

Competition between *Hydrilla verticillata* and *Vallisneria americana* as influenced by soil fertility

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Abstract

The influence of soil fertility on competitive interactions between dioecious hydrilla [*Hydrilla verticillata* (L.f.) Royle] and American eelgrass (*Vallisneria americana* Michx) was investigated. Addition series experiments were conducted with mixed plantings of *Hydrilla* : *Vallisneria* grown at two levels of soil fertility. Competitive abilities of each plant species were determined using the reciprocal-yield model of mean plant weight. In monocultures, *Hydrilla* biomass averaged six times higher at high fertility as compared to biomass at low fertility, whereas only a two-fold increase in biomass was obtained with *Vallisneria* grown in similar fertility treatments. In mixed cultures at high fertility, *Hydrilla* was the stronger competitor relative to *Vallisneria*, with one *Hydrilla* plant being competitively equivalent to 7.2 *Vallisneria* plants in terms of their respective abilities to reduce *Hydrilla* biomass. Under nutrient limiting conditions, however, *Hydrilla* growth and its competitive advantage over *Vallisneria* were both depressed, and *Vallisneria* was the dominant species. These data indicated that differential response to increased nutrient inputs is one major determinant of competitive success in mixtures of dioecious *Hydrilla* and *Vallisneria*. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Hydrilla verticillata (L.f.) Royle is a major aquatic weed in the southern and eastern US. Once established in a body of water, this exotic invasive species readily dominates and replaces native submersed plants, such as American eelgrass (*Vallisneria americana* Michx.) (Van et al., 1976). *Hydrilla* develops a dense mat, or canopy, at the water surface eliminating almost totally sunlight penetration, thus limiting competition from other

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submersed species (Haller and Sutton, 1975). In contrast, *Vallisneria* produces a basal rosette of leaves which elongates up to the surface but does not form a canopy (Titus and Adams, 1979), and therefore, depends more on light availability near the sediment for growth and survival (Rybicki and Carter, 1986).

Plant competition has been recognized as an important factor determining species distribution in aquatic plant communities (Gopal and Goel, 1993). For example, Grace and Wetzel (1981) observed that the distributions of two cattail species were directly related to the fact that *Typha angustifolia* L. was a weak competitor relative to *T. latifolia* L. Similarly, Snow and Vince (1984) presented evidence that plant competition produces zonation patterns in an Alaskan salt marsh. Agami and Waisel (1985) reported that growth of *Najas marina* L. was significantly suppressed by *Myriophyllum spicatum* L. In nature, *N. marina* seldom occurs with *M. spicatum*, and when both species were grown in mixtures, the yield of each was reduced more than would be expected based on the results of growth in monoculture. *M. spicatum* was also reported to be a stronger competitor than *V. americana*, but the two species coexist in the littoral zones of lakes of Madison (Wisconsin) due to differences in their adaptation to low light intensity (Titus and Adams, 1979). *M. spicatum* adapts to low light via leaf sloughing and plasticity in growth form. In contrast, *V. americana* has more efficient carbon fixation at low light. The two species exhibit both temporal and spacial partitioning of the habitat. *Vallisneria* is a summer specialist whereas *Myriophyllum* grows better in winter.

In many natural environments, nutrient supply is also an important factor in determining plant community structure (Elberse et al., 1983; Pastor et al., 1984; Tilman, 1984). Nutrient enrichment of aquatic and terrestrial environments is often linked with the invasion of alien plants. For example, increasing soil nutrient levels in Australian heathlands and related shrublands caused changes in floristic and structural composition and led to the invasion of herbaceous aliens (Connor and Wilson, 1968; Heddle and Specht, 1975). Similarly, accelerated eutrophication resulting from human activities has been strongly implicated as a major cause for the invasion of *Hydrilla* and other exotic species in the US (Belanger et al., 1989; Dye, 1995). Changes in species composition after an increase in nutrient supply are caused to a great extent by changes in the competitive balance between plant species (Berendse, 1983; Heil and Bruggink, 1987). In this study, we used addition series methods to examine the effects of increased nutrient inputs on growth and competitive abilities of the invasive aquatic weed *Hydrilla verticillata* and a native species, *Vallisneria americana*.

2. Materials and methods

The study was conducted at the University of Florida, Fort Lauderdale Research and Education Center, which is located at coordinates 26°05'N and 80°14'W. Mixtures of *Hydrilla* and *Vallisneria* were grown from 6 April to 27 July 1994 in outdoor concrete tanks to assess their relative competitive abilities under two different levels of soil fertility. Water temperatures in the tanks during the study averaged 28°C (minimum 24°C, maximum 35°C). *Hydrilla* and *Vallisneria* plants were obtained from stock cultures maintained over a period of several months at the Center. *Hydrilla* was of the dioecious

type originally collected from Rodeo Lake in Davie, FL, and *Vallisneria* from Nova Pond, also in Davie, FL. Stem apices 15 cm long (*Hydrilla*) and whole plants (*Vallisneria*) were used, with mean individual plant dry weights of 164 ± 23 mg (mean \pm S.D.; $N = 10$) and 228 ± 55 mg measured at the start of the experiments, respectively. The culture pans were 30 cm by 34 cm and 15 cm deep, and filled with sand to within 2.5 cm from the rim (approximately 15 kg sand per pan), and fertilizer was mixed in before more sand was added to top off the pan. The commercial fertilizer Sierra¹, with nitrogen, phosphorous, and potassium (18 : 6 : 12) formulated for an 8- to 9-month release rate at 21°C, was used.

2.1. Growth Studies

Growth of single plants of *Hydrilla* and *Vallisneria* in sand amended with different amounts of fertilizer, consisting of 0, 1.8, 3.5, 8.8, 17.5, and 35.0 g of Sierra per 15 kg sand in a culture pan, was examined using the procedures described by Sutton (1986). The culture pans were placed in a concrete tank in a completely randomized design with three replicates. The tanks were 3.1 m in width by 6.2 m in length, and filled with pond water to 0.8 m high. Pond water was from the same source as described previously (Van and Steward, 1986), and flowed into the tanks at a rate which allowed for a complete volume exchange every 24 h. Each culture pan was enclosed by a vertical cage made with fiberglass window screening material forming a water column of 0.16 m² surface area and 0.8 m high. Periodically, each cage was cleaned with a siphon to remove debris or algae or both, which built-up on the bottoms and sides of the cages and the tanks. The experiment was harvested 10 weeks after planting, and plant biomass was measured after desiccation to constant weight at 70°C. Relative growth rates (RGR) were calculated based on the formula $RGR = (\ln W_2 - \ln W_1) / (t_2 - t_1)$ where W_2 and W_1 are plant dry weights at time t_2 and t_1 , respectively (Hunt, 1990).

2.2. Competition Studies

For competition studies, two rates of fertilizer, 2.0 g Sierra (low fertility) and 25.0 g (high fertility) per 15 kg sand were used. The experimental design followed an addition series (Spitters, 1983) consisting of factorial combinations of different densities of the two competing plant species. The *Hydrilla* : *Vallisneria* planting densities were 0 : 3, 0 : 9, 3 : 0, 3 : 3, 3 : 9, 9 : 0, 9 : 3, 9 : 9 plants per container, equivalent to total densities from 19 to 112 plant/m² at the start of the experiment. Sutton et al. (1980) reported high levels of intraspecific competition of *Hydrilla* at these planting densities under comparable growing conditions. The *Hydrilla* : *Vallisneria* density matrices were repeated to provide two sets of addition series, one for each soil fertility level. The resulting 16 treatments were arranged factorially (eight plant density combinations by two soil fertility levels) and placed in a concrete tank in a randomized block design.

¹ Scotts-Sierra, Marysville, OH. Mention of a trademark name, proprietary product, or specific equipment does not constitute a warranty by the US Department of Agriculture, and does not imply its approval to the exclusion of other products that also may be suitable.

Three replicated tanks (blocks) were used. All plants were harvested 16 weeks after planting. The two plant species were separated, and biomass (g dry weight) of above-ground (shoots) and below-ground (roots) were measured separately for each species.

2.3. Data Analyses

The competitive ability of each species was estimated using the reciprocal-yield model (Spitters, 1983). Basically, this involves multiple linear regressions of the form:

$$\frac{1}{W_h} = a_{h0} + a_{hh}N_h + a_{hv}N_v$$

$$\frac{1}{W_v} = a_{v0} + a_{vv}N_v + a_{vh}N_h$$

where W_h and W_v are the mean dry weight per plant for *Hydrilla* and *Vallisneria*, respectively, and N_h and N_v represent their respective densities. The intercepts (a_{h0} and a_{v0}) estimate the reciprocal of the maximum weight of isolated plants. Intraspecific competition was estimated by the partial regression coefficients a_{hh} and a_{vv} , while interspecific competition was estimated by a_{hv} and a_{vh} . Scatter plots of the residual vs. standardized predicted values were used to determine the homogeneity of variances and the degree of model fit. Tests of significance (F -tests) were performed using the General Linear Model procedure (SAS Institute, 1988) to determine the significance of the regression coefficients. In addition, the ratios of coefficients (a_{hh}/a_{hv} and a_{vv}/a_{vh}) were tested using F -tests to determine if intraspecific and interspecific competition were significantly different. The double ratio $(a_{hh}/a_{hv}) \times (a_{vv}/a_{vh})$ was used to assess partitioning of resources between species (Spitters, 1983). Values greater than unity indicate increased resource partitioning, i.e., niche separation.

Regressions for the two fertility levels were compared using a procedure for comparison of multiple regression described by Zar (1984). A dummy variable was used to indicate the two levels of fertility, and F -tests of regressions of the pooled data indicated if the parameter coefficients were significantly different due to soil fertility.

3. Results

In monocultures, *Hydrilla* responded much more strongly to the application of nutrients than did *Vallisneria* (Fig. 1). At low fertility, the relative growth rate (RGR) of *Hydrilla* ($266 \text{ mg g}^{-1} \text{ week}^{-1}$) was lower than that of *Vallisneria* ($295 \text{ mg g}^{-1} \text{ week}^{-1}$). However, RGR of *Hydrilla* increased to $450 \text{ mg g}^{-1} \text{ week}^{-1}$ at high fertility, surpassing the corresponding RGR of *Vallisneria* ($359 \text{ mg g}^{-1} \text{ week}^{-1}$) at the same fertilization rate. Due to the stronger response to fertilization, *Hydrilla* biomass averaged six times higher in high fertility at the end of the experiment as compared to biomass in low fertility, whereas only a two-fold increase in biomass was obtained with *Vallisneria* grown in similar fertility treatments (Fig. 1). This was also the case in the experiment where *Hydrilla* and *Vallisneria* were grown in mixed cultures (Table 1). Total plant biomass of

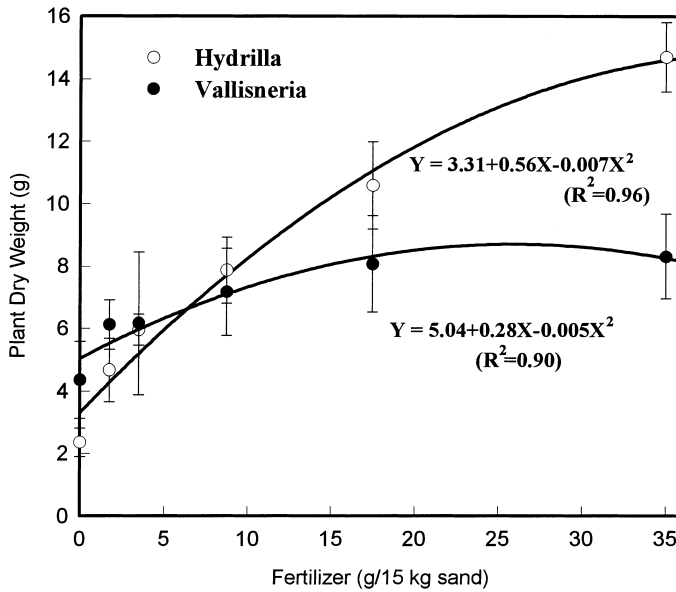


Fig. 1. Growth response of *Hydrilla* and *Vallisneria* to different fertilizer rates in monocultures after 10 weeks. Vertical bars indicate the standard deviations.

both species were on average greater at high fertility than at low fertility, but *Hydrilla* shoot mass showed the greatest increase while *Vallisneria* root mass did not change. Furthermore, *Vallisneria* allocated a much higher proportion of its biomass to its root system than did *Hydrilla* (Table 1). In both species, the relative amount of biomass allocated to the roots was lower at high fertility than at low fertility. This phenotypic change with regards to nutrient availability is common to many plant species (Brouwer, 1962).

Since the individual species responded differently to nutrient availability, the outcome of competition between *Hydrilla* and *Vallisneria* changed depending on the fertility level.

Table 1
Biomass of *Hydrilla* : *Vallisneria* mixed plantings after 16 weeks at two different levels of soil fertility

Fertility treatment ^a	<i>Hydrilla</i> ^b			<i>Vallisneria</i> ^b		
	Shoot (g)	Root (g)	Root/shoot ratio	Shoot (g)	Root (g)	Root/shoot ratio
Low	12.28 d	1.49 d	0.15 c	6.85 d	2.73 c	0.47 c
High	75.31 c	3.91 c	0.05 d	13.59 c	2.54 c	0.23 d

^aLow and high fertility treatments were 2 g and 25 g Sierra fertilizer per 15 Kg sand, respectively.

^bData were pooled for all *Hydrilla* : *Vallisneria* planting densities at each soil fertility level. Values followed by different letters are significantly different ($P < 0.05$) between fertility levels according to the Waller–Duncan test.

At high fertility, regression analysis of the mean plant weight using the reciprocal-yield model gave the following equations:

$$\frac{1}{W_h} = 0.65 \times 10^{-2} + 0.99 \times 10^{-2}N_h + 0.14 \times 10^{-2}N_v, \quad R^2 = 0.90, \quad N = 18 \quad (1)$$

$$\frac{1}{W_v} = 0.77 \times 10^{-2} + 7.32 \times 10^{-2}N_h + 3.74 \times 10^{-2}N_v, \quad R^2 = 0.78, \quad N = 18 \quad (2)$$

With respect to *Hydrilla* Eq. (1), the ratio of coefficients comparing intraspecific to interspecific competition (a_{hh}/a_{hv}) = $0.99/0.14 = 7.2$ ($P < 0.0001$). This ratio implies that intraspecific competition from other *Hydrilla* plants was more important than interspecific competition from *Vallisneria* in mixed plantings. In this case, adding one *Hydrilla* plant has the same impact on the mean *Hydrilla* weight as adding 7.2 *Vallisneria* plants, i.e., *Hydrilla* was competitively equivalent to 7.2 *Vallisneria* plants under conditions of high soil fertility.

The partial regression coefficients for *Vallisneria* in Eq. (2) also are significant. With respect to *Vallisneria*, the ratio (a_{vv}/a_{vh}) = $3.74/7.32 = 0.5$ ($P < 0.0001$) indicating that one *Vallisneria* was competitively equivalent to one-half *Hydrilla* plant in terms of their impact on the mean *Vallisneria* weight. The double ratio (a_{hh}/a_{hv}) \times (a_{vv}/a_{vh}) = $(7.2) \times (0.5) = 3.6$ indicates increased resource partitioning, i.e., niche separation (Spitters, 1983).

Similar analysis of the data from the low fertility treatment yielded the following equations:

$$\frac{1}{W_h} = 6.78 \times 10^{-2} + 2.41 \times 10^{-2}N_h + 9.44 \times 10^{-2}N_v, \quad R^2 = 0.83, \quad N = 18 \quad (3)$$

$$\frac{1}{W_v} = -5.87 \times 10^{-2} + 2.97 \times 10^{-2}N_h + 11.04 \times 10^{-2}N_v, \quad R^2 = 0.77, \quad N = 18 \quad (4)$$

For Eq. (3), the ratio of coefficients (a_{hh}/a_{hv}) = $2.41/9.44 = 0.3$ ($P < 0.0001$) implies that *Hydrilla* became the weaker competitor relative to *Vallisneria* at low fertility. In this case, one *Hydrilla* plant was competitively equivalent to 0.3 *Vallisneria* plant in terms of their respective abilities to reduce the biomass of *Hydrilla*. Similarly, Eq. (4) for *Vallisneria* also supported the same conclusion of a competitively stronger *Vallisneria* in the low fertility treatment. The intercept estimates the reciprocal of the yield of an isolated plant. Therefore the negative intercept in Eq. (4) is biologically irrational and is probably caused by random errors (Spitters, 1983). Our estimate of the intercept is of limited utility because it is outside the data range of the regressions. A more accurate estimate of the intercept could be made by incorporating observations at very low densities into the experiment.

The change in competitive relationship between *Hydrilla* and *Vallisneria* at the two levels of soil fertility is illustrated by the three-dimensional graphs of the reciprocal yield models (Fig. 2). The slopes of the regression planes corresponded to the competition coefficients in Eqs. (1)–(4), and the greater the slope the larger the competitive coefficients. Since the scales for the independent axes are the same, comparison of the slopes could be made across *Hydrilla* and *Vallisneria* densities. For example, (Fig. 2(A)

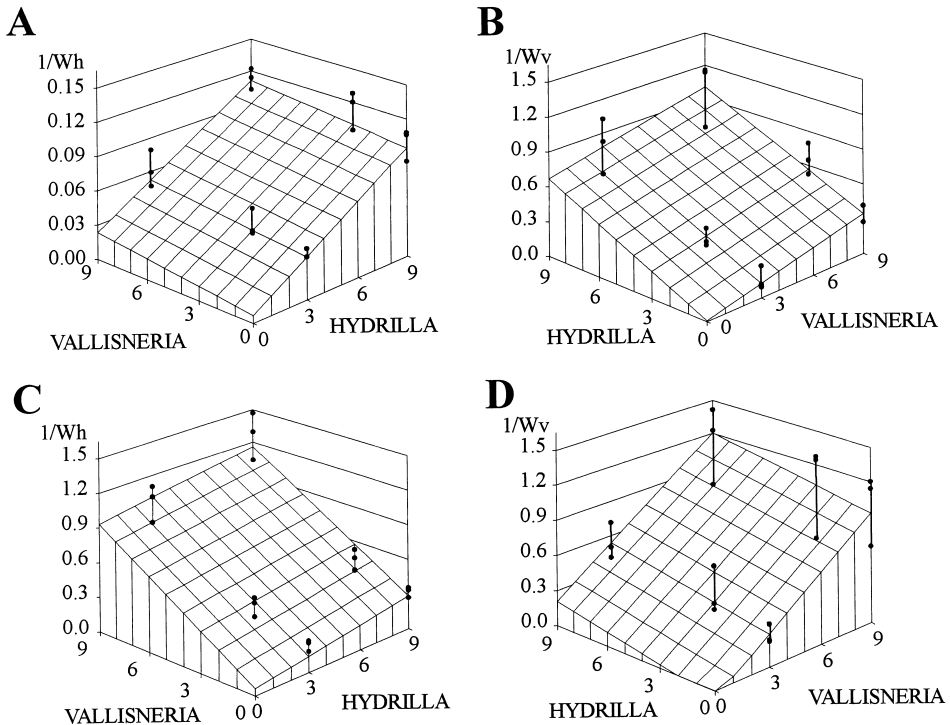


Fig. 2. Multiple regression planes demonstrating the effects of soil fertility and plant densities on the reciprocal of the mean dry weight per plant for *Hydrilla* ($1/W_h$) and *Vallisneria* ($1/W_v$). A and C compare relative competitive abilities of *Hydrilla* in high fertility and low fertility, respectively. B and D compare relative competitive abilities of *Vallisneria* in high fertility and low fertility, respectively. Points represent actual observations ($n = 18$), and the vertical lines between data points indicate the ranges. Values in X-axis are plant densities of *Hydrilla* and *Vallisneria* at the start of the experiment.

and (B)) both show a much steeper slope associated with the density of *Hydrilla* plants, reflecting the superior competitive ability of *Hydrilla* in high fertility. *Hydrilla* plants grew luxuriantly in high fertility forming a dense canopy, restricting competition from *Vallisneria*. Under conditions of low fertility, however, the outcome of interaction between the two species reversed, and *Vallisneria* became the dominant species (Fig. 2(C) and (D)).

4. Discussion

The competitive advantage of *Hydrilla* relative to *Vallisneria* has been reported previously (Steward, 1991; Smart, 1993). At high fertility, *Hydrilla* allocated as much as 95% of its biomass into photosynthetic tissues (Table 1) forming a dense canopy near the water surface, thus acquiring a considerable advantage in competition for light. In contrast, *Vallisneria* dedicated as much as 47% of its biomass into root production, thus

increasing its competitive ability for belowground resources, and became the dominant species under conditions of low soil fertility. These results conform to common observations that tall canopy-forming plants dominate nutrient-rich, highly productive areas, while oligotrophic communities are characterized by short rosette-like species (Hutchinson, 1975). Similarly, Gaudet and Keddy (1995) observed that species distributions along natural resource gradients are related to their relative competitive performances, such that species with high competitive performance occur in nutrient-rich (fertile) areas and species with low competitive performance in low-nutrient (infertile) areas.

Changes in species composition after an increase in nutrient supply (Van den Bergh, 1979; Heil and Diemont, 1983; Aerts and Berendse, 1988) are caused to a great extent by changes in the competitive balance between plant species (Berendse, 1983; Heil and Bruggink, 1987). In fact, the relative growth of plant competitors can be manipulated by adding nutrients to favor one species over another, thereby altering their respective competitive hierarchies (Bazzaz and Harper, 1976; Fowler, 1982). Similarly, fertilization experiments indicated that increased rates of nitrogen or phosphorus supply were important factors causing *Erica*-dominated communities to be replaced by *Molinia* stands in wet heathlands in the Netherlands (Aerts et al., 1990). Our results also indicated that a differential response to increased nutrient inputs is one major determinant of competitive success in mixtures of dioecious *Hydrilla* and *Vallisneria*.

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