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Silvia E. Ibarra-Obando
Centro de Investigacion Cientifica y de Educacion Superior de Ensenada

Kenneth L. Heck Jr.
Dauphin Island Sea Lab

Patricia M. Spitzer
Dauphin Island Sea Lab

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Response of Turtlegrass to Natural and Reduced Light Regimes Under Conditions of Rhizome Isolation

SILVIA E. IBARRA-OBANDO, KENNETH L. HECK JR., AND PATRICIA M. SPITZER

To evaluate if rhizome integrity influenced the response of turtlegrass (*Thalassia testudinum*) shoots to experimental light reduction, we performed a field experiment in Perdido Bay, FL, from May to Oct. 2001. We used a factorial design, with light, rhizome integrity, and time as main factors. Light was reduced to about 40% with respect to ambient irradiance by means of a polyethylene mesh, and rhizomes along the external border of the 0.5-m^2 experimental plots were severed with a knife at the beginning and middle of the experiment. Severing surrounding rhizomes had a significant ($P < .05$) negative effect on net aboveground primary production (NAPP), but this was only apparent from June to July, and there were no significant severing effects on aboveground biomass. Shading showed negative effects through time on aboveground biomass and NAPP, although the differences were not significant. Time was significant for belowground biomass, NAPP, shoot density, and leaf length and width and there were significant time-by-shading interactions for NAPP, aboveground biomass, and density. We conclude that the results of turtlegrass shading studies done over several months during the peak of the growing season are not influenced to any large extent by whether rhizomes are intact or not, indicating that previous studies of the effects of shading on turtlegrass can be compared without bias.

Numerous experiments have been conducted in order to understand the effects of light reduction on seagrass biomass and growth (e.g., Backman and Barilotti, 1976; Bulthuis, 1983; Neverauskas, 1988; Gordon et al., 1994; Czerny and Dunton, 1995; Fitzpatrick and Kirkman, 1995; Lee and Dunton, 1997; Ruiz and Romero, 2001). Results from these studies show substantial variation in the magnitude of responses, depending on season and the level of shading (Fitzpatrick and Kirkman, 1995). Carbohydrate translocation to rhizomes under low light conditions is recognized as a means of overcoming unfavorable growing conditions, and it is employed by both terrestrial and marine clonal species (e.g., Hartnett and Bazzaz, 1983; Fourqurean and Zieman, 1991; Rey and Stephens, 1996; Marbà et al., 1996; Lee and Dunton, 1997; Alcoverro et al., 2001). However, the extent to which seagrass responses to light reduction are influenced by clonal integration is incompletely understood.

Our search of the literature on shading experiments with seagrasses identified two groups of studies: 1) those that did not take into account the effect of clonal integration of seagrass shoots on the observed results (e.g., Backman and Barilotti, 1976; Bulthuis, 1983; Ruiz and Romero, 2001) and 2) those that did account for this effect by severing rhizome connections at the border of the shaded areas to interrupt rhizome connections (Neverauskas, 1988; Tomasko and Dawes, 1989; Gordon et al., 1994; Czerny and Dunton, 1995; Lee and Dunton, 1997). This second group of studies contains a great deal of variability in sample size and in the length of the experimental period. For example, sample size varied from a single shoot (Tomasko and Dawes, 1989), to hundreds (Czerny and Dunton, 1995; Lee and Dunton, 1997), or thousands of shoots in experimental plots (Gordon et al., 1994; Neverauskas, 1988), and the duration of the experimental period has ranged from 2 wk (Tomasko and Dawes, 1989) to 16 mo (Lee and Dunton, 1997).

Conflicting results can be found in the shading responses of plants connected to, or isolated from, their neighbors through rhizome severing. For example, during winter and spring, similar leaf growth rates for unsevered *Heterozostera tasmanica* shoots under four shading treatments and an unshaded control were reported by Bulthuis (1983). Similarly, severed *Thalassia testudinum* shoots showed no significant differences in leaf elongation rates between shading treatments [reductions to 14% and 10% of surface irradiance above the sea surface (SI)] and controls (50% SI) in spring and winter (Czerny and Dunton, 1995), and increased leaf length as a result of light reduction has been reported for both unsevered (Bulthuis, 1983) and severed shoots (Neverauskas, 1988). On the other hand, unsevered

Zostera marina shoots showed reduced density in only 18 d after shading (Backman and Barilotti, 1976), whereas severed *Posidonia* shoots maintained their density during 6 mo of shading (Neverauskas, 1988).

One could argue that the above studies are not truly comparable, because species, locations, seasons, and lengths of the experiments were different. However, when results from the two studies in which the response to experimental light reduction on severed and unsevered rhizomes was simultaneously analyzed, the same type of variability in clonal integration was observed. For *Posidonia australis,* Fitzpatrick and Kirkman (1995) found that cutting rhizomes had no effect on leaf growth in either a shading treatment (clear and black plastic shades) or in unshaded controls. Rey and Stephens (1996) found a significant reduction in soluble carbohydrate content in leaves and rhizomes of severed shoots of *Syringodium filiforme* after 40 d, but they also noted that severing rhizomes had no effect on unshaded plots.

With this inconsistency in experimental design and outcome of previous studies in mind, we investigated how rhizome integrity might influence *T. testudinum* responses to shading. From a management perspective, it is important to know if rhizome severing could influence the results of shading studies that have been used to set water clarity standards to protect seagrass meadows. For example, failure to sever rhizome connections could give misleading results about the amount of light required for seagrass growth and survival if stressed shoots were subsidized by unstressed shoots outside the experimental plots. To evaluate the effects of rhizome integration on the response of turtlegrass shoots to shading, we manipulated light levels and rhizome integrity during the major portion of the turtlegrass growing season.

Materials and Methods

Study Site.—Perdido Key is located in northwest Florida near the Alabama border (30°18.5′N 87°23′W). It is a natural barrier island stretching for about 23 km along the northern Gulf of Mexico. The climate is subtropical with an average summer temperature of 27 °C and average winter temperature of 13 °C. Average rainfall is 157.5 cm. Lunar tides are diurnal and average 0.5 m. Winds are predominantly from the northwest in winter and the southeast in summer, and they control the height of waves and direction of long-shore transport (Kent, 1976). The waves have moderately high energy, with breaker heights between 27 cm and 1.5 m (Gorsline, 1966). Major rivers drain into Pensacola Bay and into the Gulf of Mexico through Pensacola Pass, at the eastern end of Perdido Key. Variable flow regimes sometimes set up an east–west salinity gradient along the exposed shoreline, depending on winds, tides, and river discharge (Schropp et al., 1991; Rakocinski et al., 1996; Wear et al., 1999). Sediment is dominated by fine- to medium-grained quartz sand with small amount of shell hash and organic matter (< 6%) (Kent, 1976; Rakocinski et al., 1993). Monospecific and mixed beds of the three seagrass species most widely distributed in the Gulf of Mexico, and along the coast of Florida are present: *T. testudinum* Banks ex König, *Halodule wrightii* Ascherson, and *S. filiforme* Kützing (Wear et al., 1999). The site selected for this study is known as Johnson Beach, and it is located within the federally protected Gulf Islands National Seashore. *T. testudinum* was selected for study, because it is the dominant species in the extensive seagrass meadows in the Gulf of Mexico and the Caribbean Sea (Den Hartog, 1977).

Experimental design.—A shallow seagrass bed (about 1.5 m depth) dominated by *T. testudinum* but also containing smaller amounts of *H. wrightii,* was selected for study. The experimental area in the bed was selected haphazardly and the location of each treatment was randomly assigned (randomized block design). For each treatment, square plots of 0.5-m^2 area were marked with rebar stakes and PVC tubes at the four corners.

The effects of variation in light and rhizome integrity were tested over a 5-mo period during the major part of the growing season. For light, ambient (control) and an approximate reduction to 40% from ambient were used. The light reduction to about 40% was established as a midpoint of reported values of 50% reduction during brown tide conditions (Dunton, 1994; Onuf, 1996), and 35–50% under prior experimental manipulations (Bulthuis, 1983; Neverauskas, 1988), both of which produced significant changes in structural and functional characteristics of seagrass species. In addition, in Perdido Bay, a local 50% reduction in SI levels because of dock shading was reported by Shafer (1999). This also guided our choice of shading level. Irradiance at the bottom of each experimental plot was measured twice a month with a Licor spherical (4 Π) sensor and LI-1000 data logger. These readings coincided with field trips to mark and retrieve shoots for assessment of net aboveground primary produc-

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tion (NAPP; see below). Light readings were always made at the beginning of the sampling, before sediments had been disturbed by investigators.

Light was reduced with 0.635-cm polyethylene mesh attached to the top, south, and east sides of rebar frames placed in the randomly selected plots. By placing the mesh on these three sides we were blocking the summertime incident radiation without turning the experiment into an "enclosure experiment". Every month, at the end of the sampling, the mesh was scrubbed to reduce the cumulative effects of fouling and siltation on photosynthetically active radiation (PAR) within the cages (Valentine and Heck, 2001). Light data were normalized relative to the unshaded control, because we were interested in expressing our results relative to ambient in situ light, not to surface light. Light intensity in experiments such as these is generally expressed as a percentage of SI. However, we believe that a more appropriate way of comparing shaded vs ambient conditions is by normalizing shading intensities to ambient (control) intensities, the reason being that there is no shoot growth under control conditions if the control is SI, because shoots will be damaged by excessive solar radiation. For comparative purposes, we can express measured light intensities as % SI Mean ± 1 SE for ambient and shaded conditions are: 37.76 ± 2.03 (n = 87), and 13.99 ± 1.15 (n = 87), respectively. In other words, light intensity measured at the bottom of the unshaded plots already represents 40% of SI; the shading reduced treatment conditions to about 40% of the unshaded.

Rhizome integrity was interrupted along the external border of the 0.5-m^2 experimental plots by severing the root/rhizome layer in the upper 15 cm of sediment at the beginning and middle of the experiment with a large knife (c.f. Heck and Valentine, 1995). For each treatment four 0.5-m^2 replicates were used, giving a total of 16 plots.

The experiment lasted approximately 5 mo, from June to Oct. The following variables for *T. testudinum* were measured on a monthly basis: shoot density (number of shoots m^{-2}); average number of leaves per shoot; length and width (mm) of oldest leaf; above and belowground biomass [g ash-free dry weight (AFDW) m^{-2}]; epibiont biomass (g AFDW m^{-2}); and NAPP (g AFDW m^{-2} d^{-1}).

Field and laboratory work.—Cores of 7.6 cm internal diameter × 15 cm deep were used to collect *T. testudinum* from individual plots; sampled areas were marked with plastic flags inserted into the sediment to prevent resampling. Seagrass samples were sieved through a 1.0-mm mesh, placed in marked plastic bags, and kept cool until arrival to the lab where they were frozen for later analyses. Cores provided material to assess shoot density, average number of leaves per shoot, length and width of oldest leaf, epibiont biomass, and above- and belowground turtlegrass biomass.

Turtlegrass epibionts were removed by scraping leaves with a razor blade, and their biomass (± 0.01g), along with that of the leaves to which they were attached, was determined by placing the material in aluminum pans, oven drying the material at 60 C for 24 hr, and ashing dried samples in a muffle furnace at 500 C for 5 hours (Valentine et al., 2000). Roots and rhizomes were processed similarly.

Areal NAPP was assessed by the method described by Dennison (1990). For each plot, all turtlegrass leaves on all shoots inside a 0.01-m^2 quadrat were marked with a probe at the top of the leaf sheath. Marked shoots were flagged to facilitate relocating them after 11 to 14 d, when they were removed with a corer and returned to the lab where they were frozen until being processed. Areal NAPP was estimated by measuring new growth distal to the hole in punctured blades, and all new growth of unpunctured leaves that appeared on the marked shoots. Biomass of all new leaf tissue formed during the 11–14 d incubation period represented aboveground production. This material was dried to constant weight (± 0.01 mg) at 60 C, and its AFDW determined as indicated previously for leaf biomass. Production was expressed as g AFDW m^{-2} d^{-1}.

Water temperature and salinity were determined during every visit to the field with an Orion 140 conductivity meter.

Statistical analysis.—Treatment effects were analyzed with a mixed three-way ANOVA, with light and rhizomes as fixed factors, and time as random factor. All data passed tests for normality and variance homogeneity. The significance level was set at 0.05. The Tukey a posteriori test was used to identify where the significant differences were located. Software used was Sigmastat 3.1 and Sigmaplot 9.0 (SYSTAT Software Inc).

Results

Environmental conditions.—Mean water temperature during the study period was 26.9 ± 1.1 °C (±1 SE). Values of 29 °C or higher were

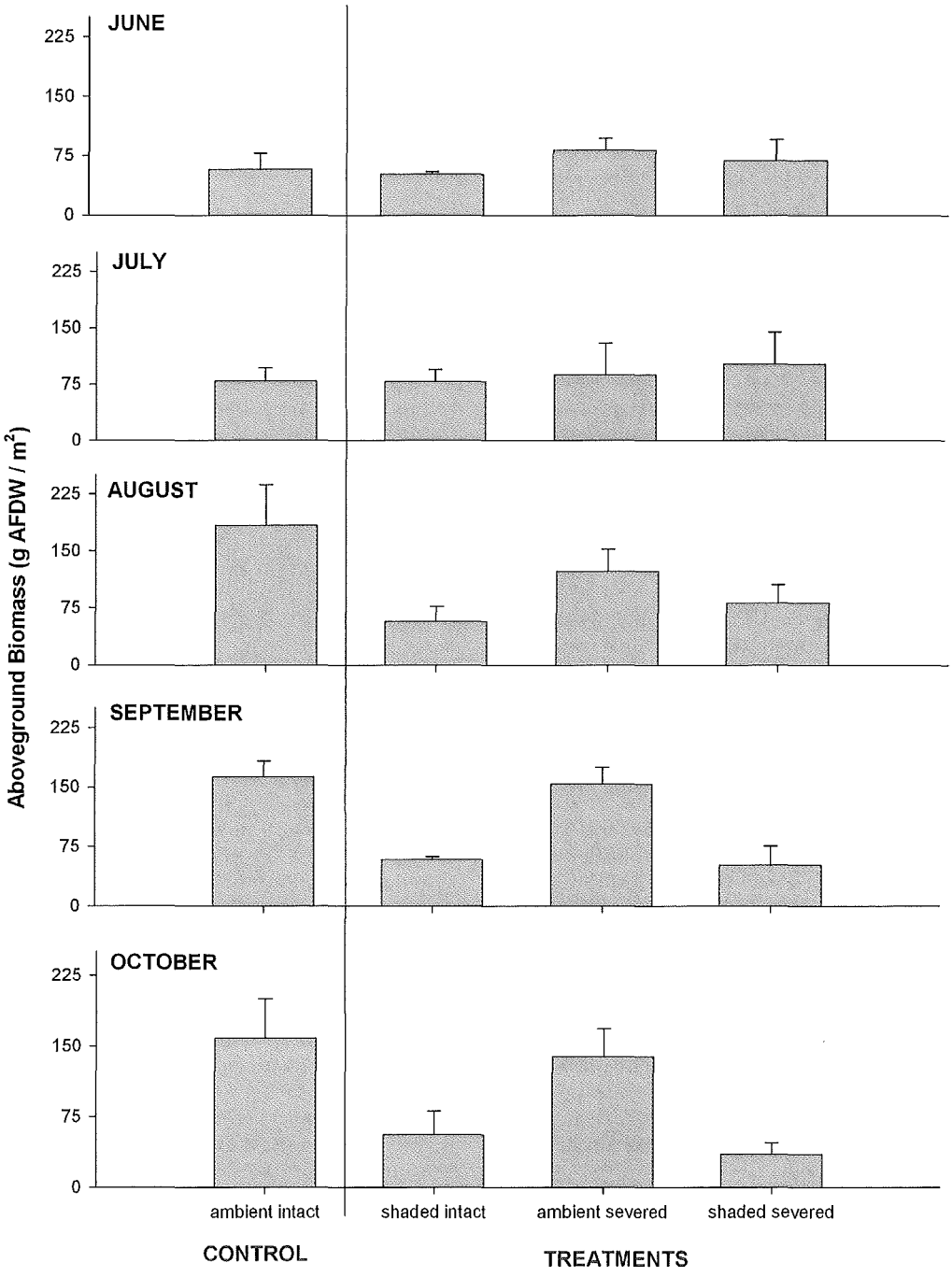

Fig. 1. Turtlegrass aboveground biomass (g AFDW m^{-2}) as a function of light, rhizome integrity, and time. Bars represent ±1 SE.

measured between 14 June and 5 Sept., with a peak of 31.4 °C on 24 July. A steady reduction characterized the end-of-summer–beginning-of-autumn period, with a value of 17.9 °C recorded by the end of the experiment. Salinity varied between 30.3‰ (15 May) and 24.0‰ (20 Aug.), with a mean of 27.08 ± 0.6‰. Low salinities were associated with summer rains.

Experimental conditions.—For the ambient treatment (control), bottom light varied between 210 ± 14 μE sec^{-1} m^{-2} on 20 Aug., and 1,625 ± 189 μE sec^{-1} m^{-2} on 12 July. The grand

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TABLE 1. Aboveground biomass ANOVA values for main factors and their interactions. (* = significant differences.)

Factors and interactions	df	F value	*P* value
Time	4	1.787	0.143
Rhizomes	1	0.051	0.832
Light	1	6.042	0.069
Time × rhizomes	4	0.478	0.751
Time × light	4	3.732	0.008*
Rhizomes × light	1	1.191	0.336
Time × rhizomes × light	4	0.471	0.756

TABLE 2. Belowground biomass ANOVA values for main factors and their interactions. (* = significant differences.)

Factors and interactions	df	F value	*P* value
Time	4	6.444	0.0002*
Rhizomes	1	0.287	0.62
Light	1	0.653	0.464
Time × rhizomes	4	0.831	0.511
Time × light	4	1.682	0.166
Rhizomes × light	1	2.827	0.168
Time × rhizomes × light	4	0.156	0.959

TABLE 3. Epibiont biomass ANOVA values for main factors and their interactions. (* = significant differences.)

Factors and interactions	df	F value	*P* value
Time	4	2.401	0.060
Rhizomes	1	0.133	0.733
Light	1	0.087	0.782
Time × rhizomes	4	0.943	0.445
Time × light	4	0.943	0.445
Rhizomes × light	1	8.274	0.045*
Time × rhizomes × light	4	0.639	0.637

mean for the study period was 893 ± 51 μE sec^{-1} m^{-2}. For the shaded treatment values fluctuated between 52 ± 4 μE sec^{-1} m^{-2} (20 Aug.), and 652 ± 67 μE sec^{-1} m^{-2} (24 July), with a grand mean of 325 ± 27 μE sec^{-1} m^{-2}. Average light in shaded treatments was 38 ± 2% relative to unshaded conditions (n = 87), indicating that we achieved the reduction we were looking for, and that fouling and siltation effects were kept to a minimum.

Response variables.—Between June and Oct., aboveground biomass was lower in shaded shoots than in ambient light shoots (Fig. 1), although severing rhizomes connections had no significant effect (Table 1). Belowground biomass increased significantly through time (Fig. 2), but no significant effects were associated with either shading or severing treatments (Table 2).

Epibiont biomass showed a significant response to the simultaneous effect of severing rhizome connections and reducing light (Table 3). However, this effect is visually evident in the data only in Oct. (Fig. 3).

NAPP decreased significantly as a result of severing surrounding rhizomes, but this was most evident in July when values were significantly less than in June (Tukey test, P = 0.033).The effect of light reduction through time negatively affected NAPP, producing a significant light × time interaction, but no significant light effect (Fig. 4; Table 4). Shoot density showed significant differences through time, with a general trend to increase between June and Oct. (Fig. 5). There was a significant time × light interaction (Table 5).

In addition, average leaf length showed a significant effect of severing rhizomes that was only apparent in Sept. and Oct. (Table 6; Fig.

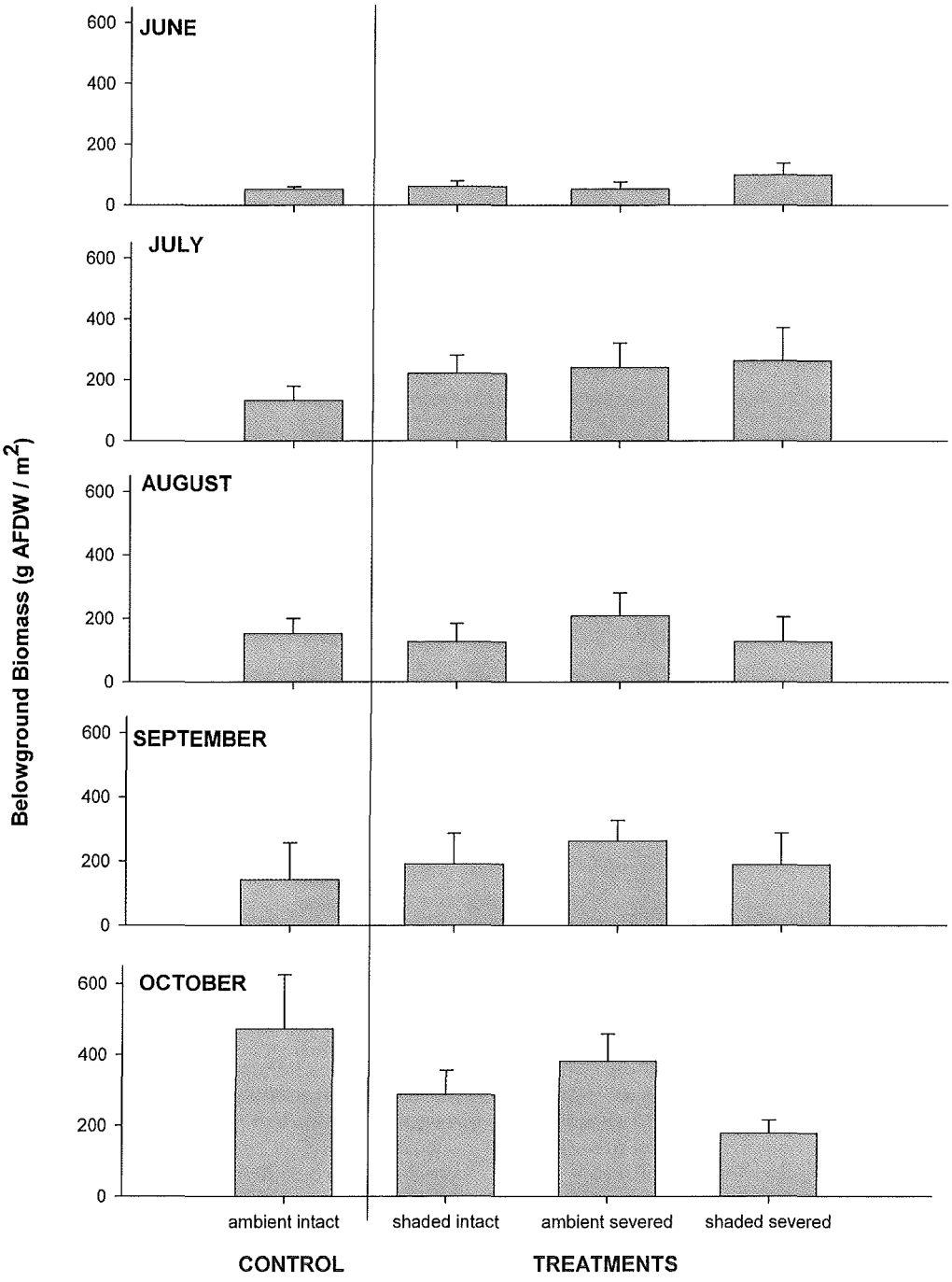

Fig. 2. Turtlegrass belowground biomass (g AFDW m^{-2}) as a function of light, rhizome integrity, and time. Bars represent ±1 SE.

6). Average leaf width also varied significantly through time, with increasing values between June and Sept. Shading or severing treatments did not have any significant effect (Fig. 7; Table 7). The average number of leaves per shoot did not show any significant difference as a function of time, shading, severing surrounding rhizomes, or their interactions (figure and table omitted). The overall mean was 3.01 ± 0.1 leaves per shoot.

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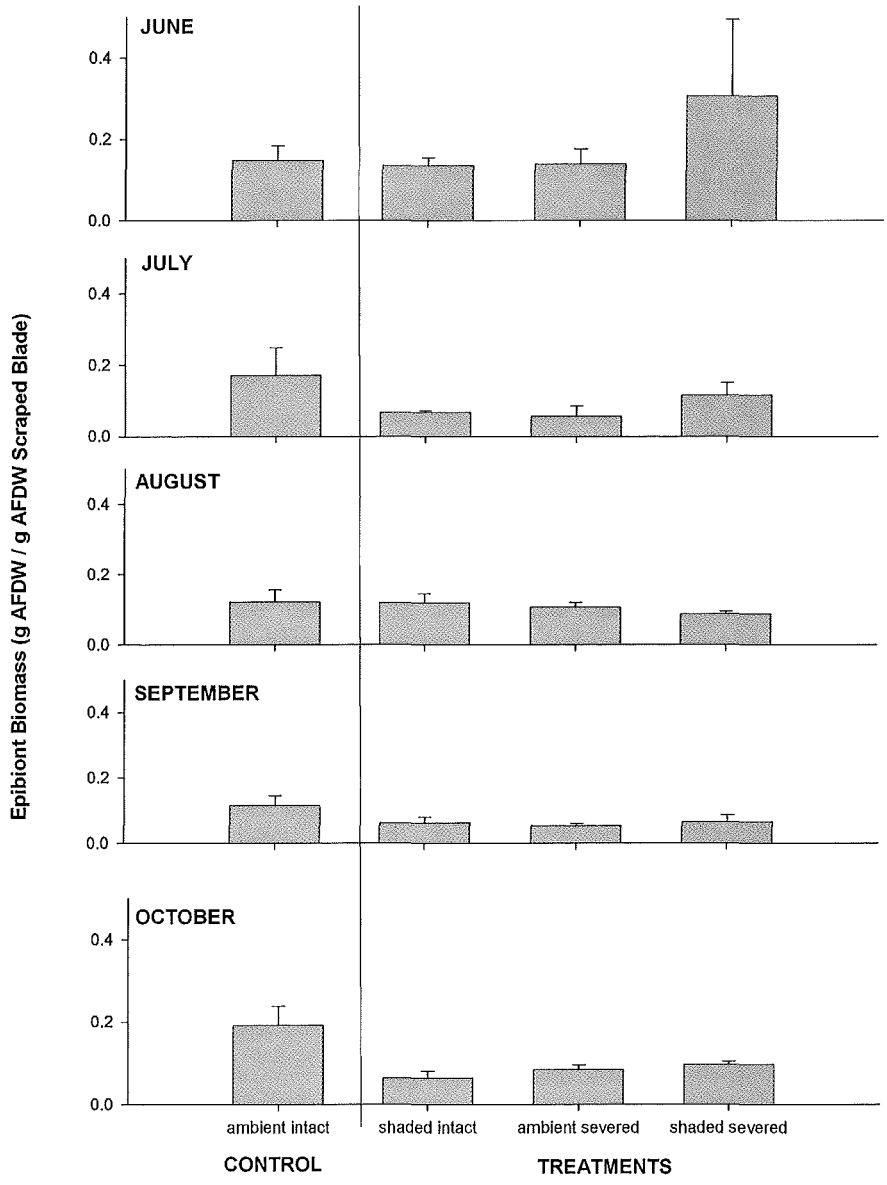

Fig. 3. Epibiont biomass (g AFDW/g AFDW scraped blade) as a function of light, rhizome integrity, and time. Bars represent ±1 SE.

Discussion

Our results were characterized primarily by independent, rather than interactive, effects to variation in light or rhizome integrity. The only significant response to the interactive effect of light and rhizome integrity was in epibiont biomass, although this result is difficult to interpret. Overall, responses to light reduction were more common than were responses to severing rhizome connections, and the only obvious response to rhizome severing was a reduction in NAPP from June to July.

In an experimental study in which individual *T. testudinum* short shoots were shaded and isolated from their neighbors, Tomasko and Dawes (1989) reported a reduction in leaf growth rate, when compared to shaded connected short shoots and controls. Tomasko and Dawes (1989) did not observe the response of isolated short shoots under natural light conditions, in order to determine whether shoots were responding to shading or severing treatments. In our study, we could not find a simultaneous effect of severing rhizomes

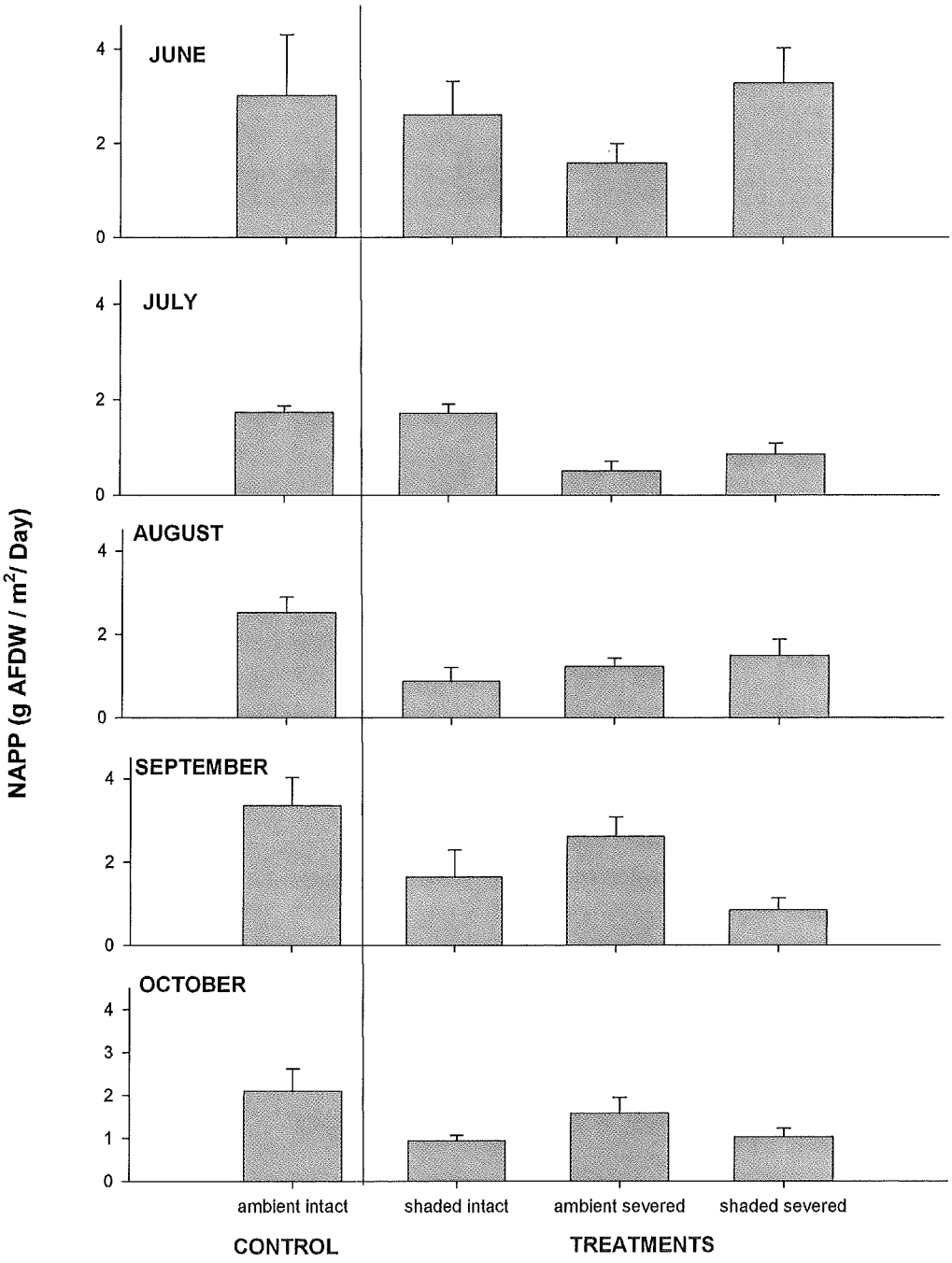

Fig. 4. NAPP (g AFDW m^{-2} d^{-1}) as a function of light, rhizome integrity, and time. Bars represent ±1 SE.

connections and shading conditions as found by these authors. We found that shaded connected shoots reduced their NAPP with respect to the control, a result in disagreement with Tomasko and Dawes. This difference in response may be attributed to experimental time span; our study lasted 5 mo, and theirs lasted only 2 wk. Our data indicate that physiological integration in *T. testudinum* is present over lateral distances of at least 0.5 m, the size of our enclosures. The use of quadrats of differing sizes could allow determination of the scales of this integration. For *Cymodocea nodosa,* Terrados et al. (1997) demonstrated that the pro-

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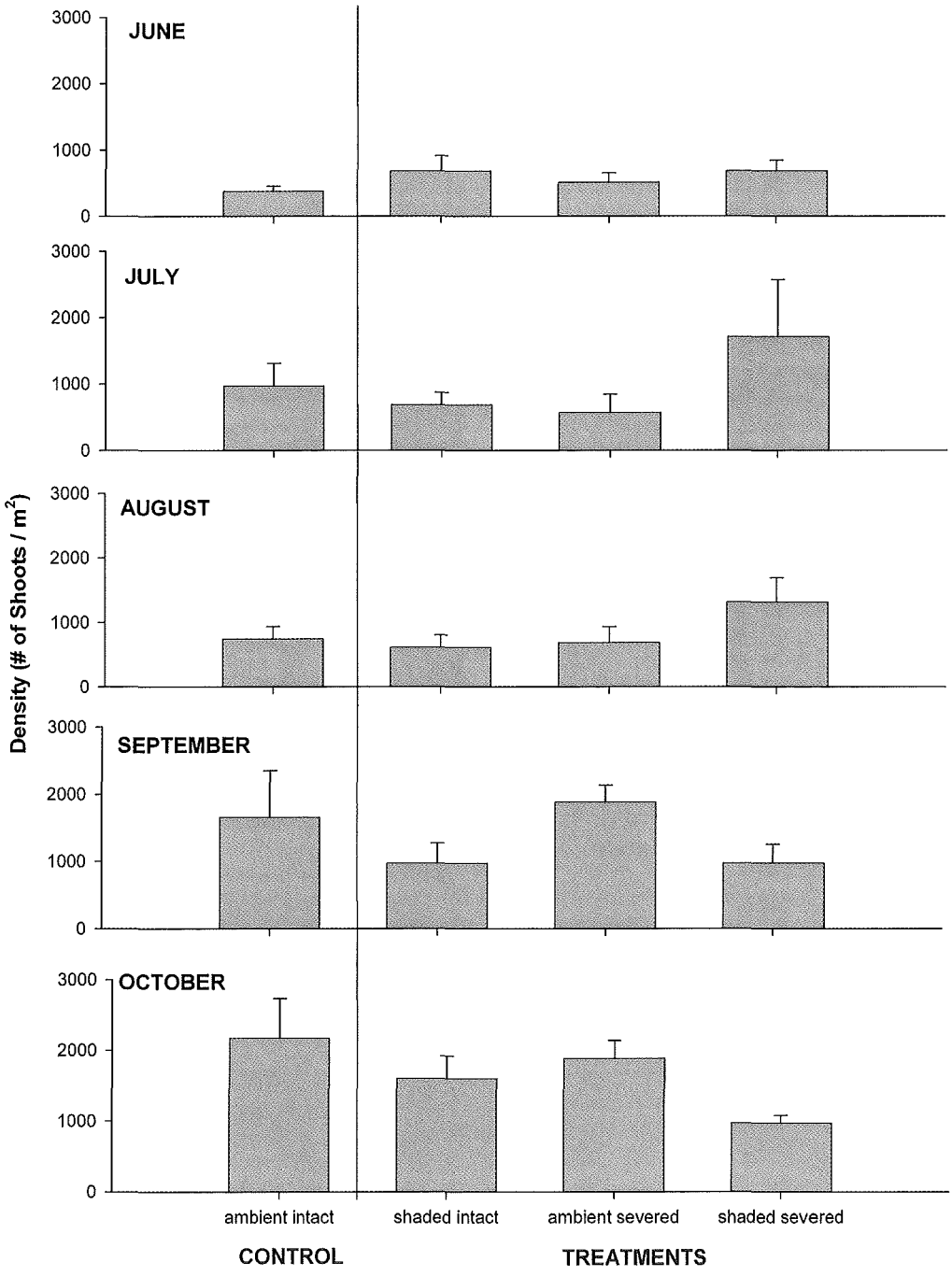

Fig. 5. Shoot density (# shoots m^{-2}) as a function of light, rhizome integrity, and time. Bars represent ±1 SE.

duction of biomass by the apical meristem depends on resources provided by shoots situated farther than 0.5 m from the rhizome apex.

We noticed that the severing effect on NAPP seems to be a transient response; significant differences were only found from June to July. Morever, the Aug. severing did not produce any significant effect. A reduction in turtlegrass blade productivity between Aug. and Nov. was reported by Tomasko and Dawes (1990) in Tampa Bay, FL. In their experiment, shoots isolated from their neighbors by severing rhi-

TABLE 4. NAPP ANOVA values for main factors and their interactions. (* = significant differences.)

Factors and interactions	df	F value	*P* value
Time	4	5.206	0.001*
Rhizomes	1	12.562	0.024*
Light	1	1.407	0.301
Time × rhizomes	4	0.467	0.759
Time × light	4	3.351	0.015*
Rhizomes × light	1	5.334	0.082
Time × rhizomes × light	4	0.901	0.469

TABLE 5. Shoot density ANOVA values for main factors and their interactions. (* = significant differences.)

Factors and interactions	df	F value	*P* value
Time	4	5.872	0.0004*
Rhizomes	1	0.259	0.637
Light	1	0.223	0.661
Time × rhizomes	4	0.791	0.535
Time × light	4	2.772	0.035*
Rhizomes × light	1	0.745	0.437
Time × rhizomes × light	4	1.160	0.337

TABLE 6. Average leaf length ANOVA values for main factors and their interactions. (* = significant differences.)

Factors and interactions	df	F value	*P* value
Time	4	33.206	0.000*
Rhizomes	1	9.732	0.036*
Light	1	1.120	0.350
Time × rhizomes	4	0.154	0.960
Time × light	4	0.323	0.861
Rhizomes × light	1	0.181	0.692
Time × rhizomes × light	4	0.633	0.640

TABLE 7. Average leaf width ANOVA values for main factors and their interactions. (* = significant differences.)

Factors and interactions	df	F value	*P* value
Time	4	6.113	0.0003*
Rhizomes	1	0.950	0.385
Light	1	0.496	0.52
Time × rhizomes	4	0.739	0.569
Time × light	4	0.497	0.738
Rhizomes × light	1	0.611	0.478
Time × rhizomes × light	4	0.982	0.424

zomes connections had blade growth rates not significantly different from controls in Nov. This seasonal reduction could have influenced the lack of a significant effect of severing on NAPP in the second half of our experimental period.

Terrados *et al.*, (1997) found that shoots on the severed horizontal rhizomes of *C. nodosa* reduced the production of new internodes, shoot number, size, leaves per shoot, and leaf width of the second youngest leaf. However, the elimination of subapical shoots promoted the growth of the horizontal rhizome branches. This was interpreted as a mechanism to overcome the effects of disturbance and the creation of gaps. This mechanism could ex-

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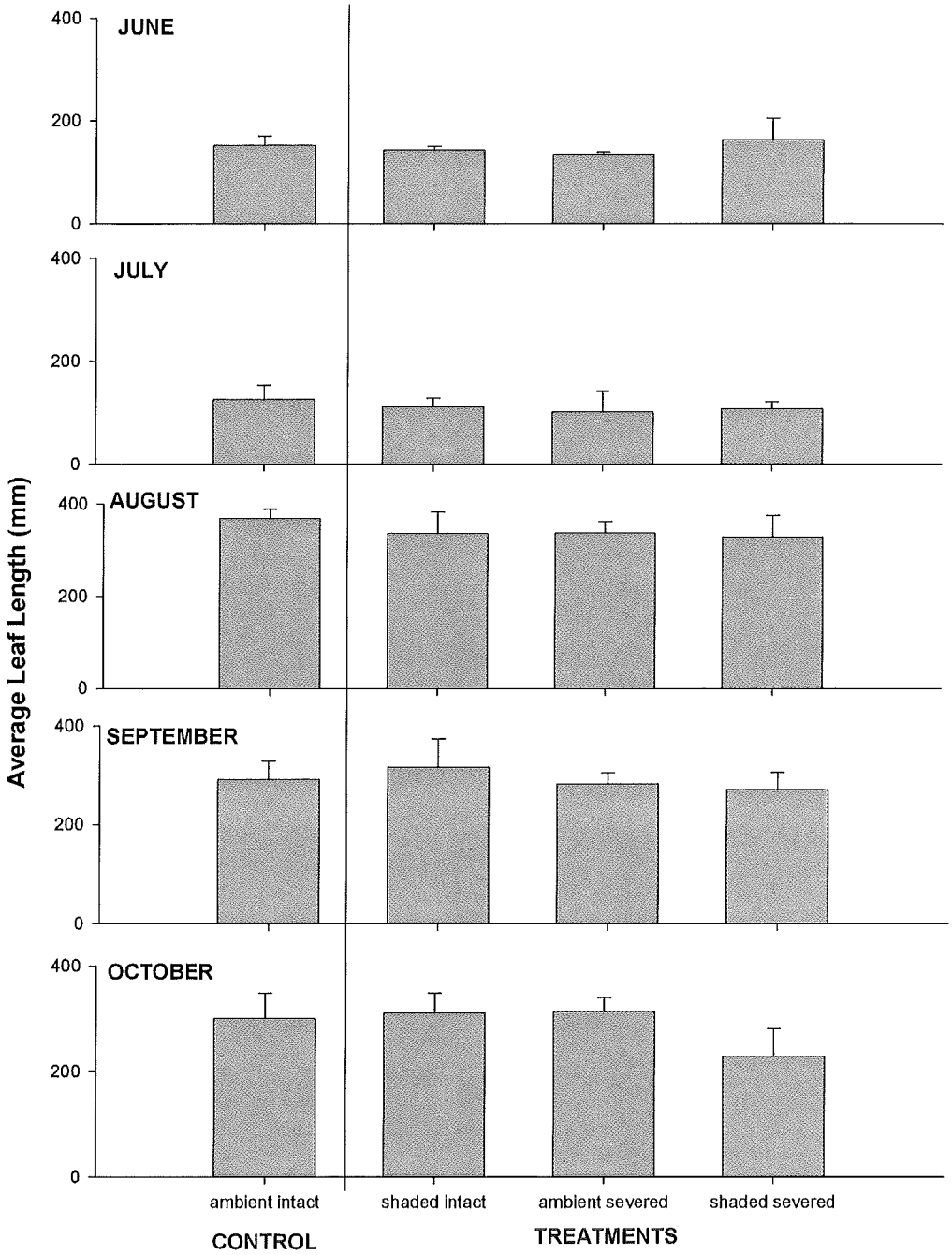

Fig. 6. Leaf length (mm) of oldest leaf as a function of light, rhizome integrity, and time. Bars represent ±1 SE.

plain why we did not find significant treatment effects on above and belowground biomass, leaf number, length or width.

In our study, 4 mo of shading to about 40% ambient light (14% SI) was needed to effect a significant reduction in turtlegrass growth rate (NAPP), whereas Czerny and Dunton (1995) found a negative effect in only 30 d at 14–10% surface irradiance. This difference likely results from seasonal effects, because our experiment took place from May to Oct., the peak of the growing season; Czerny and Dunton's

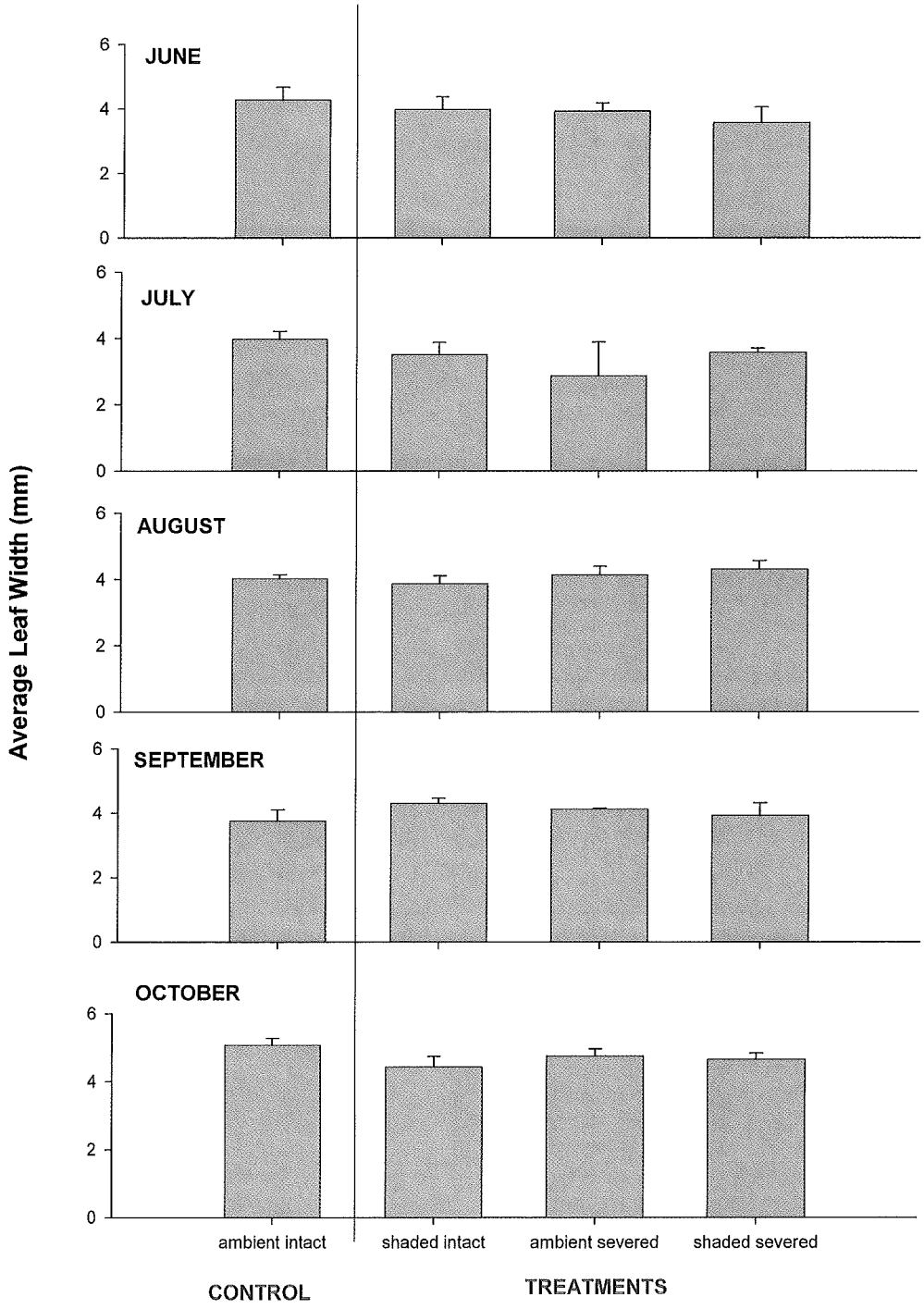

Fig. 7. Leaf width (mm) of oldest leaf as a function of light, rhizome integrity, and time. Bars represent ±1 SE.

(1995) study started in Oct., near the end of the growing season. In agreement with Czerny and Dunton (1995) and Lee and Dunton (1997), we also found a reduction in *T. testudinum* shoot density as a result of shading.

A general problem not often discussed, and one not easily addressed, is that of knowing and correcting for the degree to which rhizome connections exist between experimental and unmanipulated plots. For example, rhi-

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zome severing may not have had a significant effect on any of our response variables because in our study area rhizome integration between shaded and unshaded plots may have been uncommon. Alternatively, we may have had average values of rhizome integration, but this was simply inadequate to prevent the negative effects of such substantial shading. The benefits of ramet physiological integration are believed to be greater where the spatial heterogeneity of resource limitation varies on a physical scale similar to that of ramet distribution (Alpert and Mooney, 1986). In addition, the location effect on ramet physiological integration is confounded by age-dependent effects on ramet integration, complicating the interpretation of results from field experiments (Tomasko and Dawes, 1990).

In conclusion, our data suggest that rhizome integrity did not substantially affect the responses to shading that we measured during the peak months of the growing season, and that previous (and future) turtlegrass shading experiments should provide comparable results whether rhizome connections are intact or not.

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