

Increasing canopy shading reduces growth but not establishment of *Elodea nuttallii* and *Myriophyllum spicatum* in stream channels

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Abstract Submersed macrophytes are often important drivers of instream structure and function, but can be problematic when overabundant. The establishment success, growth rates, and morphology of submersed macrophytes could be affected by alteration of instream light levels during riparian restoration (via removing or planting canopy-forming vegetation), potentially influencing the success of riparian restoration projects aimed at improving aquatic habitats. To examine the effects of canopy shading on two common submersed macrophytes—*Elodea nuttallii* (native) and *Myriophyllum spicatum* (non-native)—I conducted experiments in artificial stream channels in two locations in California, USA. Initial establishment of stem fragments of both species was close to 100% in all shade levels, including shade that reduced incident light by 94%. Growth rates of the two species were similar across shade levels, and lowest in the highest shade. Full light appeared to have a photoinhibitory effect on *E. nuttallii* at the higher elevation site. Higher shade

increased the length:biomass ratio and decreased the branching of *E. nuttallii*. My findings suggest that altering canopy cover during riparian restoration is unlikely to affect the ability of these species to establish, but higher shade levels should slow their growth and create more favorable conditions for other instream organisms.

Keywords Riparian restoration · Propagule establishment · *Myriophyllum spicatum* · *Elodea nuttallii* · Shade · Sierra Nevada Aquatic Research Laboratory

Introduction

Whether at the scale of large rivers or small creeks, the goals of riparian restoration generally include improving instream habitat for native flora and fauna (Palmer et al., 2007; Roni et al., 2008). Follow-up monitoring of riparian restoration, though rare, has generally focused on fish, birds, mammals, invertebrates, or native riparian vegetation (Bash & Ryan, 2002; Roni et al., 2008; Feld et al., 2011; Gardali & Holmes, 2011). Submersed macrophytes often play critical roles in the structure and function of stream ecosystems (Rejmánková, 2011), but the effects of riparian restoration on these communities are rarely addressed.

The response of submersed macrophyte communities to riparian restoration, in terms of increased or decreased abundance, invasion of new species, or loss

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of species, can affect whether or not overall goals of improving instream habitat quality and restoring ecosystem function are achieved. Submersed macrophytes provide food, substrate, and habitat for aquatic and terrestrial organisms (Newman, 1991; Rejmánková, 2011) and drive important physical and chemical processes: they create heterogeneity in water velocity and substrate texture (Sand-Jensen & Mebus, 1996), trap sediments and particulate matter, oxygenate the water column and rhizosphere, and absorb and transform nutrients (Carpenter & Lodge, 1986). Yet, submersed macrophytes can also pose management challenges: excessive growth of weedy macrophytes can lead to reduced water velocity, increased water temperature, lower dissolved oxygen, and degraded fish spawning areas (Unmuth et al., 2000; Anderson, 2011). Invasion of non-natives can competitively reduce desirable native macrophytes (Madsen et al., 1991; Boylen et al., 1999) which may reduce fish and invertebrate diversity and abundance (Krull, 1970; Keast, 1984; Wilson & Ricciardi, 2009; Schultz & Dibble, 2012). Therefore, practitioners should be concerned with both the positive and negative ways submersed macrophytes can influence the success of riparian restoration projects, and should consider how restoration could affect these important communities.

While restoration of riparian zones may affect submersed macrophyte communities in a number of ways (e.g., changes in water quality and flow rates), here I focus on one important mechanism: alteration of light availability. Light is an important limiting resource for submersed macrophytes (Lacoul & Freedman, 2006; Bornette & Puijalon, 2011), and riparian restoration can either decrease or increase this resource. Riparian restoration practitioners generally aim to revegetate stream banks with native plants, often with an explicit goal of creating more shade over streams (decreasing light) to moderate temperatures and improve instream habitat for fish and other organisms (Opperman & Merenlender, 2004). Conversely, non-native riparian plants are often removed in the initial stages of restoration, and removing canopy-forming species can cause an immediate increase in instream light levels.

In plant communities, increases in resources (such as light) are commonly linked with greater invasion potential (Davis et al., 2000), and competitive dominance of non-native over native species (Daehler, 2003). Decreases in canopy cover might, therefore, be expected to facilitate establishment and growth of non-native

macrophytes at the detriment of native macrophytes, while increasing canopy shading may hinder invasion and benefit natives, but these hypotheses are rarely, if ever, tested in submersed macrophyte communities.

Most submersed macrophytes reproduce primarily asexually through fragmentation of stems and dispersal of stem fragments (Sculthorpe, 1967). Vegetative propagules are created through natural and anthropogenic processes (e.g., mechanical harvesting and boat propellers), and can range widely in size (Northwest Hydraulic Consultants, 2010). The ability for stem fragments of different sizes to *initially establish* under different levels of canopy cover is particularly important to understand, because non-native invasive macrophytes can be extremely difficult, if not impossible, to eradicate once established (Anderson, 2011). On the other hand, fostering or maintaining the ability of native submersed macrophytes to establish in restoration sites through natural recruitment or active planting may be desirable.

To make predictions and guide management decisions on the effects of altered canopy cover on submersed macrophyte propagule establishment and growth, practitioners would ideally look to studies conducted in flowing conditions, but such studies are usually conducted in tanks with stagnant water (e.g., Sand-Jensen & Madsen (1991), Barrat-Segretain (2004), Mielecki & Pieczynska (2005), and Angelstein & Schubert (2009)). Results of experiments in non-flowing conditions may not directly apply to macrophytes in flowing conditions, as water velocity can affect macrophyte physiology. Increasing water velocities can enhance photosynthesis and growth by increasing the rate of nutrient and gas exchange, yet when velocities are too high, increased shear stress can cause a decrease in photosynthetic rates and plant growth (Madsen & Sondergaard, 1983; Madsen et al., 1993). As such, controlled experiments concerning the establishment and growth of submersed macrophytes in streams should ideally be conducted in flowing conditions, yet this is rarely done (but see Dawson and Kern-Hansen 1979).

Morphological responses of macrophytes to shade levels (e.g., differences in stem branching or density) may also be important, because macrophyte growth forms influence instream habitat structure. Differences in macrophyte density and structural complexity have been shown to affect the growth rates, abundance, and behavior of fish and invertebrates (Crowder & Cooper, 1982; Warfe & Barmuta, 2006).

To better understand the effects of riparian restoration on submersed macrophyte communities, I studied the establishment and growth of two macrophyte species under different shade levels in artificial stream channels, using *Elodea nuttallii* (Planch.) H. St. John (western waterweed) and *Myriophyllum spicatum* L. (Eurasian watermilfoil) as study species. Both are widespread throughout North America—the former a native and the latter a notoriously invasive non-native—and both are perennials that reproduce almost exclusively through vegetative fragmentation (Sculthorpe, 1967). In the summer of 2011, I conducted one experiment with *E. nuttallii* only, and one with both *E. nuttallii* and *M. spicatum*, in artificial stream channels at a higher elevation site, the Sierra Nevada Aquatic Research Laboratory (SNARL), and a lower elevation site, the University of California, Davis (UC Davis), respectively. I conducted experiments in two different locations to gain a sense of the generality of results across systems with different abiotic conditions. Because submersed macrophyte vegetative propagules can vary in size, I tested whether two different sizes of fragments differed in ability to establish across shade levels.

For the experiment conducted with *E. nuttallii* alone (SNARL), I hypothesized that establishment success (rooting into soil), growth rates, and branching would decrease with increasing shade. For the experiment with both species (UC Davis), I hypothesized that while each species would show reductions in growth rates with greater shade, the non-native species would perform better than the native in the lower shade levels, but the native would do as well or better in the higher shade levels (i.e., an interaction between species and shade). For both experiments, I expected that smaller stem fragments would have lower establishment success than larger fragments in the higher shade treatments but not the lower shade treatments (i.e., an interaction between shade and initial fragment length).

Methods

Sierra Nevada Aquatic Research Laboratory experiment

Site description

The Sierra Nevada Aquatic Research Laboratory (SNARL), a University of California Natural Reserve

Table 1 Water quality data for SNARL and UC Davis

Sampling date	SNARL		UC Davis	
	August 29, 2011		September 15, 2011	
Water quality parameter	Mean	Range	Mean	Range
Temperature (°C)	17.75	(17.6-17.9)	19.44	(19.01-19.82)
pH (SU)	8.21	(8.16-8.24)	8.11	(8.03-8.18)
Specific conductance (µS/cm)	112	(112-112)	716	(716-717)
Turbidity (NTU)	7.5	(7.5-7.6)	8.0	(7.8-8.2)
Dissolved oxygen (% saturation)	81.2	(80.0-82.3)	111.5	(103.6-117.9)

operated by UC Santa Barbara, is located in Mono County, California in the eastern Sierra Nevada mountains (37°36'51"N, 118°49'47"W, elevation 2,160 m). Water from Convict Creek, an oligotrophic stream that drains Convict Lake, is diverted through a system of nine replicated artificial concrete-lined channels, three of which were used for this experiment. Each channel is 1-m wide and 50-m long. The channels have concrete walls and a rock and gravel substrate. Sandy soil from the surrounding area was added to the centers of plots to provide a more uniform surface for plant establishment, and any existing aquatic plants were removed before the experiment began. Wooden weirs were placed in the middle and downstream ends of each channel to create a more uniform depth throughout the channel. Depth was on average 19 cm, and ranged from 10 to 30 cm.

Temperature, pH, dissolved oxygen, specific conductance, and turbidity were measured with a YSI multi-probe sonde (YSI Inc., Yellow Springs, Ohio, USA) at upstream and downstream points in each channel in the afternoon of August 29, 2011 (Table 1). Flow into each channel was controlled by sluice gates, and water velocity was kept uniform among the channels. Due to weather and stream flow variation, water velocity fluctuated throughout the duration of the experiment. During sampling on August 29, velocity averaged 0.1 m/s, but was probably as high as 0.2 m/s (estimated) near the start of the experiment. Water nutrients were not measured for this study, but historical data indicate that very low nitrogen and

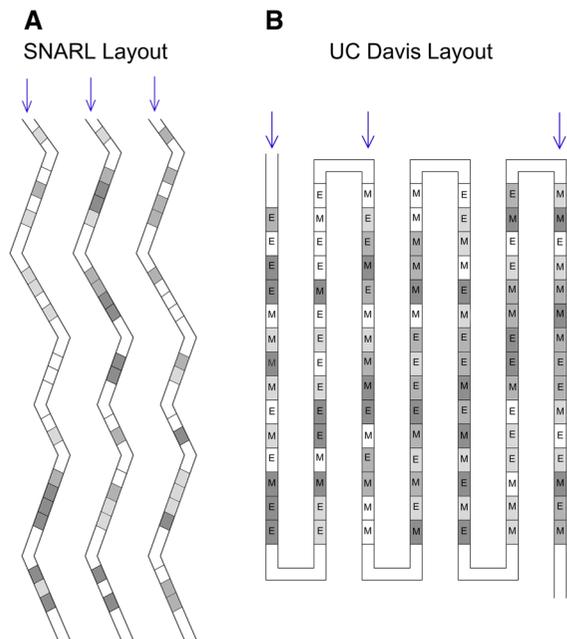


Fig. 1 Diagram of channel layouts for **A** SNARL and **B** UC Davis experiments (not to scale). Plots are shown as *rectangles* shaded according to assigned shade level—zero, low, medium, or high. In all plots, four short and four long stem fragments were planted. For the UC Davis layout, the species planted in each plot is indicated with a letter (*M* = *M. spicatum*; *E* = *E. nuttallii*). At SNARL, only *E. nuttallii* was planted. Water inputs are indicated with arrows. At SNARL, each treatment had 15 replicates initially, but high winds caused the loss of nine high shade plots and one medium shade plot. At UC Davis, the most downstream replicate of each of the eight treatments was not collected due to time constraints, so final $N = 12$

phosphorus levels are typical for Convict Creek (SNARL, personal communication).

Experimental design

To test the effects of shade on the establishment and growth of two different fragment sizes of *E. nuttallii*, shade treatments were randomly assigned to plots, with fragment sizes nested within plot in a split-plot design.

Each of the three channels was divided into 20 1.5-m-long plots (Fig. 1A). Into the center of each plot, four 5-cm (“short”) stem fragments and four 10-cm (“long”) stem fragments of *E. nuttallii* were placed 5 cm apart from each other on the substrate surface in a 4×2 arrangement alternating long and short fragments. The fragment lengths chosen are within the typical range of naturally dispersing

propagule sizes observed for a similar *Elodea* species in a California stream (Northwest Hydraulic Consultants, 2010). Source material for the fragments was collected on site, and any roots, branches, periphyton, or invertebrates were removed from the initial fragments before planting. Each fragment included an apical tip. Stem fragments were secured in the plots with plastic-coated metal ground staples. All fragments were planted on July 9, 2011. Additionally, 5 and 10 cm fragments (ten each) were dried overnight in an electric drying cabinet (Fisher Hamilton Scientific Inc., model # 218S632) at 60°C to determine average initial weights for calculating dry weight biomass gained (final—initial weight, hereafter, “biomass gained”), and relative growth rate (RGR).

Each of the 60 plots was randomly assigned one of four levels of shade using 30, 60, or 90% black polyethylene shade cloth or no shade cloth. Subsequent analysis of the actual amount of light reduction produced by the shade cloth, as measured in full sun with a LI-COR LI-193 spherical quantum sensor (LI-COR, Lincoln Nebraska, USA), revealed that the 30, 60, and 90% shade cloth reduced incident photosynthetically active radiation (PAR) by an average of 40, 72, and 94%, respectively. Therefore, shade levels will henceforth be referred to as “zero” (no shade cloth), “low,” “medium,” and “high.” Shade cloth was placed over plots approximately 0.2 m above the water surface.

On August 29, 2011 at mid-day, PAR was measured with a LI-COR LI-193 spherical quantum sensor below the water in the four shade treatments to assess the amount of light reaching the planted macrophytes. Measurements were 1,578, 990, 419, and 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ for the zero, low, medium, and high shade levels, respectively.

Data collection

During the experiment, high winds detached some of the 60 and 90% shade cloth, reducing the number of replicates for the medium and high treatments from 15 to 14 and 6, respectively. In the remaining plots, individual stem fragments were harvested from August 30–September 1, 2011, after growing for an average of 53 days. This length of time was expected to allow plants time to establish and experience the effects of shade without becoming limited by other factors (e.g., substrate nutrients and space). Each plant

was measured for number of branches and total length (sum of lengths of all branches). The presence of roots was noted for each fragment as an indication of successful establishment, but roots were removed along with any attached algae and invertebrates to obtain above-substrate biomass. For each plot, the (initial) short fragments were combined separately from the long fragments, and dried in an electric drying cabinet at 60°C for 48 h. Using these plot-level total biomass values, average per-plant values were calculated for biomass gained, RGR, and length:biomass ratio.

Statistical analysis

Mixed effects ANOVA models were used to evaluate the effects of shade level, initial fragment length, and their interaction on biomass gained, RGR, length:biomass ratio, and the number of branches per plant. “Plot” was included as a random effect with initial fragment length nested within plot. Relative growth rate was calculated as $(\ln(\text{final weight}) - \ln(\text{initial weight})) / \text{days}$. For length:biomass ratio and RGR, weighted least squares approaches were used due to unequal variances among treatment groups. Number of branches was log transformed (base 10) to comply with normality assumptions. Differences among shade treatments within each response variable were analyzed using least squares means with Tukey adjustments in *p*-values. All analyses were conducted in SAS software version 9.2 (SAS Institute Inc., Cary, North Carolina, USA).

University of California, Davis experiment

Site description

A series of connected stream channels was created at the University of California, Davis (UC Davis) Putah Creek Riparian Reserve in the Central Valley of California (38°31'42" N, 121°47'7" W, elevation 21 m). The soil at this site is classified as Yolo Silt Loam, and the terrestrial plant community was dominated by non-native grasses and forbs. Seven channels were excavated, each ~24-m long, 1-m wide, and 0.6-m deep. The channels were connected into a single system so that water diverted from an aquaculture facility flowed through all of the channels, with water inputs at three of the sections (Fig. 1B).

Water velocity averaged 0.05 m/s throughout the experiment.

Temperature, pH, dissolved oxygen, specific conductance, and turbidity were measured on September 15, 2011 with a YSI multi-probe sonde in the center of the three middle channels (Table 1).

Experimental design

Elodea nuttallii and *M. spicatum* source material were collected locally from Putah Creek (38°31' 36" N, 121°48' 13"W), cleaned of attached algae and invertebrates, and cut into 4-cm (“short”) and 8-cm (“long”) apical fragments. These fragment sizes are in the modal range for vegetative propagules of *E. nuttallii* and *M. spicatum* found locally in Putah Creek (Northwest Hydraulic Consultants, 2010). Any roots or branches were removed from fragments. Ten additional fragments of 4 and 8 cm each were dried overnight in an electric drying cabinet at 60°C to determine average initial weights for calculating biomass gained and RGR.

Each channel was divided into 1.5-m-long plots, and each plot was randomly assigned one of eight treatment combinations comprised two species—*E. nuttallii* and *M. spicatum*—crossed with four shade levels—zero, low, medium, and high (see actual percent light reduction of shade cloth levels above). In each plot, four long and four short fragments of either *M. spicatum* or *E. nuttallii* were staked to the soil surface underwater using plastic-coated ground staples in a 2x4 arrangement alternating short and long fragments. Fragments were placed 10 cm apart and were planted on July 25 and 26, 2011. Shade cloth was placed over plots approximately 0.2 m above the water surface.

To assess the amount of light reaching the planted macrophytes, PAR levels were measured underwater near the sediment surface at mid-day with a LI-COR LI-193 spherical quantum sensor on September 15, 2011. Measurements were 1,721, 1,062, 419, and 168 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for the zero, low, medium, and high shade levels, respectively.

Data collection

At the time of harvesting (50–51 days after planting), many plants had become very large and intertwined and were fragmenting at the slightest touch, making it

impossible to collect individual plant-level data. Therefore, analyses were based on plot-level biomass only. From September 14 to 16, a total plot biomass was collected, dried in a 60°C oven for 48 h, and weighed. Twelve replicates of each treatment were obtained.

Statistical analysis

Differences in plot-level biomass gained and RGR across species and shade levels were analyzed using two-way weighted least squares ANOVA. Biomass gained was log transformed (base 10) to comply with normality assumptions. A shade * species interaction term was included in the models to determine whether the two species responded differently to the four shade levels. To analyze differences among shade levels within each species, ANOVA was followed by means comparisons using Tukey's Honest Significant Difference method. One outlier, as identified by a Grubb's outlier test (Grubbs, 1950), was excluded from all analyses. (This outlier was the first plot in the first channel, and may have grown larger due to higher water velocity in that location.) Analyses were completed using the "stats" package in R, version 2.15.2 (R Development Core Team, Vienna, Austria).

Results

SNARL experiment—effects of initial fragment length and shade on *E. nuttallii*

A total of 348 individual plants (87% of originally planted) in 50 plots were harvested and measured. The remaining 52 plants were missing entirely, and had apparently washed away. No significant effects of shade level or original length on the number of remaining plants in each plot were detected ($P = 0.19$, $P = 0.46$, respectively), all remaining plants had rooted and grown, and I did not see any evidence of plant death within any plots at any point during the experiment; therefore, I concluded that survival of *E. nuttallii* was close to 100% in all shade levels for both initial lengths.

ANOVA statistics for the effects of initial fragment size and shade level on *E. nuttallii* growth metrics are shown in Table 2. See Online Resource 1, Table A for mean values and standard errors for each initial length * shade level combination.

Table 2 ANOVA table for SNARL experiment

Factor	F value	P
Dry weight biomass added		
Shade level	8.31	<0.001
Fragment size	1.43	0.235
Shade * fragment size	0.32	0.809
Relative growth rate		
Shade level	9.06	<0.001
Fragment size	41.58	<0.001
Shade * fragment size	0.33	0.802
Length: DW biomass ratio		
Shade level	21.18	<0.001
Fragment size	1.16	0.285
Shade * fragment size	0.34	0.794
Number of branches		
Shade level	7.62	<0.001
Fragment size	0.06	0.801
Shade * fragment size	0.44	0.727

Boldfaced values are significant at the $\alpha = 0.0125$ level. For all response variables, $DF = 3$ for shade level and shade * fragment size, and $DF = 1$ for fragment size

Initial fragment length had significant effects on RGR, with short fragments having 28% higher growth rates than long fragments across shade levels. However, initial fragment length had no significant effects on biomass gained, length:biomass ratio, or number of branches. The interaction between shade level and initial fragment length was not significant for any of the response variables.

Shade level, in contrast, had highly significant effects on biomass gained, RGR, length:biomass ratio, and number of branches, but the pattern of response to shade level differed between response variables. These differences were explored using Tukey means comparisons on the main effect of shade (Fig. 2).

Biomass gained and RGR were highest in intermediate shade levels. (Figure 2A and B). The plants in low and medium shade gained on average 75 and 64% more biomass than the high shade level, and 33 and 25% more biomass than the zero shade level, respectively.

Length:biomass ratio (Fig. 2C) increased significantly with higher shade: the medium shade level had a 24% larger ratio and the high shade level a 83% larger ratio than the zero and low treatments combined (which were not significantly different from each other). Though not measured, I observed that the

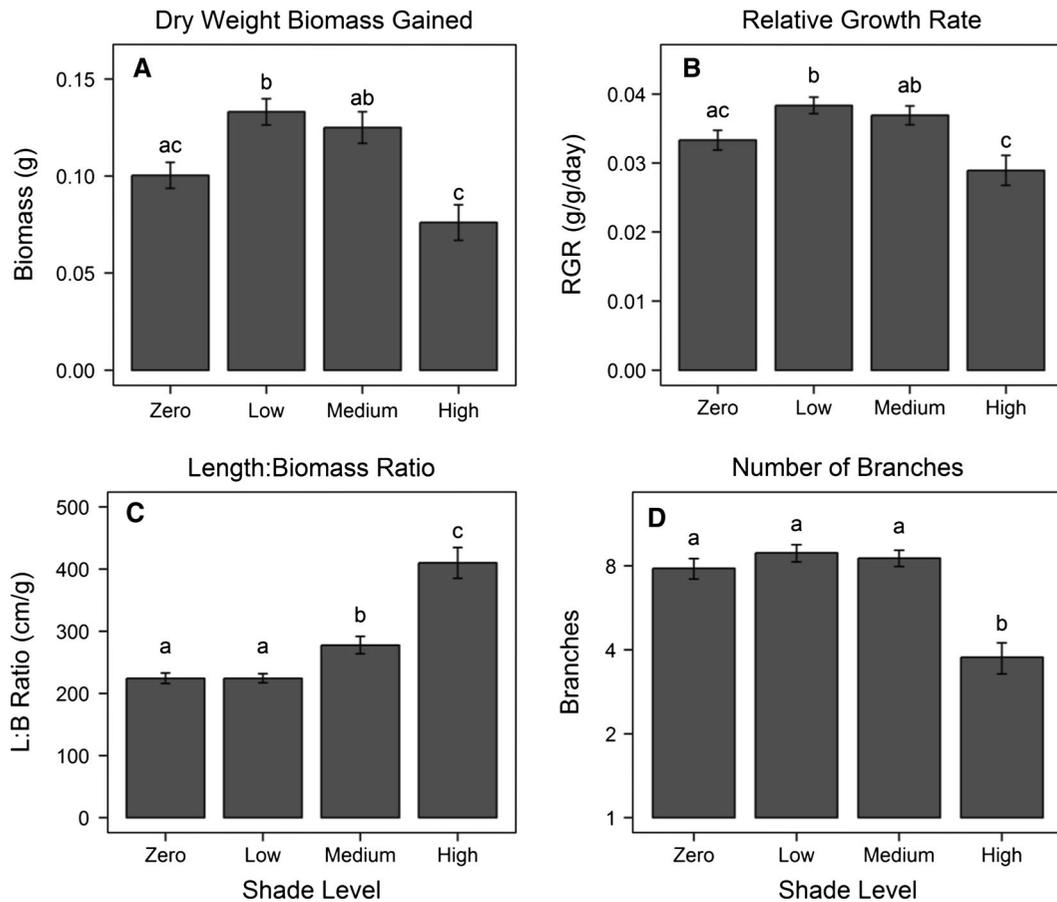


Fig. 2 Response of *E. nuttallii* plants to shade level in SNARL experiments. Short and long fragments were averaged to show main effects of shade. Error bars show standard errors. Letters

above columns indicate results of Tukey means comparisons (treatments with the same letter are not significantly different at the $\alpha = 0.05$ level). Number of branches is shown on a log axis

internode lengths of *E. nuttallii* were consistently longer in the higher shade levels. These findings suggest a plastic response of stem elongation in lower light environments.

The number of branches produced by *E. nuttallii* plants was similar in the zero, low, and medium shade levels, but significantly lower in the high shade level (Fig. 2D). Plants in the high shade level produced 55% fewer branches compared to the three lower shade levels combined.

UC Davis experiment—effects of shade on *E. nuttallii* and *M. spicatum*

No propagule mortality was observed in any of the plots for either species, though exact numbers were

impossible to discern; individuals were intertwined and rooted in multiple locations in most zero, low, and medium shade plots, and attempts at separating individuals resulted in stem fragmentation. Based on observations made during harvesting, it appeared that close to 100% of fragments of both species and initial lengths established in all shade levels. All collected plants had rooted into the substrate.

ANOVA tables for the effects of shade and species on biomass gained and RGR are shown in Table 3. Both shade level and species had significant effects on plot-level biomass gained and RGR, but there was no significant interaction, indicating similar responses to shading between species. Results of Tukey means comparisons within species across shade levels are shown in Fig. 3. See Online Resource 1, Table B for

Table 3 ANOVA table for UC Davis experiments

Factor	F value	P
Biomass gained (log transformed)		
Shade	76.78	<0.001
Species	52.72	<0.001
Shade * species	0.59	0.622
Relative growth rate		
Shade	72.94	<0.001
Species	11.52	0.001
Shade * species	0.40	0.753

Boldfaced values are significant at the $\alpha = 0.025$ level. For both response variables, $DF = 3$ for shade level and shade * species, and $DF = 1$ for species

mean values for each species * shade level combination.

Elodea nuttallii gained 85% less biomass in the high shade level compared to the zero shade level. Despite an apparent linear trend in decreasing biomass with greater shade (Fig. 3A), the zero, low, and medium treatments were not significantly different from each other.

Myriophyllum spicatum biomass gained was not significantly different in the zero and low shade levels, suggesting that light may be saturating at these levels. Biomass gained was significantly reduced in the higher shade levels, with 42% less biomass gained in the medium shade level and 87% less in the high shade level compared to the low and zero shade levels combined.

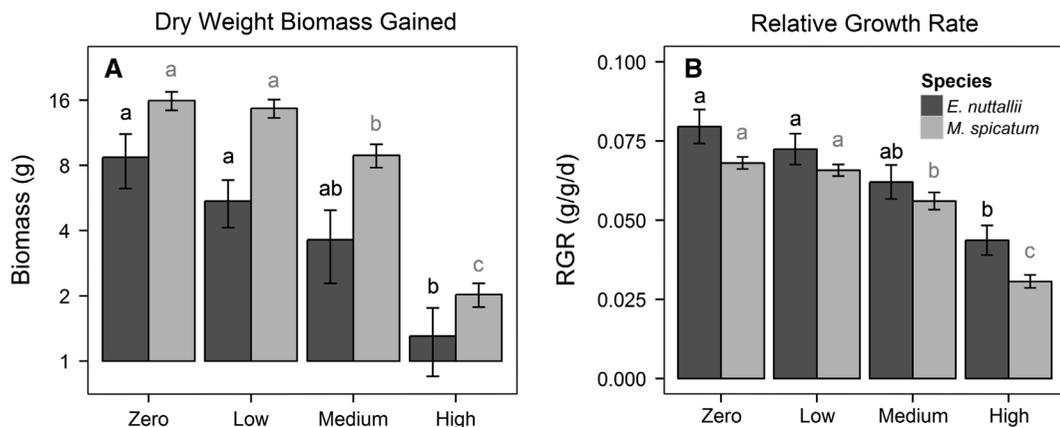


Fig. 3 Response of *E. nuttallii* and *M. spicatum* to shade level in UC Davis experiments. Results are based on plot-level biomass. Error bars show standard errors. Lowercase letters show results of Tukey means comparisons within species across

Biomass gained and RGR were significantly different between the two macrophyte species across shade levels, but conclusions on the relative performance of the species depend on which metric is used for evaluation (Fig. 3). *Myriophyllum spicatum* gained more biomass than *E. nuttallii* in all four shade treatments. However, RGR was higher in *E. nuttallii* than *M. spicatum* in all treatments. This disparity can be accounted for by the fact that while the lengths of the fragments in the plots of both species were the same initially, *M. spicatum* fragments had 3.8 times more dry weight biomass per unit length, on average. Therefore, *E. nuttallii* had higher growth than *M. spicatum* relative to the initial fragment weights.

Discussion

The ability of both native and non-native submersed macrophytes to establish and grow in flowing conditions under different levels of shade has important implications for restoration projects that alter canopy cover over streams, especially if establishing native plants and preventing the establishment of non-natives are a goal. Because macrophytes often play important ecological roles in streams, practitioners may want to foster native macrophyte establishment and (moderate) growth while reducing the likelihood of invasion or proliferation of non-native submersed macrophytes. These topics are also relevant to managers of canals,

shade level (treatments with the same letter are not significantly different at the $\alpha = 0.05$ level). Note the log scale for biomass gained

irrigation ditches, and other waterways where both native and non-native submersed macrophytes can be a nuisance.

My results suggest that the alteration of canopy cover is unlikely to affect the ability of *E. nuttallii* or *M. spicatum* to establish. Contrary to my hypothesis, both species were able to establish with high success in all shade levels, even under shade cloth that reduced PAR by 94%. Despite this large reduction in incident light, PAR levels in the highest shade treatment were measured at 168 and 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ underwater around peak daylight for UC Davis and SNARL, respectively. These light levels, which were possibly elevated because of light scattering underwater, are high enough to support growth of both macrophyte species. Angelstein & Schubert (2009) found under experimental conditions that 8 cm stem fragments of *E. nuttallii* could grow in as low as 10 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and Van et al. (1976) found the light compensation point of *M. spicatum* to be 35 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Barrat-Segretain (2004) found that 5 cm stems of *E. nuttallii* had lower survival in 28 than in 48 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, but these light levels are quite low. My results show that in flowing conditions with a natural photoperiod over the summer, light levels under 94% shade were still high enough to support establishment and growth of *E. nuttallii* and *M. spicatum*.

I hypothesized that shorter stem fragments would be less successful than longer fragments in establishing, particularly in the higher shade treatments, but found that both fragment sizes appeared to have close to 100% establishment success for both species. Riis et al. (2009) showed that smaller fragments of *Elodea canadensis* (a closely related species to *E. nuttallii*, often morphologically indistinguishable) had lower establishment success than longer fragments, but the fragment sizes used in their experiment were smaller than in mine—1 and 0.5 cm. They also found 100% establishment of *M. spicatum* fragments of 2–5 cm. The plants in their experiments were grown in non-flowing conditions and higher light levels (225 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in a 16/8 h light/dark cycle) than my highest shade treatment, and therefore may have been expected to have different outcomes. Taken together, the results of these studies suggest that only very small stem fragments in very low light may be unable to establish successfully, given adequate conditions for other growth factors. Shading from riparian vegetation

alone may not reduce light to low enough levels to reduce establishment success in shallow, clear-water streams in the summer, but establishment may be reduced if canopy shade is combined with greater water depth, turbidity, and/or color.

Shade level had significant effects on all response variables in both locations. At SNARL, *E. nuttallii* gained the most biomass and had the highest RGRs in the low and medium shade levels, and had significantly lower biomass in the zero and high shade levels. Finding that high shade reduced growth was not surprising, but the demonstration of a possible photoinhibitory effect of full light was unexpected. *Elodea nuttallii* has been called a “sun-adapted” plant (Jahnke et al., 1991), and often forms a canopy at the water’s surface (Barrat-Segretain, 2004). Photoinhibition in submersed macrophytes is rarely studied or documented (but see Hussner et al. 2010), possibly because most studies of light’s effect on macrophyte growth use artificial light. Neither species showed reduced growth in the zero shade treatment at UC Davis, but plants in the UC Davis experiment probably experienced lower levels of irradiance compared to SNARL due to greater water depth, lower site elevation, and later experimental initiation. It is also important to note that results from both experiments suggest that light saturation may have been reached at the low (~40%) shade level, which means that alterations to canopy cover that increase or reduce shade within the 0–40% range in shallow, clear-water systems may not have a significant effect on growth of these species.

Plant morphology was affected by shade level as well. At SNARL, *E. nuttallii* stems in the highest shade level were elongated (greater length:DW biomass ratio) and had fewer branches, likely an adaptation for reaching toward light at the water’s surface. Plants in the three lower shade treatments had similar amounts of branching and generally had more prostrate growth forms with many adventitious roots. Though not directly measured, I observed the same phenomenon for *E. nuttallii* in the UC Davis experiment. Similar trends in morphological variation under different shade levels have been demonstrated in *E. canadensis* in experiments by Barko et al. (1982) and Sand-Jensen & Madsen (1991) in non-flowing conditions, suggesting that these morphological responses to shade are consistent in a variety of environmental conditions. Because *E. nuttallii* reproduces primarily through fragmentation of stems, reduced branching in

high shade levels could also mean lower potential for populations to spread.

Shade-driven morphological differences could also have important implications for other instream organisms. For example, compared to plants with sparser, elongated stems, mat-like plants with many rooting branches may provide more effective hiding locations for invertebrates and small fish, but may exclude larger fish. Intermediate stem densities are probably best for fish populations (Crowder & Cooper, 1982), which my research suggests may occur at medium to high shade levels.

Contrary to the hypothesis that natives perform better than non-natives in lower resource conditions and vice versa, the native *E. nuttallii* and the non-native *M. spicatum* had very similar performance in terms of establishment success and growth across shade levels: relative growth rate was higher in all shade levels for *E. nuttallii* than *M. spicatum*, but the opposite was true for biomass gained. Classifying the two species as “native” and “non-native” is perhaps less ecologically meaningful than for other species pairs, because *E. nuttallii* is an aggressive invader and competitor in its non-native range, including regions where *M. spicatum* is native (Angelstein & Schubert, 2009). Results of my experiment suggest that canopy cover may not strongly influence the dominance of one species over the other, but competition experiments with both species planted together in one plot under different shade levels would better explore these dynamics. Interestingly, variance within treatments was consistently greater for *E. nuttallii*, suggesting that *E. nuttallii*'s growth rate may be more influenced by other factors (e.g., soil nutrients and water velocity) that may have varied randomly in this experiment, while growth of *M. spicatum* may be more highly influenced by light level.

Conclusions

Increasing riparian shading has been proposed as a management tool to reduce problematic growth of macrophytes (Dawson & Kern-Hansen, 1979; Anderson, 2011), and the potential efficacy of this idea has been demonstrated by multiple studies. For example, field surveys by Canfield & Hoyer (1988), Madsen & Adams (1989), Julian et al. (2011), Köhler et al. (2010), Ali et al. (2011), and Wood et al. (2012) all found that higher levels of riparian shade were

associated with lower submersed macrophyte abundance. Experiments have also shown reduced submersed macrophyte growth in higher shade, but these studies are almost always conducted in non-flowing conditions (e.g., Barko & Smart, 1981). My studies provide experimental evidence under stream-like conditions that increasing riparian shading could be effective in reducing growth rates and biomass of two common submersed macrophytes, but only at relatively high shade levels, and even then it may not reduce their establishment rates. Conversely, my results suggest that well-intentioned removal of invasive canopy-forming riparian vegetation could have an unintended consequence of increasing the density of submersed macrophytes.

It should be noted that because the effects of riparian shading on macrophyte growth can vary depending on season and plant growth phase (Wood et al., 2012), the timing of restoration in relation to macrophyte lifecycles may influence the outcomes of management actions. Further research into the important connections between riparian restoration and macrophyte communities (for example, similar studies on different species or in different seasons) could help restoration practitioners anticipate aquatic responses to riparian restoration, leading to more targeted and effective management actions.

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