



## Effect of light and simulated herbivory on growth of endangered northeastern bulrush, *Scirpus ancistrochaetus* Schuyler

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Received 13 January 1998; accepted in revised form 20 July 1998

**Key words:** Clipping, Conservation biology, Light availability, Sedge, Wetlands

### Abstract

The independent and interactive effects of light and simulated herbivory on growth and biomass allocation in the endangered emergent sedge, *Scirpus ancistrochaetus* Schuyler, were examined in a 15-week common garden experiment. Light level was manipulated through the use of shade cloth to attain shading levels of 0%, 30%, 63% and 90%, while herbivory was simulated by reducing plant height by 50% six weeks into the experiment. Multivariate Analysis of Variance (MANOVA) of final total (shoot + root) plant mass, leaf width and root to shoot ratio (R:S) indicated overall significant effects of both light and the interaction of light and clipping. Means of these variables decreased with decreasing light level. Furthermore, means of these variables were generally higher for clipped plants than unclipped plants in 0% shade, while they tended to be lower in clipped plants in all other levels of shade. Maximum leaf height was also significantly affected by light. Leaf height was similar in all treatments for the first 11 weeks. For the last four weeks of the experiment, however, leaf height was lowest in plants grown in 0% shade, highest in plants grown in 63 and 90% shade, and intermediate in plants grown in 30% shade. Clipped plants tended to be taller than unclipped plants at lower levels of shade, while the opposite was true at higher levels of shade, although effects were marginally significant. Both light and the interactive effect of light and clipping were important determinants of growth of *S. ancistrochaetus* in this experiment and therefore may be important influences on its distribution within and among pond habitats.

### Introduction

Seasonal freshwater ponds are home to a number of endemic or otherwise rare animal and plant species (Baskin 1994; King et al. 1996; DesMeules & Nothnagle 1997). Such vernal ponds are very sensitive to habitat loss through environmental perturbation and are therefore prone to local extinctions, in part because of their small size (Baskin 1994). In contrast to the number of studies on coastal emergent plants and other plants from open marsh habitats, relatively few studies have been conducted on emergent plants from temporary woodland ponds, especially in the eastern United States. Northeastern bulrush, *Scirpus ancistrochaetus* Schuyler, is a perennial emergent sedge found primarily in small vernal ponds. In Pennsylvania, most

ponds in which *S. ancistrochaetus* is found range from ~200–900 m<sup>2</sup> in area and are typically 1–1.5 m deep when full in early spring. Most ponds containing this species experience gradual drawdowns as the season progresses and can be completely dry as early as July. *S. ancistrochaetus* is limited to approximately 60 populations ranging from West Virginia to Massachusetts and is listed as 'endangered' by the U.S. Fish and Wildlife Service (1991). Little information is available on the life history attributes of this species (but see Bartgis 1992; Lentz & Dunson 1998; Lentz & Johnson 1998), first described by Schuyler (1962). As suggested by Brussard (1991), the collection of basic life-history information, including the influence of environmental factors on growth, can be very useful in

the conservation and preservation of rare species such as *S. ancistrochaetus*.

One environmental factor well known to influence plant growth, reproduction, and distribution is light availability (Boardman 1977). Plants grown in low light often experience decreased rubisco activity, reduced CO<sub>2</sub> assimilation rates, and increased biomass allocation to stems and leaves at the expense of roots or other storage organs (Bjorkman & Holmgren 1963; Boardman 1977; Stitt & Schulze 1994). In addition, low light-grown plants are often smaller and reproduce less than plants grown in higher light (Boardman 1977; Harper 1989). The distribution pattern of *S. ancistrochaetus* in the field strongly suggests that light availability may be an important controlling influence. Percent forest canopy cover of ponds containing *S. ancistrochaetus* in Pennsylvania can range from approximately 0 to 90% (K. Lentz, unpublished data), although the presence of this species in a given pond is usually associated with percent forest canopy cover levels of less than 60% (Lentz 1998). The centers of these ponds usually receive the most light, while the edges of the ponds receive more shade from the adjacent forest cover, similar to the light distribution in treefall gap environments (e.g., Denslow et al. 1990). *S. ancistrochaetus* typically grows toward the center of these small ponds, in percent cover conditions ranging from 0 to 50%, and is less apparent around the edges. This observational evidence suggests that light environment may be an important factor regulating the growth and distribution of this species both within and among ponds.

Herbivory is another environmental factor known to influence the growth, reproduction, and distribution of many plant species (Stephenson 1980; Marquis 1984; Vranjic & Gullan 1990). Although plants vary in their ability to compensate for herbivore damage, even moderate levels of damage have been shown to reduce plant growth and fitness (Rosenthal & Kotanen 1994). While *S. ancistrochaetus* incurs relatively little damage by insects, most populations of this species in Pennsylvania experience grazing by white-tailed deer (K. Lentz, pers. obs.). Because ponds in which *S. ancistrochaetus* is found are typically small, shallow, and experience gradual drawdowns throughout the season, deer have access to most individuals in a given pond for most of the growing season. Thus, herbivory may be another factor influencing the growth and distribution of *S. ancistrochaetus* in the field. In addition, many authors have argued that the negative consequences of herbivory should be more severe to

light-limited, slow-growing plants (Bryant et al. 1983; Coley et al. 1985) and this interactive effect has been shown experimentally in a grass species (Pierson et al. 1990). Therefore, in the field, light availability and herbivory may influence the growth and distribution of *S. ancistrochaetus* both independently and interactively.

In order to obtain more information on the potential effect of environmental factors on the growth of *S. ancistrochaetus* in the field, we investigated the independent and interactive effects of light level and simulated herbivory on growth and biomass allocation of this species in a common garden experiment. We demonstrate that growth and biomass allocation in this species were strongly affected by light and its interaction with herbivory, while simulated herbivory alone had little effect.

## Methods

*S. ancistrochaetus* is frequently subjected to terrestrial conditions when ponds become increasingly dry toward the end of the growing season and this species can be easily grown in a semi-terrestrial environment in the laboratory (Lentz & Dunson 1998). Therefore, to increase experimental feasibility, plants were grown under terrestrial conditions in the field at Penn Nursery, Centre County, Pennsylvania. Sixteen 1 m<sup>2</sup> plots were established in a 12 m × 12 m grid, in four separate blocks, with each plot separated by at least 1 m. Soil in each plot was tilled to a depth of 30 cm and all weeds removed prior to planting. On 27 May 1997, nine haphazardly-selected rhizomatous offshoots from greenhouse stock plants were planted in each plot in three rows approximately 25 cm apart (three plants per row). Greenhouse stock plants were generated from field-collected material from eight independent populations. Representatives of these populations were haphazardly distributed among all treatments in our design. All plants were ~20 cm in height at planting.

On 20 June 1997, shading treatments were initiated by draping forest-green nylon shade cloth over 1 m<sup>3</sup> support frames made from 2 cm diameter plastic pipe to cover each plot. Shading levels of 0% (frame only, no cloth), 30%, 63% and 90% were used, with one replicate of each of these four treatments in each of the four blocks. Shade cloth covered the entire frame (sides and top) except for a 20 cm strip at the bottom edge of the support frame to allow for air circula-

tion and the modulation of temperature and moisture. Plots were watered during periods of dry weather and manually weeded as needed several times throughout the experiment. To protect from the possibility that moisture differences between shading treatments due to differential evaporation could confound interpretation of our results, plots were watered in relation to their degree of shading. When watered, plots under 0% shade each received 4 l of water, those under 30% shade received 3.5 l, those under 63% shade received 3 l, and those under 90% shade received 2.5 l. To examine the effect of our differential watering scheme, soil moisture availability was measured on three separate dates in three haphazardly-chosen areas in each plot with a moisture meter with an arbitrary scale reading from 1 to 10 (Amertac, Monsey, NY). Maximum leaf height of each plant (length from soil surface to tip of longest leaf blade) was measured in approximate three-week intervals from the initiation of the shading treatment. Plants were fertilized with Peter's 20-20-20 N-P-K soluble fertilizer (Grace-Sierra, Milipitas, CA) each time height was measured. Full strength Peter's fertilizer consists of 0.0025% (w/v) each of N, P<sub>2</sub>O<sub>5</sub>, and K<sub>2</sub>O, plus Mg, B, Cu, Fe, Mn, Mo and Zn in minor amounts. Maximum mid-day light levels in each plot were measured on two separate occasions with a quantum radiometer/photometer (Li-Cor, Model LI-185B, Lincoln, NB).

On 10 July 1997, herbivory was simulated in four randomly-chosen plants in each plot by clipping each plant to 50% of its height on that date with scissors. This treatment reduced total aboveground biomass of each plant by ~35–40% at the time of clipping and was designed to simulate grazing by white-tailed deer (K. Lentz, pers. obs.). While the absolute amount of biomass removed by this treatment slightly differed among plants, the proportion removed was controlled. On 7 September 1997, final height was measured on each plant and the entire plants were harvested. Soil was removed from the roots, and the roots, shoots, and flowers were separated. Leaf width of five haphazardly-chosen leaves from each plant was measured. All plant material was then dried at 100 °C for 48 h and weighed. Shoot biomass removed by clipping was not included in the final measures of plant mass. Since flowering was rare in this experiment and randomly distributed among treatments, flower culm mass was included in the shoot mass of each plant for analyses.

Total (shoot + root) mass, leaf width and root:shoot mass ratio (R:S) data were log-transformed

and analyzed using a split-plot Multivariate Analysis of Variance (MANOVA), with shading as the fixed main plot factor and clipping as the fixed subplot factor (SAS Institute 1989). Height data were analyzed using a separate split-plot MANOVA, with height at each sampling date as separate variables in the model (von Ende 1993). Separate univariate Analyses of Variance (ANOVAs) were conducted when significant effects were found in the MANOVA to more closely examine on which variables significant treatment effects were most noticeable. Plants that had either died or not visibly grown (16 out of 144) since the original planting were excluded from the analysis. Four outliers were identified and removed for the purposes of achieving statistical normality. An analysis was also run including the outliers using a Kruskal–Wallis Rank Sum test. The results of this test were qualitatively similar to the parametric tests without the outliers; thus we chose to discard the outliers and use the relatively more robust parametric tests. In the MANOVA, *F* values were calculated from the Wilk's  $\lambda$  test statistic. Light and moisture levels were analyzed with separate ANOVAs, with fixed block, shading and date factors. The alpha level used for all tests was 0.05.

## Results

Shading treatments reduced light intensity in the expected order and magnitude ( $F_{3,15} = 373.15$ ,  $p < 0.0001$ , Table 1). Despite our differential watering regime, soil moisture content (shown averaged over the three sampling dates) was slightly different between shading treatments ( $F_{3,30} = 6.21$ ,  $p = 0.002$ , Table 1), but was not inversely related to light availability. MANOVA indicated that light significantly affected final total plant mass, R:S and leaf width ( $F_{9,17} = 5.35$ ,  $p = 0.001$ ). In the separate univariate ANOVAs, light significantly affected total mass, R:S and leaf width ( $F_{3,9} = 17.89$ ,  $p = 0.0001$ ;  $F_{3,9} = 28.57$ ,  $p = 0.0001$ ; and  $F_{3,9} = 15.34$ ,  $p = 0.0001$ , respectively). Total mass decreased from ~31–48% with each 30% increase in shading (Figure 1). Although generally decreasing with increasing shade, R:S did not differ significantly between 0%, 30%, and 63% shade. However, R:S was significantly lower in 90% shade than in each of the other three treatments (Figure 2). Leaf width did not differ between 0%, 30%, and 63% shade, but was significantly lower under 90% shade (Figure 3).

Table 1. Mean ( $\pm$  SE) light and moisture levels in each shading treatment, averaged over three sampling dates. Treatments with the same letters are not significantly different.

Shading level	Light (in $\mu\text{E}/\text{m}^2 \text{ s}$ )	Moisture (in arbitrary units)
0%	1755 $\pm$ 72	a 5.0 $\pm$ 0.8 ab
30%	1238 $\pm$ 28	b 4.4 $\pm$ 0.6 a
63%	685 $\pm$ 28	c 4.2 $\pm$ 0.6 a
90%	90 $\pm$ 9	d 5.3 $\pm$ 0.6 b

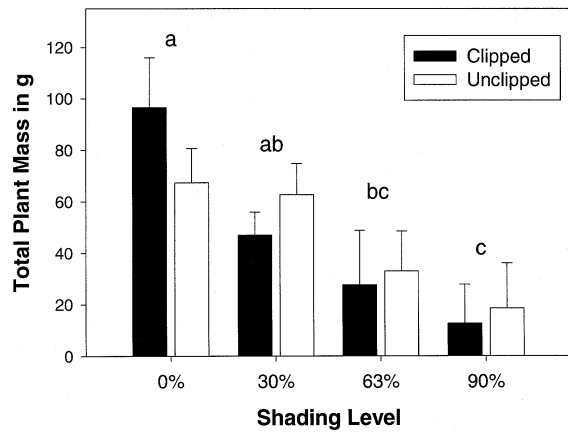


Figure 1. Total above- and belowground mass (mean  $\pm$  SE) of clipped and unclipped plants in each shading level. Different letters above bars indicate significant differences between shading treatments only (see text for discussion of clipping effects).

MANOVA indicated that the overall effect of clipping on total mass, R:S, and leaf width was not significant ( $F_{3,103} = 1.09, p = 0.4$ ), while the interactive effect of light and clipping on these variables was significant ( $F_{9,251} = 2.26, p = 0.02$ ). R:S was found to be significantly affected by the interaction of light and clipping in the univariate ANOVA ( $F_{3,105} = 4.17, p = 0.008$ ), while leaf width and total plant mass were not affected by the interaction ( $F_{3,105} = 1.27, p = 0.3$  and  $F_{3,105} = 1.57, p = 0.2$ , respectively). In general, total mass, R:S, and leaf width tended to be higher in clipped plants than in unclipped plants under 0% shade, but tended to be lower in clipped plants than in unclipped plants under all other shading treatments (Figures 1–3).

Light also significantly affected maximum leaf height throughout the experiment ( $F_{15,14} = 3.41, p = 0.01$ ) while clipping had no effect ( $F_{5,101} = 0.45, p = 0.8$ ). Plants grown under 63% and 90% shade

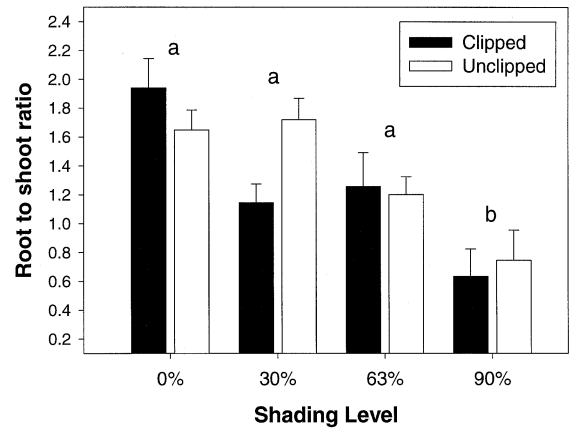


Figure 2. Root to shoot ratio (mean  $\pm$  SE) of clipped and unclipped plants in each shading level. Different letters above bars indicate significant differences between shading treatments only (see text for discussion of clipping effects).

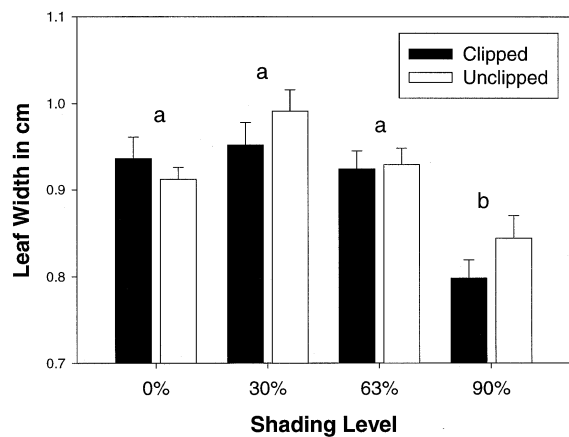


Figure 3. Leaf width (mean  $\pm$  SE) of clipped and unclipped plants in each shading level. Different letters above bars indicate significant differences between shading treatments only (see text for discussion of clipping effects).

were significantly taller than plants under 0% shade by the last two measurement dates while plants from 30% shade were intermediate in leaf height (Figure 4). The interactive effect of light and clipping on leaf height was nearly significant ( $F_{15,279} = 1.65, p = 0.06$ ). By the last two sampling dates, clipped plants tended to be taller than unclipped plants in 0% and 30% shade, while unclipped plants tended to be taller than clipped plants under 63% and 90% shade.

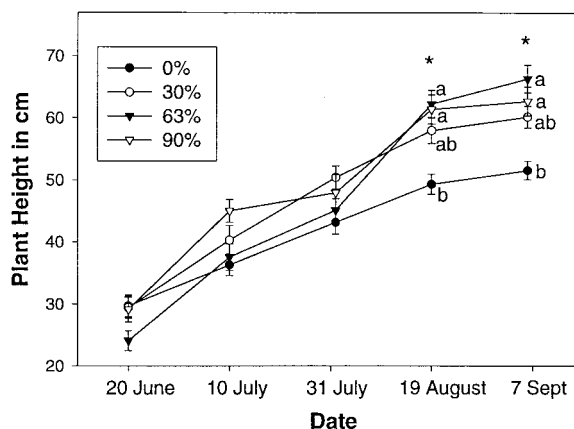


Figure 4. Maximum leaf height (mean  $\pm$  SE) of plants in each shading level over time, averaged over both clipping treatments. Asterisks indicate that the univariate ANOVA was significant for that date. Within each date, treatments with the same letter are not significantly different from each other.

## Discussion

In this study, light level strongly affected growth and biomass allocation of *S. ancistrochaetus*. Plants grown in progressively lower light accumulated much less biomass and exhibited lower R:S than those grown in higher light. Reduced R:S indicates that experimental plants preferentially allocated biomass to shoot production to maintain height and maximize light reception in low light conditions, part of the classic 'shade avoidance' syndrome (e.g., Dudley & Schmitt 1996). This response was so strong that shaded plants, although of less mass, were actually taller than unshaded plants by the end of the experiment. Differences in R:S between treatments were not merely a size-dependent artifact (Coleman et al. 1994; Gedroc et al. 1996). For example, R:S of plants was lower under 30% and 63% shade than under 0% shade, but differences were not significant. However, total mass declined greatly from 0% to 63% shading. Likewise, plants maintained constant leaf width up to 63% shading, independent of changes in total mass. However, plants grown in 90% shade had extremely low R:S and maintained height, but were unable to maintain leaf width or total mass.

The plant responses to light that we observed are consistent with those of many other studies (see Stitt & Schulze 1994) and suggest that allocational plasticity may be an important life-history trait in this species (Dudley & Schmitt 1996). Although moisture levels also differed slightly among treatments (Table 1), the pattern of plant response more closely matches the pattern of the light gradient than the moisture gradient.

Therefore, we attribute the variation in plant response to shading treatments to variation in light availability and not to moisture availability. Our results indicate that *S. ancistrochaetus* exhibits phenotypic plasticity in response to light, but that increases in shading, which can result from forest canopy closure, are likely to increasingly reduce growth and fitness of this species in the field and may partly explain its distribution within and among ponds.

In contrast to the effect of light, removal of up to 40% of aboveground biomass midway through the experiment had a much smaller overall effect on growth and biomass allocation in *S. ancistrochaetus*. Although plant species vary greatly in their ability to tolerate leaf area removal (Rosenthal & Kotanen 1994), this degree of tolerance is remarkable (but see Paige & Whitham 1987; Obeso & Grubb 1994). High-yielding agronomic species can often tolerate this level of damage with little effect on fitness (e.g., Cipollini 1997), but as little as 10% leaf area removal has been shown to significantly reduce growth and fitness in many wild species (e.g., Marquis 1984). Although the overall effects of clipping alone were not large, the interaction of shading and clipping was significant. Total mass, R:S, and leaf width were all greater in clipped plants grown in 0% shade relative to unclipped plants, while the means of these variables were generally lower in clipped plants than in unclipped plants under all other levels of shading (Figures 1–3). A similar interactive effect was observed for plant height, although the effect was marginally significant. These results indicate that the tendency to totally compensate (or overcompensate) for lost leaf area found in unshaded plants was attenuated in shaded plants, likely due to light limitation, a finding in agreement with Pierson et al. (1990). Other resource-limiting factors shown to affect growth of herbaceous plants interactively with herbivory include the presence of competitors (Lee & Bazzaz 1980), flooding (Oosterheld & McNaughton 1991), and nutrient supply (Obeso & Grubb 1994).

Several authors have associated R:S with compensatory ability following shoot herbivory (e.g., van der Meijden et al. 1988, Cipollini 1997). Specifically, the possession of a high R:S at the time of damage might allow for the rapid mobilization of stored root reserves for regrowth (Lefevre et al. 1991). Our finding that R:S was smaller in clipped plants than in unclipped plants, particularly under shade, indicates that the preferential allocation of biomass to shoots at the expense of roots was part of the compensatory mechanism in *S. ancistrochaetus* (Rosenthal & Kota-

nen 1994). Plants with the highest R:S at the time of damage (those under 0% shade) were best able to compensate for damage, while those with lower R:S under all other levels of shading were less able to compensate. Thus, the ability of *S. ancistrochaetus* to compensate for shoot herbivory in this study was positively associated with both the possession of a high R:S and with high light availability, two factors that are difficult to separate in a species that exhibits such allocational plasticity in response to light. Reduced R:S has also been noted in response to increasing water level in *S. ancistrochaetus* (Lentz & Dunson 1998). If compensatory ability is indeed positively associated with a high R:S, the growth of *S. ancistrochaetus* in the field may be increasingly reduced by herbivory as water levels increase.

The high degree of tolerance to leaf area removal exhibited by this species is also related to its intrinsic growth form. A 50% reduction in height does not damage the basal leaf meristems of *S. ancistrochaetus*. The possession of basal leaf meristems is a trait thought to confer a high degree of herbivore tolerance in grasses (e.g., McNaughton & Chapin 1985). Leaf growth rate from these meristems apparently increased as a mechanism to recover lost leaf area and did so to such a degree that unshaded plants actually overcompensated for damage.

Although flowering could have been more adversely affected by clipping than vegetative growth, flowering was so rare in this experiment that this possibility could not be examined statistically. Nevertheless, growth is an important measure of fitness in this species because it propagates vegetatively to a large degree in the field (Bartgis 1992). In any case, our results indicate that growth and fitness of *S. ancistrochaetus* are unlikely to be greatly affected by a single bout of grazing by deer in the field of the magnitude and timing that we imposed. However, chronic grazing or grazing that is severe enough to damage basal leaf meristems may have much more negative effects on growth and fitness. Our results also suggest that grazing may have more severe effects in shaded plants relative to unshaded plants, and may interactively exacerbate the growth-reducing effects of low light.

In conclusion, we suggest that light level is a key environmental factor regulating growth and distribution of *S. ancistrochaetus* in the field. While this species can occupy fairly heavily-shaded ponds, it appears as though this species performs much better when light is not limiting. While severe grazing may

negatively affect this species, moderate levels of leaf area removal appear to be tolerated extremely well, especially in high light environments. However, the interactive effects of chronic or severe grazing and low light are likely to severely reduce growth in this species, which could influence its distribution in the field, and may lead to local extinctions.

### Acknowledgements

We would like to thank W. Dunson for his role as advisor to K. A. L. We would also like to thank M. Kreider, T. Manyin, H. Pattison, T. Schmidt, C. Smith, and J. Woods for their contributions to this work. Two anonymous reviewers greatly improved an earlier version of this manuscript. The Department of Conservation and Natural Resources/Bureau of Forestry kindly provided space at Penn Nursery. A. Day and J. Kozar were especially helpful in this regard. The PA Wild Resource Conservation Fund provided funding for this project. K. A. L. was further supported by the Henry W. Popp fellowship during manuscript preparation.

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