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Vol. 54: 299–305, 1989 | MARINE ECOLOGY PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published June 22

Evidence for physiological integration between shaded and unshaded short shoots of *Thalassia testudinum*

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ABSTRACT: Physiological integration of *Thalassia testudinum* short shoots enables clones to function at a higher level of physiological organization than that of the short shoots themselves. Shaded short shoots connected to non-shaded short shoots had blade growth rates and proximate organic constituent levels equal to non-shaded controls. Shaded short shoots physically isolated from neighboring short shoots had blade growth rates and organic constituent levels different from both controls and shaded short shoots connected to non-shaded short shoots. Support of shaded short shoots appeared to be primarily from older short shoots connected to the shaded short shoots. The amelioration of localized light limitation results in an increased ability of clones to persist in heterogeneous environments. This increases the probability of the clone later encountering more favourable sites through a wider physical spread.

INTRODUCTION

Thalassia testudinum Banks ex König, the dominant seagrass in the Gulf of Mexico (Phillips 1960, den Hartog 1970), displays monopodial growth, with new rhizomes branching from older upright short shoots (Tomlinson & Vargo 1966, Tomlinson 1974). Although *T. testudinum* is a dioecious angiosperm (Grey & Moffler 1978), flowering is infrequent in many areas of the Gulf of Mexico (Phillips 1960, Orput & Boral 1964, McMillan 1976, Eleuterius 1977). In addition, spatial segregation of sexes within meadows (Durako & Moffler 1985) and high rates of microbial infection of seeds and fruits (Moffler et al. 1981) suggest that sexual reproduction is not usually successful (Lewis et al. 1985).

Seagrasses appear to use vegetative propagation (sensu Harper 1977) as the primary method of maintaining and expanding individual meadows (Tomlinson 1974, Dawes 1981). This growth pattern is a common feature of all clonal plants (Harper 1977, Cook 1983). Physiological integration of ramets (repeated horizontal modules) has been shown to occur in clonal genets (genetic individuals) (Ginzo & Lovell 1973, Harrison 1978, Hartnett & Bazzaz 1983, Salzman & Parker 1985, Alpert & Mooney 1986), although not all plants with clonal growth exhibit ramet physiological integration (Ashmun et al. 1982). Physiological integration allows the reduction of stress on an individual ramet experiencing resource limitation (Ong & Marshall 1979, Hartnett & Bazzaz 1983, Salzman & Parker 1985, Alpert & Mooney 1986, Lau & Young 1988), and enables the genet to 'grow through' resource-poor sites (Slade & Hutchings 1987). The ability to traverse unfavorable sites increases the probability that the genet may later encounter better sites through its wider physical spread (Sutherland & Stillman 1988).

In clonal plants, the physical connection of ramets does not constitute evidence for physiological integration. Three basic growth patterns characterize clonal plants (Hartnett & Bazzaz 1983). In the first, individual ramets are physiologically independent entities. No difference in performance is evident between stressed and physically isolated ramets versus stressed ramets with intact connections to non-stressed ramets. In the second growth pattern, the physical connection between ramets is important only in that it serves as a common storage organ. Intact connections may provide stressed ramets with a greater resource store, and result in a difference in performance when compared to stressed and isolated ramets. However, no differences in physiological processes are evident in non-stressed

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0171-8630/89/0054/0299/$ 03.00

ramets connected to stressed ramets. In the third growth pattern, ramet physiological integration results in distinct differences between the responses of stressed-isolated ramets and those of stressed ramets with intact connections to non-stressed ramets. In addition, imposition of local stress results in measurable effects on the physiological processes of connected non-stressed ramets.

Thus, the physical connection of *Thalassia testudinum* short shoots through the rhizome system could be associated with individual short shoots not functioning as separate physiological entities. Although translocation between short shoots has been shown for the seagrasses *Zostera americana* den Hartog (Harrison 1978) and *Posidonia oceanica* (L.) Delile (Libes & Boudouresque 1987), the implications of physiological integration of short shoots on the ability of short shoots to withstand localized resource scarcity have not been studied.

As clonal plants have varying degrees of ramet physiological integration, the actual size of a genet may not answer the question of what defines the physiological and ecological individual (Hartnett & Bazzaz 1983). The present study was designed to determine if short shoots in *Thalassia testudinum* are physiologically integrated, and if so, the benefits and costs associated with integration of localized light limitation. These goals were accomplished through experiments designed to (1) compare responses of shaded short shoots physically isolated from other short shoots to the responses of shaded short shoots connected to non-shaded short shoots, and (2) determine the effects of shading individual short shoots on physically connected non-shaded short shoots.

MATERIAL AND METHODS

The study site for the experiment was a monospecific *Thalassia testudinum* meadow ca 200 m offshore of Mullet Key, Florida, USA, (27° 37.2' N, 82° 41.7' W) at the mouth of Tampa Bay. The seagrass meadow at this location is delimited by an offshore sandbar at its shallow edge (0.6 m below MLW), and an offshore edge at ca 2.0 m (MLW), which is near the maximal depth for seagrass beds in Tampa Bay (Lewis et al. 1985). The experiment was begun on April 15, 1988 and ended 2 wk later. At this time of year, water temperatures are around 25 °C and increasing from about 16 °C in February to an annual high of 31 °C in July and August. Blade growth at this time of year is increasing from a low value of around 2 mg dw g dw^{-1} d^{-1} in January and February to an annual high of about 40 mg dw g dw^{-1} d^{-1} in July and August (Tomasko unpubl.) (dw = dry weight).

A permanent transect line was placed such that it ran parallel to the shoreline at a depth of ca 1.3 m (MLW). Knots were placed at 1 m intervals along the transect line and 51 short shoots closest to these knots were tagged and assigned at random to one of 3 treatments: shaded and isolated (SI), shaded and connected to non-shaded (SC), and controls (C) (Fig. 1). Isolated short shoots had their rhizome connections to neighboring short shoots severed by cutting with a dive knife at a point halfway between neighboring connected short shoots. Rhizome connections were found by touch, and sediment disturbance was kept to a minimum. Nonetheless, as a control, shaded connected and control short shoots were exposed to the same disturbance, but rhizomes were not cut.

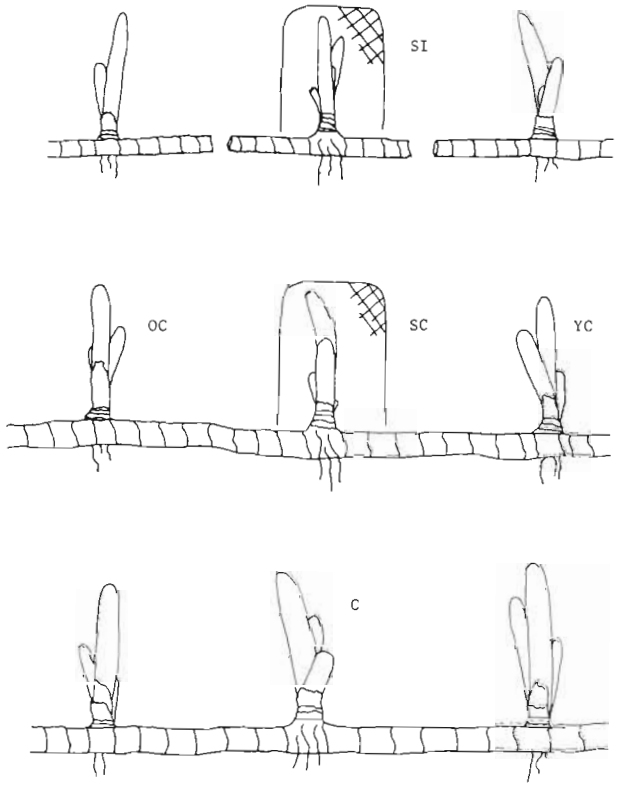

Fig. 1. *Thalassia testudinum* short shoot treatments used in the experiment. SI: shaded short shoot isolated from other short shoots; SC: shaded short shoot with intact connections to non-shaded short shoots; OC: older short shoot connected to a shaded short shoot; YC: younger short shoot connected to a shaded short shoot; C: control short shoot

Shading units were made of neutral density shade cloth sewed onto a steel frame made from planting staples. Staples were also placed next to controls as a precaution against effects of the frame. Frames were ca 30 cm high (taller than the longest blades at the time) and allowed blades to sway back and forth inside the frame. Frames were tested for light attenuation underwater using a spherical quantum meter, and were

found to reduce light availability by ca 45 %. Siltation, rather than biofouling, was the major problem with changes in shading effect and shade units were cleaned twice during the 2 wk study. After 1 wk, the blades of each shoot were marked by inserting a hypodermic needle through the blade bundle at a point 1 cm above the blade-sheath junction of the oldest intact blade.

At the end of the experiment, all tagged short shoots were excavated such that roots and rhizomes remained intact. For shaded connected (SC) short shoots, older short shoots connected to SC short shoots (OC) and younger short shoots connected to SC short shoots (YC) were also identified and excavated (Fig. 1). Older short shoots could be distinguished from younger short shoots based on the rhizome scale leaves, which are unidirectional in morphology (pers. obs.).

After transfer to the laboratory in coolers, newly formed blade material was separated from total blade material and older blades were cleaned of epiphytes by gently scraping in dilute phosphoric acid. The newly formed blade material did not bear epiphytes so scraping and acid cleaning was not necessary. New blade material was weighed after damp drying and subsequently used for chlorophyll, protein, soluble carbohydrate, and photosynthesis assays. A wet weight to dry weight conversion (0.199 mg dw mg ww^{-1}) was determined so that new blade material could be used to measure leaf relative growth rate (mg dw g dw^{-1} d^{-1}). Chlorophylls *a* and *b* were extracted by grinding in 80 % acetone and absorbances measured at 664 and 647 nm using a Gilford-250 spectrophotometer.

Photosynthetic rates were determined using 2 mm long sections of newly formed blade material 2 to 8 cm above the blade-sheath junction. Blade sections were then aspirated. This procedure floods the lacunal spaces and avoids gas buildup in the blade lacunae (Dawes & Tomasko 1988). To avoid wound respiration, the blade sections were not tested for 12 h. Photosynthetic rates were determined over a 2 h period using a Gilson respirometer at an irradiance level of 300 µE m^{-2} s^{-1}, and at 25 °C, the ambient water temperature. At this depth (1.3 m) in spring, 300 µE m^{-2} s^{-1} appears to be a near-saturation light level (Tomasko unpubl.). *Thalassia testudinum* at all but the deep meadow edges does not normally light saturate, and thus a convenient but adequate irradiance level was used.

Short shoots were separated and the fiber material from sloughed-off blades was removed. The topmost 2 cm of the short shoots was dried in a vacuum desiccator for later constituent assays. Rhizome sections directly beneath the tagged short shoots were cut such that 5 internodes extended toward both the older and younger connected short shoots. This material was then dried as well for constituent analysis. Roots attached to short shoots and rhizome sections were separated and dried. Samples were kept separate and ground into a fine powder using a mortar and pestle. In order to avoid pseudoreplication, at no point were samples pooled. Protein levels of dried material were determined using the method of Appenroth & Augsten (1987). Soluble carbohydrate levels were determined using the method of DuBois et al. (1956).

Statistical comparisons of the data used the non-parametric Kruskal-Wallis 1-way analysis of variance test with a 95 % confidence level ($p < 0.05$). Upon detection of significant treatment effects, multiple comparison tests used were either the STP procedure (Sokal & Rohlf 1981) or, for replicate numbers less than 8, the original pairwise comparison test of Dunn (1964).

RESULTS

Shaded-connected short shoots (SC) had blade production rates equal to controls (C), while shaded-isolated short shoots (SI) had rates significantly lower than both controls and shaded-connected short shoots (Table 1). No significant differences in photosynthetic rates were found between shaded-connected, shaded-isolated and controls. Older-connected short shoots (OC), but not younger-connected short shoots (YC), had significantly higher photosynthetic rates than shaded-connected short shoots (Table 1). Photosynthetic rates, measured using a differential respirometer, and expressed in µl O_2 g dw^{-1} h^{-1}, are not directly comparable to rates obtained in previous studies which used oxygen meters to study photosynthesis in *Thalassia testudinum*. Photosynthetic rates appear to be similar upon conversion to the same units. However, the conversion factor is prone to error due to possible differences in water temperature and atmospheric pressure between experiments. No differences were found for any of the treatments for blade chlorophyll content (Table 1) or blade protein levels (Table 2).

Protein levels of shaded-isolated short shoots were significantly lower than all other treatments, but protein levels in rhizomes of shaded-isolated short shoots were not significantly different from control rhizomes. Rhizome and root protein levels of older-connected short shoots were higher than controls (Table 2), while shaded-connected, shaded-isolated, and younger-connected root protein levels were equal to controls.

Soluble carbohydrate levels of blades of shaded-isolated and older-connected short shoots were lower than levels of blades of shaded-connected and control short shoots (Table 3). Shaded-connected short shoots had higher soluble carbohydrate levels than all other treatments except shaded-isolated short shoots. The levels of soluble carbohydrate in shaded-isolated short

Table 1. *Thalassia testudinum*. Leaf relative growth rate (mg dw g dw^{-1} d^{-1}), total chlorophyll content (mg g dw^{-1}), and net photosynthetic rate (µl O_2 g dw^{-1} h^{-1}) for all treatments. Values are means with standard errors in parentheses. Shared underlines denote a lack of significant difference at $p \leq 0.05$. See Fig. 1 for diagram of treatments

	Shaded-isolated	Control	Shaded-connected		
Growth rate (n = 17)	19.19 (2.34)	28.19 (2.23)	31.32 (1.88)		
	Shaded-isolated	Older-connected	Younger-connected	Control	Shaded-connected
Chl content (n = 8)	2.29 (0.20)	2.68 (0.08)	2.74 (0.17)	2.75 (0.44)	2.86 (0.30)
	Shaded-isolated	Shaded-connected	Control	Younger-connected	Older-connected
Photosyn. rate (n = 4)	473 (106)	659 (216)	959 (257)	1704 (645)	1745 (208)

Table 2. *Thalassia testudinum*. Protein levels (mg g dw^{-1}) in blades, short shoots, rhizomes and roots for all treatments. Values are means (n = 6) with standard errors in parentheses. Shared underlines denote a lack of significant difference at $p \leq 0.05$. See Fig. 1 for diagram of treatments

	Shaded-isolated	Younger-connected	Older-connected	Control	Shaded-connected
Blade	70.4 (9.4)	72.3 (11.5)	85.0 (10.2)	85.3 (13.1)	118.5 (11.8)
	Shaded-isolated	Younger-connected	Control	Shaded-connected	Older-connected
Short shoot	34.2 (6.0)	70.0 (8.5)	71.1 (16.8)	76.7 (9.0)	79.7 (11.3)
	Shaded-connected	Control	Shaded-isolated	Younger-connected	Older-connected
Rhizome	10.1 (1.5)	11.4 (2.7)	16.8 (1.7)	17.4 (2.1)	18.1 (0.9)
	Shaded-connected	Shaded-isolated	Control	Younger-connected	Older-connected
Roots	12.0 (3.3)	15.3 (1.4)	15.7 (2.7)	24.8 (3.4)	29.9 (4.1)

Table 3. *Thalassia testudinum*. Soluble carbohydrate levels (mg g dw^{-1}) in blades, short shoots, rhizomes and roots for all treatments. Values are means (n = 6) with standard errors in parentheses. Shared underlines denote a lack of significant difference at $p \leq 0.05$. See Fig. 1 for diagram of treatments

	Shaded-isolated	Older-connected	Younger-connected	Control	Shaded-connected
Blade	10.5 (2.7)	18.3 (2.3)	25.9 (3.9)	38.3 (3.6)	45.4 (5.8)

	Younger-connected	Older-connected	Control	Shaded-isolated	Shaded-connected
Short shoot	280 (29)	311 (16)	375 (33)	397 (7)	474 (21)

	Shaded-isolated	Younger-connected	Shaded-connected	Control	Older-connected
Rhizome	325 (24)	386 (40)	448 (16)	451 (20)	502 (12)

	Shaded-isolated	Younger-connected	Control	Shaded-connected	Older-connected
Roots	111 (11)	147 (22)	175 (16)	191 (8)	238 (26)

shoots were not significantly different from controls. While the levels of soluble carbohydrate in shaded-connected, older-connected, and younger-connected rhizomes were not significantly different from controls (Table 3), the levels in rhizomes of shaded-isolated short shoots were lower than both controls and shaded-connected. The soluble carbohydrate levels of roots of shaded-isolated short shoots were lower than both controls and shaded-connected, which were not significantly different from each other.

DISCUSSION

Short-term localized shading is common in *Thalassia testudinum* meadows off west Central Florida, as drift algae of the genera *Digenia, Laurencia, Gracilaria,* and *Acanthophora* can accumulate in large masses with typically patchy distributions (Dawes 1985). Although decreased light availability due to water depth is associated with changes in demography, morphology, and physiology of seagrass meadows (Giraud 1977, Boudouresque et al. 1980, Dennison & Alberte 1982, 1985, Dawes & Tomasko 1988), no work has been performed on responses to the type of light reduction caused by the patchy occurrence of drift algae.

In clonal plants, the degree of physiological integration varies greatly between species (Watson & Casper 1984). In those plants with physiological integration, integration may be restricted to times of localized resource limitation (Ong & Marshall 1979, Hartnett & Bazzaz 1983, Alpert & Mooney 1986, Slade & Hutchings 1987). The benefits of physiological integration between ramets may be greatest in situations where the physical scale of resource limitation is on the level of individual ramets (Alpert & Mooney 1986), for example, times of drift algal accumulation in seagrass meadows.

Blade growth rates were similar to those reported by Dawes & Tomasko (1988) for *Thalassia testudinum,* and Dennison & Alberte (1982, 1985) for *Zostera marina.* Shaded-isolated short shoots exhibited decreased leaf

growth rates versus controls. As such, they responded in a manner similar to previous experiments where in situ shade units were designed to cover large ($> 1\ m^2$) areas (i.e. Dennison & Alberte 1982, 1985, Bulthuis 1983). The similarity in responses may be due to the fact that individual short shoots under large-scale shade units are all equally stressed and support from neighboring non-stressed short shoots is not available. Shaded-isolated short shoots also have no source of support from other short shoots. In contrast, shaded-connected short shoots had leaf growth rates equal to controls. Shaded-connected short shoots had greater blade growth rates than shaded-isolated short shoots, but were not different from shaded-isolated short shoots when comparing photosynthetic rates. Thus, a possible change in allocation patterns of assimilated carbon, rather than a change in rates of carbon fixation, may result in the different blade growth rates of shaded-connected versus shaded-isolated short shoots. The ability of shaded-connected short shoots to maintain leaf growth rates on a level equal to controls, in spite of the 45% decline in light availability, may be associated with the elevated soluble carbohydrate levels in the short shoot. Increased short shoot carbohydrate levels in shaded-connected shoots may be due to support from older non-shaded connected short shoots, as indicated by changes in photosynthetic rates and proximate organic constituents.

The changes in photosynthetic rates and organic composition of older-connected shoots in response to localized shading may help in understanding the mechanism of physiological integration. Hartnett & Bazzaz (1983) showed unshaded ramets connected to shaded ramets had increased photosynthetic rates. This response may be due to the enhancement of photosynthesis by the development of a strong carbon sink, the shaded ramet, acting on a dynamic carbon source, the connected ramet (Thorne & Koller 1974). The data here indicate that the subcellular physiological changes involved in source-sink relations (Foyer 1987) may be detected even when using leaf segments rather than entire leaves. In the present study, the support of shaded-connected short shoots also seems to be associated with lower blade soluble carbohydrate levels and increased protein levels in the roots and rhizomes of older-connected short shoots. Decreased blade soluble carbohydrate levels in older-connected short shoots may reflect a decline in short-term energy stores brought about by increased translocation of fixed carbon out of the blades. The increased protein levels in roots and rhizomes of older-connected shoots may be due to higher levels of metabolic activity in these organs. Although the differences in blade growth rates between treatments are interpreted here in terms of carbon fluxes, the possible roles of translocation of nitrogen, phosphorous or oxygen cannot be dismissed. Unfortunately, insufficient data are available from terrestrial and marine clonal plants on the subject of between-ramet translocation of nitrogen, phosphorous or oxygen.

In spite of the physiological costs, the benefits of support to a shaded short shoot are numerous. Shaded-connected shoots were not significantly different from controls in any of the tested characters except for elevated short shoot soluble carbohydrate levels. In contrast, shaded-isolated short shoots lagged behind controls in leaf growth rate, short shoot protein levels, and blade, rhizome and root soluble carbohydrate levels. While shaded-isolated shoots had short shoot soluble carbohydrate levels equal to controls, the increased levels in shaded-connected short shoots may be important in maintaining blade production during short-term reductions in light availability. The data further indicate that with a lack of support, isolated short shoots utilize rhizome soluble carbohydrate stores upon imposition of shading. No such change was seen in rhizomes of shaded-connected short shoots.

Although physiological integration of *Thalassia testudinum* short shoots involves some energetic costs, the benefits of supporting a shaded short shoot appear to outweigh those costs. If the costs of physiological integration consistently exceed the benefits, a clonal plant would exhibit decreased fitness at the genet level (Slade & Hutchings 1987). Such a situation would increase the selective pressure against that clone, and produce an expected early genet mortality (Cook 1983). Physiological integration increases the probability of genets surviving in heterogeneous environments by ameliorating conditions of ramets experiencing localized resource limitation (Salzman & Parker 1985, Alpert & Mooney 1986, Lau & Young 1988), and by spreading mortality risks out amongst the connected ramets (Cook 1979).

Seagrasses are ideal plants with which to study clonal growth dynamics. The abundance of physiological data on seagrasses (as opposed to terrestrial clonal plants) allows an interpretation of sub-organismic processes involved in clonal growth. The present study shows that physiological integration does occur between *Thalassia testudinum* short shoots, and indicates some of the mechanisms of physiological integration. The structure of *T. testudinum* meadows is currently being studied with relation to physiological integration between ramets as affected by abiotic factors such as season and water depth, and biotic factors such as the local density experienced by individual short shoots.

Acknowledgement. The authors thank 3 anonymous reviewers for their detailed and constructive criticisms of prior versions of the manuscript.

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This article was submitted to the editor

Manuscript first received: September 16, 1988
Revised version accepted: March 21, 1989