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Competitive Interactions between Eurasian Watermilfoil and Northern Watermilfoil in Experimental Tanks

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ABSTRACT

Two submersed macrophytes, the exotic Eurasian watermilfoil (*Myriophyllum spicatum* L.) and the native northern watermilfoil (*Myriophyllum sibiricum* Kom.), were grown in 0.30-m^3 outdoor experimental tanks in single- and mixed-species cultures of low (75 stems m^{-2}) and high densities (150 stems m^{-2}). Elongation rates (cm $week^{-1}$) and average individual stem and root dry mass were evaluated. Northern watermilfoil unexpectedly gained a head start because stem cuttings formed roots and began to grow before Eurasian watermilfoil cuttings were established. Still, Eurasian watermilfoil elongated much more rapidly than northern watermilfoil in all treatments ($p < 0.001$) and was equal in length to northern watermilfoil by the conclusion of the experiment. Density and culture type (mixed vs single) had no effect on elongation rates. Intraspecific competitive effects on mean individual stem mass was significant in Eurasian watermilfoil monocultures ($p = 0.05$) and marginally significant in northern watermilfoil monocultures ($p = 0.07$). Stems and roots were heavier in the low-density treatments than in the high-density treatments (both $p < 0.01$). Interspecific competition between stems was present in the mixed-culture treatments. Given preemption, northern watermilfoil was the superior competitor. Northern watermilfoil suppressed biomass accumulation of Eurasian watermilfoil stems ($p = 0.006$). Biomass accumulation of northern watermilfoil was not affected when grown with Eurasian watermilfoil. In shallow, clear water, established northern watermilfoil appears to be the superior competitor, at least for biomass accumulation. These findings contrast to long-term field observations of Eurasian watermilfoil displacing northern watermilfoil. Water clarity and depth may be important factors affecting competitive interactions of Eurasian watermilfoil with other species of submersed macrophytes.

Key words: ecology, growth, competition, *Myriophyllum spicatum*, *Myriophyllum sibiricum*, water clarity, depth.

INTRODUCTION

The exotic Eurasian watermilfoil (*Myriophyllum spicatum* L.) is a nuisance aquatic plant that has infested lakes across North America. Since its introduction to North America in the 1940s (Couch and Nelson 1985), Eurasian watermilfoil has continued to spread across the continent and is now considered one of the most troublesome aquatic weeds (Smith and Barko 1990). Successful colonization by Eurasian watermilfoil in much of North America can be attributed to its rapid and effective dispersal by plant fragments and its ability to form a canopy (Grace and Wetzel 1978, Smith and Barko 1990). Eurasian watermilfoil becomes most troublesome when environmental conditions permit canopy formation. Thick mats of Eurasian watermilfoil covering the surface of lakes impede boat traffic and shade out other submersed species, thereby reducing species diversity and richness (Madsen et al. 1991b).

The native northern watermilfoil (*Myriophyllum sibiricum* Kom., formerly *M. exalbescens* Fern.) is found in the northern half of North America (Aiken et al. 1979) and is closely related to Eurasian watermilfoil (Aiken 1979). The phylogenetic relationship between these species was debated in the past and northern watermilfoil was considered a variety of Eurasian watermilfoil by some botanists (Aiken 1981). Northern watermilfoil is not usually considered a nuisance species because it generally does not form a dense canopy at the water surface (Aiken 1979). Although both species prefer similar habitats (Nichols 1992), coexistence is rare and Eurasian watermilfoil tends to displace northern watermilfoil (Nichols 1994). Displacement is most likely due to canopy formation by Eurasian watermilfoil (Madsen et al. 1991b). Coexistence of Eurasian and northern watermilfoil appears to be more common in undisturbed shallow habitats with conditions of high water clarity (Newman personal obs.)

Field observations suggest Eurasian watermilfoil is a superior competitor to northern watermilfoil (Nichols 1994); however, experimental evidence is lacking. Competitive interactions between Eurasian watermilfoil and other species of macrophytes have previously been assessed and results have varied. Wakeman and Les (1994) found no interspecific competition when large leaf pondweed (*Potamogeton amplifolius*) was cultured with Eurasian watermilfoil. Abernethy et al. (1996) found Eurasian watermilfoil to be an inferior competitor when grown with Canada waterweed (*Elodea canadensis*). However, Eurasian watermilfoil was found to have superior competitive abilities when cultured with spiny naiad (*Najas marina*, Agami and Waisel 1985) and wild celery (*Vallisneria americana*, Titus and Adams 1979).

Less is known about the competitive abilities of northern watermilfoil. Moen and Cohen (1989) assessed competitive

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abilities of northern watermilfoil. They found northern watermilfoil to be the inferior competitor when grown with sago pondweed (*Potamogeton pectinatus*) in 30-cm deep aquaria. Aiken and Picard (1980) is the only study that has compared growth of both Eurasian and northern watermilfoil under identical experimental conditions. Although this was not a competition experiment per se, they found that Eurasian watermilfoil grew better than northern watermilfoil in one year, yet, the contrary was true in another year under the same conditions. The objectives of our study were to assess intra- and interspecific competitive interactions of Eurasian and northern watermilfoil by varying density and mixture combinations, and to examine differences in growth strategies that may explain why Eurasian watermilfoil displaces northern watermilfoil in the field.

MATERIALS AND METHODS

To assess competitive interactions we planted cuttings of each species at two different densities (high or low) and combinations (monoculture or mix-culture). High-density treatments (arbitrarily defined as N; McCreary 1991), were set at 150 stem cuttings m^{-2}. Selection of this density was based on observed stem densities of several Eurasian watermilfoil beds in Minnesota (Newman et al. 1996). Numbers of stems in the low-density treatments were half the number of stems in the high-density treatments (N/2; McCreary 1991). Six treatments were used, with four replicates of each treatment: (1) high density Eurasian watermilfoil monoculture (N); (2) low density Eurasian watermilfoil monoculture (N/2); (3) high density northern watermilfoil monoculture (N), (4) low density northern watermilfoil monoculture (N/2); (5) high density mix of both species (N/2 Eurasian watermilfoil + N/2 northern watermilfoil = N); and (6) low density mix of both species (N/4 Eurasian watermilfoil + N/4 northern watermilfoil = N/2).

This experiment took place outdoors for five weeks (30 Jul. through 28 Aug. 1997) in nine 0.60-m^3 (1.85 m by 0.65 m by 0.5 m) stock tanks and six 0.30-m^3 (1 m by 0.5 m by 0.6 m) plastic tanks. The larger tanks were bisected in order to create a total of 24 independent 0.30-m^3 experimental units. Watermilfoil growth experiments have traditionally been performed in <1 m of water (i.e., Titus and Adams 1979, Aiken and Picard 1980, Agami and Waisel 1985, Moen and Cohen 1989, Abernethy et al. 1996) and we did not have access to replicate deeper experimental tanks.

Homogenized sediment collected from Otter Lake, Anoka Co., MN, was placed in the bottom of all tanks to a depth of approximately 5 cm. Fifteen fertilizer sticks were placed into the sediment of each tank to facilitate growth. Forty-five cm of water was then added to the tanks and dechlorinated before the 15-cm milfoil cuttings were planted. Northern watermilfoil cuttings were collected from Christmas Lake, Hennepin Co., MN. Eurasian watermilfoil cuttings were collected from Wayzata Bay in Lake Minnetonka, Hennepin Co., MN. Treatments were assigned to tanks in a stratified, random manner such that each of the 0.30-m^3 tanks received one replicate of each treatment and the same treatment was not assigned to both halves of the bisected tanks. Northern watermilfoil cuttings were planted one week prior to Eurasian watermilfoil cuttings in order to compensate for time differences we expected in root establishment.

Prior to the experiment, we planted Eurasian and northern watermilfoil cuttings from a greenhouse stock into a tank to determine how long it would take for cuttings of both species to form roots. We observed Eurasian watermilfoil to form roots in one week, and northern watermilfoil in two. We therefore planted northern watermilfoil cuttings a week before the Eurasian watermilfoil cuttings. All cuttings were equally spaced and stems of the two species were alternated in the mixed treatments. Zooplankton and snails were placed into each tank to control algal and periphyton growth. Nylon mesh screens were placed on the top of each tank to prevent entry of wind blown debris.

One week after Eurasian watermilfoil was planted, roots of both species were established and length measurements could begin. Length of each plant was measured from the sediment surface to the tip of the longest meristem. In addition to length, temperature ranges and photosynthetically active radiation (PAR) were recorded weekly. Maximum/minimum thermometers were placed 10 cm below the water surface in each of the plastic tanks. Another maximum/minimum thermometer was used to record atmospheric temperature. PAR was measured weekly with a LI-COR light meter (model LI-185). Readings were recorded at the water surface both under the screen covers and uncovered, and 10 cm below the covered surface. The covers reduced surface light intensities by an average of 37% and light intensities at 10 cm below the surface were on average 74% of surface light intensities. Environmental variables are summarized in Table 1.

Table 1. Range of weekly environmental characteristics of the tanks at 10 cm beneath the covered surface and sediment attributes (±2 SE) at the beginning and end of the experiment. N = 24 for all results except water temperature.

	Water temp. (°C)	Sub-surface PAR μ mol s^{-1} m^{-2} (mean)	% Organic matter	Bulk density (g ml^{-1})	Pore water NH_4^+ (mg l^{-1})
Week 1	21-34	486-896 (752)	7.6 ± 0.2	0.60 ± 0.01	5.40 ± 0.33
Week 2	22-34	400-1025 (643)	—	—	—
Week 3	19-34	350-925 (506)	—	—	—
Week 4	18-31	115-300 (166)*	—	—	—
Week 5	16-30	350-750 (595)	8.9 ± 0.8	0.61 ± 0.02	0.866 ± 0.16‡
All weeks	16-34	350-1025 (624)**	—	—	—

*Readings recorded under cloudy skies.
**Excluding week 4 values.
‡Mean pore water NH_4^+ declined from the start of the experiment (t-test, $p < 0.001$).

Sediment was analyzed at the beginning and end of the experiment for bulk density, organic matter, and pore water ammonia following methods described by Newman et al. (1996), modified from Barko and Smart (1986). Three sediment cores (3.5 cm in diameter by length of 4 to 5 cm) from each tank were combined and homogenized. A 5 ml sediment subsample from each tank was dried at 105 C for 48 h and then weighed to obtain bulk density (g dry mass ml^{-1}). Dried sediment was then ashed at 550 C for 4 h to obtain percent organic matter (ash-free-dry-mass dry $mass^{-1}$*100). Pore water was extracted from the remaining sediment by centrifugation, acidified to less than pH 2 and stored in a refrigerator. Within seven days, the NH_4^+ concentration was determined by selective electrode (APHA 1989). Table 1 summarizes sediment conditions.

Plants were harvested at the end of week five. Individual stems (with leaves) and roots were separated and plants from each tank were spun dry (salad spinner) before fresh weights were recorded. Fresh weights of roots were obtained after excess water was squeezed out of roots. Stems and roots were then dried at 105 C and weighed.

Statistical analyses. Traditionally, competitive interactions between plants have been assessed using a reciprocal-replacement series (RS) design and analysis, developed by de Wit (1960, Connolly 1986). However, this type of analysis is inherently flawed because effects of interspecific competition cannot be isolated from effects of intraspecific competition (Firbank and Watkinson 1985, Connolly 1986, 1988), particularly when only one density is used. Connolly (1997) cautions against use of RS experiments to establish competitive hierarchies in plant communities or to infer competitive exclusion. Analysis of variance (ANOVA) appears to provide a more robust analysis of competition and has become a popular statistical tool for plant competition experiments (i.e., Moen and Cohen 1989, Chambers and Prepas 1990, Abernethy et al. 1996, Mal et al. 1997, Weihe and Neely 1997). Accordingly, we chose to assess competitive interactions by ANOVA.

Data were analyzed using JMP IN statistical software (Sall and Lehman 1996). Three-way ANOVA was carried out with elongation rates (cm wk^{-1}) and log-transformed values (to correct for normality) of individual stem and root dry mass to determine the effects of species, density, and culture type. Significance is concluded at the $p < 0.05$ level.

RESULTS AND DISCUSSION

Due to sunny, warm weather, and source of the northern watermilfoil cuttings (Christmas Lake), northern watermilfoil roots formed much earlier than expected (5 days), and stems had almost reached the surface (avg. length = 37 cm) by the time Eurasian watermilfoil roots were established. The variation in rooting times observed with northern watermilfoil suggests that source of cuttings (greenhouse vs lake) and weather greatly affect rooting times and thus initial growth. Eurasian watermilfoil cuttings formed roots in about seven days, as expected.

The head start by northern watermilfoil did not appear to have a large impact on the elongation of Eurasian watermilfoil because stem lengths of both northern and Eurasian watermilfoil in all treatments were approximately equal at the

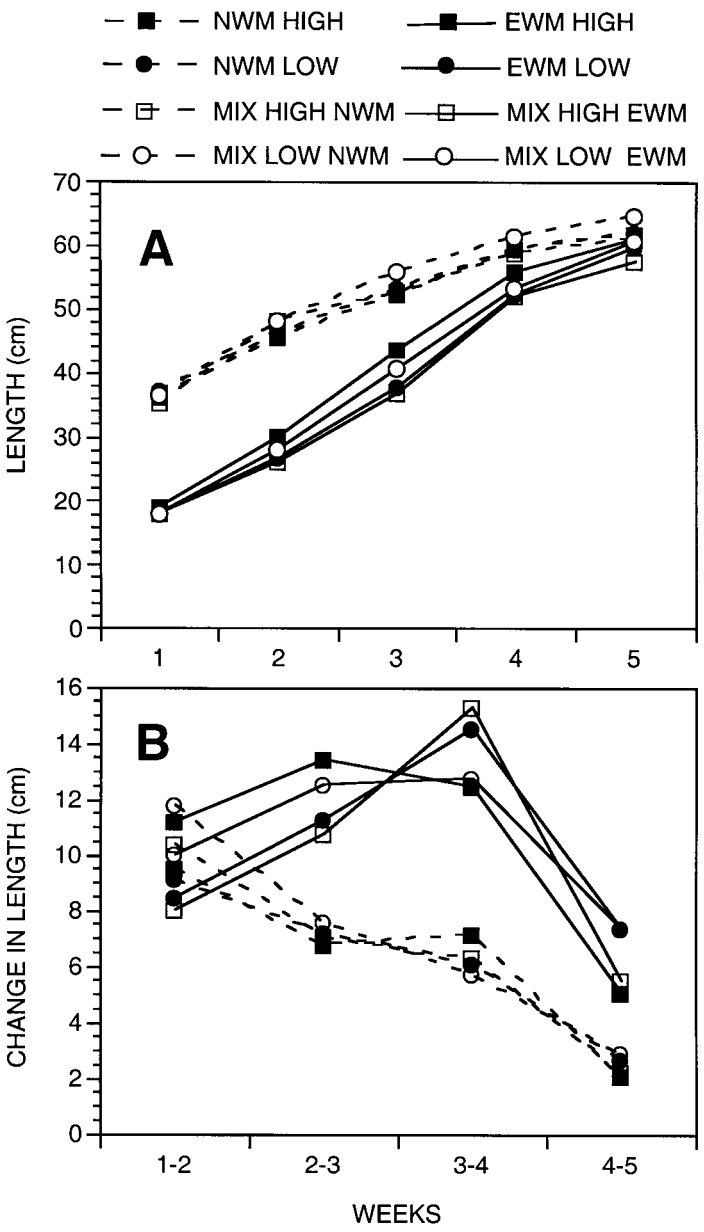

Figure 1. Mean weekly length (cm) of plants in each treatment (A), and elongation (B; change in length) of Eurasian (EWM) and northern watermilfoil (NWM) over the course of the experiment. High density was 150 stems m^{-2} and low density was 75 m^{-2}; mixed densities were half these levels for each species (i.e., 75 stems m^{-2} of each species for mixed high). Standard errors of mean values were all small (avg. SE of length = ± 1.28 cm and avg. SE of elongation = ± 0.29).

conclusion of the experiment (Figure 1A). Stems of both species grew an additional 16 cm once they reached the water surface and formed a thin mat of vegetation on the surface. Some stems of both Eurasian and northern watermilfoil formed flowers in all tanks, indicating a biomass peak (Smith and Barko 1990). No leaf sloughing of Eurasian watermilfoil was present in any of the treatments, indicating there was adequate light penetration throughout the water column (Madsen et al. 1991a). Average length of Eurasian watermilfoil in all treatments at week three (grand mean = 40 cm) was

approximately equal to the starting length of northern watermilfoil stems (grand mean = 37 cm). Therefore, to compensate for the head start by northern watermilfoil, length values of Eurasian watermilfoil between weeks three and five, and length values of northern watermilfoil between weeks one and five were used for statistical analysis of weekly elongation rate.

Three-way ANOVA indicated a significant species effect on elongation rate but there were no density or culture-type effects (Table 2). Northern watermilfoil grew 23 cm (37 cm to 61 cm) in four weeks, whereas Eurasian watermilfoil grew approximately the same amount in two weeks (Figure 1A). Elongation of both Eurasian and northern watermilfoil stems in all treatments slowed once they reached 38 cm in length, yet Eurasian watermilfoil still grew at a much faster rate (grand mean = 10.07 cm wk^{-1}) than northern watermilfoil (grand mean = 6.77 cm wk^{-1}) in all treatments after this length was reached (ANOVA $p < 0.001$; Figure 1B). Although no two-way interactions were present, ANOVA did detect a significant three-way interaction with elongation rate (p = 0.013). Eurasian watermilfoil elongation was slower in the high-density monoculture treatment (mean = 8.75 cm wk^{-1}) compared to the other treatments (mean = 10.5 cm wk^{-1}). Although northern watermilfoil elongated much slower than Eurasian watermilfoil in all treatments, stems of northern watermilfoil elongated faster in the low-density mixed cultures (mean = 7.55 cm wk^{-1}) compared to the other treatments (mean = 6.51 cm wk^{-1}).

Three-way ANOVA with root mass revealed only a density effect (p = 0.003; Table 2). Roots of both species were heavier in the low-density treatments. Qualitative comparison of average individual root and stem mass depict the same pattern between treatments (Figure 2). Because of the large variance of individual dry root mass among replicates (avg. coefficient of variation = 60), ANOVA failed to indicate any differences between species.

Three-way ANOVA also indicated a density effect on stem mass (Table 2). Average individual stem mass was significantly higher in the low-density treatments than in the high-density treatments ($p < 0.001$). Intraspecific competition suppressed biomass accumulation of Eurasian watermilfoil stems in the high-density monoculture treatments; stems of Eurasian watermilfoil were heavier in the low-density monocultures compared to stems in the high-density monocultures (t-test, p = 0.04). Marginal intraspecific competitive effects on

TABLE 2. RESULTS OF THREE-WAY ANOVAS SHOWING THE EFFECTS OF DENSITY (HIGH AND LOW), CULTURE-TYPE (MONO AND MIXED), AND SPECIES (EURASIAN AND NORTHERN WATERMILFOIL) ON WEEKLY ELONGATION RATE AND LOG-TRANSFORMED MEAN INDIVIDUAL STEM AND ROOT MASS. FOR EACH RESPONSE, 24 DEGREES OF FREEDOM ARE ASSOCIATED WITH THE ERROR MEAN SQUARE.

Elongation rate (cm wk^{-1})	DF	Sum of squares	*P*-value
Density	1	3.063	0.118
Culture-type	1	1.593	0.253
Species	1	86.724	<0.001
Density × Culture-type	1	0.616	0.474
Species × Culture-type	1	0.035	0.864
Species × Density	1	0.852	0.401
Species × Density × Culture-type	1	8.282	0.013
Avg. indiv. root dry mass (g)			
Density	1	5.232	0.003
Culture-type	1	0.003	0.942
Species	1	1.133	0.140
Density × Culture-type	1	1.369	0.107
Species × Culture-type	1	0.944	0.177
Species × Density	1	0.495	0.323
Species × Density × Culture-type	1	0.001	0.962
Avg. indiv. stem dry mass (g)			
Density	1	0.942	<0.001
Culture-type	1	0.015	0.589
Species	1	1.316	<0.001
Density × Culture-type	1	0.011	0.645
Species × Culture-type	1	0.454	0.006
Species × Density	1	0.125	0.124
Species × Density × Culture-type	1	<0.001	0.891

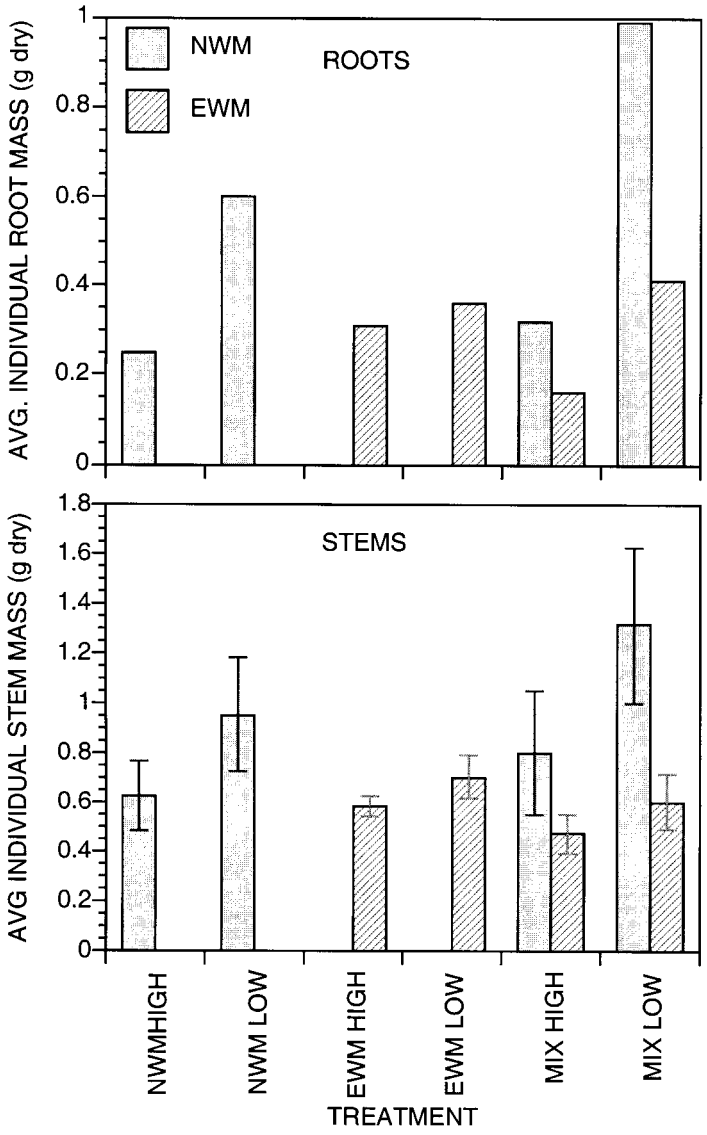

Figure 2. Mean individual root and stem mass of Eurasian (EWM) and northern (NWM) watermilfoil. High density was 150 stems m^{-2} and low density was 75 m^{-2}; mixed densities were half these levels for each species (i.e., 75 stems m^{-2} of each species for mixed high). Variance of root mass between replicates was large (avg. coefficient of variation = 60). Stem mass vertical bars are ±2 SE, based on the mean of 4 replicates for each treatment.

northern watermilfoil stem mass were present with lower average individual stem mass in the high-density treatments (t-test, $p = 0.07$).

It was less clear whether or not the head start by northern watermilfoil had a large impact on interspecific interactions. Comparison of monoculture treatments revealed no differences in stem mass between the two species (t-tests, $p > 0.10$). However, ANOVA revealed a species by culture-type interaction, with northern watermilfoil stems weighing more than Eurasian watermilfoil stems in the mixed-culture treatments ($p = 0.006$) (Figure 2). The lavish growth and profuse basal branching of northern watermilfoil suppressed biomass accumulation of Eurasian watermilfoil in the mixed-culture treatments. The presence of Eurasian watermilfoil had no significant effect on biomass accumulation of northern watermilfoil. In fact, northern watermilfoil had higher mean stem mass in both mixed treatments than in comparable monocultures (Figure 2), whereas Eurasian watermilfoil did not grow as well in mixed compared to monoculture treatments. Total biomass of Eurasian watermilfoil in the high-density mixed-treatments was suppressed to 64% of its yield in monoculture treatments of the same component density (Figure 3). Abernethy et al. (1996) also found significant suppression of Eurasian watermilfoil biomass when grown with Canada waterweed in shallow, clear water. Although the relatively short duration of both studies may have influenced the outcomes, the presence of many flowing plants in all of our treatments and the decreased elongation rates suggest that the length of our experiment was adequate to attain maximum biomass of both species. Of course, differing over-

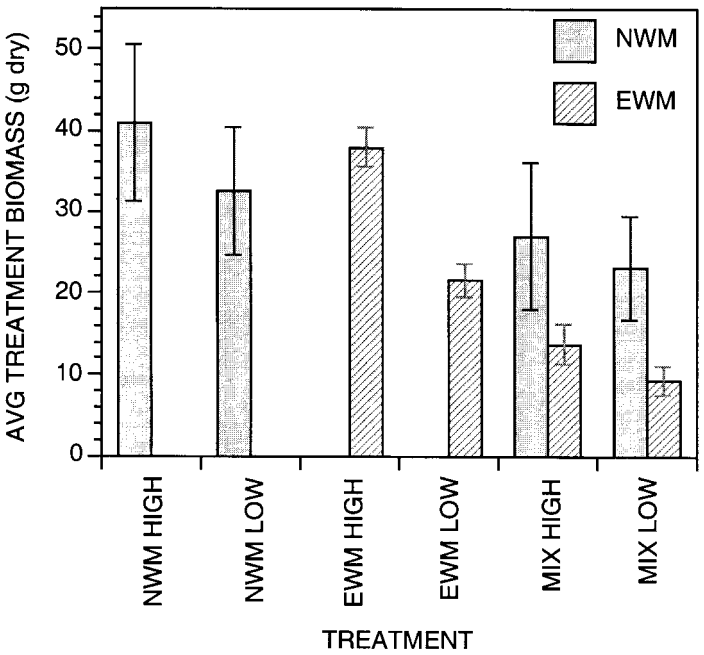

Figure 3. Average dry stem biomass of Eurasian (EWM) and northern (NWM) watermilfoil per treatment (0.5 m^2). High density was 150 stems m^{-2} and low density was 75 m^{-2}; mixed densities were half these levels for each species (i.e., 75 stems m^{-2} of each species for mixed high). Vertical bars are ±2 SE, based on the mean of 4 replicates for each treatment.

winter or spring regrowth abilities could alter the outcome over several growing seasons.

Northern watermilfoil likely preempted potentially valuable resources with its head start, thus, we cannot confidently conclude that northern watermilfoil will often be a superior competitor to Eurasian watermilfoil. Our results may not be applicable to deeper or more turbid water with well established Eurasian watermilfoil. Although growth of both species begins in early April (Aiken 1979), established populations of Eurasian watermilfoil may effectively displace northern watermilfoil in situ, particularly in deeper water, because it elongates more rapidly than northern watermilfoil, and unlike northern watermilfoil often forms a surface canopy. Disturbances (i.e., changes in water clarity or depth) may accelerate establishment of Eurasian watermilfoil (Smith and Barko 1990) and may facilitate eventual extirpation of northern watermilfoil. However, our results suggest that habitats with established northern watermilfoil may suppress the growth and biomass accumulation of newly invading Eurasian watermilfoil, at least in shallow, clear water.

Water clarity and depth may be important in determining competitive abilities of Eurasian watermilfoil. Eutrophic conditions of low light and high temperatures stimulate shoot elongation and canopy formation in Eurasian watermilfoil (Smith and Barko 1990). Eurasian watermilfoil, unlike most other native macrophytes, is poorly tolerant of shade; therefore, canopy formation is most likely a response to insufficient light penetration (Madsen et al. 1991a). Thus, northern watermilfoil may be shaded by Eurasian watermilfoil in turbid or deep habitats. Experimental tests of this hypothesis are needed.

Given the conditions of persistent clear or shallow water where light penetration is high, Eurasian watermilfoil may not develop an extensive surface canopy, thereby allowing coexistence with other macrophytes (Smith and Barko 1990). Considerable species diversity, including northern watermilfoil, has been found in Twin City metro lakes containing Eurasian watermilfoil that have Secchi depths ≥3.5 m (Newman et al. unpublished data). We also have observed northern watermilfoil to be common in shallow areas (<1.5 m) of Eurasian watermilfoil beds. Northern watermilfoil may be better suited to higher light conditions, however, we are unaware of comparative studies of photosynthetic characteristics of northern watermilfoil, as have been done with Eurasian watermilfoil (i.e., Titus and Adams 1979, Madsen et al. 1991a).

Instead of allocating its resources towards biomass production, Eurasian watermilfoil will allocate initial energy towards shoot elongation (Smith and Barko 1990). This may explain the faster growth rates of Eurasian watermilfoil compared to northern watermilfoil. Much like our study, Abernethy et al. (1996) discovered that despite suppression of biomass, shoot elongation of Eurasian watermilfoil was unaffected by the presence of a competitor (Canada waterweed). The rapid shoot elongation of Eurasian watermilfoil may be advantageous in deeper, light-limited habitats, because it can form a canopy that shades out potential competitors (Madsen et al. 1991b). Where light is not limiting, Eurasian watermilfoil may be at a competitive disadvantage with other macrophytes, such as northern watermilfoil and Canada

waterweed, for other resources, such as nutrients and space. Most studies of competitive abilities of watermilfoils have been conducted in very shallow, clear water.

The results of our experiment suggest Eurasian watermilfoil is the inferior competitor in newly invaded shallow habitats where northern watermilfoil is already established and that eventual dominance of Eurasian watermilfoil may be dependent on water clarity and depth. Competitive displacement of northern watermilfoil by Eurasian watermilfoil is likely a slow process and may be contingent upon Eurasian watermilfoil's ability to form a dense canopy. If high water clarity prevails throughout the growing season, successful colonization and subsequent domination of Eurasian watermilfoil into areas with abundant northern watermilfoil may not occur. However, competition experiments that vary water clarity or depth are needed to better support this claim, and will be needed to better understand conditions facilitating invasions and declines of Eurasian watermilfoil.

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