-grained" sampling of patchy environments (Pitelka and Ashmun, 1985) and aids in survival on, and escape from, unfavorable patches (Hartnett and Bazzaz, 1983). This subject has been addressed in many species of terrestrial plants (e.g., Hartnett and Bazzaz, 1983; Pitelka and Ashmun, 1985; Alpert and Mooney, 1986; Lau and Young, 1988), but only recently has physiological integration been studied in seagrasses (Tomasko and Dawes, 1989, 1990). These authors demonstrated complete physiological integration between adjoining ramets of *T. testudinum*. Their results indicated support of shaded shoots by connected unshaded shoots, and seasonal and spatial variation in the degree of ramet interdependence. These authors also demonstrated a decrease in soluble carbohydrate levels in blades of unshaded short shoots connected to shaded ones in spite of increases in photosynthetic rates in the former. Our results are consistent with physiological integration in *S. filiforme*, and indicate that the process may function over distances longer than adjoining ramets. However, this study was not designed to test for integration in this species, but simply to examine the changes in soluble carbohydrate stores of *S. filiforme* in response to shading and isolation. Much more

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detailed data are needed, including data on other constituents, quantitative biomass data, and examination of the response of unshaded ramets to shading of ramets to which they are connected to determine the degree of integration in this species.

Conclusion

Severe shading significantly affected carbohydrate levels in both blades and rhizomes of *S. filiforme*. Effects were evident during every time period and in almost every treatment. Significant effects of isolation on carbohydrate levels were also evident, but these were less consistent than the shading effects. It appears from the carbohydrate data that connected shoots could somewhat compensate for the effects of shading, at least at the scale measured in this study, which suggests a limited degree of physiological integration. On the other hand, the decline in short shoot density in the isolated-shaded plots and not in the connected-shaded ones suggests that the degree of integration may be greater than the carbohydrate data alone indicate.

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