

Responses of eelgrass *Zostera marina* seedlings to reduced light

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ABSTRACT: We subjected seedlings of *Zostera marina* L. to High (72%), Medium (23%), and Low (10%) daily irradiance (mean daily PAR of 24.4, 7.9, and 3.3 E m⁻² d⁻¹ respectively) over 12 wk. We measured plant response in terms of survivorship, lateral shoot production, morphology, growth rate, photosynthesis and respiration, and leaf pigment concentration. Decreasing the light available to eelgrass seedlings from 72 to 23% resulted in a reduction of lateral shoot formation, lower plant biomass, and longer and wider leaves. Shoot area, growth rate, and pigment concentrations remained similar. A reduction of incident light to 10% decreased survival to 74% and had a negative effect on shoot growth, size, and above- and belowground biomass. Pigment concentrations increased with respect to seedlings raised at medium light. In general, the responses of seedlings to reduced light are similar to those reported for mature *Z. marina*. Rapid expansion of seedling patches can only occur at irradiance levels greater than 7.9 E m⁻² d⁻¹. Morphological changes resulting from exposure to mean daily PAR levels of less than 8 E m⁻² d⁻¹ such as thinner leaves and low belowground biomass, have serious implications for decreased seedling survival in the field.

KEY WORDS: Eelgrass · Seagrass seedlings · Light · *Zostera marina* · Shade adaptation

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INTRODUCTION

Temperate eelgrass *Zostera marina* L. meadows are produced and maintained largely by the asexual extension and branching of rhizomes (Phillips et al. 1983, Olesen & Sand-Jensen 1994a). However, several studies have documented the importance of seeds and seedlings in establishing patches in bare areas within and outside of existing beds (Orth & Moore 1983, Harrison 1987, Olesen & Sand-Jensen 1994a,b, Olesen 1999 and others). In addition, in several areas of the world, annual eelgrass populations are maintained entirely by the production of seeds and seedlings (Keddy & Patriquin 1978, Harlin et al. 1982, McMillan 1983, Harrison 1991). The production of seeds within an eelgrass meadow is considerable and may reach 70 000 m⁻² (van Lent & Vershuure 1994, Fishman &

Orth 1996, van Katwijk et al. 1998). For this reason, using seeds for restoration and mitigation may hold great potential (Harwell & Orth 1999, Granger et al. 2000). Seedling germination is between 30 and 90% (Churchill 1983, Hootsmans et al. 1987, van Lent & Verschuure 1994, Granger et al. 2000), but seedling mortality is often substantial (Robertson & Mann 1984, Duarte & Sand-Jensen 1990, Olesen & Sand-Jensen 1994a, de Jonge et al. 1996). The ultimate success of germinated seedlings and the formation of viable beds appears to depend upon several factors, including sediment burial, light attenuation, nutrient limitation, and initial patch size (Churchill 1983, Duarte & Sand-Jensen 1990, Orth et al. 1994).

Using transplanted seedlings and sowing seeds are both being explored as viable restoration techniques in the Dutch Wadden Sea (de Jonge et al. 2000). However, an obstacle to the use of these techniques is that much of the basic quantitative information needed to assess the potential of different sites is unavailable

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(de Jonge et al. 1996, van Katwijk et al. 2000). Virtually all of our knowledge of *Zostera marina* physiology and environmental requirements is derived from studies of mature plants in established populations (Backman & Barilotti 1976, Bulthuis 1983, Dennison & Alberte 1982, 1985, Olesen & Sand-Jensen 1993). An example is the relationship between plant growth and survival and the availability of photosynthetically active radiation (PAR). The responses of mature, established plants to changes in light exposure have been well documented (e.g. Dennison & Alberte 1982, 1985, 1986, Short 1991, Olesen & Sand-Jensen 1993). While these studies have been integral to understanding the role of light in the maintenance of eelgrass meadows, there have been only a few studies on the response of young, seed generated plants to changes in PAR (Zimmerman & Alberte 1996, van Katwijk et al. 1998).

To determine the survival and growth potential of seed generated *Zostera*, we subjected seedlings to a gradient of light exposure and measured their response in terms of survivorship, asexual reproductive success, production and respiration rates, morphology, growth rate, and leaf pigment concentrations.

MATERIALS AND METHODS

Experimental system and design. SCUBA divers harvested seed-bearing shoots of *Zostera marina* in July and August of 1997, in Narragansett Bay, Rhode Island, USA (41° N, 71° W). The plants were allowed to release their seeds in outdoor flowing seawater tanks adjacent to the lower bay. We separated seeds from the detrital remains of the spathe through several steps of screening and winnowing, and held the seeds in ambient flowing seawater for several months (Granger et al. 2000).

Seeds were planted in late December 1997. Four seeds were buried at 2 cm depth in individual 10.2 cm

Table 1. Mean daily quantum flux (PAR) ($E\ m^{-2}\ d^{-1}$) at the sediment surface and the percentage of days seedlings experienced a PAR of at least $100\ \mu E\ m^{-2}\ s^{-1}$ $\geq 6\ h$ and $\geq 10\ h$ in the high, medium and low treatments

Treatment	Quantum flux d^{-1}		% d at $100\ \mu E\ m^{-2}\ s^{-1}$	
	Summer range	Summer mean	$\geq 6\ h$	$\geq 10\ h$
High	22.0–28.8	24.4	98	89
Medium	7.1–9.3	7.9	84	51
Low	3.0–4.0	3.3	46	0

diameter pots in low organic (0.17 to 0.56% weight loss on ignition at 550°C) sandy sediment collected in Block Island Sound. We allowed the seeds to germinate in outdoor tanks with flowing seawater 50 cm deep, under conditions of ambient light and temperature. Seedlings began emerging on January 21, 1998. Each of 3 light treatments was apportioned 80 pots, giving a total of 240 pots.

By May 15, the seedlings reached a mean height of 4 cm and we thinned the plants to leave 1 seedling per pot before moving them to outdoor tanks with a water depth of about 80 cm over the sediment surface. Every week the tank walls were scrubbed clean of periphyton, and epiphytes were gently removed from the leaves by hand. The water column remained clear throughout the experiment as water continually flowed through the tanks. Salinity was measured 2 to 3 times per week with a digital salinometer, and varied between 29 and 32 psu. The experiment lasted for about 12 wk, from May 25 through August 20, 1998. Mean daily water temperatures during this period ranged from 16 to 24°C (Fig. 1).

The minimum light requirement for mature *Zostera marina* appears to lie between 8 and 30% of incident PAR (Duarte 1991, Dennison et al. 1993, van Katwijk et al. 1998). We used neutral density, greenhouse shade screens placed over the water to establish experimental conditions in which seedlings were exposed to 72% (high), 23% (medium) and 10% (low) of incoming irradiance at the sediment surface. Irradiance was measured at the base of the plants with a LI-COR 2 pi quantum underwater sensor and a LI-1000 data logger (LI-COR, Lincoln, NE). The high light treatment was not screened so that attenuation was due solely to the overlying water.

Hourly light data were collected by the Marine Ecosystems Research Laboratory with a LI-1000 data logger located on the dock at the Graduate School of Oceanography. These data were used with the respective attenuation coefficients to calculate mean daily quantum flux (PAR, $E\ m^{-2}\ d^{-1}$) at the sediment surface for each treatment over the course of the 12 wk experiment (Table 1).

Light climate. Mean daily PAR for the high light treatment was about 3 times greater than that received

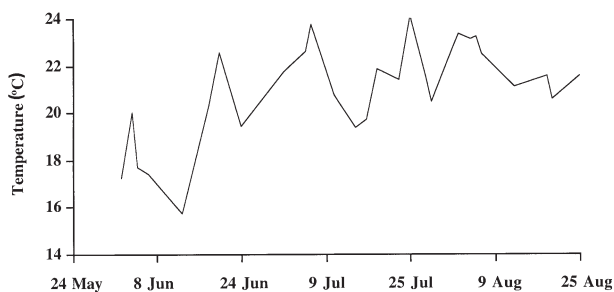


Fig. 1. Mean daily water temperature in experimental tanks. Temperature was recorded using continuous probes in conjunction with daily thermometer readings

in the medium light treatment, and about 7 times greater than in the low light treatment (Table 1). Seedlings grown at the highest light level received at least $100 \mu\text{E m}^{-2} \text{s}^{-1}$ for more than 6 h d^{-1} on nearly every day of the experiment (Table 1). Seedlings in the low treatment never received $100 \mu\text{E m}^{-2} \text{s}^{-1}$ for more than 10 h d^{-1} .

Survivorship, reproduction, morphology and growth.

Growth and leaf production rates were calculated each month from June to August by randomly selecting 16 plants from each treatment and piercing at the top of the youngest sheath through all existing leaves of the primary shoot, using the method of Kentula & McIntire (1986). Marked seedlings were collected approximately 20 d later. Following photosynthetic production and respiration incubations (see below), seedlings were rinsed with deionized water, and dissected by separating the leaves at the top of the sheath and from the rhizome at the top of the newest rhizome node. The length and width of each leaf from the top of the sheath to the tip of the leaf was recorded for both primary and lateral shoots. Old leaves had clearly visible piercing scars and new leaves were unscarred. The distance from the top of the sheath to the pierce scar was considered to be new growth. The new growth was multiplied by the leaf width, summed for all new leaf material, and divided by the number of days since marking to get growth as $\text{cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$. Growth rates correspond to the primary shoot only (i.e. not laterals).

Shoot and root/rhizome material was dried at 65°C for a minimum of 48 h or until they reached a constant dry weight (DW). Any lateral shoots present were counted, measured, and weighed along with the primary shoot. Since we measured growth as the increase in leaf surface area, we developed a dry weight to surface area regression for each sampling period and for each treatment. We used the slope of the regression line to calculate the biomass of new material produced from the calculated new surface area (Table 2). Root/rhizome productivity was calculated as the dry weight of the entire rhizome from the top of the newest rhizome node divided by the number of days from the beginning of the experiment.

The plastochrone interval (PI) is the length of time between the generation of 2 successive new leaves on a single shoot and was calculated using the equation of Jacobs (1979). Relative growth rate (RGR) of shoots, which is the fraction of total above ground material produced per unit time, was calculated following van Lent & Verschuure (1994). The leaf life span was calculated by multiplying the calculated PI by the mean number of standing leaves per shoot (F. T. Short pers. comm.).

Photosynthesis and respiration. Measurements of production and respiration rates were made on 3 occa-

sions for each treatment, after approximately 10 d (June), 50 d (July), and 85 d (August) of treatment. Measurements were made under conditions of ambient bay water temperature and natural sunlight. The 16 randomly chosen seedlings which had been pre-marked for growth measurements 20 d before were removed from their pots by gently rinsing away the sediment, so that the shoot and rhizome remained intact. Individual whole plants with lateral shoots if present were placed in 300 ml BOD bottles filled with filtered ($1 \mu\text{m}$) Narragansett Bay water. Clear and opaque 'blank' bottles were used to correct for plankton metabolism. Of the 16 seedlings collected from each treatment, 4 were incubated in high light, 4 in medium light, 4 in low light and 4 were placed in dark bottles for determination of respiration rate.

Rates of net production and respiration were measured as change in oxygen concentration (mg l^{-1}) in the BOD bottles during a 5 h incubation. Photosynthetic production rates were normalized to leaf surface area and respiration rates were normalized to whole plant biomass. Oxygen measurements were conducted before and after each incubation using a calibrated BOD oxygen probe (Model 5905, YSI Inc., Yellow Spring, OH) and a DO meter (YSI Model 58). Incubations were conducted during the same period of the day (10:00 to 16:00 h) on sunny days. Mean light levels on the days that the experiments were conducted never varied by more than $62 \mu\text{E m}^{-2} \text{s}^{-1}$ in the high light treatment, $20 \mu\text{E m}^{-2} \text{s}^{-1}$ under the medium light screen, and $8 \mu\text{E m}^{-2} \text{s}^{-1}$ under the low light screen.

Leaf pigment content. Six of the 16 pierced shoots collected and dissected on each date over the course of the summer were also analyzed for pigment content. A 1 cm^2 section from the tip of the youngest leaf was removed for analysis and weighed to the nearest 0.01 mg. If the youngest leaf contained less than 1 cm^2 , the difference was made up with a piece from the tip of the second youngest leaf. Chlorophyll extraction was carried out using the method of Dennison (1990).

Table 2. Slope (r^2) for linear regressions of dry weight (mg) versus surface area (cm^2) for each mo and each treatment used to calculate the amount of dry weight biomass produced over each marking period. $n \approx 10$ plants

Month	High light	Medium light	Low light
Jun	4.2 (0.98)	4.0 (0.93)	3.6 (0.97)
Jul	6.0 (0.99)	4.7 (0.92)	3.3 (0.89)
Aug	6.2 (0.97)	3.9 (0.99)	5.5 (0.69)*

*The low r^2 for this regression is due to one point out of 8 that deviates from the trend line. Excluding this point raises the r^2 to 0.94 but only changes the slope to 5.1

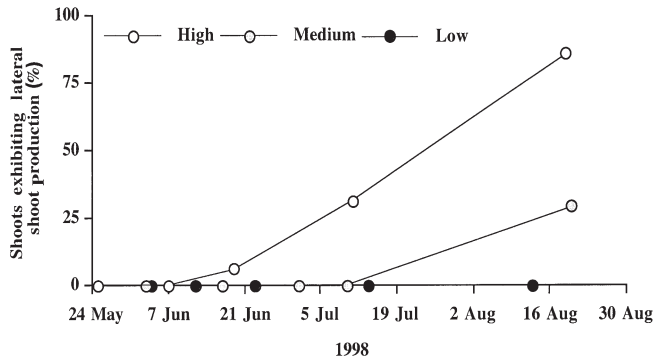


Fig. 2. Percentage of seedlings exhibiting vegetative reproduction in High, Medium and Low light over 12 wk. Each point represents a sample of 16 seedlings. May 25 was the initial condition before experimental treatment

Absorbance at 645, 663 and 725 nm was determined with a DU 640 spectrophotometer (Beckman Instruments, Carlsbad, CA) on duplicate samples.

Statistical analysis. We used normal probability plots to test for normality on all of the data. None of the parameters were normally distributed except for chlorophyll *a*. A 1-way ANOVA on the ranked data (Kruskal-Wallis test) was used to test for the effect of light level on photosynthesis, morphological, and growth parameters. If there was a significant difference ($p < 0.05$) between treatments, a post-hoc Bonferroni multiple comparison test was used ($p < 0.016$) (SPSS Inc. 1998). A paired *t*-test of least significant difference followed by a Tukey pairwise comparison was used to test for the effect of light level on chlorophyll concentrations. All statistical analyses were performed in SAS (Cody & Smith 1997).

RESULTS

Seedling survival was high in all treatments; 74% in the low, 94% in the medium, and 100% in the high light. Seedlings grown at high ambient light began producing lateral shoots within a few weeks of transfer to the experimental tanks, and 86% of the plants collected had produced at least 1 lateral shoot after 12 wk (Fig. 2). In the medium light treatment, lateral shoot initiation was delayed, and it was completely suppressed in the low light treatment.

Seedlings that were exposed to high light for 12 wk had significantly larger shoots, more below ground biomass (Fig. 3), and more leaves on the primary shoot compared to seedlings grown in low light (Table 3). After 12 wk, lateral shoots from the high light treatment comprised a mean of 23% of total leaf shoot weight and 28% of total leaf shoot area. Lateral shoots

from the medium light treatment comprised a mean of 14% of total leaf shoot weight and 10% of total leaf shoot area.

Primary shoots grown at 23% incident light had significantly wider leaves and greater specific leaf area than seedlings from the other treatments (Table 3). However, they were not significantly different from seedlings grown at 72% light in the majority of morphological and growth parameters measured. A 90% reduction in light resulted in smaller shoots with less below ground biomass (Fig. 3). Growth rates of primary shoots and rhizomes were negatively affected (Table 3).

Seedlings grown in high light established a short and relatively constant plastochrone interval (PI) of 1 new leaf every 9 to 12 d throughout the experiment. Plants grown at medium light were able to produce a new leaf every 13 d in June and July, but after 12 wk, they were producing a new leaf only every 21 d

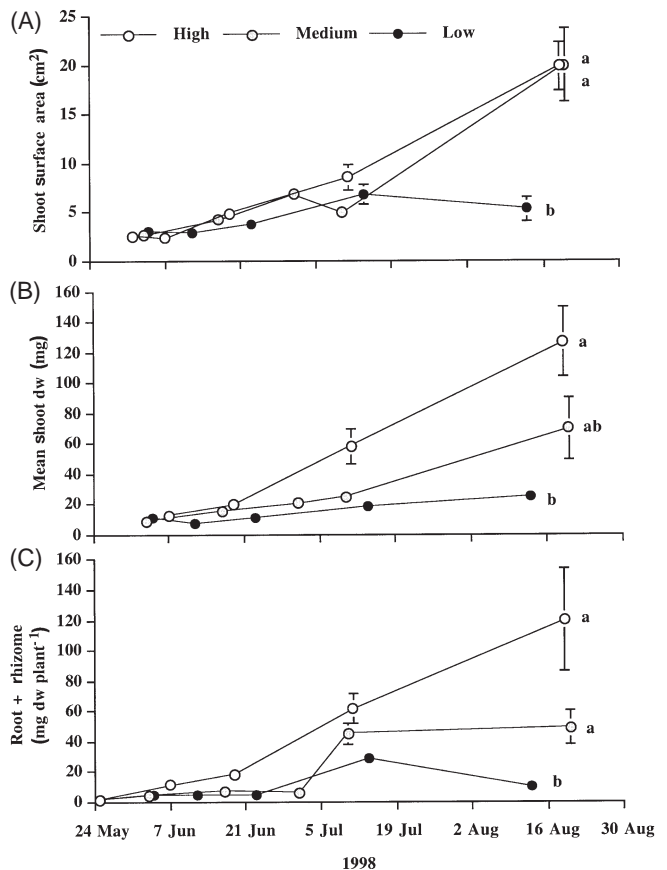


Fig. 3. Surface area and above- and belowground dry weight of seedlings grown in High, Medium and Low light over a 12 wk period. (A) Mean shoot surface area; (B) mean shoot dry weight; (C) mean root + rhizome dry weight. Bars represent standard errors of the mean. Symbols followed by the same letter indicate no statistical difference at 12 wk. All parameters include lateral shoots

Table 3. Physiological and morphological characteristics of *Zostera marina* seedlings after 12 wk exposure to high, medium, and low light. Values in rows followed by the same letter indicate no statistical difference between treatments. Data are means (\pm SE)

Variable	High	Medium	Low
Seedling morphology			
Shoot size including laterals (mg dw seedling ⁻¹)	126.5 ^a (23)	69.8 ^{ab} (20)	25.2 ^b (5)
(cm ² seedling ⁻¹)	19.9 ^a (2.5)	19.9 ^a (3.7)	5.3 ^b (1.2)
Below ground biomass including laterals (mg dw seedling ⁻¹)	120 ^a (34)	49 ^a (11)	10 ^b (1)
% Biomass below ground	51 ^a (3)	43 ^{ab} (3)	30 ^b (4)
Root:shoot ratio ^a	1.14 ^a (0.14)	0.77 ^a (0.10)	0.48 ^a (0.12)
Whole plant biomass (mg)	268 ^a (55)	119 ^b (31)	35 ^b (6)
No. of leaves primary shoot ⁻¹	4.5 ^a (0.2)	3.2 ^{ab} (0.4)	3.0 ^b (0.2)
Maximum leaf length (cm)	16.5 ^a (1.4)	26.2 ^a (2.3)	17.3 ^a (2.7)
Maximum leaf width (cm)	0.21 ^b (0.02)	0.28 ^a (0.02)	0.14 ^c (0.01)
Specific leaf area (cm ² mg dw ⁻¹)	0.16 ^b (0.01)	0.28 ^a (0.02)	0.19 ^b (0.03)
Mean no. of laterals seedling ⁻¹	1.2 ^a (0.2)	0.4 ^b (0.2)	0.0 ^b (0.0)
Growth and production of primary shoot			
Shoot growth rate (cm ² shoot ⁻¹ d ⁻¹)	0.38 ^a (0.04)	0.43 ^a (0.09)	0.12 ^b (0.04)
(mg dw shoot ⁻¹ d ⁻¹)	2.24 ^a (0.30)	1.65 ^a (0.35)	0.46 ^b (0.08)
Relative growth rate (cm ² cm ⁻² d ⁻¹)	0.027 ^a (0.001)	0.022 ^a (0.002)	0.019 ^a (0.002)
Rhizome productivity (mg dw shoot ⁻¹ d ⁻¹)	1.64 ^a (0.39)	0.56 ^{ab} (0.13)	0.12 ^b (0.02)
PI (days) ^b	11	21	20
Leaf life span (days)	48	59	67
Leaf pigments of primary shoot			
Chl <i>a</i> (mg dm ⁻²)	2.60 ^{ab} (0.16)	1.96 ^b (0.22)	2.87 ^a (0.23)
Total chlorophyll (<i>a</i> + <i>b</i>) (mg dm ⁻²)	3.74 ^{ab} (0.22)	2.97 ^b (0.34)	4.44 ^a (0.35)
Chl <i>a</i> : <i>b</i> ratio	2.12 ^a (0.22)	1.91 ^b (0.01)	1.83 ^b (0.04)
^a Ratio of mg root + rhizome dw to mg shoot dw			
^b Plastochrone interval (days between leaf initiation; Jacobs 1979)			

(Table 3). Seedlings grown at low light displayed a prolonged and variable PI of 19 d in June, 14 d in July, and 20 d in August. After 12 wk of treatment, seedlings grown at low light held their leaves 8 d longer than those at medium light, and 20 d longer than those at high light.

After 12 wk of shading, seedlings from the low light treatment had a significantly greater chlorophyll *a* and total chlorophyll (*a* + *b*) concentration (mg dm⁻²) compared to seedlings grown in medium light (Table 3). However, seedlings maintained in low and medium light had a significantly lower ratio of chlorophyll *a* to *b* than seedlings grown in high light.

Short-term photosynthetic rates ($\mu\text{mol O}_2 \text{ dm}^{-2} \text{ min}^{-1}$) were significantly lower in seedlings from the low light treatment versus the high and medium treatments in June, but not in July or August (Table 4). There were no significant differences in respiration rates ($\mu\text{mol O}_2$

Table 4. *Zostera marina*. Net production and respiration rates in June, July and August of whole seedlings grown in High, Medium and Low light. Production ($\mu\text{mol O}_2 \text{ dm}^{-2} \text{ min}^{-1}$) is normalized to leaf surface area. Respiration ($\text{O}_2 \text{ mg dw}^{-1} \text{ min}^{-1}$) is normalized to whole plant dry weight. Units are μmol . Values in columns followed by the same letter indicate no statistical difference between treatments. Data are means (\pm SE)

	Jun	Jul	Aug
Net production			
High	2.65 (0.39) ^a	1.51 (0.29) ^a	3.48 (0.18) ^a
Medium	2.21 (0.21) ^{ab}	2.12 (0.12) ^a	1.19 (0.40) ^a
Low	0.96 (0.24) ^b	1.05 (0.16) ^a	1.65 (0.48) ^a
Respiration			
High	0.46 (0.21) ^a	0.55 (0.12) ^a	0.44 (0.05) ^a
Medium	No data	0.36 (0.16) ^a	0.30 (0.10) ^a
Low	0.66 (0.07) ^a	0.23 (0.02) ^a	0.27 (0.04) ^a

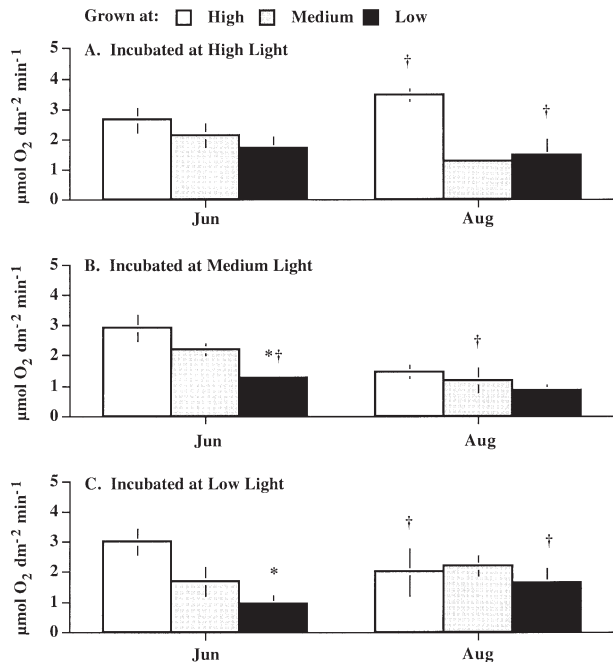


Fig. 4. Net photosynthetic production of seedlings grown in High, Medium and Low light treatments and incubated for 5 h at each light level. Errors represent the SE of the mean. *Indicates statistical difference between the Low and High treatment at the light level of incubation. Bars with a † above indicate less than 4 replicates were used to determine statistical differences. Statistical differences were calculated using an ANOVA on ranked data followed by a post hoc Bonferroni test ($p < 0.016$)

mg plant dw⁻¹ min⁻¹) among treatments during the course of the experiment.

The actual success of the photoadaptive responses of *Zostera marina* seedlings can be assessed by comparing photosynthetic performance of plants from each experimental shading treatment when placed in the other treatments. Calculated values of net production normalized to shoot surface area provide an index of photosynthetic performance. In June, plants grown for ca 10 d in low light had significantly lower photosynthetic production rates compared to plants grown for ca 10 d in high light when placed in medium or low light, whereas they were not different in August (Fig. 4). The inability to show a statistical difference in August may be due to low sample size ($n = 2$) in some cases coupled with high variability among individual plants. There were no significant differences in photosynthetic production rates between seedlings from any treatment when placed in any of the incubation light levels. For example, plants from the low light treatment had similar production rates whether they were placed in high, medium or low light in both June and August.

DISCUSSION

Survivorship, reproduction, morphology, and growth rate

The high survival and photosynthetic production rates of even the heavily shaded seedlings suggest that adaptive responses were adequate, at least for the first summer of growth. However, long-term vegetative survival was unlikely, since no laterals were formed and below ground biomass was severely reduced. The retardation of vegetative reproduction suggests that seedlings require a minimum of $8 \text{ E m}^{-2} \text{ d}^{-1}$ PAR on average during their first summer of growth in order to increase bed size.

Changes in specific leaf area with reduced light for adult *Zostera* have not been consistent (Table 5). The increase in SLA in our seedlings may be an explanation for the ability of the medium light seedlings to maintain growth rates and surface area equivalent to plants grown in high light. Thinner leaves, coupled with an increase in chlorophyll *a* per unit mass, would result in a decrease in the relative amount of non-photosynthetic tissue and an increase in light absorption per unit biomass (Goldsborough & Kemp 1988). However, while thinner leaves may increase the maximum photosynthetic rate (Enríquez et al. 1995), they may also be more prone to breakage (Kopp 1998).

Increases in chlorophyll *a* under conditions of reduced light, such as we found in our seedlings, are commonly reported for mature *Zostera* (Table 5). An increase in chlorophyll *a* in marine macrophytes increases light absorption according to a law of diminishing returns (Enríquez et al. 1994), so that a large increase in chlorophyll *a* increases light absorption only marginally. This suggests that any increase in chlorophyll initiated by the most highly shaded plants could not have been sufficient to enable them to sustain growth rates and leaf initiation rates similar to plants maintained at higher light levels.

The similarity in shoot surface area between seedlings grown in high and medium light treatments is somewhat surprising, as shoots collected from the high light treatment had both more primary shoots with lateral shoots and also more laterals per primary shoot. The explanation may lie in other aspects of shoot morphology. Seedlings grown in medium light had a longer leaf lifespan, which allowed leaves to grow taller and wider, increasing surface area.

Since leaf production is directly linked to rhizome production, with each new leaf corresponding to a new rhizome node (Jacobs 1979), a longer PI results in a lower rhizome production rate and, therefore, lower below ground biomass. Lowered allocation of production to rhizomes has been reported as a consequence of

Table 5. General results of studies on *Zostera* species subjected to lowered irradiance levels. +: increase, -: decrease. ns: no significant difference

Source	Leaf pigments	Growth rate	PI	Chl a:b ratio	Specific leaf area: dm ² gdw ⁻¹	Lateral shoot initiation	Rhizome allocation	Shoot biomass	P _{max}
Dennison & Alberte (1982)	+	-	+	-	ns			+	-
Dennison & Alberte (1985)	+		+	ns	-			ns	-
Dennison & Alberte (1986)	+	-	+	-	ns		-	-	-
Short 1991		-						-	
Olesen & Sand-Jensen (1993)	+	-			+		-	-	
Abal et al. (1994)*	+	-	+			-	-	+	
van Lent & Verschuure (1994)	+								
Goodman et al. (1995)									-
van Lent et al. (1995)		-						-	
Zimmerman et al. (1995)		-		ns					ns
This study	+	-	+	+	+	-	-	-	-

* *Z. capricornii*

shading in mature *Zostera marina* (Table 5). Energy reserves accumulated during the summer months are crucial for support of metabolic activity and growth during the low light periods of winter and spring (Madsen 1991, Olesen & Sand-Jensen 1993, Kraemer & Alberte 1995, Zimmerman et al. 1995). Therefore, although seedlings grown in low light could survive an entire summer with an average daily PAR of 3.3 E m⁻² d⁻¹, they would be unlikely to survive the winter due to inadequate rhizome reserves.

Photosynthesis and respiration

Short-term photosynthetic rates per unit leaf area of seedlings were 2 to 3 times higher than reported for mature *Zostera*, even when plants were growing at high irradiance (Dennison & Alberte 1982, 1986, Marsh et al. 1986). A recent study of *Cymodocea nodosa* reported higher PAR saturated photosynthetic rates (and higher respiration rates) in seedlings versus lateral or primary shoots (Nielsen & Pederson 2000). They attributed this difference to greater nutrient availability in seedling patches compared to larger adult meadows, however they did not address the issue of self-shading within established meadows. The reduction in net photosynthetic rates in plants grown in low light even when temporarily subjected to high light implies that they are unable to exploit short-term increases in light that occur in estuarine habitats.

Dennison & Alberte (1982) found that when plants received 100 µE m⁻² s⁻¹ less than 10 h d⁻¹, growth rates were strongly affected. When they received less than 6 h, both growth and survival were compromised. During our experiment, growth rates of seedlings experi-

encing 8 h of 100 µE m⁻² s⁻¹ d⁻¹ were unaffected, but they were seriously reduced when the plants only received 4 h d⁻¹. This suggests that the length of time seedlings are exposed to light may be as important as the fraction of incident light they receive.

CONCLUSIONS

Decreases in light availability had effects on *Zostera marina* seedlings that are summarized in Fig. 5. In the field, the survival of planted or naturally occurring patches of seedlings depends on growth, mortality, and reproduction of the population. In this study, although survival was high even at very low light, above and below ground growth rates, and vegetative reproduction were negatively affected. Our results suggest that seedlings need considerably greater than 4 h of irradiance exceeding 100 µE m⁻² s⁻¹, and greater than 8 E m⁻² d⁻¹ mean daily PAR during their first summer of growth to become established perennial beds. Our results also indicate that rapid vegetative expansion of patches composed of seedlings can only occur at relatively high light intensities. Although some expansion can occur at a mean summer PAR of 8 E m⁻² d⁻¹, seedlings are more likely to invest energy in longer and wider leaves, rather than in lateral shoot production. Additionally, the increase in SLA (thinner leaves) and the decrease in below ground material may have consequences for seedling survival in the field. Thinner leaves are more susceptible to breakage and low below ground biomass may decrease anchoring capacity and nutrient acquisition. When mean daily quantum flux drops to 3.3 E m⁻² d⁻¹ during the first summer of growth, the potential for multi-year seedling survival is low.

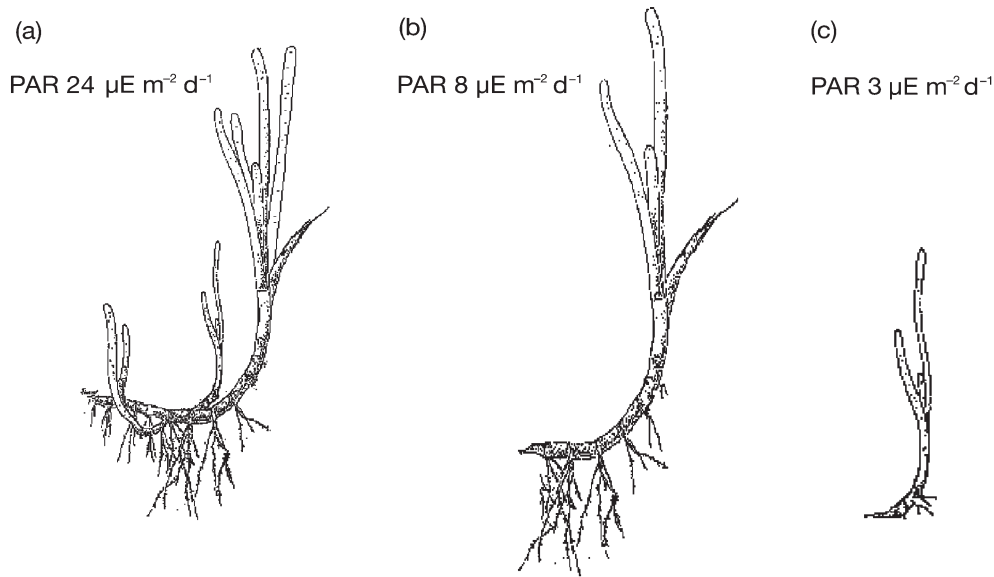


Fig. 5. Summary of seedling response to 12 wk of growth at High, Medium and Low light. Values for daily PAR are means for the 12 wk period. Drawings adapted from Thayer et al. (1984). (a) 100 % survival, 85 % produce lateral shoots, large shoots by weight, high below ground biomass, equal weight allocation above and below ground, 4–5 leaves per primary shoot, low area per unit biomass, rapid primary shoot growth rate, rapid rhizome production rate, short PI, high chl *a*:*b* ratio; (b) 94 % survival, 29 % produce lateral shoots, 3–4 leaves per primary shoot, long, thin and wide leaves, rapid primary shoot growth rate, long PI, low pigment concentrations, low chl *a*:*b* ratio; (c) 74 % survival, no lateral shoots, small shoots by weight and area, low below ground biomass, greater biomass allocation above than below ground, 3 leaves per primary shoot, narrow leaves, slow primary shoot growth rate, slow rhizome production rate, long PI, high pigment concentration

Acknowledgements: We acknowledge and thank S. Granger, S. Sherwood, B. Buckley and M. Brush for technical and scientific advice throughout the experiment, and S. Granger and M. Traber for seed collection and separation. We would also like to thank Dr V. de Jonge and the anonymous reviewers who provided very helpful comments on this manuscript. Rhode Island Sea Grant provided funding for this research

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Editorial responsibility: Victor de Jonge (Contributing Editor), Haren, The Netherlands

Submitted: June 12, 1999; Accepted: April 3, 2001
Proofs received from author(s): November 15, 2001