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Aquatic Plant Control Research Program

Competition Between *Hydrilla verticillata* and *Vallisneria americana* Under Different Environmental Conditions

by *R. Michael Smart, John W. Barko, Dwilette G. McFarland*
Environmental Laboratory

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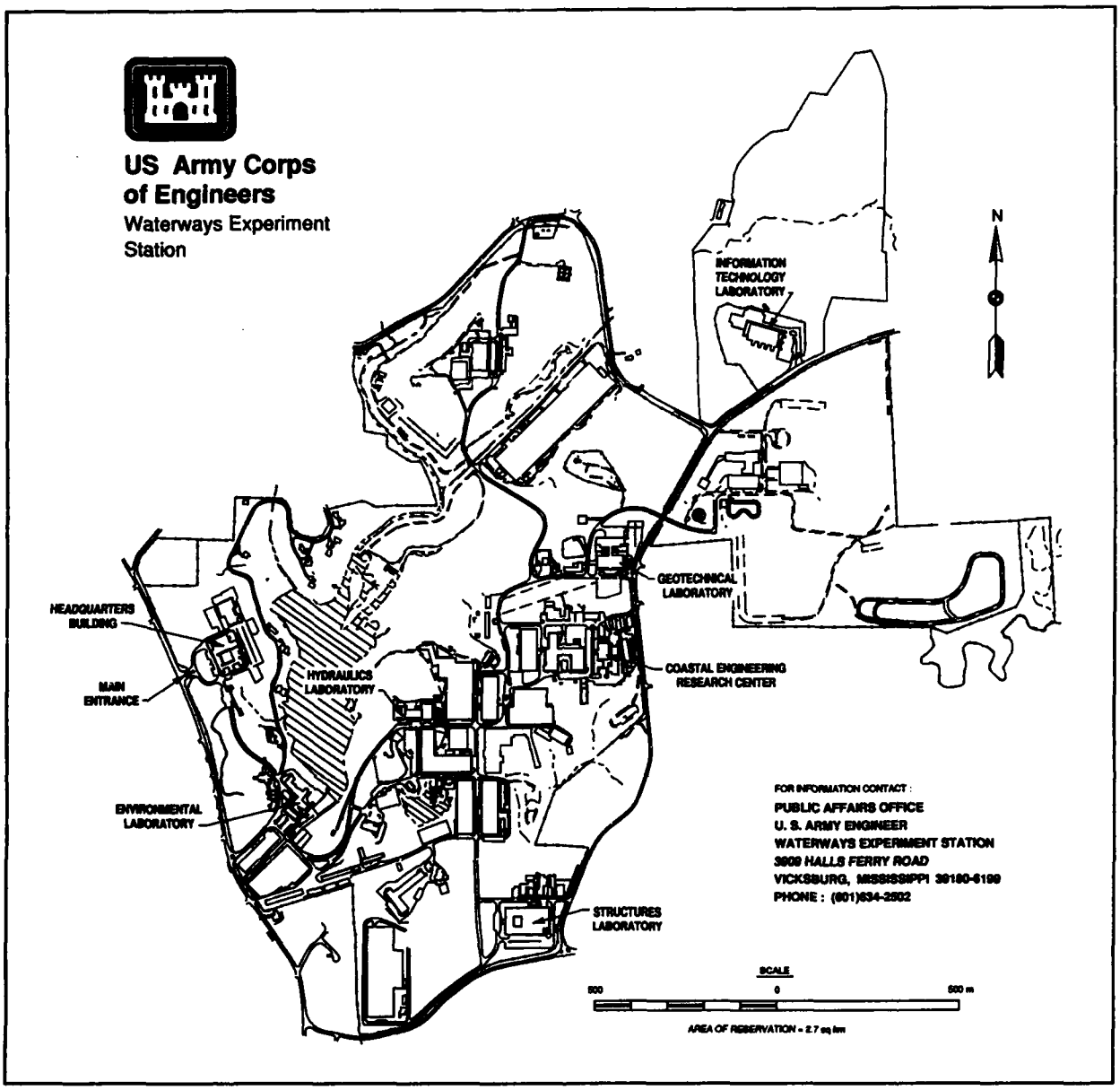

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Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP), Work Unit 32577. The APCRP is sponsored by the Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of the Army Appropriation Number 96X3122, Construction General. The APCRP is managed under the Environmental Resources Research and Assistance Programs (ERRAP), Mr. J. L. Decell, Manager. Mr. Robert C. Gunkel was Assistant Manager, ERRAP, for the APCRP. Technical Monitor during this study was Ms. Denise White, HQUSACE.

Principal Investigator for this study was Dr. R. Michael Smart, Ecosystem Processes and Effects Branch (EPEB), Environmental Processes and Effects Division (EPED), EL, WES. Technical assistance was provided by Ms. Gail Bird, Ms. Wanda Dee, Mr. Harry Eakin, Ms. Evelyn Henderson, Ms. Avis Howell, Ms. Kimberly Mauermann, and Ms. Susan Monteleone. The report was reviewed by Drs. Robert Doyle and John Madsen, EPED. Dr. Smart, Dr. John W. Barko, and Ms. Dwilette G. McFarland prepared this report.

This investigation was performed under the general supervision of Dr. Richard E. Price, Chief, EPEB, Mr. Donald L. Robey, Chief, EPED, and Dr. John Harrison, Director, EL.

At the time of publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Bruce K. Howard, EN.

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1 Introduction

Several attributes of a submersed aquatic plant community largely determine whether or not an aquatic plant control problem exists. These include species composition, biomass production, and the areal extent and location of the community. Of these, species composition is most important. Certain species, such as Eurasian watermilfoil (*Myriophyllum spicatum*) and *Hydrilla* (*Hydrilla verticillata*), have been identified as noxious exotic plants and are considered to cause problems wherever they occur. Biomass production is also important, and in extremely infertile, oligotrophic systems or in deep, turbid waters, aquatic plant problems may not develop in spite of the presence of these problem species. Unfortunately, these conditions are relatively rare, and many of the reservoirs and waterways under stewardship of the Corps of Engineers (particularly those with sizeable areas of shallow, slow moving water) are capable of supporting problem levels of submersed aquatic plants.

Since only a few of the many species of submersed aquatic plants cause problems requiring control or management operations, the growth characteristics of these problem species should be examined. Populations of problem submersed aquatic plant species, typified by Eurasian watermilfoil and *Hydrilla*, generally produce much of their biomass at or near the water surface, often forming an extensive canopy or mat of intertangled branches (Haller and Sutton 1975; Nichols and Shaw 1986). This surface mat can cause a variety of environmental problems and often interferes with use of water resources. Since their surface mat also physically impedes the exchange of gases across the air-water interface, these species often cause diminished oxygen concentrations (Buscemi 1958) and wide swings in pH (Van, Haller, and Bowes 1976). Heavy infestations can also severely reduce the flow of water, causing stagnant conditions leading to further degradation of water quality. These conditions, which are characteristic of extensive, monospecific beds of canopy-forming submersed aquatic plants, provide a habitat that is generally detrimental to fish and other desirable aquatic organisms (Newroth 1985). Extensive surface mats also interfere with navigation and water supply, can eliminate contact recreation such as swimming and water skiing, and may limit or prevent access to open water by boaters and fishermen.

Many nonproblem, native species exhibit a distinctly different growth form. These species, typified by *Vallisneria* (*Vallisneria americana*), distribute their biomass more uniformly throughout the water column (Haller and Sutton 1975;

Titus and Adams 1979). Since these species do not produce an extensive mat at the water surface, they generally do not cause significant adverse environmental conditions or interfere with use of water resources. In fact, the presence of these native submersed aquatic plant communities enhances aquatic habitats, providing both food and shelter for invertebrates and fish (Nichols 1986). These plant communities also increase water clarity by filtering suspended matter, reducing nutrient concentrations that promote algal blooms, and stabilizing deposited sediments. The objective of aquatic resource management should be not only to control occurrences and prevent the spread of problem exotic species, but also to protect, preserve, and promote communities of beneficial, native aquatic plants.

Although only a relatively few species of submersed aquatic plants cause problems requiring management attention, these species are very common. The widespread occurrence of these problem species and their strong dominance of many submersed aquatic plant communities require study. Problem species, such as *Hydrilla*, must be either more highly adapted to their environment than are most native species, or they may be competitively superior to these native species. The biological, ecological, or environmental reasons leading to the frequent dominance of submersed aquatic plant communities by problem exotic species should be determined. This information should then be considered in formulating aquatic plant management plans that include promoting the establishment and persistence of beneficial native plant communities in an attempt to slow or prevent the regrowth, reinvasion, or further spread of problem species.

Since the concern is with the management of aquatic resources that are either presently infested with (or are likely to be infested with) problem submersed aquatic plants, the factors controlling the distribution and abundance of these problem species must be considered. Examinations of the environmental factors affecting the growth of both introduced and native species have provided much information on the requirements of individual species of both groups. These studies have considered light (Barko and Smart 1981a; Barko, Hardin, and Matthews 1982), temperature (Barko and Smart 1981a; Barko, Hardin, and Matthews 1982), sediment composition (Barko and Smart 1981b, 1983, 1986), and fertility (Barko et al. 1988); water chemistry (Smart and Barko 1986, 1988, 1990) and salinity (Twilley and Barko 1990); and inorganic carbon supply (Smart and Barko 1988, 1990) as well as various combinations of these factors (Barko 1982, 1983; McFarland and Barko 1987; Smart and Barko 1990). While individual species exhibit quantitatively different responses to these environmental factors, qualitatively, most submersed aquatic plants respond to the environment in quite similar fashion. In other words, most of the species tested have exhibited roughly similar light, temperature, and nutrient requirements. Certainly, there are no consistent differences in the collective responses of problem and nonproblem groups of submersed aquatic plants.

Since both problem and nonproblem species exhibit fairly similar environmental requirements and tolerances, and since a variety of environmental

conditions can be found in most aquatic systems, it is unlikely that the distribution of problem species can be attributed to unique environmental conditions. Therefore, one must look elsewhere for an explanation of the widespread occurrence of problem exotic species and their often complete domination of the submersed aquatic plant community.

Although the environment may elicit similar responses from both problem and nonproblem submersed aquatic plant species, individual physiological responses to environmental conditions may differ sufficiently between species that more efficient species may outcompete less efficient species when they are growing together. If problem exotic species were physiologically more efficient at photosynthesis under low light levels (Van, Haller, and Bowes 1976; Bowes et al. 1977) or were more effective at light capture than were nonproblem species (Haller and Sutton 1975), then this might explain their dominance in deep or turbid waters where light is limiting biomass production. Similarly, if problem species were more effective than nonproblem species at nutrient uptake, this might explain their dominance under nutrient-limiting conditions. In either case, a higher efficiency of the physiological response to an environmental factor should confer a competitive advantage under conditions where that environmental factor is growth limiting. The widespread and often dominant occurrence of problem exotic species such as *Hydrilla* or Eurasian watermilfoil may be the result of some competitive advantage over native species (Haller and Sutton 1975; Madsen et al. 1991).

If dominance in submersed aquatic plant communities is attributable to competitive ability, then competitive, native species that could be used to replace problem exotic species in these communities might be identified. These communities of native submersed aquatic plants would provide water quality and habitat benefits without the adverse effects associated with the excessive growth and surface mat development of communities dominated by problem exotic species. By following aquatic plant control operations with the establishment of competitive, native species, the recurrence of aquatic plant problems might be slowed or even prevented. This would prolong the effectiveness of the control operation, perhaps resulting in a lower overall cost of management. Additional benefits would include improved aquatic habitat, water quality, and, in the case of chemical control, lesser use of herbicides.

The research reported here involved an evaluation of the relative competitive abilities of a problem exotic species, *Hydrilla verticillata*, and a beneficial native species, *Vallisneria americana*, under different environmental conditions. The objectives of the research were to identify the factors and mechanisms involved in short-term competition between thesc two species.

2 Materials and Methods

The experiment was conducted in a system of 1,200-L white fiberglass tanks, measuring 150 by 90 by 90 cm deep, and housed in a greenhouse facility of the Environmental Laboratory at the U.S. Army Engineer Waterways Experiment Station (WES), Vicksburg, MS. Experimental treatments were randomly assigned to tanks in the greenhouse. Solutions were maintained at 25 ± 1 °C with thermostatically controlled liquid circulators (Remcor Corp., Chicago, IL). Gas exchange and mixing were facilitated by administering humidified, compressed air through twin air lifts in each tank. Experimental tanks were fitted with lucite covers to prevent the entry of dust and other contaminants.

The experimental solution used in the study (Table 1) approximates the average composition of bicarbonate lake waters (Hutchinson 1957) and is a modification of the alkaline solution of Smart and Barko (1985). Specific modifications included (a) a reduction in calcium (Ca) to minimize precipitation of calcium carbonate ($CaCO_3$) and (b) an increase in potassium (K) since prior studies indicated that shoot uptake of K by submersed aquatic plants often exhausted lower levels of solution K (Smart and Barko 1988, 1990). A similar low Ca, low dissolved inorganic carbon (DIC) solution produced maximal biomass of *M. spicatum* (Smart and Barko 1986). The solution was formulated by additions of reagent grade chemicals to deionized (reverse osmosis) water. Gaseous carbon dioxide (CO_2) was administered to solution prior to adding required amounts of $CaCO_3$ to achieve solubility (Smart and Barko 1984, 1985). The chemical composition of the solution was subsequently verified by chemical analysis. Water samples were collected from each of the experimental tanks and analyzed for sodium (Na), K, Ca, and magnesium (Mg) by atomic absorption spectrophotometry. Electrical conductivity (25 °C) was determined with a YSI Model 32 conductivity meter. DIC was determined with a Beckman Model 915A Total Organic Carbon Analyzer; pH was measured with a Beckman Expandomatic IV expanded scale pH meter; and alkalinity was calculated from these measured values according to equations provided in Stumm and Morgan (1981).

Sediment used in the experiment was collected from Brown's Lake, a turbid reservoir located on the grounds of WES. Brown's Lake sediment (collected from areas free of submersed aquatic plants) has been used for many years as a substrate for culturing rooted submersed aquatic plants. This fertile,

Table 1
Chemical Composition and Characterization of Experimental Solution Used in the Investigation

Chemical Composition		Solution Formulation	
Parameter	**Concentration mg/L**	**Reagent**	**Quantity mg/L**
Na	15.3	$NaHCO_3$	55.95
K	9.8	$KHCO_3$	25.00
Ca	15.2	$CaCO_3$[a]	37.92
Mg	4.0	$MgSO_4$ (anh.)	9.90
		$MgCl_2$	7.83
DIC[b]	20.0		
SO_4^{-2}	7.9		
Cl^-	5.8		
Alkalinity	66.0		

[a] Requires addition of CO_2 gas to achieve solubility.
[b] Note that half of the DIC is derived from gaseous CO_2.

fine-textured sediment supports good growth of submersed aquatic plants (Barko and Smart 1986). Physical and chemical characteristics of the sediment were similar to those provided earlier (Barko and Smart 1986). Prior to use, the sediment was thoroughly mixed in an electrically driven mortar mixer. After mixing, sediment was placed in 1-L plastic containers (pots), and these were randomly assigned to different experimental treatments.

Previous laboratory and field research has shown that light level, sediment nutrient availability (Barko 1992), and inorganic carbon supply (Smart 1990) are major determinants of biomass production by rooted submersed aquatic plants. Since these resources are also likely to be limiting biomass production of natural submersed aquatic plant communities, differences in efficiency of uptake or utilization of these resources are likely to translate into differences in competitive ability. The species that more efficiently acquires or utilizes the limiting resource should be competitively superior (Tilman 1982, 1988, 1990). To examine possible interactions among the three potential limiting resources, the experiment was conducted in a factorial arrangement with two light levels, two sediment fertility levels, and two rates of inorganic carbon supply, for a total of eight environmental treatment combinations.

The experiment employed two light levels that were achieved by placing neutral density shade fabric (73 percent shade) over the entire greenhouse and over half of the experimental tanks (low light treatments). Shading reduced solar irradiance to maximal midday photosynthetically active radiation (PAR) levels of about 550 (high) and 125 (low) $\mu E/m^2/sec$ (Figure 1), or

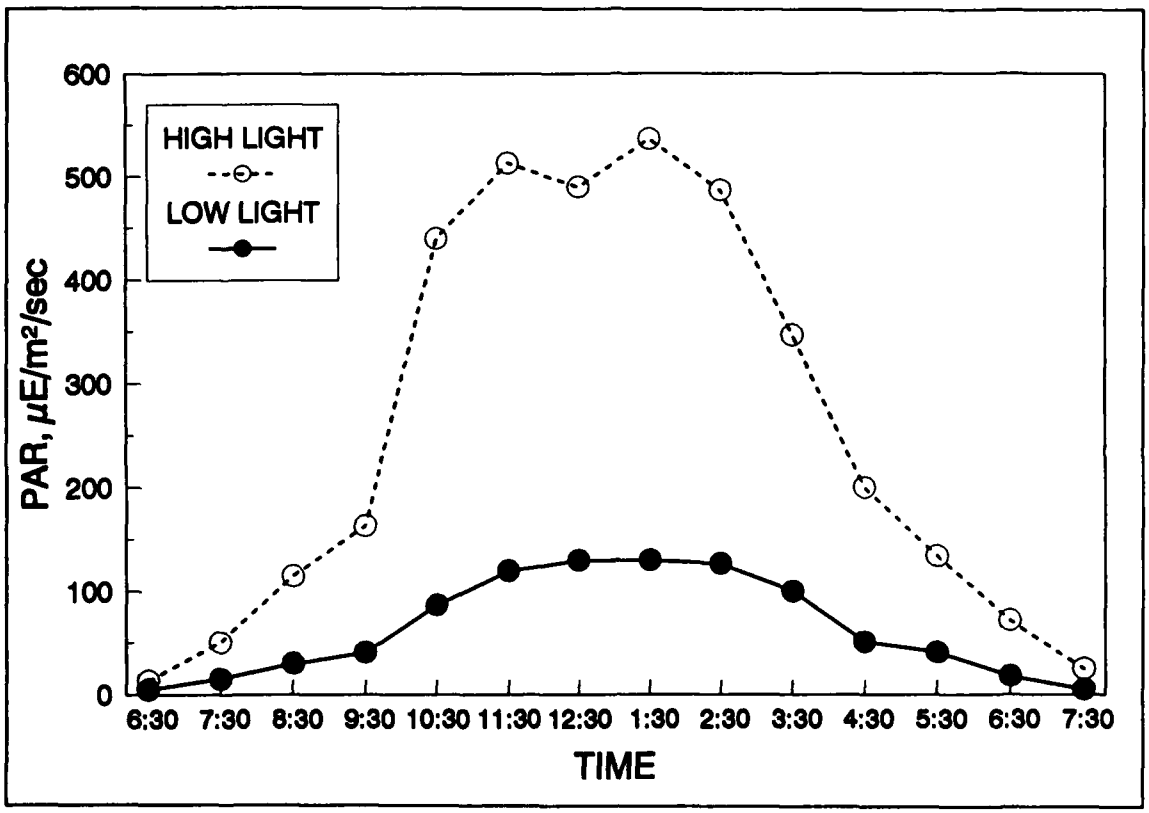

Figure 1. Experimental light levels used in the investigation. Values are means of three separate measurements taken on a typical sunny day. Standard errors of the means generally fell within the area of the markers

approximately 25 and 5 percent, respectively, of full sunlight. PAR was measured with a LiCor irradiance meter equipped with an underwater quantum sensor.

The two fertility levels were achieved by using freshly collected sediment (high fertility treatments) and sediment that had previously supported the growth of submersed aquatic plants (low fertility treatments). A prior period of growth results in much lower sediment nitrogen (N) levels and a corresponding reduction in biomass production (Barko et al. 1988).

The two rates of inorganic carbon (C) supply were achieved by varying the concentration of CO_2 in the aerating gas. Under ambient air aeration, photosynthesis by actively growing submersed aquatic plants causes decreases in HCO_3^- concentration, increases in pH, and frequently results in DIC depletion because of the combined effects of photosynthetic DIC uptake and $CaCO_3$ precipitation (Smart and Barko 1986). DIC depletion was not prevented by administering air enriched fourfold in CO_2 (Smart and Barko 1988), but can be partially alleviated by supplying air containing 10 times ambient CO_2. To ensure that the additional CO_2 would maintain higher levels of DIC, a tenfold enrichment as a high C supply treatment was employed. Low inorganic C

supply treatments received ambient air aeration from a compressor supplied with outside air, while high C supply treatments received compressed air that had been enriched tenfold in CO_2 (350 and 3,500 µL/L, respectively). Concentrations of CO_2 in the aerating gas were obtained by metering pure CO_2 into a metered air stream provided by a separate compressor. Each of the air streams was filtered and then humidified by bubbling through deionized water columns. CO_2 concentrations were verified by infrared gas analysis (Beckman Model 865).

The size and complexity of the experiment required that it be conducted in two phases. The first phase included all combinations involving the high fertility treatments. The second phase, which included only the low fertility treatments, employed nutrient-depleted sediment left over from the first phase. The two phases bracketed the summer solstice, and each phase employed an 8-week period of growth.

Relative competitive abilities of the two species were evaluated by comparing the responses of plants grown monospecifically (without competition) and in mixture. Two types of mixtures were used in an attempt to separate the effects of root and shoot competition (Figure 2). Pot mixtures, with both species growing in the same pot, subjected the plants to both root and shoot competition. Tank mixtures, with each species rooted in separate pots, subjected the plants to shoot competition only. Each tank contained forty 1-L pots arranged in eight columns of five. The large number of pots ensured that shoot competition would begin early in the experiment. Each competition experiment included the four competition treatments (*Hydrilla* monoculture, *Vallisneria* monoculture, pot mixture, and tank mixture) grown under each of the eight environmental treatment combinations. Each of the 32 competition environmental treatment combinations was randomly allocated to a single tank, except that combinations involving tank mixtures were allocated to two tanks to achieve a total of 40 pots of each species for each combination (Figure 2). Overall, the experiment employed 40 tanks and 1,600 pots.

Apical shoots of *Hydrilla*, 15 cm in length, were taken from a greenhouse culture that had been maintained at 25 °C and at light levels similar to the higher level used in the study. Dormant field-collected winter buds of *Vallisneria* were obtained from a commercial source in Wisconsin. Four propagules (apices or winter buds) were planted in each pot (Figure 2). Pots allocated to monospecific and tank mixture treatment combinations received four propagules of only one of the species, while pots designated to be used in pot mixture combinations received two propagules of each species. After planting, a 2-cm layer of washed silica sand was placed over the sediment to minimize physical exchanges with the overlying water.

At the end of the 8-week growth period, 10 replicate containers were harvested for each treatment combination. Plant shoots were clipped at the sediment surface, and the number of shoots (plants or rosettes in *Vallisneria*) were counted and measured for length. After these measurements were obtained, shoots were rinsed, bagged, and dried at 80 °C in a forced draft oven to

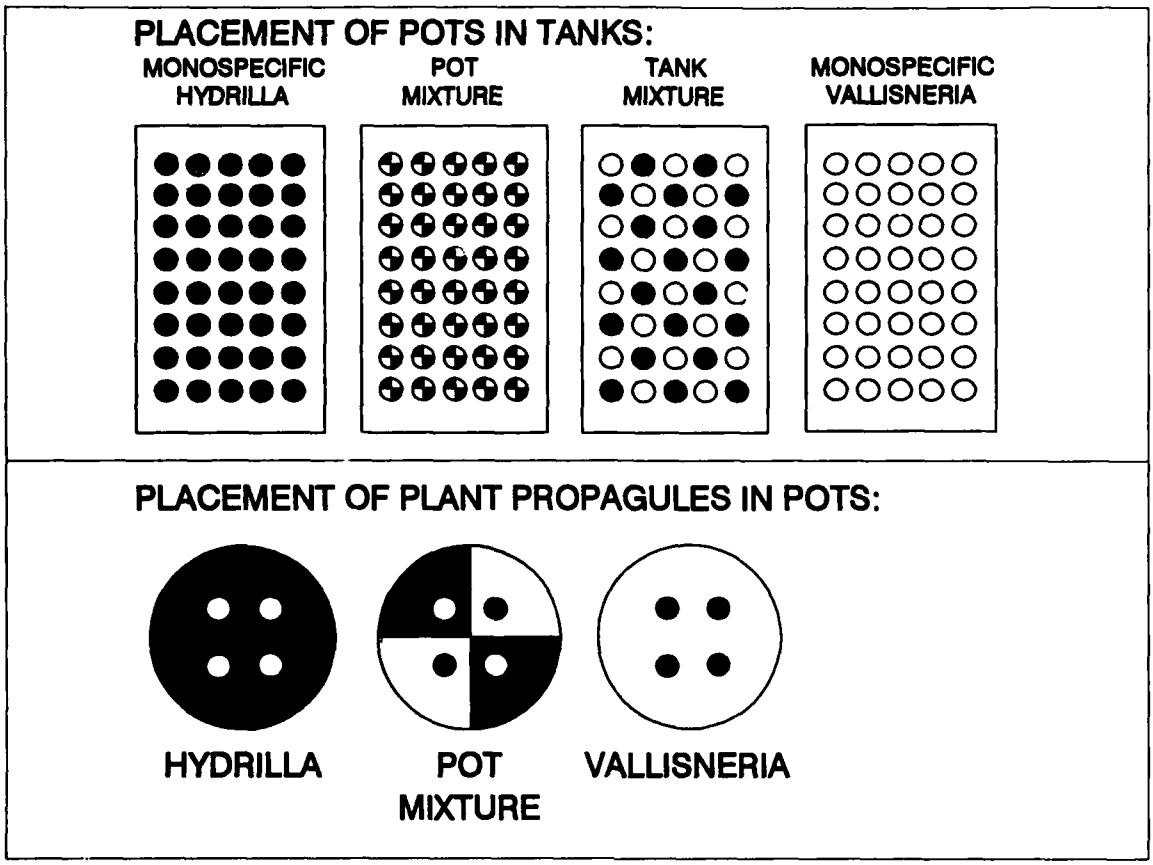

Figure 2. Schematic of planting configurations used in the investigation

constant weight. Roots were washed over a 1-mm sieve to remove sediment and debris and dried as for shoots. Weights of root and shoot samples were recorded to the nearest milligram. Biomass attained by the end of the experimental period was considered to be indicative of plant growth for both of the species as, in every case, the initial biomass comprised less than 5 percent of final biomass.

Root and shoot samples were ground in a Wiley mill to pass a 40-mesh sieve. Subsamples of the dried and ground material were combusted in a muffle furnace at 550 °C to determine ash content. Additional subsamples were digested in H_2O_2 - H_2SO_4 (Allen et al. 1974) and then analyzed on a Technicon Autoanalyzer to determine total N and total phosphorous (P). Major cations (Na, K, Ca, and Mg) were determined on the same digestate by atomic absorption spectrophotometry.

Solution chemical composition was determined at the beginning, after 5 weeks, and at 8 weeks shortly before termination. Samples were analyzed for Na, K, Ca, Mg, DIC, conductivity, and pH. Decreases in solution concentration of a particular element between the beginning and the end of the growth period in the monospecific treatments should be indicative of the

demand and/or efficiency of plant uptake of that element. Decreases occurring in the species mixtures would then be indicative of the intensity of competition for that element.

Light attenuation by the plant communities was determined just prior to harvest by measuring PAR at the water surface and near the sediment surface (75-cm depth). These measurements were made at midday in the center of the tanks. Light attenuation in monospecific treatments should be indicative of the efficiency of each species to capture this resource, while light attenuation in the mixtures would provide a measure of the intensity of competition for light.

Data were tested to ensure that they were normally distributed using the Shapiro-Wilk normality test (Zar 1984). Homogeneity of variance was examined using Fisher's test for variances. Where data were normally distributed and variances were homogeneous, they were subjected to parametric two-, three- and four-way analysis of variance (ANOVA) procedures as appropriate. Mean comparisons were generally performed using Student-Newman-Keuls test or independent t tests. Where variances were not homogenous, mean comparisons were performed using Welch's t Test. In the few cases where data were not normally distributed, nonparametric procedures were employed (Wilcoxon Ranks Test). Statistically significant differences referred to in the text were evaluated at the 5-percent (or less) level of statistical probability. All statistical analysis was performed using PC-SAS (Statistical Analysis System, Cary, NC).

3 Monospecific Responses

Statistical Analysis of Growth Responses

Results of a four-way ANOVA (Table A1) indicate that total biomass production was significantly affected by all four main effects (species, light, fertility, and C supply). However, all of the two-factor interactions and two of the three-factor interactions were also significant, indicating that the main effects were not independent. The occurrence of significant interactions requires a reexamination of the main effects (Steel and Torrie 1960).

In an attempt to further clarify the results, the data were analyzed by species. The resultant three-way ANOVAs (Tables A2 and A3) indicate that total biomass of both species was significantly affected by all three main effects (light, fertility, and C supply), and again several of the interaction terms were significant. Although these interactions will require further analysis of the main effects, the three-way ANOVAs illustrate both a similarity and a major difference in the responses of the two species. While total biomass of *Hydrilla* was primarily affected by light and aeration, total biomass of *Vallisneria* was more affected by light and fertility. That light level exerted a dominant influence on biomass production of both species was not unexpected at the relatively low level (<125 $\mu E/m^2/sec$) provided in the low light treatment. However, the qualitative and quantitative differences in the two species' responses to the other environmental factors (fertility and C supply) are perhaps indicative of fundamental differences in physiological adaptation to the aquatic environment.

Differences in the two species' responses to fertility and C supply are also revealed in the two-way ANOVAs performed on total biomass produced under each of the two light levels (Table A4). Total biomass production of *Hydrilla* was affected by C supply under both light levels, but was affected by fertility only under the higher light level. In contrast, total biomass production of *Vallisneria* was affected mainly by fertility and, to a lesser extent, by C supply at both light levels. In both species, the magnitude of their responses to fertility and C supply were greatest at the higher light level. Increased light afforded greater biomass production and consequently placed greater demands on the supply of other resources such as nutrients and inorganic C.

ANOVA tables for length and density responses of each of the two species are also included in Appendix A (Tables A2, A3, and A4).

Biomass and Morphology

Taking the low light, low C supply, and low fertility treatment combination as a baseline, the responses of each of the species to either single factor (light, C supply, fertility) or multiple factor additions can be evaluated (Figure 3). *Hydrilla* clearly responded to an increase in light (+L) by producing more total biomass (Figure 3a). *Hydrilla* also responded to an increase in C supply (+C, +C+F), but not to an increase in sediment fertility alone (+F). Under the higher light level (+L) where growth was less constrained by light, total biomass in *Hydrilla* responded to increased C supply (+L+C) and, to a lesser extent, to increased fertility (+L+F). Under the higher light, higher C supply treatment (+L+C), shoot biomass responded to increased sediment fertility (+L+C+F). Maximal total biomass of *Hydrilla* was produced only when all three factors were provided at the higher level (+L+C+F).

Shoot length in *Hydrilla* (Figure 3c) reached its maximum under the low light, higher C supply treatments (+C, +C+F). Moreover, all of the low light treatments (BASE, +C, +F, +C+F) produced longer shoots than did the higher light treatments (+L, +L+C, +L+F, +L+C+F). This ability of *Hydrilla* to alter its morphology depending on the light environment is illustrated in the changing relationship between shoot length and shoot biomass shown in Figure 4a. Under the low light level, any increase in shoot biomass results in a corresponding and considerable increase in shoot length. Under the higher light level, shoot length is reduced and appears to be unrelated to shoot biomass. This morphological plasticity would seem to be highly adaptive considering the uncertain light climate of most freshwater environments.

Shoot density in *Hydrilla* increased twofold to fivefold over initial planting densities (four shoots/pot) under all of the environmental treatments (Figure 3e). Relative to base conditions, shoot density in *Hydrilla* did not increase in response to single factor additions (+C, +F, +L), but required both higher light and the higher level of either C supply (+L+C) or fertility (+L+F). Like total biomass production, maximal shoot density occurred only when all three factors were provided at the higher level (+L+C+F).

In comparison with the baseline condition, total biomass production in *Vallisneria* (Figure 3b) responded to an increase in light (+L), but not to an increase in C supply (+C) or fertility (+F). Under the higher light level (+L) where growth was less constrained by light, total biomass in *Vallisneria* responded to increased fertility (+L+F), but not to increased C supply (+L+C). Once light and nutrient limitations were overcome, under the higher light, higher fertility treatment (+L+F), biomass production in *Vallisneria* was responsive to an increase in C supply (+L+C+F). Like *Hydrilla*, maximal total biomass of *Vallisneria* was produced only when all three factors were provided at the higher level (+L+C+F).

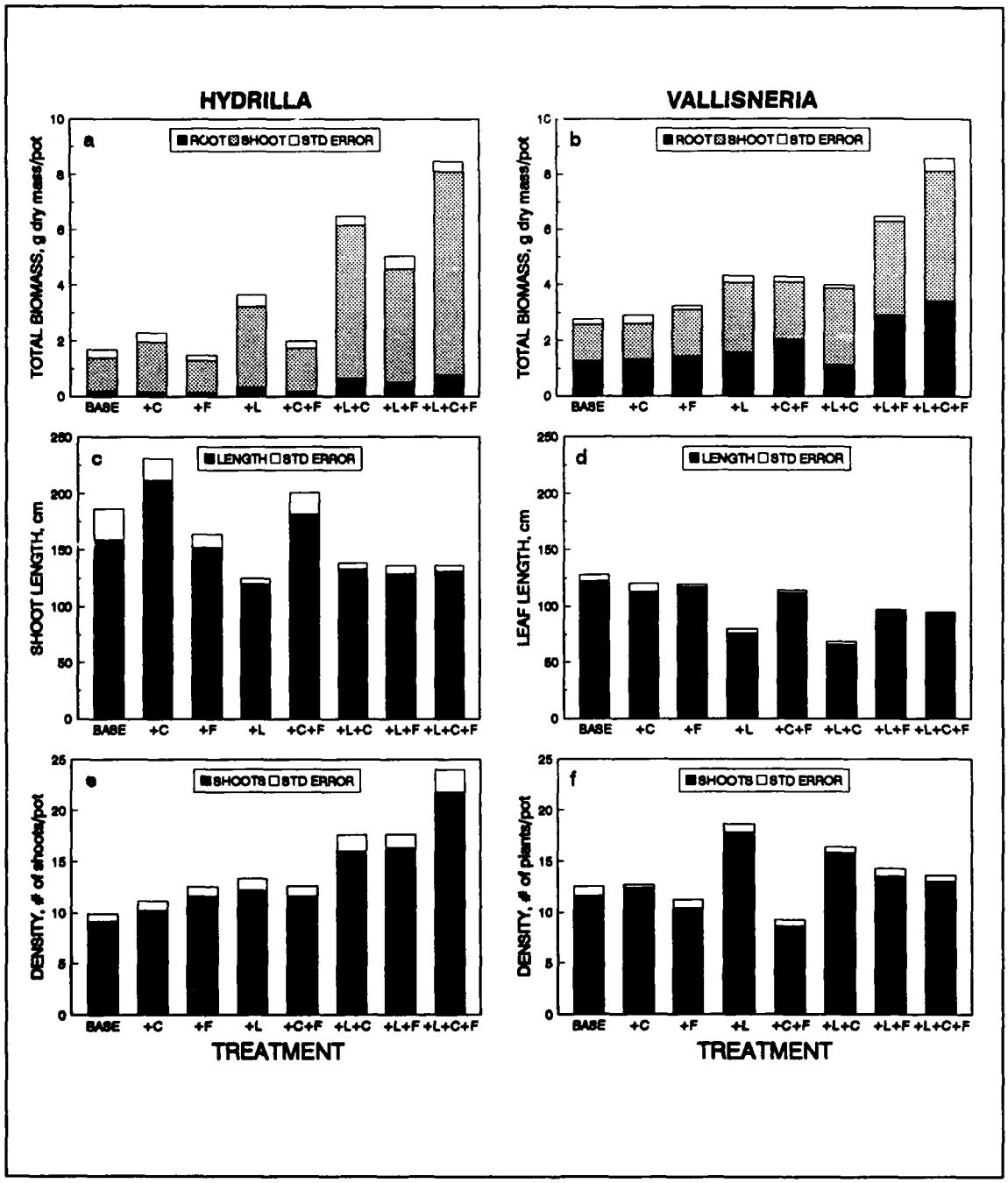

Figure 3. Root, shoot, and total biomass production (a, b), shoot or leaf length (c, d), and shoot or plant density (e, f) of *Hydrilla* and *Vallisneria* grown monospecifically under different environmental conditions. "Base" denotes the low level of light (L), C supply (C), and sediment fertility (F), and "+" indicates the higher level of the factor. Means and standard errors of the means are based on 10 replications

Leaf length in *Vallisneria* (Figure 3d) was maximal under the low light treatments (BASE, +C, +F, +C+F). Like shoot length in *Hydrilla*, leaf length in *Vallisneria* decreased in response to an increase in light (+L, +L+C).

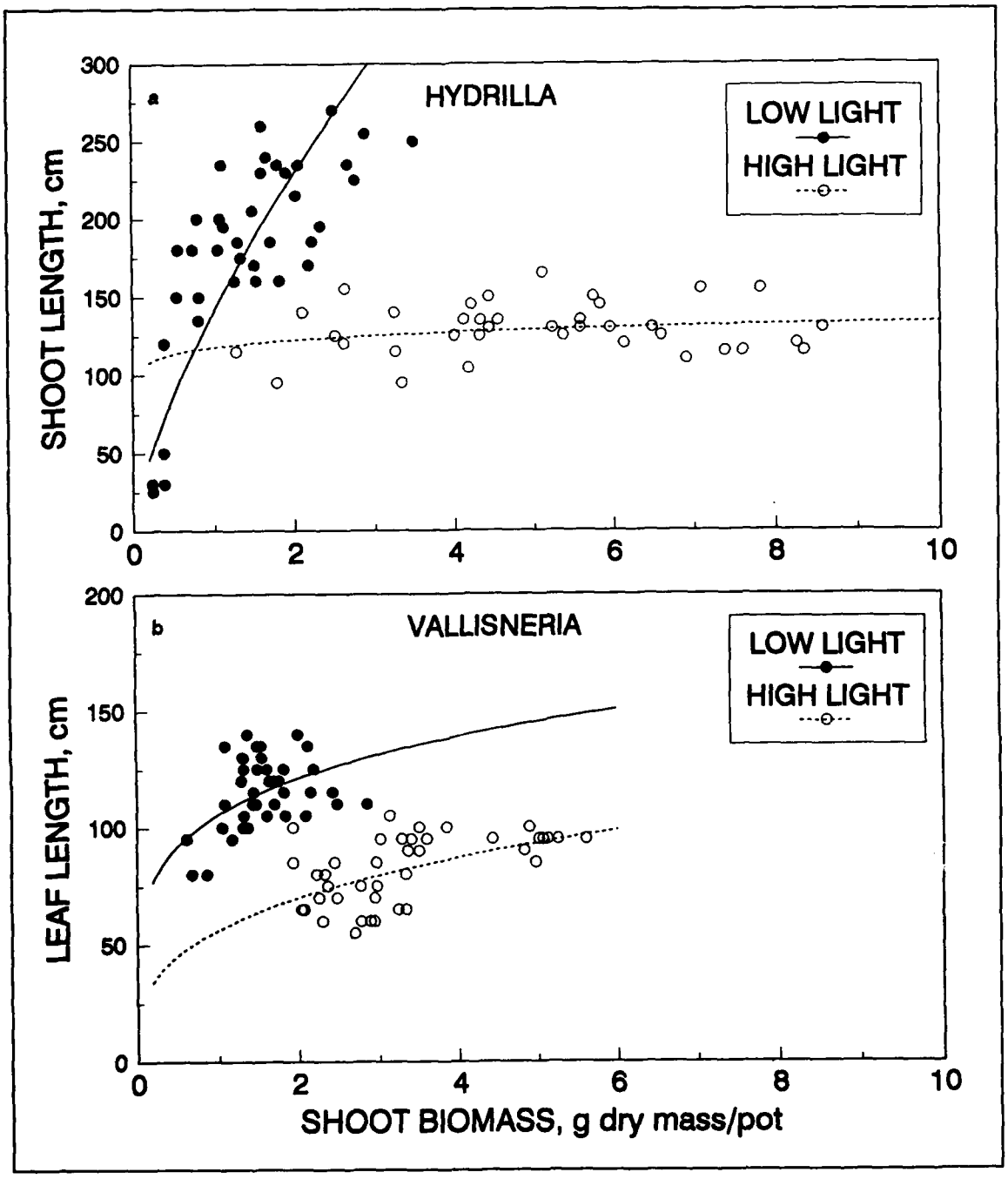

Figure 4. Relationships between shoot length and shoot biomass in *Hydrilla* (a) and leaf length and shoot biomass in *Vallisneria* (b) grown monospecifically under low and high light conditions. Values are for individual replicates (rather than means) to better illustrate relationships

However, unlike *Hydrilla*, at the higher light level (+L, +L+C), an increase in fertility resulted in an increase in leaf length (+L+F, +L+C+F). *Vallisneria* exhibited less morphological plasticity than *Hydrilla* (Figure 4b). Although leaves produced under low light were longer than those produced under the higher light level, the relationship between leaf length and shoot biomass was

similar for plants grown under both light levels. Leaf length in *Vallisneria* also spanned a narrower range than did shoot length in *Hydrilla*.

Plant density in *Vallisneria* was roughly comparable to that of *Hydrilla* and increased twofold to fourfold over initial planting densities (four winter buds/pot) under all of the environmental treatments (Figure 3f). Relative to base conditions, plant density in *Vallisneria* increased in response to increased light (+L) and decreased in response to increased fertility (+F, +C+F), but was unaffected by C supply (+C). Plant density in *Vallisneria* also decreased in response to increased fertility (+L+F, +L+C+F) at the higher light level (+L, +L+C). Oddly, plant density in *Vallisneria* was maximal at an intermediate level of biomass production.

Biomass allocation differed greatly between the two species. Root:shoot ratios in *Hydrilla* were generally less than 0.15 and were not greatly affected by environmental treatments (Figure 5a). Root:shoot ratios in *Vallisneria*, however, were generally about sixfold higher and were responsive to environmental treatments (Figure 5b). Biomass allocation to roots was highest under the low light condition. Surprisingly, under the higher light condition, root:shoot ratios were lowest on the low fertility sediment. This pattern is unusual because plants growing under nutrient limitation generally allocate a higher proportion of biomass to roots (Barko and Smart 1986; McFarland, Barko, and McCreary 1990). In the present study, "root" biomass included not only roots, but all biomass contained below the sediment-water interface, including roots and stolons. The possible significance of this will be examined in a later section.

Hydrilla, in keeping with its pattern of biomass allocation, produced shoots that were generally much longer than the leaves produced by *Vallisneria*, particularly low light conditions (Figure 4a and 4b). The increased length of *Hydrilla* shoots was most apparent under the low light, high C supply conditions (+C, +C+F in Figure 3c).

Both *Hydrilla* and *Vallisneria* exhibited increased vegetative proliferation under the higher light conditions (Figure 3e and 3f). However, while shoot density in *Hydrilla* continued to increase with increasing shoot biomass, plant density in *Vallisneria* decreased with increasing shoot biomass. Under both light levels, an increase in sediment fertility resulted in a decrease in *Vallisneria* plant density in comparison with base conditions.

Hydrilla is highly adapted to a variable light environment by virtue of its ability to regulate the vertical distribution of its shoot biomass within the water column, placing its photosynthetic machinery where it will be most productive. This regulation is achieved by virtue of its ability to control production of new shoots from the root crown, shoot elongation, and branching in response to light (Barko and Smart 1981a; Smart unpublished data).

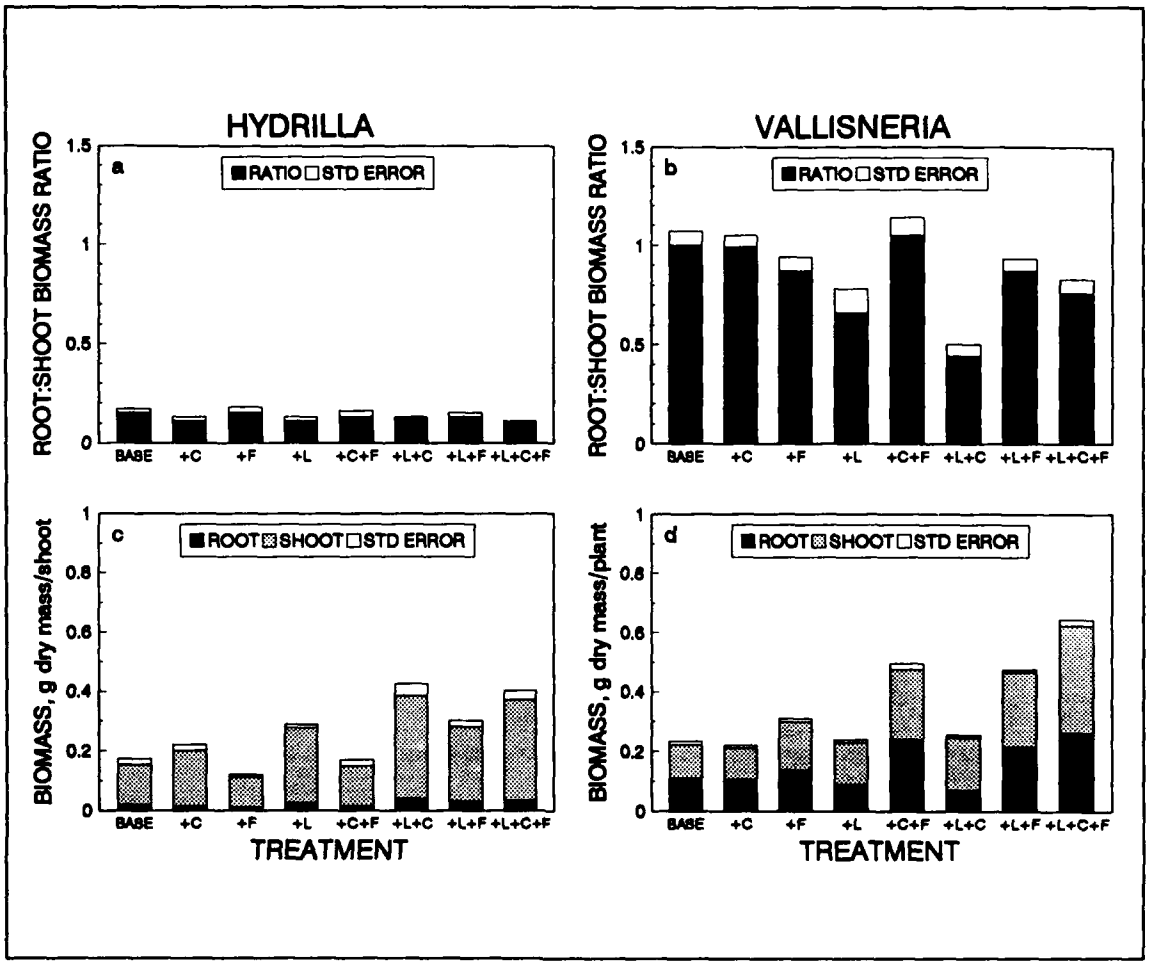

Figure 5. Root:shoot ratio (a, b) and root, shoot, and total biomass per shoot or per plant in *Hydrilla* (c) and *Vallisneria* (d) grown monospecifically under different environmental conditions. Treatments are as indicated in Figure 3. Means and standard errors of the means are based on 10 replications

Vallisneria, with its meristematic tissue constrained to the bottom, is more limited in its ability to alter the distribution of its biomass in response to light. Under low light conditions, ramet (daughter plant) production in *Vallisneria* is limited, resulting in low plant densities (Figure 3f). Production of fewer plants partially moderates decreased biomass production under low light conditions and may enable the increase in leaf length observed under field conditions (Titus and Stephens 1983) and in the laboratory (Barko, Hardin, and Matthews 1982). However, density regulation under the low light conditions employed here was accompanied by increased allocation of biomass to belowground organs (Figure 5b) and was not sufficient to prevent a reduction in ramet (individual shoot) biomass (Figure 5d). While leaf length increased under low light conditions, ramet biomass generally decreased. The increase in leaf length was therefore not achieved solely by density regulation. These low light leaves either had a lower specific mass (less mass per unit area) or there were fewer leaves per plant.

An increase in sediment fertility facilitated morphological adaptation in *Vallisneria* grown under the lower light level. Density of *Vallisneria* was reduced in the higher fertility treatments under both light levels (Figure 3f), and plants grown on the higher fertility sediment under both light conditions maintained a higher biomass per plant than those grown on the lower fertility sediment (Figure 5d). This increased biomass per plant resulted from both an increase in biomass production on the higher fertility sediments and also from a decrease in plant density. Under the low light condition, *Vallisneria* leaf length was unaffected by sediment fertility even though biomass per plant was increased. If the increase in biomass per plant was not used to increase leaf length under these low light conditions, it must have been used in the production of greater numbers of leaves. *Vallisneria* may respond to different environmental conditions by varying the number of leaves produced per plant. Unfortunately, the large number of samples precluded counting of leaves during the harvest.

Under the higher light condition, total biomass, biomass per plant, root: shoot ratio, and leaf length all increased on the higher fertility sediment. Given adequate light and nutrients, *Vallisneria* develops an intermediate number of large plants with long leaves and a high proportion of root/stolon biomass—characteristics that would seem to be competitive. Under less optimal light conditions, root:shoot ratio and leaf length increase, but both the number and mass of plants decrease. Under less optimal nutrient conditions, the number of plants increases while the mass of plants, root:shoot ratio, and leaf length all decrease. Clearly, *Vallisneria* will be much less competitive under low fertility conditions.

Light Interception

Light interception by the *Hydrilla* canopies that developed under the low and high light conditions are presented in Table 2. In spite of rather large treatment-related differences in shoot biomass attained by plants grown under the higher light level, light interception by these *Hydrilla* canopies was quite uniform. Although light interception by *Hydrilla* canopies developing under low light was somewhat reduced relative to those that developed under the higher light condition, even these canopies were quite effective. The efficiency of these *Hydrilla* canopies, in spite of the limited amount of shoot biomass attained under the low light treatments, is remarkable and attests to the adaptive value of morphological plasticity in this species.

Although biomass production of *Hydrilla* was quite limited under the low light treatments, this species adapted to these conditions by producing fewer, but longer shoots, particularly when provided ample inorganic carbon (+C, +C+F). Under natural conditions, these shoots would extend into shallower depths, reaching a more favorable light environment, perhaps even reaching the surface and full sunlight. Under the higher light treatments, biomass production was much greater, and *Hydrilla* produced a greater number

Table 2
Light (Photosynthetically Active Radiation) Attenuation by Canopies of *Hydrilla* and *Vallisneria* Growing Monospecifically Under Low and High Light Conditions[1]

Species	Light Level	Canopy Attenuation		PAR[2] µE/m²/sec	
		% of Surface	Std Error	Above	Below
Hydrilla	Low	80.3	4.6	125	25
	High	90.6	1.3	550	51
	Overall	85.4	2.9		
Vallisneria	Low	75.5	1.9	125	31
	High	78.6	5.7	550	118
	Overall	77.1	2.9		

[1] Means and standard errors are based on measurements of four populations at each light level.
[2] Typical maximum midday PAR values were calculated from mean light attenuation values.

of shorter, more highly branched shoots. This strategy is highly adaptive to a variety of aquatic conditions. In shallow or very clear waters, *Hydrilla* produces a large number of shoots that can completely fill the water column. In moderate depths or in more turbid waters, *Hydrilla* produces fewer, more elongated shoots, but these shoots branch to form an extensive canopy at or near the water surface. Finally, in deeper, or very turbid waters, *Hydrilla* produces very few, highly elongated shoots; and if tnese shoots extend into a favorable light environment, they also begin to branch and form a canopy.

Light interception by *Vallisneria*, which also exhibited large differences in shoot biomass under these different conditions, was also quite uniform (Table 2). *Vallisneria* employs a different growth strategy from *Hydrilla*, distributing its biomass more uniformly throughout the water column. Although light interception by *Vallisneria* canopies may occur lower in the water column, these canopies were, never-the-less effective at light harvesting, removing over 75 percent of PAR. Similar levels of light reduction have been measured in field populations of *Vallisneria* (Titus and Adams 1979). The growth strategy employed by *Vallisneria*, though not as effective at light capture as that of *Hydrilla*, seems capable of adjusting biomass allocation and morphology to maximize light interception in spite of large differences in biomass production. This morphological adaptability, coupled with physiological adaptations allowing photosynthesis under low light levels (Titus and Adams 1979), should make *Vallisneria* competitive under low light conditions.

Plant Nutrition

Shoot N concentrations in *Hydrilla* were higher in plants grown under low light conditions, particularly those grown on the higher fertility sediment (Figure 6a). Decreases in shoot N concentration under the higher light condition reflect dilution of tissue N by increased biomass production. Tissue N levels in shoots of plants grown under both high light, high C supply treatment combinations (+L+C, +L+C+F) are within the critical (growth-limiting) concentration range of 9.2 ± 0.4 mg N/g dry mass determined for *Hydrilla* in another study (Smart, unpublished data). Tissue N concentrations within the critical range are indicative of possible N limitation. Although the significant biomass response of *Hydrilla* to an increase in sediment fertility at the higher light level here (+L+F versus +L in Figure 3a) suggests that the critical concentration range may extend as high as 16 ± 1.3 mg N/g dry mass (+L in Figure 6a), there are other indications that this is not the case. First, *Hydrilla* grown under the higher light treatment (+L) responded more to an increase in C supply than to increased fertility (+L+C versus +L+F in Figure 3a), suggesting growth limitation by C rather than by N. Second, *Hydrilla* grown under the high light, high fertility condition (+L+F), which had a similar shoot N concentration (16.9 ± 0.3), was not likely limited by N since plants grown under these conditions clearly responded to an increase in C supply (+L+C+F versus +L+F in Figure 3a).

Root N concentrations in *Hydrilla* (Figure 6b) were also lower in plants grown under the higher light level treatments, again reflecting dilution by increased biomass production. These low root N concentrations are also indicative of possible N limitation of *Hydrilla* growth under the higher light, low fertility treatments. However, much less is known of the diagnostic value (if any) of root N concentrations in this species.

Shoot P and K concentrations in *Hydrilla* plants grown under the different environmental conditions (Figure 6c and 6e) exhibit patterns almost identical to those for shoot N (Figure 6a). This is not an unusual occurrence in submersed aquatic plants and seems to reflect a high degree of coupling in the uptake of N, P, and K (Barko and Smart 1986; Barko et al. 1988; Smart and Barko 1990). Shoot concentrations of both P and K in *Hydrilla* (Figure 6c and 6e) were considerably higher than suggested critical concentrations for these elements, indicating that growth was unlikely limited by either P or K under any of the experimental conditions employed here.

Root concentrations of P and K in *Hydrilla* plants grown under the different environmental conditions (Figure 6d and 6f) were very similar to shoot concentrations of these elements (Figure 6c and 6e).

Shoot N concentrations in *Vallisneria* plants grown under low light conditions were higher than those of plants grown under the higher light conditions (Figure 7a). Unlike *Hydrilla*, however, *Vallisneria* plants grown on the high fertility sediment under low light conditions had no higher shoot N

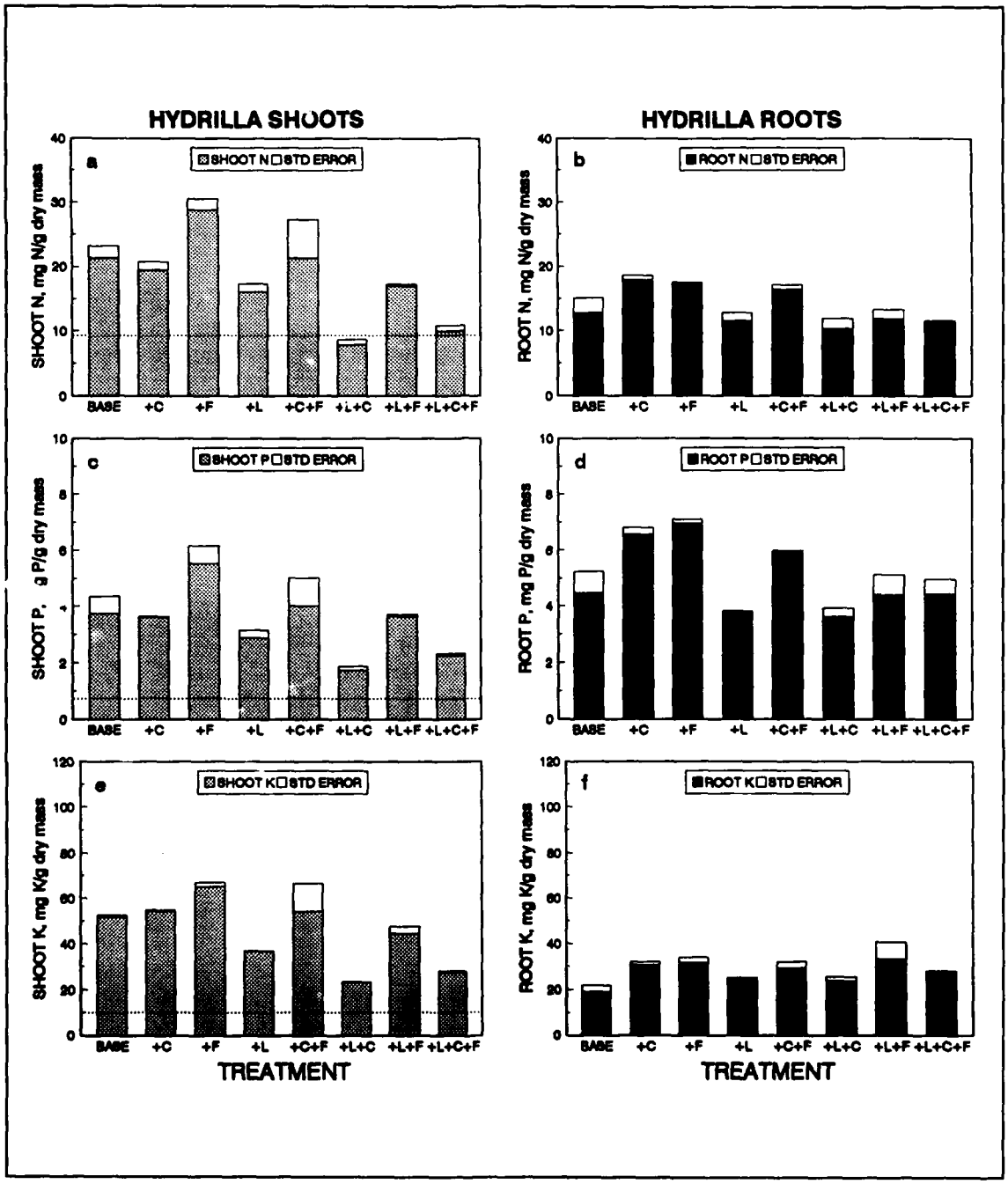

Figure 6. Shoot and root concentrations of N (a, b), P (c, d), and K (e, f) in *Hydrilla* plants grown monospecifically under different environmental conditions. Treatments are as indicated in Figure 3. Means and standard errors are based on duplicate digestion and analysis of separate composite samples obtained from pooling five replicate biomass samples. When present, horizontal dashed lines indicate critical (growth-limiting) tissue concentrations

concentrations than those grown on the low fertility sediment. *Vallisneria* plants grown on low fertility sediment under the higher light condition (+L and +L+C in Figure 3b) both responded to increased fertility with increased

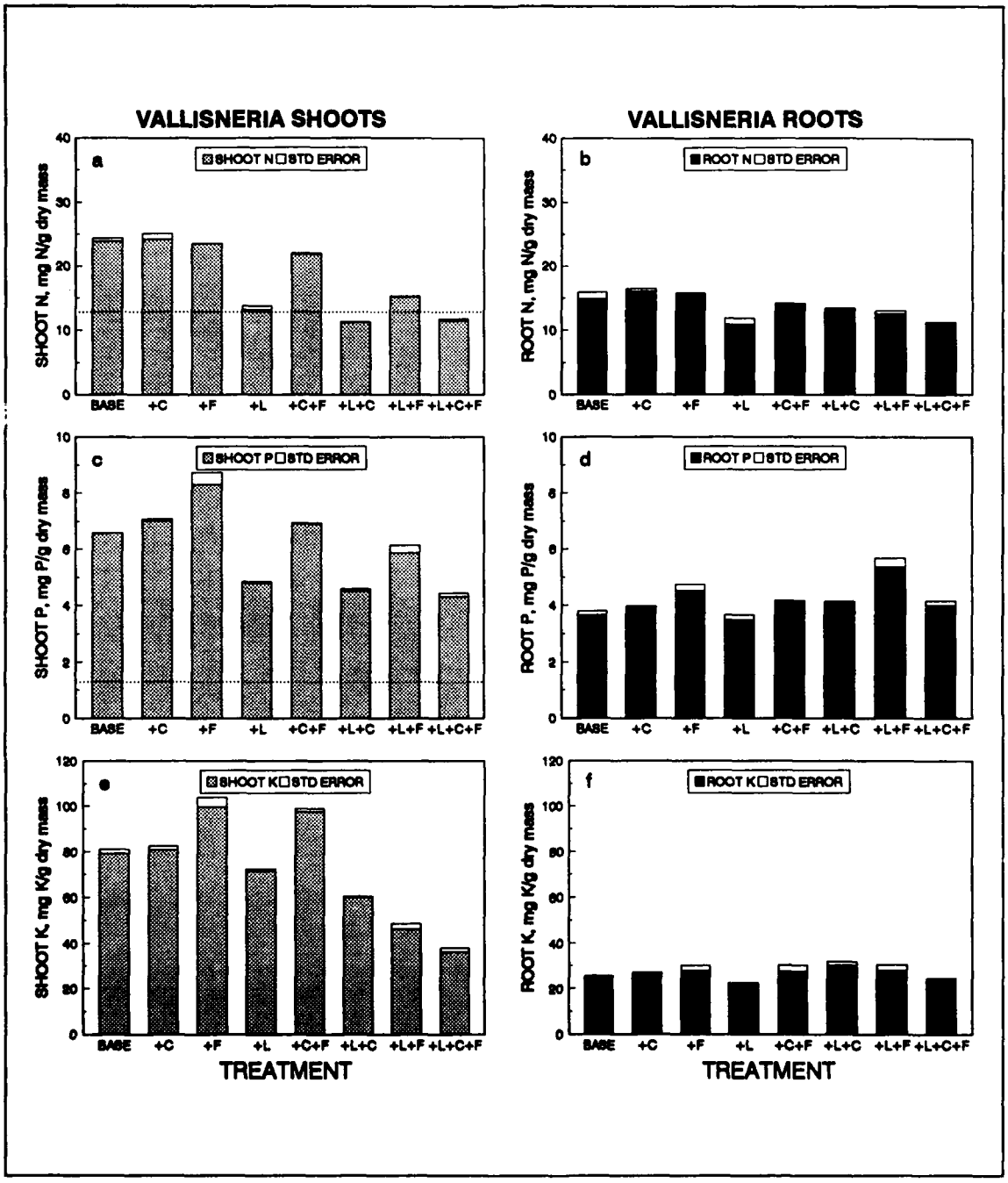

Figure 7. Shoot and root concentrations of N (a, b), P (c, d), and K (e, f) in *Vallisneria* plants grown monospecifically under different environmental conditions. Treatments are as indicated in Figure 3. Means and standard errors are based on duplicate digestion and analysis of separate composite samples obtained from pooling five replicate biomass samples. When present, horizontal dashed lines indicate critical (growth-limiting) tissue concentrations

growth, suggesting probable N limitation. Shoot N concentrations of these plants are in agreement with the critical or growth-limiting N concentration of 13 mg N/g dry mass determined for *Vallisneria* (Gerloff and Krombholz 1966). Using this criterion, the growth of *Vallisneria* under the combined high level of each of the factors (+L+C+F) appears to also have been N-limited, as was *Hydrilla.*

Root N concentrations in *Vallisneria* plants grown under the different environmental conditions (Figure 7b) exhibit a pattern almost identical to that for shoot N. Differences in root N concentration of plants grown under low and high light conditions were much less pronounced, however.

Shoot P and K concentrations in *Vallisneria* plants grown under the different environmental conditions (Figure 7c and 7e) exhibit patterns almost identical to those for shoot N (Figure 7a). Shoot P concentrations in *Vallisneria* (Figure 7c) greatly exceeded the critical concentration of 1.3 mg P/g dry mass (Gerloff and Krombholz 1966) suggesting that biomass accumulation was unlikely limited by P availability. Shoot K concentrations in *Vallisneria* were likewise high (Figure 7e) indicating that biomass accumulation of *Vallisneria* was also unlikely limited by availability of K under any of the environmental conditions examined. However, there is insufficient published information to establish a value for the critical K concentrations of *Vallisneria.*

Root P concentrations of *Vallisneria* plants grown under low light conditions (Figure 7d) exhibit patterns quite similar to those for shoots (Figure 7c), although actual concentrations are less than corresponding values for shoots. Under the higher light treatments, root and shoot P concentrations were quite similar. Root K concentrations of *Vallisneria* plants grown under the different environmental conditions (Figure 7f) exhibit patterns identical to those for root N concentrations in this species (Figure 7b). Root K concentrations in *Vallisneria* plants grown under all conditions are quite low in relation to shoot K concentrations. The large difference in K concentration between roots and shoots of *Vallisneria* suggests that the solution is the primary source of K supply for *Vallisneria.* In a study of the relative importance of sediment and solution as K sources for *Hydrilla*, concentration gradients between shoots and roots were reversible and indicative of the primary source of supply (Barko 1982).

Total N accumulation (the product of biomass and tissue N concentration) was of similar magnitude in both species (Figure 8a and 8b). Nitrogen allocation in *Hydrilla* is similar to biomass allocation in this species, most of the N accumulating in shoots. In comparison with base level conditions, N accumulation in *Hydrilla* increased in response to increased C supply (+C), sediment fertility (+F), and light level (+L). Among these single factor additions, N accumulation in *Hydrilla* was affected more by light than by sediment fertility. These results, in conjunction with high tissue N levels in plants grown under low light (Figure 6a) and the lack of a biomass response to sediment fertility Figure 3a), indicate that *Hydrilla* grown monospecifically was not nutrient limited under any low light condition. Biomass production under the higher

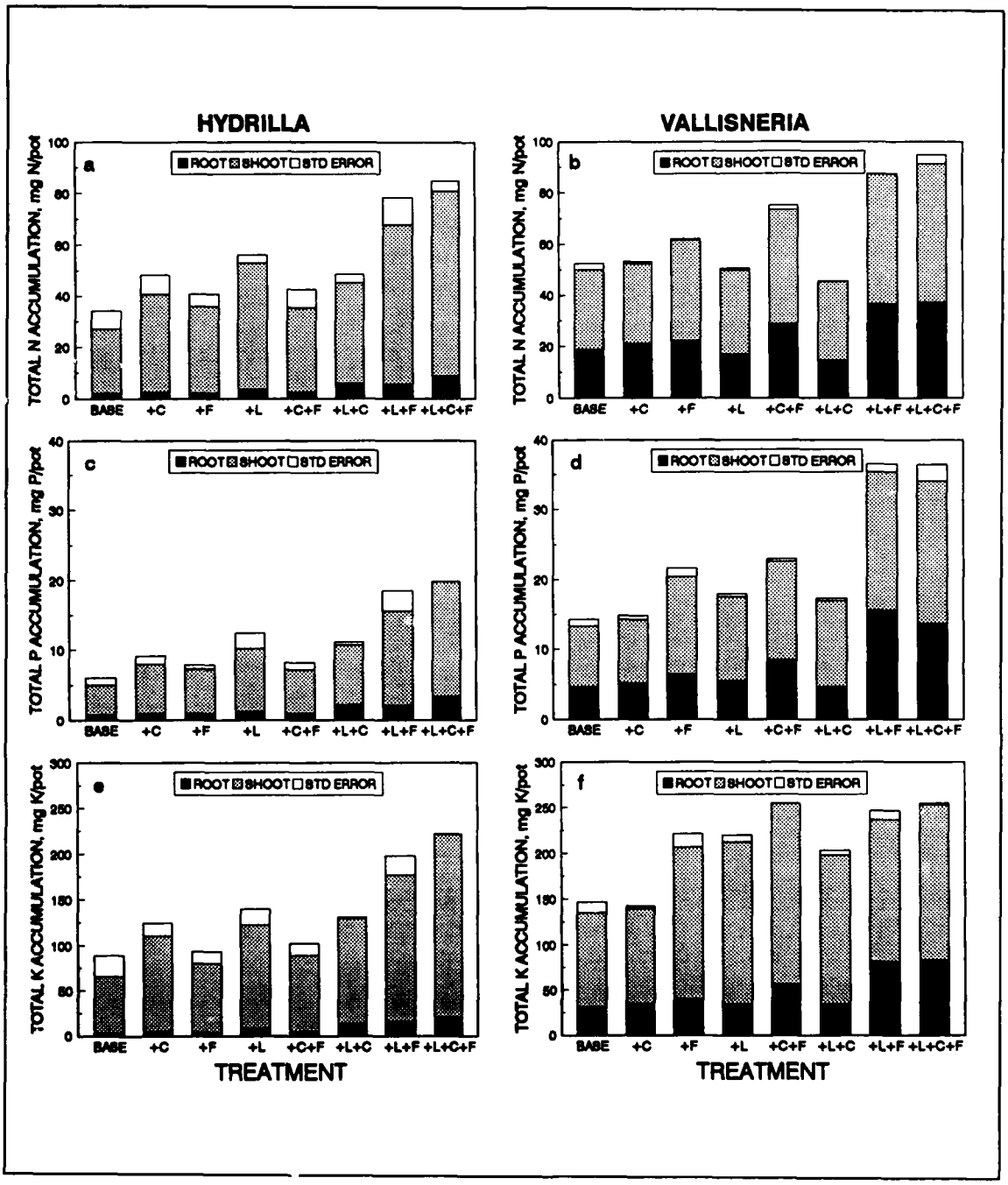

Figure 8. Accumulation of N (a, b), P (c, d), and K (e, f) in roots, shoots, and total biomass of *Hydrilla* and *Vallisneria* plants grown under different environmental conditions. Treatments are as indicated in Figure 3. Means and standard errors are based on duplicate digestion and analysis of separate composite samples obtained from pooling five replicate biomass samples

light level (Figure 3a) increased with increasing sediment fertility (+L+F) or inorganic C supply (+L+C), evidence that biomass accumulation under the higher light, low fertility condition was both C- and N-limited. Nitrogen

accumulation in *Hydrilla* grown under the higher light level (Figure 8a) also responded to an increase in sediment fertility (+L+F), but not to an increase in C supply (+L+C). While these findings suggest that the growth of *Hydrilla* on low fertility sediment under the higher light level (+L) was N-limited, tissue analysis does not substantiate N limitation, since shoot N (16.0 ± 1.3 mg N/g dry mass, Figure 6a) exceeds the experimentally determined critical N concentration (9.2 ± 0.4). Clearly, *Hydrilla* growth was limited by N under the high light, high C supply (+L+C) treatment since there both biomass and N accumulation increased in response to increased fertility (+L+C+F), and shoot N was in the critical range. Maximal N accumulation occurred in plants grown under the combination having the high level of each of the environmental factors (+L+C+F, Figure 8a).

Nitrogen allocation in *Vallisneria* is similar to biomass allocation in this species, with almost half of the N accumulating in roots (Figure 8b). Among single factor additions, N accumulation was unaffected by C supply (+C) or light (+L), but increased slightly in response to higher sediment fertility. *Vallisneria* was more effective than *Hydrilla* at accumulating N under low light. Nitrogen accumulation in *Vallisneria* was more responsive to sediment fertility under high than under low light levels. Nitrogen accumulation by *Vallisneria* plants grown under all light and C supply conditions on the low fertility sediment was similar in spite of differences in growth, suggesting that N availability may have ultimately limited growth under both of the higher light, low fertility conditions (+L, +L+C). Low tissue N levels in plants grown in these low fertility treatments (Figure 7a and 7b) and the large growth response to sediment fertility under the higher light condition (Figure 3b), provide additional evidence that *Vallisneria* grown monospecifically was N limited under the high light, low fertility condition (+L, +L+C). Maximal N accumulation occurred in plants grown under high light, high fertility conditions (+L+F, +L+C+F).

Hydrilla accumulated less P than did *Vallisneria* under all growth conditions (Figure 8c and 8d). Phosphorus accumulation in *Hydrilla* increased in the higher light treatments, particularly so in plants grown under the high light, high fertility conditions. Accumulation of P in *Vallisneria* was more responsive to sediment fertility than to light level. Like *Hydrilla*, *Vallisneria* accumulated more P under the high light, high fertility conditions.

Overall, accumulation of K in *Hydrilla* was responsive to increased light, while in *Vallisneria* K accumulation was responsive to both light and sediment fertility (Figure 8e and 8f). *Vallisneria* also accumulated higher levels of K than did *Hydrilla*. Potassium is usually taken up primarily from solution (Huebert and Gorham 1983; Barko 1982; Smart and Barko 1988, 1990) rather than from sediment. The quantities of K accumulated by *Vallisneria* under the higher growth treatments are equivalent to the total amount of K supplied in solution. The possible significance of solution K depletion will be considered in the following section.

Water Chemistry

Submersed aquatic plants have been shown to cause large changes in the chemical composition of the solution in which they are grown (Smart 1990). Measurement of the changes caused by different species might provide insight into possible competitive mechanisms related to photosynthetic C or nutrient uptake. Photosynthetic C uptake can cause large reductions in concentrations of DIC in solution, either directly, by uptake of HCO_3^-, or indirectly, by inducing precipitation of $CaCO_3$ (Smart and Barko 1986, 1988). Depletion of DIC is a function of supply and demand. Increasing the rate of supply of C should lessen depletion of DIC. Demand depends on photosynthetic rate and the mass of photosynthetic tissue; therefore, under conditions of equal C supply, DIC depletion should be more rapid under favorable growth conditions.

The potential tenfold increase in the supply of CO_2 to solution alleviated, at least in part, the depletion of DIC from solution, as indicated by the higher DIC concentrations in the +C treatments (Figure 9a-9d). Under the lower rate of C supply, DIC depletion was significantly affected by light level, and both *Hydrilla* and *Vallisneria* caused larger depletions under the higher light conditions. Sediment fertility, in spite of its effects on the growth of both species at the higher light level, did not affect DIC depletion in *Hydrilla* or *Vallisneria*. As expected, quite similar results were obtained with Ca (Figure 9d-9h), indicating that increased C supply lessened both photosynthetic C depletion and $CaCO_3$ precipitation.

In contrast to the above parameters, depletion of solution K was unaffected by C supply and was, at least in some cases, affected by sediment fertility (Figure 9i-9l). Under low light, K depletion by *Hydrilla* was greater under low fertility conditions (Base, +C in Figure 9i). Under the higher light level, K depletion was unaffected by C supply or fertility level (Figure 9j) and was comparable to depletion under the low light, low fertility treatments. Potassium depletion by *Vallisneria* (Figure 9k and 9l) was greater than that by *Hydrilla* and was only marginally affected by sediment fertility under low light. However, under the higher light level, the rate of K depletion by *Vallisneria* was greatly accelerated in the higher fertility treatments (Figure 9l). *Vallisneria* growing on higher fertility sediments completely exhausted solution K within 5 weeks, while plants growing on the lower fertility sediment reduced solution K to near zero by the end of the 8-week growth period.

Both *Hydrilla* and *Vallisneria* appear to be capable of exerting a high photosynthetic demand for solution DIC, and both of these species reduced DIC to comparable levels under equivalent environmental conditions. While photosynthetic C uptake in *Hydrilla* may be highly efficient under low light conditions (Bowes et al. 1977), this species does not appear to be equally efficient with respect to inorganic C (Van, Haller, and Bowes 1976). *Hydrilla* does not appear to be physiologically capable of reducing C availability to a level at which *Vallisneria* photosynthesis cannot occur. Although these results do not eliminate photosynthetic C assimilation as a potential factor affecting the

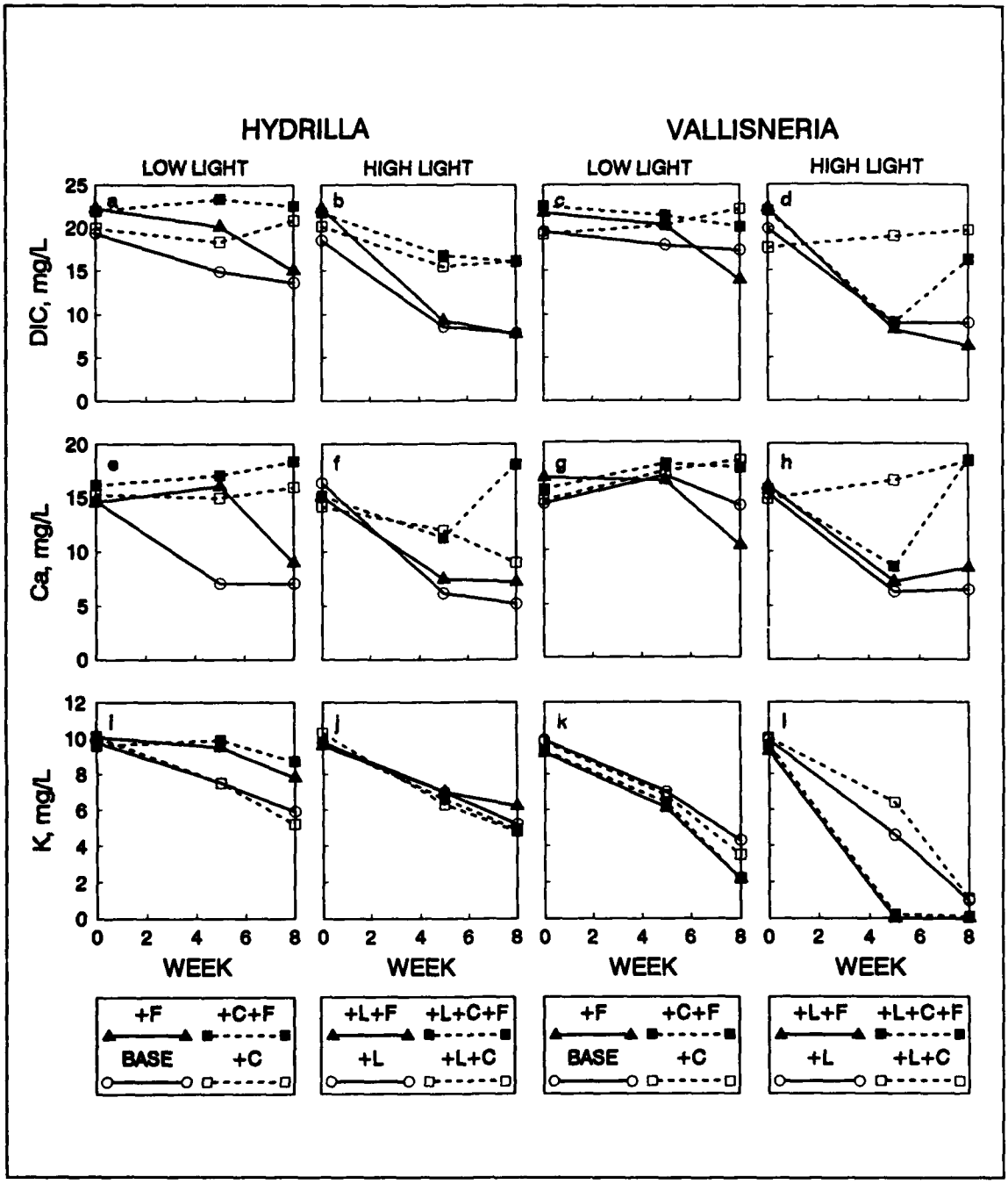

Figure 9. Changes in DIC (a-d), Ca (e-h), and K (i-l) concentrations in solutions supporting the growth of *Hydrilla* or *Vallisneria* plants grown under different environmental conditions

outcome of competition between these two species, possible differences in the physiology of photosynthesis do not seem to be sufficient to have conveyed a competitive advantage to either species during the 8-week period of this experiment.

Both K accumulation and solution K depletion were greater in *Vallisneria* than in *Hydrilla*; these results suggest that *Vallisneria* has a greater demand for K than does *Hydrilla*. Since *Vallisneria* virtually eliminated K from solution under the higher light, higher fertility treatments (<0.1 mg/L), it is tempting to speculate that *Vallisneria* may be capable of reducing solution K to levels that would be inaccessible to *Hydrilla*. Even if this were true, the potential importance of K as a limiting resource is uncertain. While *Hydrilla* (Barko 1982), *Potamogeton pectinatus* (Huebert and Gorham 1983), and *M. spicatum* (Smart and Barko 1986) have all been shown to require K in solution for normal growth under laboratory conditions, the importance of this requirement to growth in nature (where K is rarely depleted) has not been demonstrated.

Summary

When grown monospecifically, under similar environmental conditions, *Vallisneria* and *Hydrilla* produced similar quantities of biomass. Table 3 summarizes the responses of the two species to the different environmental conditions used in this investigation. Under all four low light treatment combinations (Base, +C, +F, +C+F), the growth of *Hydrilla* was limited primarily by light. In the two low light, low C supply treatment combinations (Base, +F), the growth of *Hydrilla* was also limited by C supply. Under the same low light treatment combinations, *Vallisneria* growth was limited primarily by light on three of these (Base, +F, +C+F) and secondarily by C supply (+F) and sediment fertility (Base). The remaining low light treatment combination (+C) seemed to respond equally to increases in light or sediment fertility. Under treatment combinations including the higher light level, *Hydrilla* growth was limited primarily by inorganic C in the low C supply treatment combinations (+L, +L+F) and by sediment N on the low fertility sediment receiving the higher rate of C supply (+L+C). In the treatment combination consisting of the high level of each of the three environmental factors (+L+C+F), *Hydrilla* growth was likely limited by N. Under three of the four higher light level treatment combinations (+L, +L+C, +L+C+F), *Vallisneria* growth was limited by N. On the remaining high light treatment (+L+F), *Vallisneria* growth was limited by inorganic C.

From the individual growth responses of each of the two species to the different environmental factors, it is apparent that many different factors will be growth limiting under different combinations of environmental conditions. An increase in the supply of a single limiting factor results in increased biomass production until growth becomes limited by the same or another limiting factor. Shifts in environmental conditions toward limitation by different factors may favor those species that are least limited by the availability of the limiting factor.

To characterize relative growth limitation of these two species by the different environmental factors studied here, the monospecific responses of each of the species at two levels of the factor are compared in Table 4. Overall,

Table 3
Summary of Factors Limiting the Growth Responses of *Hydrilla* and *Vallisneria* Growing Monospecifically Under Different Combinations of Environmental Conditions Used in the Investigation

Environmental Condition	Limiting Factors	
	Hydrilla	*Vallisneria*
BASE	Light, C Supply	Light, Fertility
+C	Light	Fertility, Light
+F	Light, C Supply	Light, C Supply
+L	C Supply, Fertility	Fertility (N)
+C+F	Light	Light
+L+C	Fertility (N)	Fertility (N)
+L+F	C Supply	C Supply
+L+C+F	Fertility (N)	Fertility (N)

Table 4
Overall Mean Percentage Increase in Total Biomass Production of *Hydrilla* and *Vallisneria* Growing Monospecifically in Response to Increases in Each of the Environmental Factors

Environmental Factor	Percentage Increase	
	Hydrilla	*Vallisneria*
Light[1]	243	77
C Supply	64	14
Fertility	15	60

[1] Mean of (+L versus Base, +L+C versus +C, +L+F versus +F, and +L+C+F versus +C+F).

Hydrilla responded to an increase in light from the low to the high level by increasing biomass production by 243 percent. In comparison, *Vallisneria* biomass production increased by only 77 percent overall in response to an increase in light. *Hydrilla* was, therefore, limited by light to a much greater extent than was *Vallisneria*. An increase in C supply elicited a large increase in biomass production by *Hydrilla* but not by *Vallisneria*, while an increase in sediment fertility elicited a large increase in the growth of *Vallisneria* but not Hydrilla.

From this analysis, it is apparent that the growth of *Hydrilla* was strongly light limited. These results suggest that biomass production of *Hydrilla* may

not be as physiologically tolerant of low light levels as earlier photosynthesis measurements seemed to indicate (Van, Haller, and Bowes 1976; Bowes et al. 1977). *Hydrilla* is, however, highly adapted to low fertility conditions as evidenced by its relatively minor response to fertility here. *Hydrilla* tolerates low fertility conditions and exploits high light and, to a lesser extent, high C supply environments by rapidly increasing biomass when these factors become more plentiful. *Vallisneria* tolerates low C supply conditions and exploits increases in light or sediment fertility. The differences in growth strategy and response of these two species suggest that changes in environmental conditions may alter the outcome of competition between them. This hypothesis will be tested in the following section.

4 Competitive Responses

Experimental Considerations

Plant density

To avoid undue complexity in this investigation, plant density was kept constant in monocultures and both types of mixtures. All pots received four plant propagules, and all tanks received 40 pots (160 plants). Although consideration of only one density level may somewhat limit the ability to generalize these results, this was a necessary compromise considering the size and other complexities of the experiment. A planting density was chosen (400 plants/m^2 sediment surface area) that approximates maximal values observed in natural populations (Korschgen and Green 1988). The use of only one density level in experiments dealing with vegetatively reproducing perennials is further justified in the following paragraphs.

In agronomic situations, where much of plant competition theory was developed (see Harper 1977), the investigator often deals with uniformly spaced, annual crop plants growing from sown seeds and competing with annual, weedy species that also grow from seeds germinating at about the same time. In these situations, the densities of both crop and weed seeds are likely to vary independently (whether by intention or not). Moreover, the density of competing annual weed seeds is likely to vary over several orders of magnitude and may be quite high. Annual plant communities often undergo self-thinning since many more seeds germinate than can survive to maturity. Self-thinning is most severe in plant communities undergoing the most rapid growth. Intraspecific competition (and, by inference, interspecific competition) is therefore greater under conditions where biomass production is high. Since mortality (resulting from the effects of either intra- or interspecific competition) in these plant communities is density dependent, and also since final density usually decreases with increasing site favorability, it is obvious that planting (sowing) density is a critically important design feature in competition experiments involving annual plants grown from seed.

Over the course of a single season, perennial plant species that reproduce primarily by vegetative means (clonal plants) generally do not experience appreciable self-thinning among individual modules (ramets) or, at most, do so

to a lesser extent than do annual species (Harper 1977). Unlike annual species in which seasonal maximum plant densities occur at the beginning of the season, maximum densities of clonal perennials usually occur later, or at the end of the growing season. While maximum densities of populations of annual species are constrained by the density of germinated seeds, clonal perennial plants can respond to the environment by either decreasing or increasing their density through self-thinning or vegetative reproduction, respectively. Densities at peak biomass in populations of both annual and clonal perennial species are likely to be more affected by environmental conditions than by initial densities (Harper 1977). Although populations started at different densities may reach similar densities by the time of peak biomass accumulation, these similarities between populations belie differences in the growth responses and mortality of individuals. Since clonal perennials generally do not undergo extreme changes in density over the growing season, and since these plants can regulate their densities, growth responses of these plants are much less sensitive to initial densities than are annual species.

All of the problem aquatic plant species and many of the nonproblem native species of submersed aquatic plants are clonal plants. These species generally establish from vegetative propagules at relatively low densities. Initial growth usually includes not only a large increase in biomass, but also an increase in density through vegetative reproduction. In *Hydrilla*, increases in density can occur through a variety of means, including production of new shoots from the root crown, along stolons, from axillary turions or subterranean turions (tubers), as well as from shoot fragments.

Since growth response of most of the submersed aquatic plant species of concern are less affected by initial densities, and since they generally increase in density during colonization and establishment, planting density is not a critical design element of competition experiments involving these species. McCreary, McFarland, and Barko (1991) provides supporting evidence from greenhouse tank competition experiments conducted at both low and high planting densities of *Hydrilla* and *Potamogeton americanus*. In their experiments, planting density had only a minor influence on the experimental results, leading the authors to conclude that multiple densities may not be necessary in short-term competition studies. Since planting density in this experiment approximates the higher density employed by McCreary et al., and since both *Vallisneria* and *Hydrilla* exhibited similar increases in density during the course of this study, the authors do not think that appreciably different results would have been achieved at other planting densities. The results obtained in these short-term competition experiments can thus be considered valid indicators of short-term competitive ability of the two species tested.

Analysis of competition

In evaluating the competitive abilities of two plant species growing in mixture, it is necessary to compare not only their growth in relation to each other, but also in relation to their growth alone (in monoculture). One graphical

method of making both of these comparisons at once is called a relative yield diagram (Radosevich 1987). In this diagram, the yield (total biomass) of each species is plotted against the proportion of that species in the mixture (Figure 10). In the most simple case, yield is limited by the level of a single pot resource (eg., sediment N), and the two species are equal competitors for this resource. In this case, total yield per pot is constant over all possible mixtures, and the relative yields of each species are in direct proportion to the proportion of that species in the mixture (Figure 10a). A linear relationship between yield and proportion indicates that the two species are equivalent competitors. Departures from linearity in either or both species indicate that the two species are not equal competitors (Figure 10c), and the species whose yield exceeds its proportion in the mixture is the better competitor. In this case, if the yield of the inferior competitor is also proportionately reduced, the dominant is considered to have exerted a competitive effect on the competitively inferior (suppressed) species.

These experiments included three competition treatments: monocultures, with each species growing in separate tanks (no competition); pot mixtures, with both species rooted in the same containers of sediment (root plus shoot competition); and tank mixtures, with the two species grown together in the same tanks, but in different containers of sediment (shoot competition only). In the case of monocultures and pot mixtures, yield per tank is directly related to yield per pot. Since there are 40 monospecific or 40 mixed pots per tank, $Y_T = 40 \cdot Y_P$, where Y_T and Y_P are tank yield and mean pot yield, respectively. In the case of 50:50 tank mixtures, yield per tank is equal to the sum of the yields of the individual species, or $Y_T = 20 \cdot Y_{P_{HYD}} + 20 \cdot Y_{P_{VAL}}$. In this simple case where the species are equal competitors, the yields, on a pot basis, of both *Hydrilla* and *Vallisneria* are equal, both in monoculture and in the tank mixtures (symbols in Figure 10b). When yields of the tank mixture are expressed on a tank basis, the relative yields of each species are in proportion to their proportion in the tank mixture (lines in Figure 10b).

By expressing yields on both a pot and tank basis, the nature of competition between the two species can be evaluated. If the relative yield diagrams for the two types of mixtures are similar (Figure 10a and 10b), this indicates that competition for pot (sediment) resources is not affecting the outcome of competition, and the species are competing primarily through their shoots, presumably for light or other resource available through the water column (such as C supply). However, if relative yield diagrams differ between pot and tank mixtures (Figure 10c and 10d), competition for pot resources (e.g., root competition for sediment nutrients) is affecting competitive outcome in pot mixtures. In pot mixtures (Figure 10c), species A is the superior competitor; however, in tank mixtures (Figure 10d) where root competition is prevented, species B is the superior competitor. The ability to separate the effects of root and shoot competition is a necessary first step in understanding the nature of competition between plant species (Newman 1983; Wilson 1988).

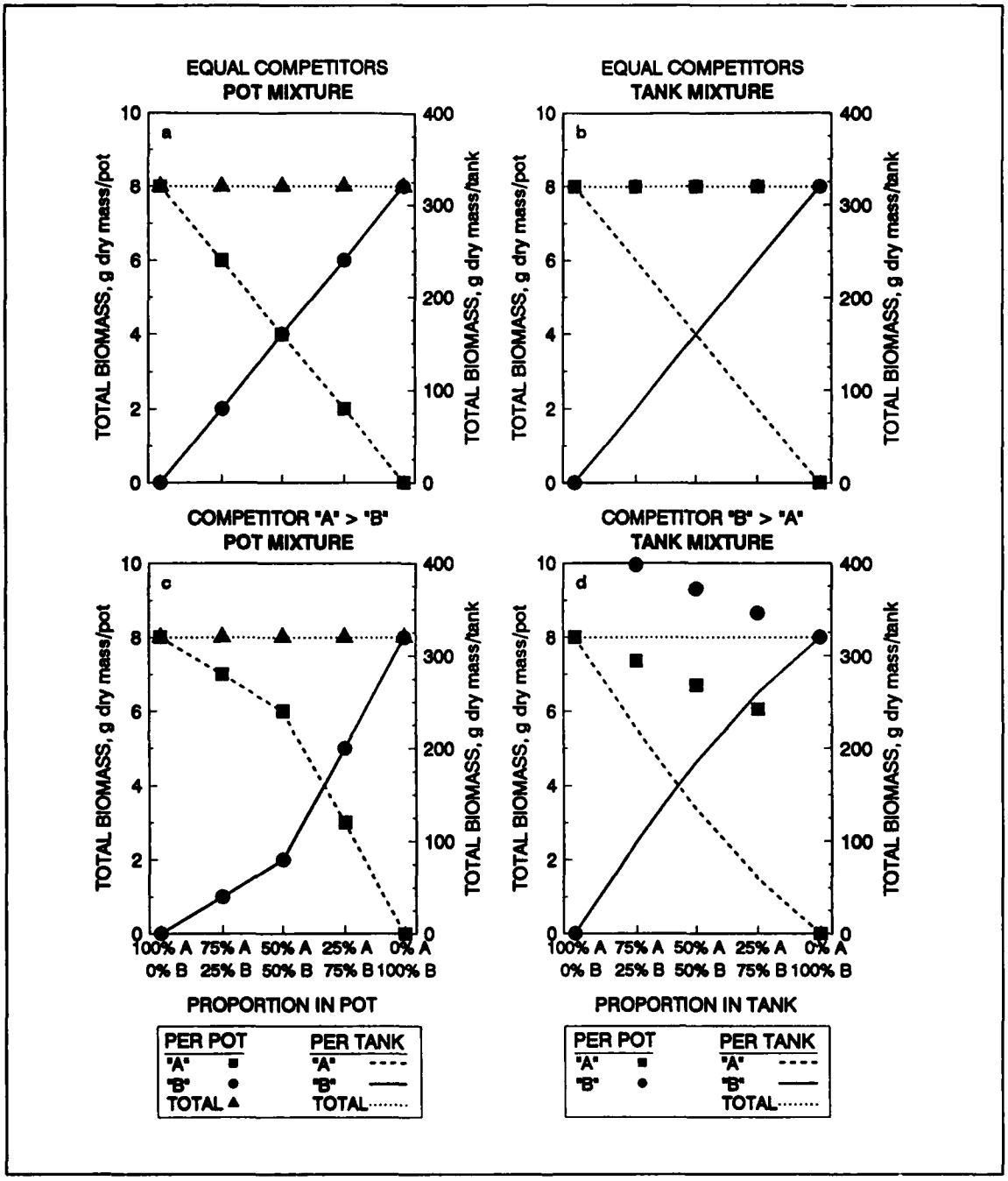

Figure 10. Example relative yield diagrams for pot mixtures and tank mixtures of two competing species. In (a) and (b) the two species are equal competitors whether competition is for sediment resources or not. In pot mixtures (c) where root competition for sediment resources is included, species "A" is the superior competitor. In tank mixtures (d) where root competition is excluded, species "B" is the superior competitor. Symbols denote yield per pot, and lines denote yield per tank calculated from individual pot values

Several statistical comparisons (t-tests) were constructed to evaluate the outcome of the different types of competition occurring under each of the environmental treatment combinations. Total biomass of each of the species grown in tank mixture was compared with that attained under monospecific conditions to evaluate the effects of shoot competition. Root plus shoot competition was evaluated by comparing monoculture yields of each species (from four propagules) with twice the 50:50 pot mixture yields (from two propagules). Competitive effect is defined as the ability of a species to reduce the growth of the other species in mixture. Competitive superiority was determined by comparing yields of the two species in mixture. Finally, the total yield of both species in mixture was compared with the average yields of the two species in monoculture.

Biomass Production

Low light responses

Under the base level conditions, *Hydrilla* accumulated less total biomass than did *Vallisneria* when the two species were grown alone (Figure 3a and 3b). However, in pot mixtures, *Hydrilla* greatly outyielded *Vallisneria* (Figure 11a). *Hydrilla* produced more biomass when growing with *Vallisneria* than when growing alone, in spite of being planted at half the density. *Hydrilla* grown in pot mixture with *Vallisneria* thus suffered less from interspecific competition with *Vallisneria* than from intraspecific competition when grown alone. Obviously, *Vallisneria* exerted no competitive effect on the growth of *Hydrilla* in these pot mixtures. The presence of *Hydrilla* did, however, reduce the growth of *Vallisneria*, indicating that *Hydrilla* was interfering with *Vallisneria*'s ability to access a limiting resource.

When grown together in tank mixture under base level conditions, the two species produced equivalent levels of biomass (Figure 11b). Biomass production of neither species in tank mixture differed significantly from that attained in monoculture. Thus the shoots of neither species exerted significant interference with the growth of the other species. The difference in the competitive responses of plants grown in pot mixtures and tank mixtures under base conditions indicates that *Hydrilla* shoots alone did not interfere with *Vallisneria* growth; however, the combined effects of root and shoot competition provided *Hydrilla* a significant competitive advantage under this particular environmental treatment combination.

An increase in C supply (+C) relative to base conditions increased total biomass production of *Hydrilla* grown monospecifically, but did not affect the growth of *Vallisneria* (Figure 3a and 3b). In pot mixture, total biomass production of *Hydrilla* was similar to that produced in pot mixture grown under base conditions (Figure 11c versus 11a). This result suggests that the growth of *Hydrilla* in pot mixture under base conditions was not limited by C supply. Total biomass production of *Vallisneria* in pot mixture did, however, respond to an increase in C supply relative to plants grown in pot mixture under base

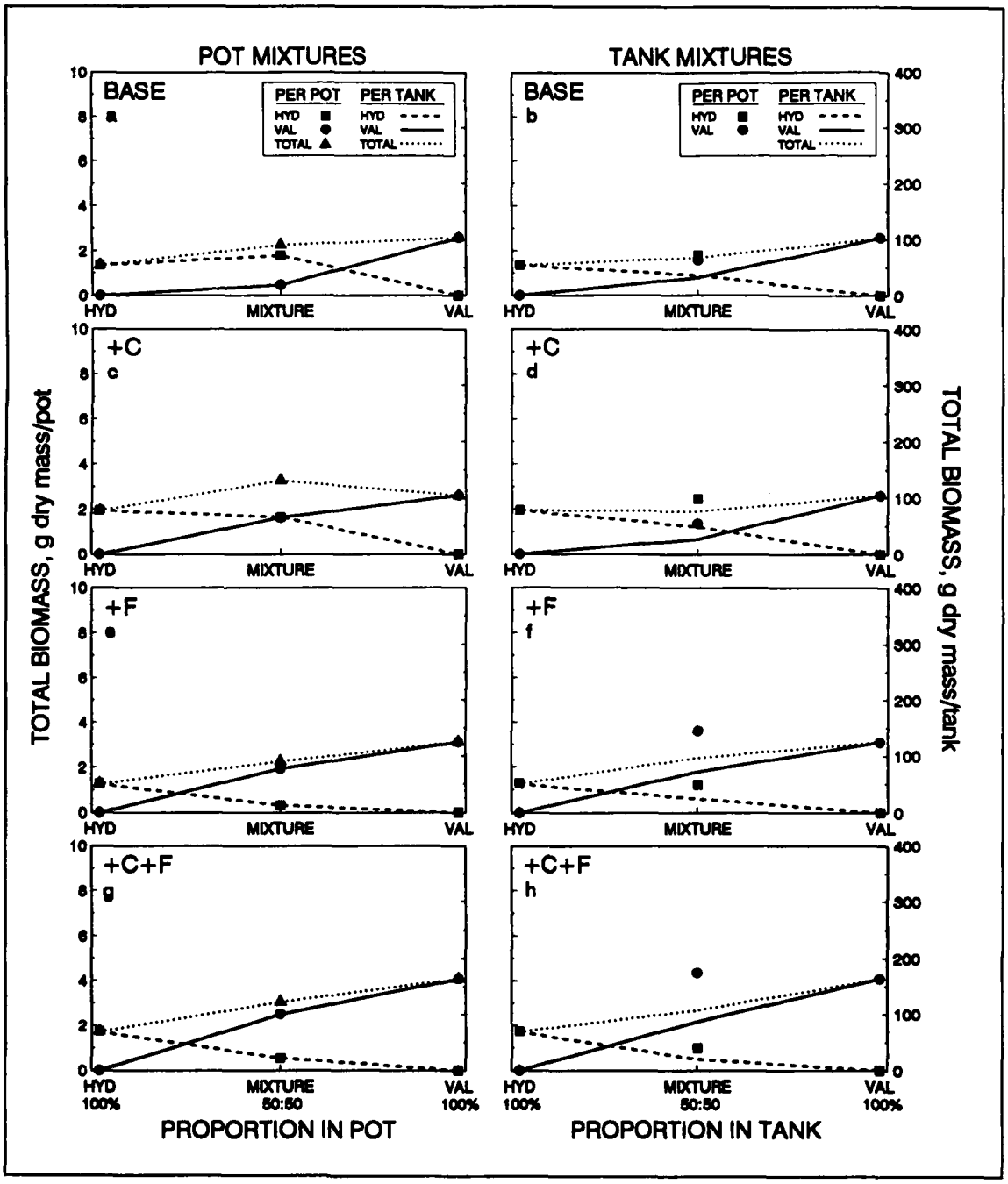

Figure 11. Relative yield diagrams for total biomass production of *Hydrilla* and *Vallisneria* grown in pot mixtures (a, c, e, g) and tank mixtures (b, d, f, h) under low light conditions. Symbols denote yield per pot based on 10 replicate pots. Lines denote yield per tank calculated from individual (N = 10) pot values

conditions (Figure 11c versus 11a) even though *Vallisneria* grown monospecifically did not. While biomass production of neither species in these pot mixtures differed significantly from that to be expected from their monoculture performance, total biomass production of the community or mixture was

significantly greater than either monoculture. This result suggests that the two species were limited by different resources (Harper 1977). When the two species were grown together, each was able to exploit additional quantities of a resource that was not limiting the growth of the other species.

Total biomass production of *Hydrilla* grown in tank mixture was stimulated by the increased C supply (+C) relative to plants grown under base conditions (Figure 11d versus 11b), but did not differ significantly from that attained in monoculture. Biomass production of *Vallisneria*, however, was unaffected by the increased C supply, whether grown monospecifically or in tank mixture. Total biomass of *Vallisneria* grown in tank mixture with *Hydrilla* was significantly reduced relative to that attained in monoculture. *Hydrilla* thus dominated the tank mixture. *Hydrilla* shoots, therefore, exerted a competitive effect on *Vallisneria* in tank mixture, but this effect was lessened when the two species were grown together in the same pot. Apparently, *Vallisneria* was able to negate some advantage of *Hydrilla* when the two species were rooted in the same sediment.

An increase in sediment fertility (+F) stimulated total biomass production by *Vallisneria* both in monoculture (Figure 3b) and in pot mixture (Figure 11e) relative to base conditions (Figure 11a). However, increased fertility did not affect the growth of *Hydrilla* grown in monoculture (Figure 3a). The increase in fertility apparently increased the competitive ability of *Vallisneria* in pot mixture, and biomass production of *Vallisneria* was enhanced relative to that of the monoculture (Figure 11e). Biomass production of *Hydrilla* was reduced in pot mixture relative to that in monoculture. *Vallisneria*, the competitive dominant, thus exerted a significant competitive effect on the growth of *Hydrilla* when the two species were grown on the higher fertility sediment.

Increased fertility also increased total biomass production of *Vallisneria* in tank mixture; however, this increased growth apparently did not greatly interfere with the biomass production of competing *Hydrilla* (Figure 11f), which was equivalent to that obtained under the monospecific condition. Although in this case the growth of *Hydrilla* was not significantly reduced by competition, *Vallisneria*, by virtue of its significantly greater biomass accrual, was the more successful competitor.

The quantitative difference in responses of plants grown in the two types of mixtures under the increased fertility condition (Figure 11e and 11f) indicates that root competition more than shoot competition enabled *Vallisneria* to outcompete *Hydrilla* in the pot mixtures.

An increase in both C supply and sediment fertility (+C+F) produced results that were similar in pattern but slightly greater in magnitude than those produced by increasing fertility alone (Figure 11g). The increased growth of *Vallisneria* greatly exceeded the growth of *Hydrilla* in both pot mixture and tank mixture (Figure 11h). In pot mixture, *Vallisneria* produced a disproportionate share of the total biomass, while *Hydrilla* was suppressed relative to its growth in monoculture (Figure 11g). Thus, under the combined high levels of

C supply and sediment fertility, *Vallisneria* exerted a competitive effect on *Hydrilla*. The competitive effect of *Vallisneria* on *Hydrilla* was also observed in the tank mixture (Figure 11h), indicating that shoot competition may have accounted for the competitive effect.

High light responses

Total biomass accumulation of both species in monoculture was increased under all conditions at the higher light level (Figure 3a and 3b). This increased growth likely increased the intensity of competition between the two species.

Under the higher light condition (+L), *Vallisneria* and *Hydrilla* produced roughly equivalent amounts of total biomass when the two species were grown alone (Figure 3a and 3b). However, in pot mixtures, biomass production of *Hydrilla* greatly exceeded that of *Vallisneria* (Figure 12a). The growth of *Hydrilla* was greatly increased relative to its proportion in mixture, indicating that *Vallisneria* exerted no competitive effect on *Hydrilla*. The growth of *Vallisneria*, however, was slightly reduced in the presence of *Hydrilla*, indicating that *Hydrilla* exerted a small, but significant, competitive effect on *Vallisneria*. The total yield of the pot mixture did not differ from that to be expected from the individual monoculture yields.

In tank mixtures, *Hydrilla* produced greater total biomass than did *Vallisneria* (Figure 12b). *Hydrilla* also produced more biomass in the mixtures than it did in monoculture. This result indicates that the growth of *Hydrilla* was inhibited more by its own shoots than by shoots of *Vallisneria*. The presence of *Hydrilla* shoots also inhibited the growth of *Vallisneria*, which produced less total biomass in tank mixture than in monoculture. The similarity in competitive results obtained in both pot and tank mixtures under the higher light (+L) condition suggests that competition was occurring primarily among shoots rather than among roots.

An increase in C supply at the higher light level (+L+C) greatly stimulated total biomass production in *Hydrilla*, but not *Vallisneria* when the species were grown in monoculture (Figure 3a and 3b). In pot mixtures, the increase in C supply greatly stimulated the growth of *Hydrilla* relative to that in monoculture (Figure 12c). This increased growth of *Hydrilla*, however, exerted no measurable competitive effect on *Vallisneria*. Since the growth of *Hydrilla* was greatly stimulated, and the growth of *Vallisneria* was unaffected by competition, the mixture yielded significantly greater biomass than did either species grown alone. This result is similar to that obtained under elevated C supply at the lower light level (Figure 11c) and also suggests that growth of the two species was limited by different resources.

Under increased light and C supply conditions (+L+C), growth of each of the two species in the tank mixtures did not differ significantly from their growth alone (Figure 12d). Although shoots of the two species were

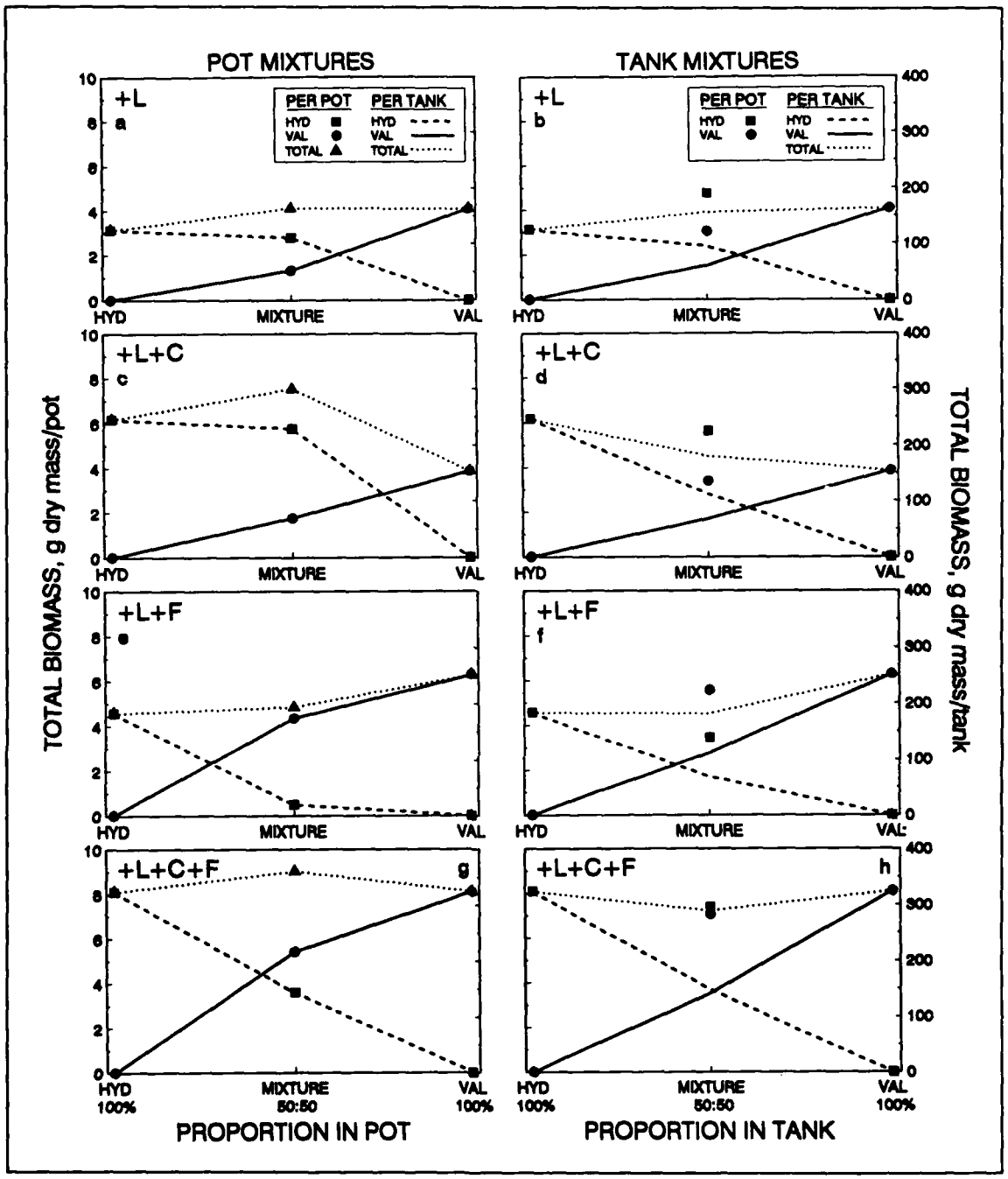

Figure 12. Relative yield diagrams for total biomass production of *Hydrilla* and *Vallisneria* grown in pot mixtures (a, c, e, g) and tank mixtures (b, d, f, h) under high light conditions. Symbols denote yield per pot based on 10 replicate pots. Lines denote yield per tank calculated from individual (N = 10) pot values

competitively equivalent, *Hydrilla*, by virtue of its significantly greater total biomass production, is considered to be competitively superior to *Vallisneria* under this condition. The difference in competitive results obtained between the pot and tank mixtures suggests that the increased C supply enhanced the competitive ability of *Hydrilla* roots.

An increase in sediment fertility at the higher light level (+L+F) stimulated total biomass production of *Vallisneria* but not *Hydrilla* when the species were grown in monoculture (Figure 3a and 3b). In pot mixtures, the growth of *Vallisneria* was greatly stimulated by increased fertility, and this increased growth of *Vallisneria* occurred at the expense of competing *Hydrilla* (Figure 12e). Total biomass production of the mixture was reduced relative to that expected from the monoculture yields of the two species. This result again suggests that the two species were limited by different resources. In this case, the competitive superior, *Vallisneria*, interfered with the ability of the suppressed species, *Hydrilla*, to access a limiting resource.

In tank mixture, total biomass production of *Hydrilla* and, to a lesser extent, *Vallisneria* was significantly reduced in comparison with respective monoculture values (Figure 12f). This result indicates that shoots of each species exerted a slight, but significant, competitive effect on the growth of the other species. The much greater competitive superiority of *Vallisneria* in pot mixture, however, indicates that although shoot competition may have occurred, root competition was of greater importance.

Under the higher level of all three factors (+L+C+F), both species reached their maximal total biomass production in monoculture (Figure 3a and 3b). In pot mixtures, the growth of *Vallisneria* was enhanced, while the growth of *Hydrilla* was unaffected (Figure 12g). Even though *Vallisneria* did not suppress the growth of competing *Hydrilla*, its greater biomass production indicates its competitive superiority under these conditions.

In tank mixtures, growth of the two species was similar, and total biomass production of both species was not significantly reduced relative to that in monoculture (Figure 12h). The two species were equivalent competitors under these conditions. Although results of the two competition treatments did not differ greatly, the competitive ability of *Vallisneria* was enhanced by root competition in the pot mixtures. Neither species exerted significant competitive effects on the other species in either of the mixtures.

Morphological Responses

Low light shoot length responses

When grown in monocultures under the base level condition, *Hydrilla* shoots attained maximal lengths in excess of 1.5 m, while *Vallisneria* leaves were less than 1.25 m in length (Figure 13a). Shoot lengths of *Hydrilla* increased, while leaf lengths of *Vallisneria* decreased in both types of mixtures, relative to these in monocultures.

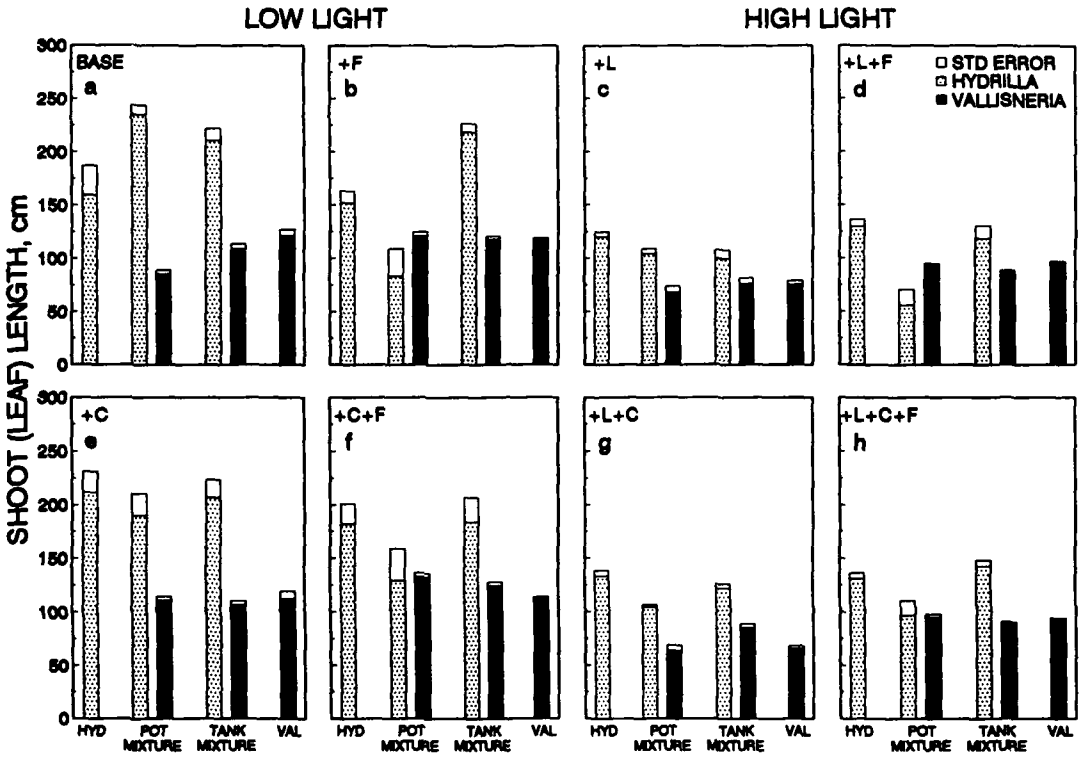

Figure 13. Maximum shoot length of *Hydrilla* and leaf length of *Vallisneria* plants grown in monocultures, pot mixtures, and tank mixtures under different environmental conditions. Bars are means and standard errors based on 10 replicate pots

Under increased C supply (+C), shoot length in *Hydrilla* and leaf length in *Vallisneria* were relatively unaffected by competition treatment (Figure 13e). *Hydrilla* shoots attained maximal lengths of 2 m, while maximal leaf lengths in *Vallisneria* averaged slightly over 1 m.

Under increased sediment fertility (+F), shoot length in *Hydrilla* was minimal in pot mixtures and maximal in tank mixtures, while leaf length in *Vallisneria* was unaffected by competition treatment (Figure 13b). In pot mixtures, length of *Vallisneria* leaves exceeded that of *Hydrilla* shoots; however, in tank mixtures, shoot length in *Hydrilla* greatly exceeded leaf length in *Vallisneria*.

Under the combination of elevated C supply and increased sediment fertility (+C+F), shoot length in *Hydrilla* was again minimal in pot mixtures (Figure 13f). Leaf length in *Vallisneria* was maximal in pot mixtures and equaled shoot length in *Hydrilla* under these conditions. The opposite occurred in tank mixtures, where *Hydrilla* shoot length greatly exceeded *Vallisneria* leaf length.

High light shoot length responses

Under all environmental treatment combinations at the higher light level, maximal lengths of both species were generally reduced relative to those occurring under the lower light level. Under the higher light level condition (+L), shoot length in *Hydrilla* exceeded leaf length in *Vallisneria* (Figure 13c). Neither species exhibited marked changes in length in response to competition treatment. Increased C supply (+L+C) did not alter the pattern described above, and shoot length in *Hydrilla* exceeded leaf length in *Vallisneria* under all competition treatments (Figure 13g).

Increasing sediment fertility at the higher light level (+L+F and +L+F+C) resulted in increased leaf length in *Vallisneria* and changed the competitive responses (Figure 13d and 13h). In both monocultures and tank mixtures, shoot length in *Hydrilla* exceeded leaf length in *Vallisneria*; however, in pot mixtures, shoot length in *Hydrilla* was reduced, allowing *Vallisneria* leaves to equal (+L+C+F) or exceed (+L+F) *Hydrilla* shoots in length. These results paralleled those observed under the higher fertility conditions at the lower light level (Figure 13b).

Density responses

In general, plant density responses (Figure 14) were similar to those observed for plant biomass. Under base level conditions, density of *Vallisneria* was reduced in competition with *Hydrilla* (Figure 14a and 14b). The effect was similar in both pot and tank mixtures, indicating that competition from *Hydrilla* shoots was the likely cause. The increased dominance of *Hydrilla* in pot mixtures suggests that root interactions increased *Hydrilla*'s competitive advantage.

With an increase in C supply (+C), the density of *Vallisneria* plants increased in pot mixtures but decreased in tank mixtures (Figure 14e and 14f). The density of *Hydrilla* shoots increased slightly in both types of mixtures.

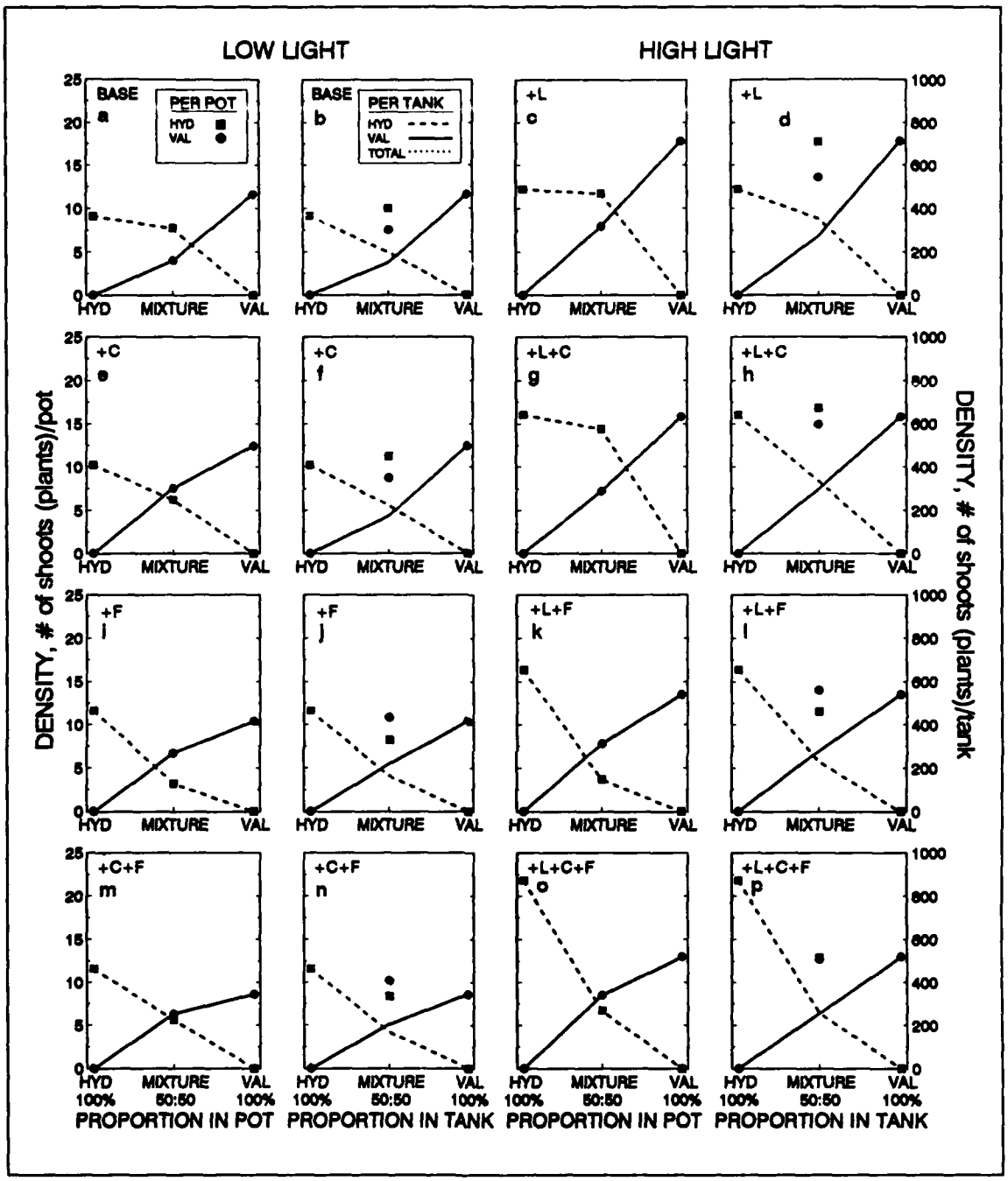

Figure 14. Density responses of *Hydrilla* and *Vallisneria* grown in monocultures, pot mixtures, and tank mixtures under different environmental conditions. Symbols denote density of shoots or plants per pot based on 10 replicate pots. Lines denote density per tank calculated from individual (N = 10) pot values

Belowground interactions occurring in the pot mixtures apparently negated *Hydrilla*'s advantage in shoot competition.

With an increase in sediment fertility (+F), the density of *Vallisneria* plants increased in pot mixtures and was unaffected in tank mixtures (Figure 14i and 14j). The density of *Hydrilla* shoots was decreased in both types of mixtures. Root interactions in the pot mixture apparently enhanced the competitive ability of *Vallisneria*.

An increase in both C supply and sediment fertility under the low light condition (+C+F) resulted in increases in density of *Vallisneria* plants in pot mixtures (Figure 14m). Density of *Hydrilla* shoots was relatively unaffected in pot mixtures, but was reduced in tank mixtures (Figure 14n). While shoot interactions apparently resulted in reduced *Hydrilla* shoot density in tank mixtures, root interactions apparently counteracted this effect in pot mixtures.

Under the higher light condition (+L), *Hydrilla* achieved higher densities in both types of mixtures (Figure 14c and 14d). Density of *Vallisneria* decreased in tank mixture but was unaffected in pot mixtures. Under increased C supply (+L+C), *Hydrilla* achieved a higher density only in pot mixtures and not in tank mixtures (Figure 14g and 14h). These results suggest that, under the low fertility condition, belowground interactions increased the competitive advantage afforded *Hydrilla* by its shoots.

Under the higher light, higher fertility conditions, *Vallisneria* density was unaffected by the presence of *Hydrilla* shoots in tank mixtures (Figure 14p). The presence of *Vallisneria* shoots did, however, reduce *Hydrilla* shoot density in both types of mixtures (Figure 14o and 14p). In pot mixtures, root competition apparently increased *Vallisneria*'s competitive advantage on the higher fertility sediment.

Length-mass relationships

The relationships observed between shoot length and biomass of *Hydrilla* and *Vallisneria* grown monospecifically under different light conditions were also observed for plants grown in both pot and tank mixtures (Figure 15a and 15b). Morphological characteristics of plants grown under the lower light level differed from those grown at higher light, but were unaffected by competition treatment. Under the higher light level, there was a tendency for *Vallisneria* shoots grown in mixture with *Hydrilla* to exhibit greater length:mass ratios than *Vallisneria* plants grown alone. This result suggests that, in mixtures, *Hydrilla* shoots caused a reduction in light available to *Vallisneria*, and that *Vallisneria* responded to this reduction by increasing its length:mass ratio.

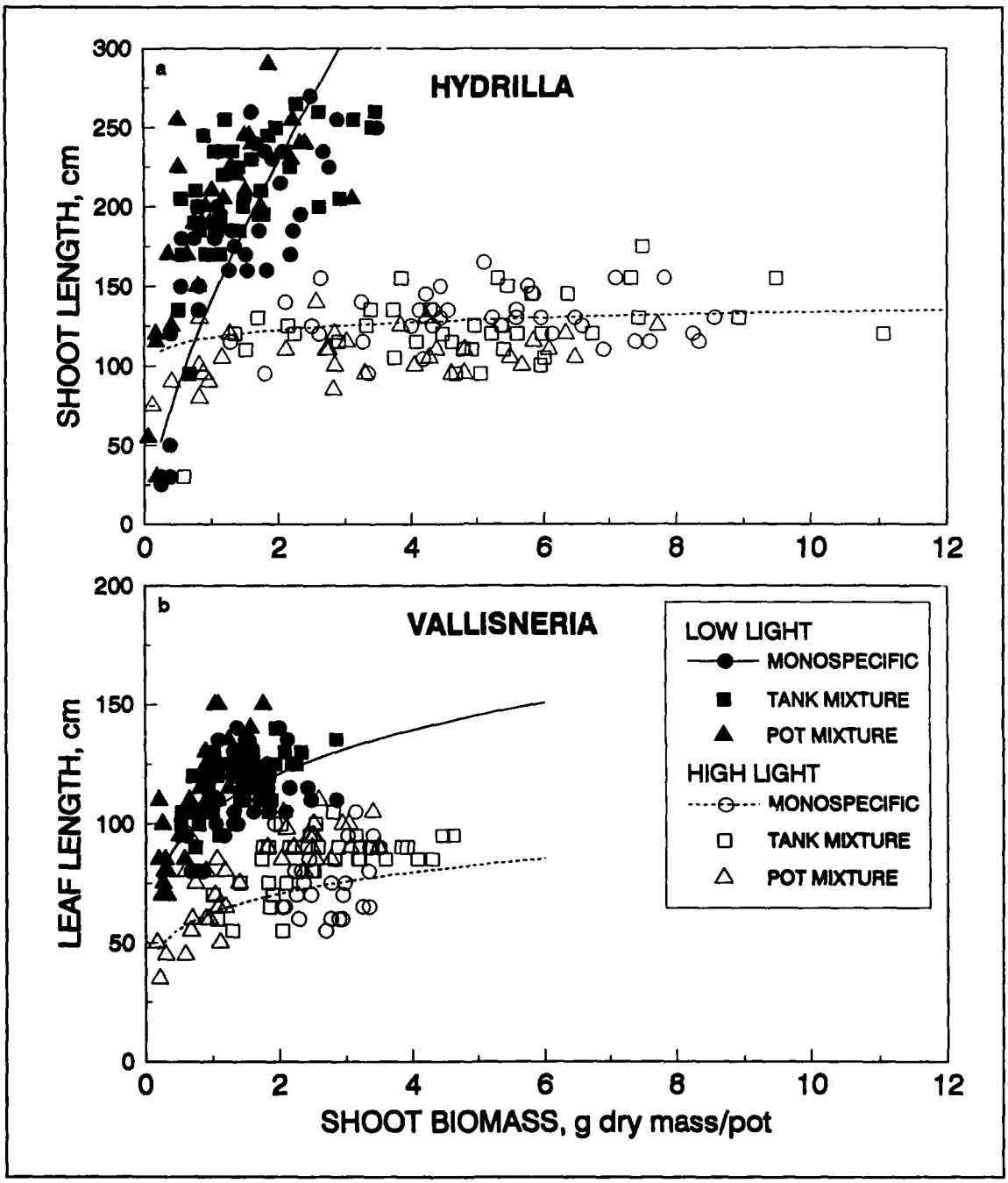

Figure 15. Relationships between shoot length and shoot biomass in *Hydrilla* (a) and leaf length and shoot biomass in *Vallisneria* (b) grown in monocultures, pot mixtures, and tank mixtures under low and high light conditions. Values are for individual replicates (rather than means) to better illustrate relationships

5 Resource Competition

Light Interception

As stated earlier, canopy development in *Hydrilla* monocultures was quite efficient, and this species altered its morphology to maximize light interception under widely different light conditions. Although canopy development and light interception in *Hydrilla* were greater at the higher light level, observed differences in shoot biomass production under other environmental conditions were not accompanied by differences in light interception. Although *Vallisneria* was, overall, less effective at light interception than *Hydrilla*, this species also intercepted a high and relatively unvarying percentage of incident solar radiation when grown in monoculture.

In view of the above, it is not surprising that light interception by mixed canopies was intermediate between that of *Hydrilla* and *Vallisneria* monocultures (Table 5). Likewise, it is not surprising that light interception in mixed canopies was fairly constant under all of the environmental conditions and competition treatments evaluated.

Although the amount of light intercepted by each species in the mixtures was not determined, *Hydrilla*, by virtue of its greater shoot length and ability to branch prolifically at the water surface, would be expected to receive a greater share of incident radiation. Although *Vallisneria* also intercepted a high percentage of incident light in monocultures, this species, since it distributes its biomass more uniformly throughout the water column, would be expected to receive a less proportionate share of the incident light than *Hydrilla* when the two species are growing together. Indirect evidence that *Hydrilla* shoots intercepted a greater share of incident light in mixtures is the change in morphological relationships of *Vallisneria* grown with *Hydrilla* in comparison with *Vallisneria* growing alone (Figure 15b).

Photographs of the plant canopies taken at the end of the experiment generally show a canopy composed predominantly of *Hydrilla* shoots, thus providing qualitative evidence supporting *Hydrilla*'s competitive superiority in surface light interception. Exceptions to this general pattern were observed in pot mixtures grown on the higher fertility sediment, particularly those grown under conditions of low C supply (+F, +L+F). Under these conditions,

Table 5
Light (Photosynthetically Active Radiation) Attenuation by Canopies of *Hydrilla* and *Vallisneria* Growing Monospecifically and in Pot Mixtures and Tank Mixtures Under Low and High Light Conditions[1]

Treatment	Light Level	Canopy Attenuation	
		% of Surface	Standard Error
Hydrilla	Low	80	4.6
	High	90	1.3
Pot Mixture	Low	80	4.3
	High	83	5.0
Tank Mixture	Low	75	5.2
	High	82	1.9
Vallisneria	Low	75	1.9
	High	78	5.7

[1] Means and standard errors are based on measurements of four communities or populations at each light level.

Hydrilla grown in pot mixtures produced very little shoot biomass, and its shoots barely reached the water surface. Under these conditions, *Hydrilla* did not form a surface canopy, and *Vallisneria* undoubtedly intercepted much of the incident solar radiation.

Nutrient Limitation

Unlike light, for which there is no simple diagnostic for ascribing plant growth limitation, nutrient concentrations in plant tissues provide evidence of the adequacy (or inadequacy) of their supply. Earlier tissue analysis was used to substantiate N limitation of the growth of *Hydrilla* growing monospecifically under the higher light, high C supply conditions (+L+C, +L+C+F). Tissue analysis also suggested N limitation in *Vallisneria* growing monospecifically under three of the four higher light treatment combinations (+L, +L+C, +L+C+F). This approach should also yield valuable information about the limiting nutrient status of plants growing in mixtures.

Shoot N concentrations

Concentrations of N in *Hydrilla* shoots growing in both types of mixtures under the higher light, high C supply conditions (+L+C, +L+C+F) were within the critical range (Figure 16a), suggesting N limitation of *Hydrilla*

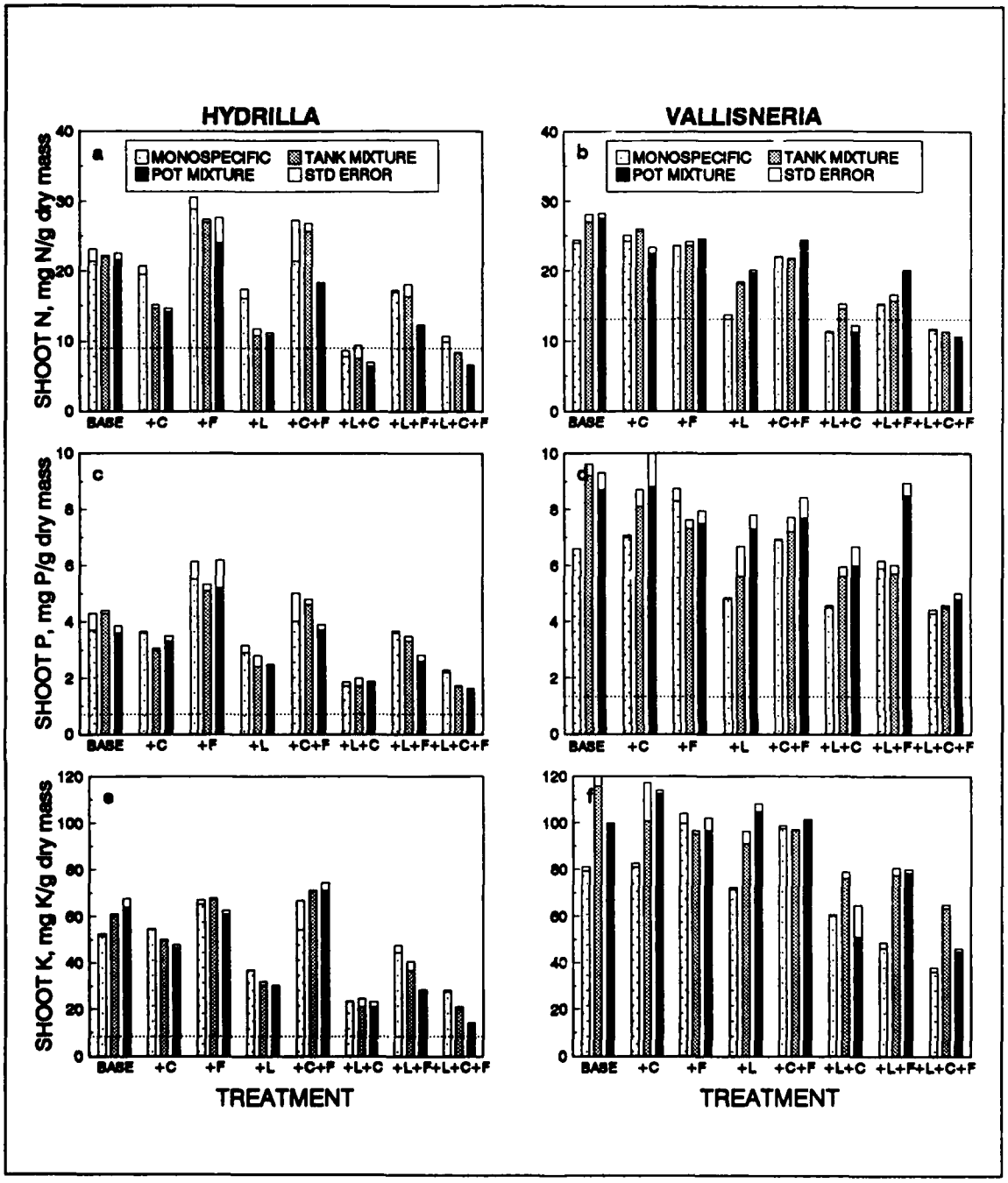

Figure 16. Shoot concentrations of N (a, b), P (c, d), and K (e, f) in *Hydrilla* and *Vallisneria* plants grown monospecifically and in tank and pot mixtures under different environmental conditions. Treatments are as indicated in Figure 3. Means and standard errors are based on duplicate digestion and analysis of separate composite samples obtained from pooling five replicate biomass samples. When present, horizontal dashed lines indicate critical (growth-limiting) tissue concentrations

growth under these conditions. Concentrations of N in *Hydrilla* shoots growing in both types of mixtures under the higher light level condition (+L) were also near critical, and the possibility of N limitation of the growth of these plants cannot be dismissed. The growth of *Hydrilla* under the remaining conditions, however, is unlikely to have been limited by N.

Concentrations of N in *Vallisneria* shoots grown in both types of mixtures under the higher light, high C supply conditions (+L+C, +L+C+F) were also within the critical range (Figure 16b), suggesting N limitation of *Vallisneria* growth under these conditions. Concentrations of N in *Vallisneria* shoots grown in mixtures with *Hydrilla* under other conditions exceeded critical concentrations for N and are not indicative of N limitation of *Vallisneria* growth under these conditions.

Shoot P concentrations

Concentrations of P in both *Hydrilla* and *Vallisneria* shoots grown under all environmental and competition treatment combinations were well above respective critical concentrations for this element (Figure 16c and 16d), indicating that neither species was limited by P availability under any of the conditions examined. Since P apparently had no effect on the growth of either *Hydrilla* or *Vallisneria*, this element will not be considered further.

Shoot K concentrations

Concentrations of K in *Hydrilla* shoots grown under all environmental and competition treatment combinations (Figure 16e) were generally well above the suggested critical concentration of 8.0 mg K/g dry mass (Barko 1982), indicating that *Hydrilla* was unlikely limited by K availability under any of the conditions examined. Although a critical concentration of K for *Vallisneria* has not yet been determined, shoot K concentrations were very high under all environmental and competition treatment combinations, indicating that *Vallisneria* was not limited by K availability under any of the conditions examined (Figure 16f). Although tissue K had no apparent effect on the growth of either *Hydrilla* or *Vallisneria*, this element is rapidly taken up from the water column by both of these species. *Vallisneria* virtually depleted the water column of K under certain conditions. In view of the importance of solution K to growth (Barko 1982), its physiological role in maintaining plant integrity (Smart and Barko 1986), and its postulated role in N acquisition (Barko et al. 1988), the possible involvement of solution K in affecting the outcome of plant competition will be considered in a subsequent section.

Nutrient Accumulation

N accumulation

Although the most direct method of measuring competitive success (and the one employed here) is to measure total biomass accrual, there are many other parameters that could be used. Resource capture, in particular, the capture of a limiting resource, is one possibility. Since N availability has often been shown to limit the growth of aquatic plants (Anderson and Kalff 1986; Smart and Barko 1988; Barko 1992), and since N limitation occurred under some of the conditions examined in this experiment, it would be interesting to use N accumulation as a measure of competitive success.

Plotting N accumulation as a relative yield diagram (Figures 17 and 18) indicates that N accumulation provides results that are almost identical to those for total biomass accumulation presented earlier. Under base level conditions, when the two species were grown together in pot mixtures, *Hydrilla* accumulated a much greater share of sediment N, while *Vallisneria* accumulated a lesser share (Figure 17a). When they were grown in separate pots in the tank mixture, *Hydrilla*'s competitive advantage was lessened, suggesting that root competition for sediment N was important to *Hydrilla*'s dominance in the pot mixture (Figure 17b).

Under increased C supply (+C), N accumulation by the two species is more equitably apportioned (Figure 17c and 17d). Increased sediment fertility (+F, +C+F) favors *Vallisneria*, particularly in pot mixtures, where root competition enhances *Vallisneria*'s competitiveness (Figure 17e and 17g).

Under the higher light level (+L), both species accumulated equivalent amounts of N in pot mixtures (Figure 18a). In tank mixtures of plants grown on the lower fertility sediments (+L, +L+C), there was no apparent competition for sediment N, and both species accumulated equivalent amounts (Figure 18b and 18d). In the pot mixtures receiving the higher C supply (+L+C), *Hydrilla* accumulated a greater share of sediment N than did *Vallisneria* (Figure 18c). However, increased N accumulation in *Hydrilla* did not reduce N accumulation by *Vallisneria.*

When plants were grown in pot mixtures on the higher fertility sediment (+L+F, +L+C+F), *Vallisneria* accumulated a much greater share of sediment N than did *Hydrilla* (Figure 18e and 18g). The increase in N accumulation by *Vallisneria* corresponded with a reduction in N accumulation by *Hydrilla.* When the plants were grown in separate pots in tank mixtures, *Vallisneria* accumulated more N than did *Hydrilla* (Figure 18f and 18h). The presence of *Vallisneria* shoots in these tank mixtures also seems to have reduced the ability of *Hydrilla* to accumulate sediment N.

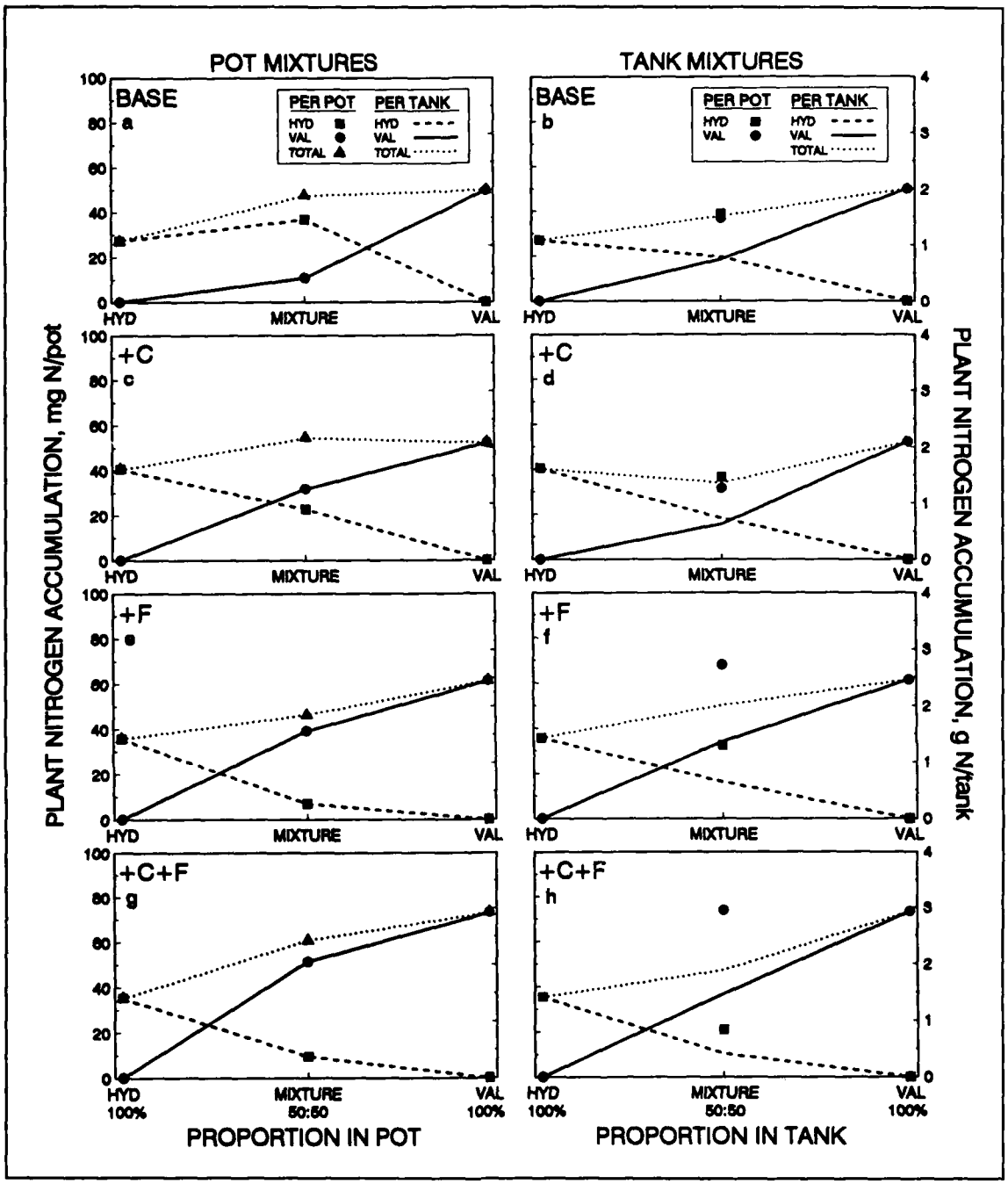

Figure 17. Relative yield diagrams for total plant N accumulation in *Hydrilla* and *Vallisneria* grown in pot mixtures (a, c, e, g) and tank mixtures (b, d, f, h) under low light conditions. Symbols denote N accumulation per pot based on duplicate digestion and analysis of separate composite samples obtained from pooling five replicate biomass samples. Lines denote N accumulation per tank calculated from individual (composited) pot values

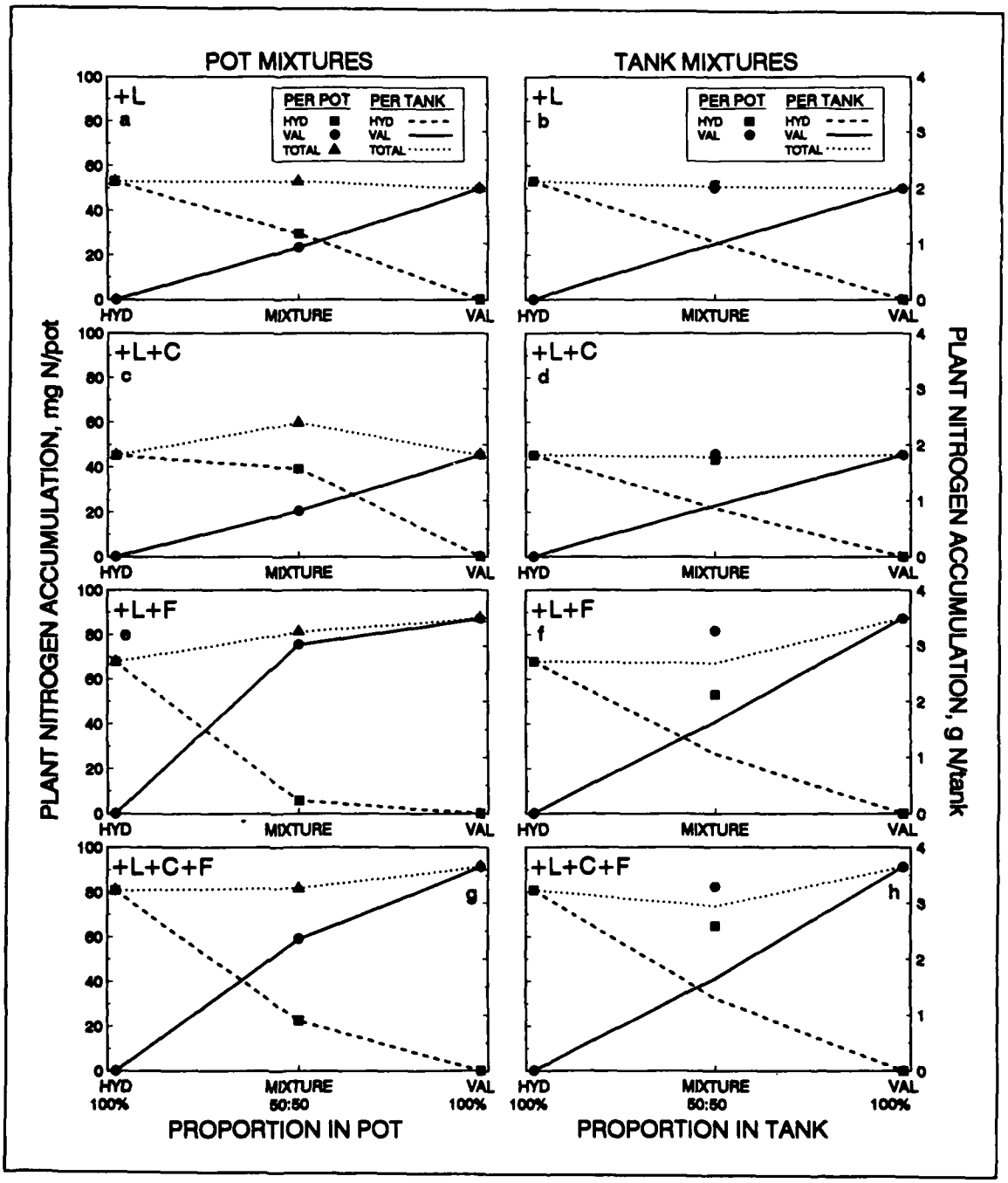

Figure 18. Relative yield diagrams for total plant N accumulation in *Hydrilla* and *Vallisneria* grown in pot mixtures (a, c, e, g) and tank mixtures (b, d, f, h) under high light conditions. Symbols denote N accumulation per pot based on duplicate digestion and analysis of separate composite samples obtained from pooling five replicate biomass samples. Lines denote N accumulation per tank calculated from individual (composited) pot values

K accumulation

Under base level conditions, when the two species were grown together in pot mixtures, *Hydrilla* accumulated a much greater quantity of K than did *Vallisneria* (Figure 19a). When they were grown in separate pots in the tank mixture, *Hydrilla*'s competitive advantage was lessened (Figure 19b), suggesting that root competition, perhaps for sediment N, was important to *Hydrilla*'s dominance in both biomass accumulation and K accumulation in the pot mixture.

Under increased C supply (+C), K accumulation in *Vallisneria* is enhanced in pot mixtures (Figure 19c), but this enhancement is not detrimental to either biomass production or K accumulation in *Hydrilla*. In tank mixture, K accumulation is more equitably apportioned between the two species (Figure 19d). There was generally a close correspondence between depletion of K from solution and K accumulation in tissues of plants grown on low fertility sediments (Figure 19a-19d). This indicates that the solution, rather than the sediment, was usually the primary source of K for plants of both species grown on the low fertility sediment.

Increased sediment fertility (+F, +C+F) favored K accumulation by *Vallisneria*, particularly in pot mixtures (Figure 19e and 19g), where root competition (perhaps for N) apparently enhanced *Vallisneria*'s competitiveness for K. Although *Vallisneria* does accumulate a greater share of K in both pot and tank mixtures (Figure 19f and 19h), this increase is not always accompanied by a decrease in K accumulation in *Hydrilla*, indicating that affinity for K may not be important in affecting the outcome of competition between these two species under the conditions tested.

Under the higher light level (+L), both species accumulated equivalent amounts of K in pot mixtures (Figure 20a). In tank mixtures of plants grown on the lower fertility sediments (Figure 20b and 20d), there was no apparent competition for K, and both species accumulated amounts similar to those in monoculture. In the pot mixtures receiving the higher C supply (+L+C), *Hydrilla* accumulated a greater share of K than did *Vallisneria* (Figure 20c). However, this increased K accumulation in *Hydrilla* did not reduce K accumulation by *Vallisneria*.

When plants were grown in pot mixtures on the higher fertility sediment (Figure 20e and 20g), *Vallisneria* accumulated a much greater share of K than did *Hydrilla*. The large increase in K accumulation by *Vallisneria* corresponded with a large reduction in K accumulation by *Hydrilla*. When the plants were grown in separate pots in tank mixtures, *Vallisneria* again accumulated more K than did *Hydrilla* (Figure 20f and 20h). The presence of *Vallisneria* shoots in these tank mixtures also seems to have reduced the ability of *Hydrilla* to accumulate K.

There was a close correspondence between depletion of K from solution and K accumulation in plant tissues (Figures 19 and 20). Under three of the

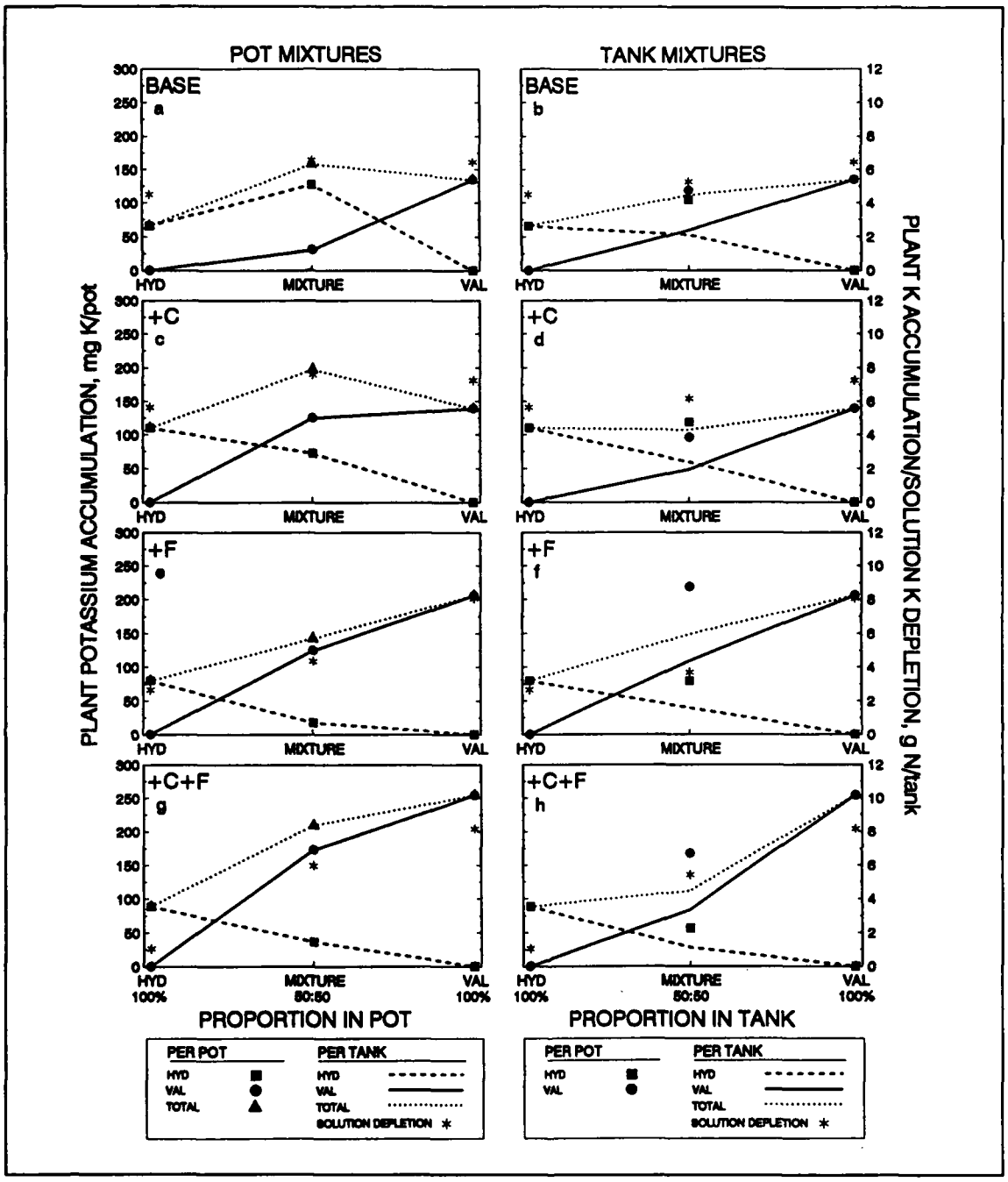

Figure 19. Relative yield diagrams for total plant K accumulation in *Hydrilla* and *Vallisneria* grown in pot mixtures (a, c, e, g) and tank mixtures (b, d, f, h) under low light conditions. Solid symbols denote K accumulation per pot based on duplicate digestion and analysis of separate composite samples obtained from pooling five replicate biomass samples. Lines denote K accumulation per tank calculated from individual (composited) pot values. Asterisks (*) denote measured amounts of K depletion from solution (expressed on a tank basis) for comparison with plant K accumulation values

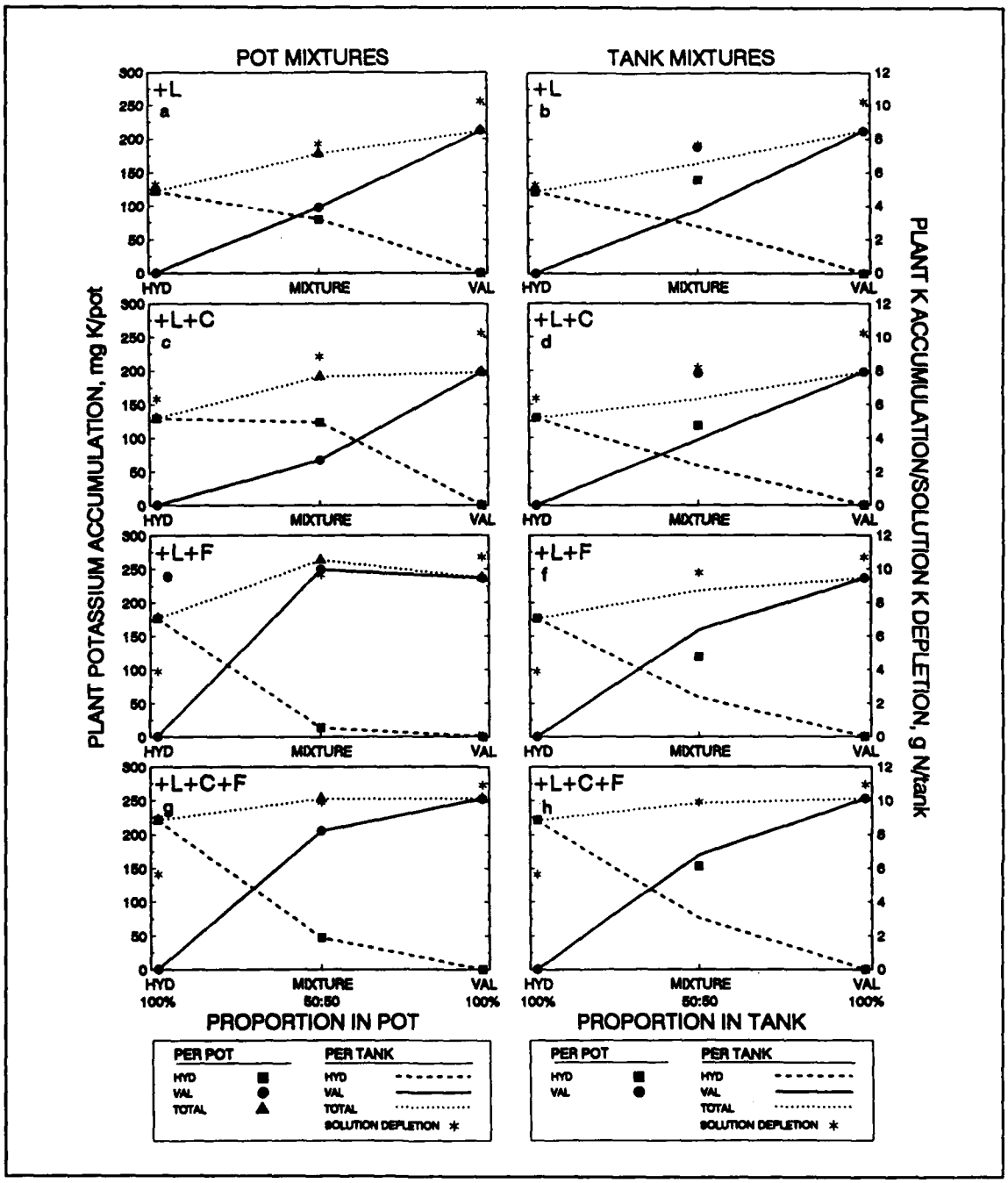

Figure 20. Relative yield diagrams for total plant K accumulation in *Hydrilla* and *Vallisneria* grown in pot mixtures (a, c, e, g) and tank mixtures (b, d, f, h) under high light conditions. Symbols denote K accumulation per pot based on duplicate digestion and analysis of separate composite samples obtained from pooling five replicate biomass samples. Lines denote K accumulation per tank calculated from individual (composited) pot values. Asterisks (*) denote measured amounts of K depletion from solution (expressed on a tank basis) for comparison with plant K accumulation values

four treatments at the higher sediment fertility (+C+F in Figure 19, +L+F, +L+C+F in Figure 20), *Hydrilla* grown in monoculture accumulated more K than could be accounted for by losses of K from solution. Under low fertility conditions, solution K depletion generally exceeded K accumulation in both *Hydrilla* and *Vallisneria* growing in monoculture. This result perhaps suggests a net transport of solution K to the sediment. It is interesting that this occurred only under the low fertility condition, since it has been suggested that foliar uptake and translocation of solution K to roots for exchange with sediment NH_4 may be a response to N limitation in *Hydrilla* (Barko et al. 1988).

Nutrient Allocation Strategies

Under the higher levels of both light and C supply (+L+C), growth of both species in monoculture was clearly limited by the availability of N. Evidence for N limitation includes both shoot N concentrations within the critical range and the significant responses to increased sediment fertility (+L+C+F). *Hydrilla* and *Vallisneria* accumulated identical quantities of N under this condition (45.2 ± 3.4 mg N/pot and 45.4 ± 0.1 mg N/pot, respectively), suggesting that the two species were comparable in terms of their abilities to acquire N when this resource was limiting.

N allocation

Although neither species possessed a physiological advantage in N acquisition, *Hydrilla* allocated 87 percent of its N to shoots and only 13 percent to roots, while *Vallisneria* allocated only 68 percent of its N to shoots. For each gram of N acquired, *Hydrilla* produced 111 g dry shoot mass, while *Vallisneria* produced only 60 g dry shoot mass. This difference in N allocation strategy between the two species arises from their different strategies for biomass allocation. *Hydrilla* maximizes shoot production at the expense of roots, while *Vallisneria* more evenly distributes its biomass between aboveground and belowground portions. Since *Hydrilla* in this investigation was predominantly light limited rather than nutrient limited (Table 4), this strategy would seem to be quite effective. By maximizing shoot production, *Hydrilla* maximizes capture of the limiting resource—light. The development of a dense canopy of shoots may also allow *Hydrilla* to effectively preempt light, thus avoiding competition from other species (Haller and Sutton 1975). *Vallisneria* in this investigation responded equally to increases in light and sediment fertility. Although allocation of a greater share of biomass to shoots would enhance *Vallisneria*'s ability to capture light, a corresponding decrease in the production of belowground biomass would limit its ability to acquire (or store) sediment N. Thus increased allocation of biomass (or other potentially limiting resources such as N) to shoots might not be advantageous for *Vallisneria*. Since *Vallisneria* distributes its biomass more evenly throughout the water column and does not often form a dense surface canopy (Haller and Sutton 1975), it would not often be able to preempt light even with a much higher

allocation to shoots. By accumulating a greater proportion of nutrients in belowground structures, *Vallisneria* may be able to retain these nutrients over multiple growing seasons. *Hydrilla*, however, may lose much of its accumulated nutrient store during senescence of shoots at the end of the growing season.

N retention

Earlier studies have demonstrated that the first season or period of growth of *Hydrilla* on previously unvegetated sediments is usually quite high (Barko et al. 1988). However, the growth of *Hydrilla* during subsequent periods is greatly diminished as a result of N depletion of the sediment. Addition of N ameliorates the reduction. Retention of nutrients (N in particular) in perennating belowground organs may thus provide substantial competitive advantages to species like *Vallisneria* during subsequent seasons.

Solution Interactions

DIC and Ca depletion

When *Hydrilla* and *Vallisneria* were grown monospecifically, they caused nearly identical changes in solution DIC and Ca. Under the lower rate of C supply, photosynthesis by both species caused reductions in solution DIC and Ca. These reductions, which were greater under the higher light level, resulted from the combined effects of HCO_3^- uptake and $CaCO_3$ precipitation. Not surprisingly, reductions in solution DIC levels in both pot mixtures and tank mixtures (not shown) were quite similar to those occurring in the monocultures. Even though plant growth may have been limited by C availability under some of the environmental conditions examined, this study provides no evidence that either species possessed any physiological advantages with respect to either C acquisition or DIC depletion.

K depletion

When *Hydrilla* and *Vallisneria* were grown monospecifically, *Vallisneria* elicited a much greater reduction in solution K than did *Hydrilla*. Under the higher fertility conditions at the higher light level, *Vallisneria* completely depleted solution K within 5 weeks. Depletion of solution K in both pot mixtures and tank mixtures (not shown) did not differ significantly from the depletion occurring in *Vallisneria* monocultures, but was significantly greater than that occurring in *Hydrilla* monocultures. Since *Vallisneria* exhibited both a high demand for K (as evidenced by its high K accumulation) as well as an ability to acquire K from solution even at low concentrations, *Vallisneria* may have a competitive advantage under K-limiting growth conditions.

Resource Limitation

Methodological considerations

In these experiments, levels of the three resources (light, inorganic C supply, and sediment fertility) most likely to limit the growth and distribution of submersed aquatic plants were varied. These resources are those most likely to affect the outcome of competition between submersed aquatic plants. Since two of these resources (light and C supply) are captured by plant shoots and the third (sediment nutrients) is acquired by the roots, an attempt was made to separately estimate the effects of shoot competition (using tank mixtures) in addition to determination of root plus shoot competition. Separate estimates of the effects of the shoot component of competition should provide additional information on the mechanisms involved in competitive interactions (Newman 1983).

To determine the environmental factors (in this case resources) affecting the outcome of competition, one must be able to assess the suitability of the factor (adequacy of the supply of the resource) for each of the species in question. One method of accomplishing this is to increase the level of the factor and observe the response. With monospecific populations, this is quite simple. If the plant responds to the increased level of the factor by increasing its growth, then the plant's growth is considered to have been limited by the resource. With a mixture, however, either of the species (or both) can respond to the increase in resource availability and the other species will then be affected, not only by the increase, but also by the response of the first species. Moreover, addition of a limiting resource may either eliminate competition for the resource by fulfilling the requirements of both species or intensify competition for the resource by increasing the disparity between the competitive winner and loser. Addition of a limiting resource may also promote limitation of either or both species of the mixture by a second resource.

Separation of the effects of shoot and root competition also proved problematical. Since the effects of shoot and root competition are not likely to be additive (Wilson 1988), assessment of the shoot and root components of plant competition requires three independent measurement conditions—shoot competition only, root competition only, and root + shoot competition. Although root competition was prevented in tank mixtures (to estimate shoot competition), this lack of additivity prevents us from estimating root competition from the difference between pot mixtures and tank mixtures. Prevention of shoot competition (to estimate root competition) with dividers as has been used with terrestrial plants is not practical for submersed aquatic plants that share the same fluid medium. Thus it will be difficult to determine the magnitude of the shoot component of the competitive interaction between the two species. The method of separating shoot competition from root + shoot competition used here actually only serves to identify cases where root competition is unimportant (tank mixtures = pot mixtures).

In spite of the above limitations of the methodology, in the following sections, the authors attempt to identify the limiting factors and some of the mechanisms involved in interspecific competition.

Limiting factors

Under base conditions, *Hydrilla* dominated pot mixtures, suppressing the growth of *Vallisneria* (Figure 11a). The growth of long *Hydrilla* shoots (230 cm in a 75-cm water column) in pot mixtures formed an effective canopy that likely exerted a competitive effect on *Vallisneria* by shading the lower growing (120 cm) *Vallisneria* leaves (Figure 13a). Competition for inorganic C for photosynthesis is less likely, as DIC depletion was not substantial under the low light condition (Figure 9a and 9c). The involvement of roots in *Hydrilla*'s competitive dominance is indicated by the lesser competitive effect in the tank mixture where only shoot competition could occur (Figure 11b). Competition for sediment N is the most likely mechanism to account for the strong belowground interaction in pot mixtures; however, tissue N levels in *Vallisneria* shoots at the end of the study were not indicative of N limitation (Figure 16b). Accumulation of N by *Hydrilla* did increase, while that of *Vallisneria* decreased in the pot mixtures (Figure 17a); but it is uncertain whether this indicates a greater competitive ability of *Hydrilla* for N acquisition or is merely a result of *Hydrilla*'s superiority in the capture of some other resource that limited the growth of *Vallisneria* in pot mixtures. The most likely explanation is that *Hydrilla* was more effective at converting sediment N into shoot biomass. Increased shoot biomass produced more root biomass and photosynthate, which fueled additional N uptake in a positive feedback loop. While *Vallisneria* may have been limited by N early in the experiment, the prolific growth of *Hydrilla* shoots so reduced light that, by the end of the 8-week period, *Vallisneria*'s growth was light limited rather than N limited. However, from the limited information obtained in this study, it is not possible to positively attribute *Hydrilla*'s dominance under base conditions to any particular factor or mechanism.

An increase in C supply would, at first thought, seem to increase *Hydrilla*'s advantage since monocultures of this species were C limited under base conditions and those of *Vallisneria* were not (Figure 3a, 3b). However, *Hydrilla* in pot mixtures was apparently not C limited, as these plants did not respond to the increased C supply (Figure 11c versus 11a). Increasing the supply of inorganic C actually lessened *Hydrilla*'s competitive advantage since the additional supply ensured that *Vallisneria* was not limited by C supply. The growth of *Vallisneria* was reduced in both tank mixtures under the low light, low fertility conditions (Base and +C in Figure 11b and 11d), indicating that *Hydrilla* shoots were exerting a competitive effect. Increasing the supply of C to pot mixtures apparently enabled *Vallisneria* to exploit additional sediment N not used by *Hydrilla* (Figure 17c).

An increase in sediment fertility under the low light condition (+F in Figure 11e) enabled *Vallisneria* to exert a competitive effect on *Hydrilla* in pot

mixtures. *Vallisneria* also increased in tank mixtures, but this increase did not cause a significant decrease in *Hydrilla* growth (Figure 11f). Belowground interactions enhanced *Vallisneria*'s competitiveness, increasing its accumulation of sediment N (Figure 17e), decreasing *Hydrilla*'s N accumulation, and decreasing the length of *Hydrilla* shoots (Figure 13b). However, tissue analysis did not substantiate N limitation of *Hydrilla* growth (Figure 16a). Similar results were obtained under both high fertility environmental treatment combinations (+F and +C+F in Figure 11e and 11g).

Under the higher light level (+L in Figure 12a and 12b), both mixtures produced similar results, with *Hydrilla* exerting a competitive effect on the growth of *Vallisneria*. This similarity indicates that belowground interaction was unimportant and that shoot competition was largely responsible for the observed results. Additional evidence for the predominance of shoot competition is the lack of a competitive effect by *Hydrilla* on N accumulation (Figure 18a and 18b). Although the exact nature of this shoot interaction cannot be determined, competition for inorganic C is likely. An increase in C supply at the higher light level increased *Hydrilla* growth in both pot mixtures and tank mixtures (+L+C in Figure 12c and 12d).

Under the higher light, higher C supply condition (+L+C in Figure 12c), *Hydrilla* strongly dominated the pot mixture, but not the tank mixture (Figure 12d). This difference in results indicates that belowground interactions were important in the pot mixture. *Hydrilla*'s increased dominance in biomass production with increased C supply corresponded with a large increase in N accumulation by this species (Figure 18c). However, increased N accumulation by *Hydrilla* did not reduce N accumulation or growth of *Vallisneria* in pot mixtures (Figure 18c), and increased C supply did not result in increased N accumulation by *Hydrilla* in tank mixtures (Figure 18d). *Hydrilla* may have been accessing sediment N that was unavailable to *Vallisneria*. Plants of both species were apparently N limited in monocultures and in both types of mixtures under the higher light, higher C supply condition (Figure 16a and 16b).

Under the higher light, higher fertility condition (+L+F), *Vallisneria* exerted a strong competitive effect on *Hydrilla* in pot mixtures and a lesser effect in tank mixtures (Figure 12e and 12f). The high degree of suppression of *Hydrilla* in pot mixtures likely involved both root and shoot competition. Although competition for sediment N seems likely, tissue analysis of *Hydrilla* shoots did not provide evidence of N limitation (Figure 16a). Shoot competition for inorganic C is likely, as C demand under these environmental conditions would be high. *Vallisneria* leaves may also have reduced the light available to *Hydrilla* shoots, as the latter were short (60 cm) and unable to form a canopy at the water surface (Figure 13d).

Under the combined high level of each of the resources (+L+C+F), both species attained their maximum biomass (Figure 3a and 3b). Neither species exerted a competitive effect on the other in either of the two types of mixtures (Figure 12g and 12h). The growth of *Vallisneria* in pot mixture was, however, stimulated relative to its growth in monoculture (Figure 12g). Growth of both

species in both types of mixtures was apparently N limited (Figure 16a and 16b), and *Vallisneria* exerted a competitive effect on *Hydrilla* N accumulation (Figure 18g). Apparently, each of the resources was available in sufficient supply to afford moderate growth of both of the species, and competitive interactions were insufficient to cause appreciable limitations of growth.

Diagnostic Indicators

Although sediment fertility (N availability) exerted a controlling influence and belowground interaction affected competitive outcome, N limitation of the competitive loser was demonstrated in only two of the eight environmental treatment combinations. The use of tissue analysis at a single point in time as an indicator of the adequacy of supply of a nutrient over an extended period is perilous, particularly for mixtures of plants species. In mixtures more so than monocultures, limiting factors are dynamic, changing from day to day as individual plants respond to the changing environment and to each other (Chapin et al. 1987). Thus nutrient limitations occurring early in the growth period may have lasting effects on the outcome of competition, but may leave little tissue evidence of their occurrence.

Diagnostic indicators of light or C limitation are even less well-developed. Morphological attributes such as internodal lengths might be used for assessing light limitation in species such as *Hydrilla* (Barko and Smart 1981a), but this measurement could not be used for species such as *Vallisneria*. Assessment of C limitation would be even more difficult, possibly requiring photosynthetic or enzyme assays.

For all of the above reasons, determination of the limiting factors or resources in competing plants remains difficult.

6 Discussion

Under the least favorable growth conditions (Base), *Hydrilla* was more competitive than *Vallisneria*. Increased light lessened *Hydrilla*'s advantage; increased C availability equalized the two species; and increased sediment fertility shifted the advantage to *Vallisneria*. Under the most favorable conditions, *Vallisneria* was somewhat more competitive, but did not suppress the growth of *Hydrilla*. Decreased light slightly increased *Vallisneria*'s advantage; decreased C availability greatly increased *Vallisneria*'s advantage; and decreased sediment fertility shifted the advantage to *Hydrilla*.

Competitive Mechanisms

Resource competition

Results of these controlled experiments indicate that the outcome of competition between two species can vary dramatically depending on the environmental conditions employed. Under low fertility conditions, *Hydrilla* is generally the superior competitor; but on higher fertility sediments, *Vallisneria* is dominant. Strong dominance by either species generally occurred only in pot mixtures, indicating that belowground interactions were a significant component of competition between these two species.

The complexity of the competitive interactions observed in these experiments precludes the determination of simple, general mechanisms of competition. The resource-based approach seems appropriate since changes in rates of supply of different resources resulted in differences in competitive outcome. However, it remains to be determined whether competitive success in submersed aquatic plants is more dependent on resource depletion (Tilman 1990) or resource capture (Grime 1979).

The occurrence of growth limitation by multiple resources seems to be fairly common among submersed aquatic plants (Barko and Smart 1986; Smart and Barko 1990; and this study). That growth (and competitive interactions) can be limited simultaneously by multiple resources further confounds the analysis of competitive interactions (Chapin et al. 1987) and complicates the determination of competitive mechanisms. Consideration must be given not

only to the more obvious limiting factors but also to other, more subtle components of the environment, since resource acquisition (whether limiting or not) bears a cost that affects the total allocation of resources within the plant (Bloom, Chapin, and Mooney 1985). Consideration must be given to the effects of tradeoffs in the acquisition, storage, utilization, and (in the case of nutrients) recycling of resources (Grace 1990). This consideration will require systematic study of the interactions occurring in the relative rates of each of these processes as they relate to the total economy of the plant and to its interaction with its neighbors.

Resource preemption

In addition to direct competition for resources, consideration must also be given the role of preemption in competitive interactions. In a newly establishing community of annual species, seed germination of the different species usually occurs over a fairly limited time period in the spring. During initial establishment of these individual species, competitive interactions are likely to be important determinants of community structure, and short-term competition experiments may be useful in predicting species composition of the resultant community. However, in an established community of perennial species, competitive interactions may be so dominated by mature individuals of a single species that these short-term experiments are not appropriate for predicting species composition. This occurs because the established perennial species has preempted the resources, thus avoiding competition from other species. This situation appears to be quite common among submersed aquatic plant communities, and productive aquatic environments are often characterized by large expanses of monospecific vegetation.

In the absence of disturbance, these monospecific communities may persist for long periods. The ability of these dominant species to persist (resist invasion by a more competitive species) depends on the degree to which they have preempted the limiting resources of the environment. Experiments designed to measure preemption may provide more relevant information on the susceptibility of different species to invasion.

Dispersal

Following a large-scale disturbance event, preemption of resources may be eliminated, once again resulting in more equitable competitive interactions among newly arriving plants. In this situation, species that can rapidly colonize disturbed sites are at an advantage. This advantage can result from the development of a resistant and long-lived seed/tuber bank or from an ability to rapidly flood an area with seed or other propagules. The latter is a very effective method of vegetative expansion, and the ability to rapidly spread by shoot fragmentation is a characteristic of our most serious submersed aquatic weed species such as *Hydrilla* or Eurasian watermilfoil.

Growth Strategies

The two species studied here clearly differ in terms of their plant growth strategies. *Hydrilla* allocates much of its biomass and nutrients to shoots, has a high requirement for both light and C supply, tolerates low sediment N availability, distributes much of its biomass at or near the water surface, exhibits a high degree of morphological plasticity in response to different environmental conditions, and likely loses a significant proportion of its accumulated biomass and nutrients during seasonal senescence. These characteristics are typical of early successional or pioneer species. These pioneer species are usually highly adapted for rapid colonization of new or disturbed sites. Typical adaptations of these ruderal (weedy) species include efficient dispersal of propagules, rapid growth rates, early reproduction, and tolerance of marginal growing conditions. *Hydrilla* also exhibits these traits with its rapid spread through fragmentation, prolific growth, and ability to exploit habitats left open by indigenous vegetation.

In contrast with *Hydrilla*, *Vallisneria* evenly allocates its biomass and nutrients between aboveground and belowground portions, has a high N requirement, tolerates low light and low C supply, distributes its biomass evenly throughout the water column, does not exhibit a great deal of morphological plasticity in response to differences in environmental conditions, and likely retains a high proportion of its accumulated biomass and nutrients from one season to the next. These characteristics are typical of later successional species. While these species are generally competitive dominants, they are usually slower growing, more demanding in terms of environmental requirements, and require relatively stable, undisturbed conditions in order to establish and achieve dominance.

The greatest attributes of *Hydrilla*, and the primary reasons for its widespread distribution, are its ability to rapidly disperse large numbers of propagules through fragmentation and its rapid growth under less than ideal conditions. Once *Hydrilla* becomes established, it is unlikely to be displaced because, with these characteristics, disturbance will always favor reestablishment rather than replacement. Although other, later successional species may be more competitive, these species may never be afforded an opportunity to replace the weedy invader. Either succession is arrested at an early stage because of frequent disturbance of the aquatic environment, or there may be insufficient propagules of the competitive, higher successional species to ensure establishment.

7 Conclusions and Recommendations

The experiments reported here demonstrate that under certain environmental conditions *Vallisneria* can be an effective competitor with *Hydrilla*. Since *Vallisneria* has a high requirement for N, a key to its success is the provision of adequate sediment N to sustain a high growth rate. Once *Vallisneria* is successfully established, its N requirement should decrease since it likely retains much of its accumulated N in belowground perennating organs (winter buds).

Two attributes of *Hydrilla* explain its dominance in disturbed aquatic ecosystems—a very effective means of propagation and dispersal, and a competitive growth morphology. *Hydrilla* is able to rapidly colonize disturbed sites through shoot fragmentation as well as from turions. Floating shoot fragments are abundant in water bodies infested with *Hydrilla*. These fragments readily root in sediment and rapidly grow to mature plants. Once established, *Hydrilla* produces a large quantity of shoot biomass from a limited supply of sediment N. Unchecked, the growth of *Hydrilla* can produce a dense surface mat or canopy of shoots that absorbs all light penetrating the water surface, preempting this resource and eliminating potential competitors.

Although *Vallisneria* is a very effective competitor with *Hydrilla* during the established phase, it is at a definite disadvantage during the colonization phase. Unlike *Hydrilla*, *Vallisneria* has no vegetative propagules for dispersing over long distances. Although *Vallisneria* does produce seed, these are not widely dispersed (Kaul 1978) and are unlikely to successfully establish in the presence of competing vegetation.

Productive aquatic environments are frequently disturbed by acts of man (drawdowns, harvesting, herbicide treatment, watershed activities that increase turbidity and sedimentation, and boating) and events of nature (water level fluctuations, severe storm events and flooding, extremes of climate, and overgrazing). Frequent disturbance favors ruderal (weedy) species such as *Hydrilla*, which are highly adapted both for colonization of these systems and tolerance of their environmental conditions. The widespread dominance of many of our water bodies by problem species such as *Hydrilla* is a symptom of this cycle of disturbance and colonization.

An alternative management approach involves the establishment of communities of beneficial native species. By following aquatic plant control operations with the establishment of competitive native species, the recurrence of aquatic plant problems might be slowed or even prevented. By planting large numbers of propagules of competitive species, the strategic advantage of weedy, colonizing species such as *Hydrilla* might be offset. The effectiveness of the control operation is prolonged by delaying the reinfestation of a managed site, perhaps resulting in a lower overall cost of management. Additional benefits would include improved aquatic habitat, water quality, and, in the case of chemical control, lesser use of herbicides.

Future research should determine the competitive abilities of other beneficial native species, determine the importance of preemption in structuring submersed aquatic plant communities, develop practical and efficient methods of propagation and establishment of native species, and evaluate competitive interactions in larger scale and longer term field studies.

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Appendix A
Analysis of Variance (ANOVA) Tables

Table A1
Four-Way ANOVA for Total Biomass Production in *Hydrilla* and *Vallisneria* Growing Monospecifically

Source	DF	F Value	Probability
Species	1	31.12	0.0001
Light	1	450.35	0.0000
C Supply	1	73.65	0.0001
Fertility	1	91.03	0.0001
Species * Light	1	23.06	0.0001
Species * C Supply	1	18.46	0.0001
Species * Fertility	1	21.04	0.0001
Light * C Supply	1	25.85	0.0001
Light * Fertility	1	46.76	0.0001
C Supply * Fertility	1	8.45	0.0042
Species * Light * C Supply	1	17.14	0.0001
Species * Light * Fertility	1	0.29	0.5928
Species * C Supply * Fertility	1	4.60	0.0337
Light * C Supply * Fertility	1	1.87	0.1738
Species * Light * C Supply * Fertility	1	0.24	0.6215

Shoot length in *Hydrilla* (Table A2) was significantly affected primarily by light level and, to a much lesser extent, by C supply. Shoot length in *Hydrilla* was not affected by fertility (Table A2). Unlike total biomass, which increased with increasing light, shoot length in *Hydrilla* decreased with increasing light. The shoot length response (increase) to C supply in *Hydrilla* occurred only under low light conditions (Table A4).

Leaf length in *Vallisneria* (Table A3) was also significantly affected primarily by light level. Like shoot length in *Hydrilla*, leaf length in *Vallisneria* also decreased with increasing light (Table A3). The significant light*fertility interaction complicates further interpretation of the main effects. In contrast with the shoot length response of *Hydrilla*, leaf length increased in *Vallisneria* in response to fertility, not C supply, and only under the higher light level (Table A4).

With respect to shoot density in *Hydrilla* (Table A2), all three main effects (light, fertility, and C supply) were significant, as was a light*C supply interaction. Like total biomass, shoot density increased with increased light. Under low light conditions, shoot density in *Hydrilla* significantly increased in response to increased fertility, but not to increased C supply (Table A4). Under the higher light conditions, shoot density significantly increased with increases in either fertility or C supply.

In *Vallisneria*, plant density significantly increased with increasing light, decreased with increasing fertility, and was unaffected by C supply (Table A3).

The decrease in plant density in *Vallisneria* with increasing fertility occurred under both light levels, but was more pronounced under the higher level (Table A4). The density decrease in response to increased fertility in *Vallisneria* is opposite to the density increase observed in *Hydrilla*.

Table A2
Three-Way ANOVA for Total Biomass Production, Shoot Length, and Shoot Density in *Hydrilla* Growing Monospecifically

Parameter	Source	DF	F Value	Probability
Total Biomass	Light	1	254.17	0.0001
	C Supply	1	62.60	0.0001
	Fertility	1	8.80	0.0041
	Light * C Supply	1	32.27	0.0001
	Light * Fertility	1	14.73	0.0003
	C Supply * Fertility	1	0.19	0.6622
	Light * C Supply * Fertility	1	0.28	0.6006
Shoot Length	Light	1	19.99	0.0001
	C Supply	1	5.50	0.0219
	Fertility	1	0.53	0.4707
	Light * C Supply	1	2.51	0.1178
	Light * Fertility	1	1.07	0.3045
	C Supply * Fertility	1	0.64	0.4268
	Light * C Supply * Fertility	1	0.06	0.8135
Shoot Density	Light	1	41.47	0.0001
	C Supply	1	8.25	0.0054
	Fertility	1	13.53	0.0005
	Light * C Supply	1	5.47	0.0222
	Light * Fertility	1	2.63	0.1091
	C Supply * Fertility	1	0.02	0.8951
	Light * C Supply * Fertility	1	0.55	0.4592

Table A3
Three-Way ANOVA for Total Biomass Production, Shoot Length, and Shoot Density in *Vallisneria* Growing Monospecifically

Parameter	Source	DF	F Value	Probability
Total Biomass	Light	1	199.26	0.0001
	C Supply	1	13.94	0.0004
	Fertility	1	144.13	0.0001
	Light * C Supply	1	0.77	0.3845
	Light * Fertility	1	39.67	0.0001
	C Supply * Fertility	1	18.36	0.0001
	Light * C Supply * Fertility	1	2.51	0.1175
Shoot Length	Light	1	154.56	0.0001
	C Supply	1	5.46	0.0222
	Fertility	1	14.69	0.0003
	Light * C Supply	1	0.03	0.8522
	Light * Fertility	1	23.63	0.0001
	C Supply * Fertility	1	1.26	0.2657
	Light * C Supply * Fertility	1	0.08	0.7800
Shoot Density	Light	1	74.91	0.0001
	C Supply	1	3.14	0.0807
	Fertility	1	37.51	0.0001
	Light * C Supply	1	0.58	0.4502
	Light * Fertility	1	1.13	0.2914
	C Supply * Fertility	1	0.31	0.5794
	Light * C Supply * Fertility	1	4.31	0.0415

Table A4
Two-Way ANOVA for Total Biomass Production, Shoot Length, and Shoot Density in *Hydrilla* and *Vallisneria* Growing Monospecifically

Species	Light	Parameter					
		Total Biomass		Shoot Length		Shoot Density	
Source		F	Probability	F	Probability	F	Probability
Hydrilla	**Low Light**						
C Supply		4.14	0.0494	4.27	0.0461	0.37	0.5461
Fertility		0.53	0.4730	0.85	0.3633	4.67	0.0375
C Supply * Fertility		0.01	0.9438	0.30	0.5874	0.37	0.5461
Hydrilla	**High Light**						
C Supply		67.67	0.0001	1.87	0.1803	8.76	0.0056
Fertility		17.02	0.0002	0.41	0.5259	9.00	0.0050
C Supply * Fertility		0.34	0.5626	1.11	0.2985	0.25	0.6180
Vallisneria	**Low Light**						
C Supply		5.63	0.0232	2.04	0.1615	0.51	0.4787
Fertility		22.41	0.0001	0.34	0.5640	12.8	0.0010
C Supply * Fertility		5.02	0.0314	0.23	0.6366	3.46	0.0709
Vallisneria	**High Light**						
C Supply		8.34	0.0065	5.24	0.0281	3.20	0.0820
Fertility		131.5	0.0001	35.6	0.0001	25.8	0.0001
C Supply * Fertility		13.52	0.0008	2.23	0.1443	1.15	0.2902

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13. ABSTRACT *(Maximum 200 words)*

The report describes results of a greenhouse investigation of short-term (8 weeks duration) competition between the beneficial native plant *Vallisneria americana* and the introduced, problem plant *Hydrilla verticillata*. Competitive interactions were evaluated in a factorial arrangement of two levels of each of three environmental factors—light, sediment fertility, and inorganic carbon supply. Plants of each species were grown alone and in 50:50 mixtures under each of the eight different environmental treatment combinations.

When grown alone, the two species generally produced comparable levels of biomass; however, allocation of this biomass differed substantially. *Hydrilla* produced a dense canopy of leafy shoots at the water surface and was more effective at light capture than *Vallisneria*, which distributed its biomass more uniformly throughout the water column. *Vallisneria* allocated a greater proportion of biomass to belowground portions of the plant than did *Hydrilla*. Both species exerted high demands for dissolved inorganic carbon.

In keeping with patterns of biomass allocation, the growth of *Hydrilla* was, overall, limited primarily by light, while that of *Vallisneria* was more limited by sediment fertility (nitrogen availability).

(Continued)

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When the two species were grown together, the outcome of competition depended on the level of the different environmental factors. When the plants competed on the lower fertility sediments, *Hydrilla* generally dominated the mixtures. At the higher fertility level, *Vallisneria* was dominant. The competitive abilities of each of the species generally increased when provided with the higher level of the resource that most limited its growth in monocultures. Of the three resources evaluated, sediment fertility (N availability) was the most important in affecting the outcome of competition.

When provided with adequate sediment N, *Vallisneria* proved to be quite competitive and suppressed the growth of *Hydrilla*. The two species exhibit different growth strategies that are correlated with their resource requirements. *Hydrilla* tolerates low nutrient environments and exploits higher light environments by allocating most of its biomass (>90 percent) to shoots, producing a dense canopy at the water surface where light is most plentiful. *Vallisneria* tolerates low light environments and exploits high sediment fertility by allocating much of its biomass (40 to 50 percent) belowground to support acquisition and storage of sediment N. *Vallisneria* has the characteristics of a higher successional species, while *Hydrilla* is more of a pioneer, or colonizing species. In the absence of disturbance, *Vallisneria* should be able to resist invasion by *Hydrilla*.