

Effects of Intraspecific Competition and Nutrient Supply on the Endangered Northeastern Bulrush, *Scirpus ancistrochaetus* Schuyler (Cyperaceae)

KENDRA A. LENTZ¹

Department of Biology, The Pennsylvania State University, 208 Mueller Laboratory, University Park 16802

ABSTRACT.—The effect of intraspecific competition and nutrient supply on the endangered northeastern bulrush, *Scirpus ancistrochaetus*, was examined in a full-factorial greenhouse experiment. Seedlings were exposed to 4 densities (1, 5, 10 or 25 plants/pot) and 3 nutrient concentrations (3, 25 or 50% of full strength) for 9 wk. Height, mass and survival generally decreased with increasing density. Root to shoot ratio (R:S) increased with density, indicating that competition primarily involved belowground resources. Nutrient concentration significantly affected average plant height, total mass and R:S but did not affect survival. Plant height and total mass generally increased with increasing nutrient concentration, whereas R:S decreased. In general, the negative effect of intraspecific competition on plant height and total mass was greatest at the highest nutrient concentration, confirming that the intensity of intraspecific competition increases with resource supply in this species. Neither density nor nutrient concentration affected the population distribution of plant sizes in densities over 1 plant/pot, suggesting that size hierarchies, and therefore asymmetric competition, are not important during seedling growth in this species. Information gained from this study can be used towards understanding seedling establishment in the field and, in turn, towards effective management and reintroduction of this endangered species.

INTRODUCTION

Northeastern bulrush, *Scirpus ancistrochaetus* Schuyler, is a perennial emergent sedge (Schuyler, 1962) typically found in small, seasonal, palustrine wetlands which are frequently isolated in the landscape. It ranges from West Virginia to Massachusetts, with the majority of populations found in Pennsylvania (see Lentz, 1998). *Scirpus ancistrochaetus* is currently limited to 60 known populations and is listed as endangered by the U.S. Fish and Wildlife Service (1991). Only a limited amount of life history information is available on this species (but see Bartgis, 1992; Lentz, 1998; Lentz and Cipollini, 1998; Lentz and Dunson, 1998; Lentz and Johnson, 1998; Lentz and Dunson, 1999), yet basic ecological information is necessary to develop effective conservation management plans (Brussard, 1991; Lesica, 1992). For example, information on ecological factors affecting seedling growth and survival can be used not only to examine factors that may cause population decline and rarity, but also to develop an effective reintroduction technique.

Because this species tends to grow in largely monospecific stands in central Pennsylvania wetlands (Lentz, 1998), intraspecific competition may be an important influence in the population dynamics of this species. Furthermore, since successful recruitment by seedlings is low and seedling densities are typically high in this species (Lentz, pers. obs.), intraspecific competition may exert a particularly strong influence during the seedling stage. Establishment by seedlings is particularly important in the re-establishment of populations from the seed bank after a reduction in population size and in the expansion into new pond habitats by animal-dispersed seeds (Lentz, pers. obs.). Expansion within a pond is achieved primarily through asexual propagation (Bartgis, 1992; Lentz, pers. obs.).

¹Present address: 5706 S. Drexel Ave #3, Chicago, IL 60637, e-mail: kall143@alumni.psu.edu

Plants can respond to increased intraspecific competition (density) through a plastic response, such as growth or reallocation of resources between the root and shoot, or through a mortality response (Harper, 1977; Bazzaz, 1996). For many plants, an increase in density results in a decrease in reproduction, total biomass, height and/or survival (Antonovics and Levin, 1980; McFarland *et al.*, 1992; Ungar, 1992; Nicotra and Rodenhouse, 1995). Increased intraspecific competition can also change patterns of resource allocation, depending upon the resource which is in the most demand (Bazzaz, 1996). For example, if light were most limiting, root to shoot ratio (R:S) would be expected to decrease with increased density as plants shift more resources towards light-gathering structures. In addition, the effect of intraspecific competition on plant growth frequently changes with resource supply (Bazzaz, 1996; Creed *et al.*, 1997; Sugiyama and Bazzaz, 1997). The intensity of intraspecific competition is thought by some to decrease with increasing resource supply (Harper, 1977; Heywood and Levin, 1986), although other studies have found the inverse to be true (Drake and Ungar, 1989; Nicotra and Rodenhouse, 1995; Creed *et al.*, 1997). Nutrient levels vary among ponds where *Scirpus ancistrochaetus* is found (Lentz, 1998) and are probably heterogeneous within ponds. Therefore, the effect of intraspecific competition on this species may vary among and within ponds with different nutrient supplies.

Intraspecific competition not only affects individuals, but can also affect the size structure of a population through the formation of a size hierarchy, a common response in many species (Weiner, 1985; Weiner and Thomas, 1986; Berntson and Weiner, 1991; Weiner, 1993). A size hierarchy is defined by Weiner and Solbrig (1984) as, "a frequency distribution of individual plant sizes in which relatively few individuals contribute most of the population's biomass and most individuals are relatively small." The few, large, dominant individuals acquire a disproportionate amount of the available resources, a type of interaction termed "asymmetric competition" (Weiner and Thomas, 1986). A size hierarchy is typically evaluated using a measure of size inequality among members of a plant population, such as the coefficient of variation (Bendel *et al.*, 1989).

Determining how *Scirpus ancistrochaetus* responds to intraspecific competition and resource supply under controlled conditions in the greenhouse may improve our understanding of factors that affect establishment of seedlings of this species in the field, therefore aiding in conservation efforts. In this study, seedlings of *S. ancistrochaetus* were subjected to four density levels and three nutrient levels to determine the effect of intraspecific competition on growth and survival of this species and how the effect may change along an environmental gradient of nutrient concentration. I hypothesized that (1) increased density would lead to decreased total plant biomass, height and survival while the degree of size inequality would increase; (2) R:S would decrease with density, since light strongly affects growth and resource allocation in this species (Lentz, 1998; Lentz and Cipollini, 1998) and (3) the addition of nutrients would ameliorate the negative effects of intraspecific competition on plant growth.

METHODS

Mature seeds (achenes) were collected from 16 separate populations of *Scirpus ancistrochaetus* in central Pennsylvania, located >1 to ~100 km apart from each other (*see* Lentz, 1998). Seeds were pooled and germinated on wet paper towels after a 2 mo cold stratification period as in Deno (1993) and Lentz and Johnson (1998). Seedlings were allowed to grow to a height of about 1 cm before transplanting. On 24 February 1997 (day 0), seedlings were transplanted in 75 ml (5.5 cm diam \times 5.5 cm depth) pots which contained coarse vermiculite and a top layer (~10 ml) of sphagnum peat moss. Seedlings were planted in densities of 1, 5, 10 or 25 plants/pot (421, 2105, 4210 and 10,526 plants/m²). Densities

used were within the range of densities found in the field (400–63,000 plants/m²) (Lentz, 1998). Densities at the high end of the natural range were not used in this study due to logistical constraints. Pots were randomly arranged in four separate blocks on a greenhouse bench, with one replicate per block. Plants were not moved during the experiment since blocking and randomization account for any slight placement differences. Pots were placed in individual plastic saucers (8 × 8 × 3 cm depth) that were constantly filled with distilled water to keep the planting medium saturated throughout the experiment. Pots were fertilized biweekly starting on day 13 with 15 ml of a nutrient solution of 3, 25, or 50% of full strength Peter's 20-20-20 N-P-K soluble fertilizer (Grace-Sierra, Milipitas, California). Full strength Peter's fertilizer consists of 0.0025% (w/v) each of N, P₂O₅, and K₂O, plus Mg, B, Cu, Fe, Mn, Mo and Zn in minor amounts. The treatments were administered in a full-factorial design (4 densities × 3 nutrient levels × 4 blocks). Natural daylengths were supplemented with sodium vapor lamps as necessary to create a 15 h photoperiod, simulating growing season light conditions. Light intensity of photosynthetically active radiation (PAR) measured with a quantum radiometer/photometer (Li-Cor Model LI-185B) ranged from approximately 400–1000 μE/m²·s PAR and greenhouse temperatures averaged 25 C.

The experiment was terminated on day 63 to avoid overcrowding of seedlings and allow separation of each seedling (roots and shoots) from each other. On day 63, entire plants were carefully removed from each pot. Height of each plant from base of leaves to the tip of the tallest leaf was measured. Plants were then dried at 100 C for 24 h and weighed. Average height, total mass and root to shoot ratio (R:S) were subsequently calculated for each pot. Plants were immature so no measure of sexual reproduction was possible. A Multivariate Analysis of Variance (MANOVA) with fixed factors of density, nutrient and block was conducted on percent survival, average height, total mass and R:S (SAS Institute, Inc., 1989). When significance was found in the MANOVA (using an F value calculated from Wilk's λ test statistic), univariate Analyses of Variance (ANOVAs) were conducted on each response variable separately, followed by a Tukey's test to determine significant differences between means. In order to evaluate the presence of a size hierarchy, the coefficient of variation was determined for plant height and mass in treatment densities > 1 plant/pot and a MANOVA was used as above. The alpha level used for all tests was 0.05. Transformations were not necessary since all data met model assumptions of normality and homoscedasticity.

RESULTS

Height, total mass, R:S and percent survival were significantly affected by both density and nutrient concentration in the MANOVA ($F_{12,40} = 16.49$, $P = 0.0001$; and $F_{8,30} = 19.11$, $P = 0.0001$, respectively). The interaction of density and nutrient concentration was also significant ($F_{24,54} = 2.22$, $P = 0.0080$). In the univariate ANOVA, density, nutrient concentration and their interaction significantly affected height ($F_{3,18} = 203.08$, $P = 0.0001$; $F_{2,18} = 191.96$, $P = 0.0001$; and $F_{6,18} = 13.56$, $P = 0.0001$, respectively). As expected, plant height decreased with increasing density (1 > 5 > 10 = 25), and increased significantly with each increase in nutrient concentration (Fig. 1A). In general, differences in height between nutrient levels were greatest at the lowest densities, with no difference in height between nutrient levels at the density of 25 plants/pot (Fig. 1A). Density, nutrient concentration and their interaction also had a significant effect on total plant mass in the ANOVA ($F_{3,18} = 45.79$, $P = 0.0001$; $F_{2,18} = 33.92$, $P = 0.0001$; and $F_{6,18} = 8.06$, $P = 0.0003$, respectively). Mean total plant mass decreased significantly with increasing density (1 > 5 > 25, 5 = 10, 10 = 25) (Fig. 1B). Total mass was significantly higher at the highest nutrient concentration than at the lower nutrient concentrations (Fig. 1B). As with plant height,

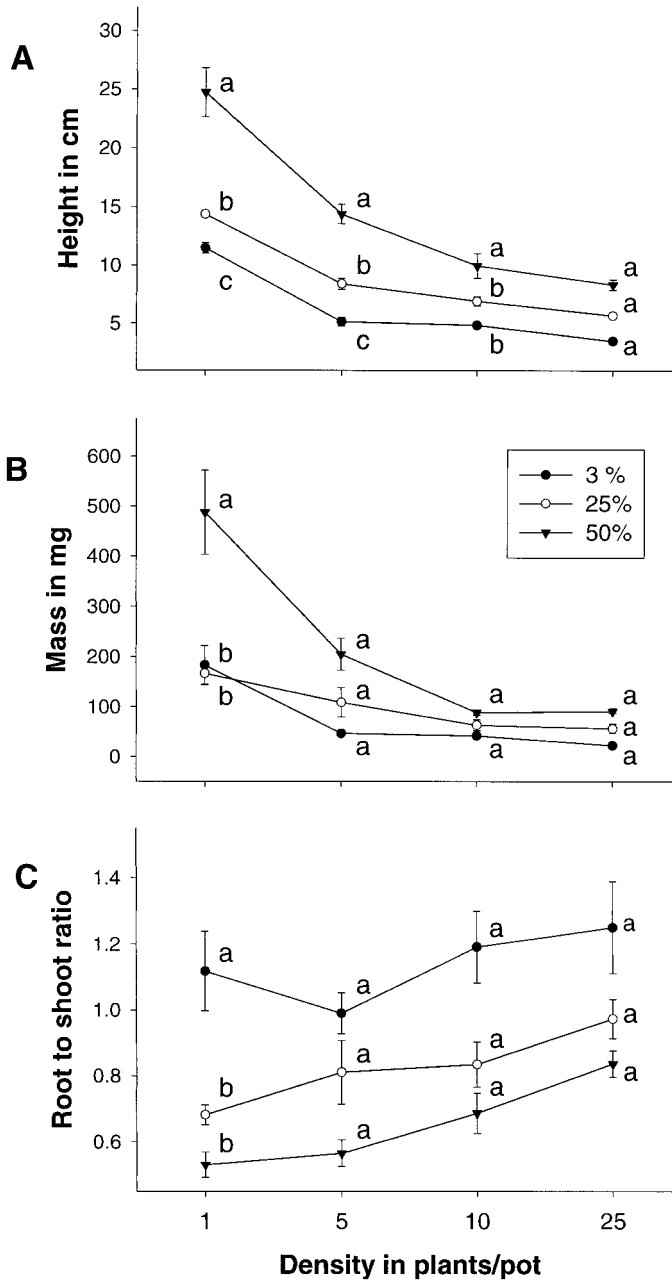


FIG. 1.—Mean \pm SE of (A) leaf height, (B) total plant mass and (C) root to shoot ratio in plants grown at four densities (1, 5, 10 and 25 plants/pot) and three nutrient concentrations (3, 25 and 50% of full strength). Within each density level, nutrient treatments with the same letters were not significantly different from each other. In some cases, standard errors are smaller than the graph symbol

differences in total mass among density levels were greatest at the high nutrient concentration (Fig. 1B).

R:S was also significantly affected by both density and nutrient concentration in the ANOVA ($F_{3,18} = 5.02$, $P = 0.0106$ and $F_{2,18} = 30.88$, $P = 0.0001$, respectively), but not the interaction of the two factors ($F_{6,18} = 0.45$, $P = 0.8333$). R:S decreased with each increase in nutrient concentration (Fig. 1C). R:S was highest in the highest density (25 plants/pot) and lowest in the two lowest densities (1 and 5 plants/pot), with the R:S of plants in the density treatment of 10 plants/pot intermediate between the two groups (Fig. 1C). In the ANOVA, survival was significantly affected by density only ($F_{3,18} = 10.65$, $P = 0.0003$). There was 100% survival in the two lowest densities, 95.9% at 10 plants/pot and 87.3% at 25 plants/pot. Survival of plants at 25 plants/pot was significantly lower than at the other three density levels.

Density, nutrient concentration and their interaction had no effect on the coefficient of variation for plant height and total mass in treatments greater than 1 plant/pot in a MANOVA ($F_{4,22} = 0.295$, $P = 0.878$; $F_{4,22} = 0.688$, $P = 0.608$ and $F_{6,22} = 0.682$, $P = 0.666$, respectively).

DISCUSSION

Intraspecific competition and resource supply significantly affected plant height and total mass, both independently and interactively. Plant height, total mass and survival decreased with increasing density, in agreement with previous studies (Antonovics and Levin, 1980; Ungar, 1992; Nicotra and Rodenhouse, 1995). As expected, plant height and total mass also increased with increasing nutrient concentration. The differences in mean plant height between plants grown alone vs. plants grown in increasing density treatments were greatest at the highest nutrient levels, as evidenced by the steeper slope in high nutrient treatments (Fig. 1A). The same pattern was found for total plant mass (Fig. 1B). This indicates that the negative effect of competition or the intensity of competition was greater at higher nutrient levels, concurring with other research (Drake and Ungar, 1989; Nicotra and Rodenhouse, 1995). These results suggest that as plants grew larger in higher nutrient environments their resource demands also increased, thereby effectively increasing the competition intensity.

R:S decreased with increasing nutrient supply and increased with increasing density, but was not affected interactively by the two factors. An increase in R:S is a common response of plants to lowered nutrient supply (Chapin, 1980; Perez *et al.*, 1994; Bazzaz, 1996). R:S of plants in this study increased with intraspecific competition, in contrast to my hypothesis and previous studies that found no change in R:S with density and in agreement with Heywood and Levin (1986). These results indicate that belowground competition is more important than aboveground competition in *S. ancistrochaetus*, possibly because the grass-like architecture of this species may not shade neighbors to a great extent at the seedling stage. Plants may shift allocation towards shoots as seedlings grow larger and shade each other more fully. Possible changes in resource competition with age in this species should be examined in future experiments.

The coefficient of variation for height and/or mass of a plant population can increase with competition (Weiner and Thomas, 1986; Sugiyama and Bazzaz, 1997) and nutrient supply (Creed *et al.*, 1997; Sugiyama and Bazzaz, 1997), which is indicative of the creation of a size hierarchy. However neither intraspecific competition nor resource supply created a population size hierarchy in this study. Weiner and Thomas (1986) discovered that, although most competition results in the formation of a population size inequality ("asymmetric competition"), some does not ("resource depletion" or "two-sided competition").

Creed *et al.* (1997) also did not find the formation of a size hierarchy with increasing density. Since asymmetric competition is due primarily to competition for light (Weiner and Thomas, 1986) and seedlings of the species in this study compete primarily for belowground resources, "resource depletion" competition may be more important in this species than asymmetric competition. Alternatively, a size hierarchy can disappear with self-thinning in a population (Weiner and Thomas, 1986; Weiner and Whigham, 1988). Self-thinning may have been a factor in the lack of formation of a size hierarchy in this study, especially in the highest density treatment where survival was significantly lower. It is important to note, however, that caution must be exercised when interpreting results concerning the formation of a size hierarchy when population sizes are small. To more completely investigate the formation of a size hierarchy in this species, experiments using higher densities must be performed, while closely monitoring survival in both the field and greenhouse.

This study shows that density can negatively affect growth of *Scirpus ancistrochaetus* in the greenhouse and that the effect of competition is greater with increased nutrient supply. It also demonstrates that the competition between seedlings of this species primarily involves belowground resources, as evidenced by a shift in resource allocation to roots with increased density. Soil rooting volume can also affect plant growth and allocation (Carmi *et al.*, 1983, McConnaughay and Bazzaz, 1991). Although pot size was small (75 ml) in this study, soil volume was probably not a factor in the results since the roots occupied a very small (<5%) volume and could easily be separated from one another. It is likely that the same basic response would be important in natural populations, although extrapolation of my results to field situations should be made cautiously until field experimentation is performed. Many other factors present in the field, such as seedling competition with adults (Aguilera and Lauenroth, 1993), could also affect intraspecific competition in the field and need to be further addressed. Other factors that may affect seedling growth in the field include inter-specific competition, water stress, herbivory, disturbance frequency and microhabitat differences (Harper, 1977; Bazzaz, 1996). The information gained from this study can be used towards conservation and management of this species. For example, use of fertilizers during reintroduction of this species by seedlings should be carefully considered in light of the increased competition intensity with increased nutrients. This study also suggests that intra-specific competition may be the reason for low recruitment by seedlings into the population, since survival and growth were strongly affected by density and the density levels used did not approach the maximum densities observed in the field.

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