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The Influence of Field Site and Natural Sediments on the Growth and Tissue Chemistry of *Vallisneria americana* Michx.

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ABSTRACT

Rosettes of Vallisneria americana were transplanted into three upstate New York lakes, all on the same fertile lake sediment, at depths which received approximately the same quantum flux density. The lakes varied in pH and dissolved inorganic carbon (DIC) concentrations. In two of the lakes, Vallisneria was also planted on native sediment.

After ten weeks, dry matter accumulation for plants grown on the fertile sediment was approximately six-fold greater in the high pH, high DIC site, but concentrations of nitrogen (N), phosphorus (P), and potassium (K) were much lower in shoots of these plants. Greater DIC availability appears to have led to more rapid biomass gain, and effectively diluted the mineral nutrients in plant tissues. The highly significant site effect also led to greater total N, P, and K content in shoots in the high DIC site.

Sediment source had a significant effect in one of two cases. Growth was reduced ca. 60% on the sediment with the lowest pore water ammonium and soluble reactive phosphate concentrations, the lowest bulk density, and the highest organic content. Collectively these traits suggest that limited nutrient availability may have accounted for reduced growth. In contrast to trends observed among sites, smaller plants had significantly lower shoot concentrations of N and P, and no difference in K concentration occurred.

Both site and sediment effects were important regulators of biomass and nutrient accumulation by Vallisneria americana under natural conditions, but site effects -- probably attributable to differences in DIC availability -- had a greater impact in this study.

INTRODUCTION

Long-standing interest in the relative importance of sediment and lake water to submersed aquatic macrophytes has provoked studies with three foci: (1) determining sources of mineral nutrients (Carignan and Kalff 1980, Huebert and Gorham 1983), (2) correlating sediment and lake water characteristics with macrophyte distribution (Moyle 1945, Spence 1967), and (3) testing sediment and lake water influences on macrophyte growth (Barko 1982, Barko and Smart 1986). Most recent experimental work on macrophyte growth has been carried out under lab conditions (Barko 1983) or with a single sediment modified by the addition of sand (Chambers and Kalff 1985, 1987) or fertilizer (Anderson and Kalff 1986). We have taken an experimental approach addressing the importance of different naturally occurring sediments and selected differences in water chemistry in situ.

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Our greenhouse investigations have shown that two related aspects of water chemistry, pH and dissolved inorganic carbon (DIC) availability, may have a profound effect on the growth and reproduction, as well as tissue chemistry, of Vallisneria americana (Grisé et al. 1986, Titus et al. 1990). Several investigators have used nutrient analysis to gain insight into growth differences that appear among treatments (Grisé et al. 1986, Barko and Smart 1986, Barko et al. 1988). In order to test the effects of pH/DIC regimes on macrophyte growth and tissue chemistry in situ, we transplanted Vallisneria americana into four lakes of differing initial pH on a sediment that had supported robust growth in previous greenhouse experiments and in the field. In two of the lakes we also used native sediments to investigate the influence of different naturally occurring sediments.

Our data suggest that certain aspects of lake waters, such as carbon availability, may rival sediment type as an important influence on growth and nutrition, and that there are alternate interpretations of low tissue nutrient levels.

METHODS AND MATERIALS

Species and Study Sites

Vallisneria americana Michx. (Hydrocharitaceae; hereafter Vallisneria), wild celery, occurs in a variety of lacustrine and riverine habitats, although it is rarely found at low pH (Crow and Hellquist 1982, Yan et al. 1985).

Otsego Lake (Otsego County, New York) is an alkaline lake that supports the growth of 35 macrophyte species including Vallisneria (Harman & Sohacki 1980). Pickerel Pond (Broome County, New York), in which Vallisneria also occurs with several Potamogeton spp. and Najas flexilis, has lightly stained water and unconsolidated, organic sediment. Orchard Lake (Sullivan County, New York) has lightly stained water and firm, mineral sediment. Several Potamogeton spp. occur near the study site, but we have not found Vallisneria in this lake. These sites were originally selected on the basis of their differing pH values: Otsego was ca. pH 8.0 (Harman and Sohacki 1980), Pickerel was ca. pH 7.0 (O'Brien 1982), and Orchard was ca. pH 6.0 in the spring of 1983. A fourth site at pH 4.6 was initially included, but Vallisneria transplanted there disappeared completely within 23 days. Subsequent tests with protected plants implicated vertebrate herbivory. However, plants in the other lakes showed little observable grazing damage.

Penetration of photosynthetically active radiation (PAR) was determined in each of the sites with a LI-COR LI-185A meter equipped with a LI-192S underwater quantum sensor before the experiments began. Temperature and pH were monitored intermittently with a YSI telethermometer and Orion 407A field pH meter, respectively. Alkalinity was determined by titration to the bromcresol green/methyl red endpoint (ca. pH 4.6). Pertinent characteristics of each lake are summarized in Table 1. The pH differences initially noted between Orchard Lake and Pickerel Pond did not persist through the growing season.

Experimental procedures

Vallisneria rosettes, 8-15 cm tall, were collected on 24 June 1983 from Otsego Lake. They were randomly assigned to 19 cm diameter plastic pots and placed in the experimental lakes. On 29 June, 12 pots with two rosettes each in Otsego sediment were placed into Otsego Lake. The experiments in the other two lakes commenced 30 June (Pickerel) and 1 July (Orchard) in which 12 pots of rosettes in Otsego sediment and 12 in native sediment were placed in each lake. Pots were attached in pairs to flats which were placed 3-4 cm apart. At each site plants were placed at the depth that received 30-35% of subsurface PAR (Table 1).

Table 1. Selected characteristics of Otsego Lake (OT), Orchard Lake (OR), and Pickerel Pond (P).

site	latitude	longitude	planting depth (m)[a]	pH	alkalinity (meq liter^{-1})	DIC (mgCO_2 liter^{-1})[b]
OT	42°42'	74°55'	2.3	7.6	2.0	96
OR	41°57'	74°45'	1.5	6.4	0.22	22
P	42°11'	75°36'	1.7	6.4	0.24	21

[a] depth of penetration of 30-35% subsurface PAR in spring
[b] calculated from summer pH, alkalinity and temperature data using equilibrium constants of Harned and Davies (1943) and Scholes (1941)

To ensure minimal loss of material to senescence, pots were harvested after 72 days in the field in the following manner: leaves, stolons, and winter buds were collected from each pot, and stolons and leaves were combined (and are hereafter referred to as shoots). Buds and shoots were weighed after being oven-dried at 75°C to constant mass. All the dried shoot material for each plant was then ground to powder in a Wiley Mill, except that the smallest plants were ground with a mortar and pestle in liquid nitrogen to minimize loss of material. Powdered samples were digested in a mixture of sulfuric acid and hydrogen peroxide (Allen et al. 1974). Nitrogen was measured by a phenolhypochloric method (Solorzano 1969, Harwood and Kuhn 1970) and total phosphorus was determined by an ascorbic acid method (Murphy and Riley 1962). Potassium was determined by flame photometry (Model #143, Instrumentation Laboratory, Inc., Lexington, MA). All methods were verified by measuring nitrogen, phosphorus, and potassium in digested certified National Bureau of Standards orchard leaves #1571. Total shoot dry mass, as well as percent and total N, P, and K, were calculated for each pot.

These data actually represent two experiments. In the first experiment the independent variable is site with all plants grown on Otsego sediment in order to test site effects. A one-way ANOVA and the Tukey-Kramer procedure were performed. The second experiment consisted of two within lake comparisons of native sediment (Orchard or Pickerel) vs. Otsego sediment. A one-way ANOVA was conducted for each lake. All statistical analyses were performed using SAS (SAS Institute 1985).

Sediments were analyzed for bulk density and loss on ignition (Allen et al. 1974). Sediment pore water chemistry was examined by modifying Hesslein's (1976) method to use plastic centrifuge tubes (M. Mitchell, pers. comm.). Tubes with Gelman Versapor-200 membrane sealed to the sides were filled with deoxygenated distilled water, capped with serum septa, maintained in water bubbled with nitrogen overnight, and placed 5 cm deep in sediment. Pots were placed beneath the water surface in temperature-controlled fiberglass tanks for six weeks. Water samples were then removed from the tubes, filtered, and analyzed for soluble reactive phosphate using Murphy and Riley's (1962) method and for NH_4^+ using a salicylic acid method (Havilah et al. 1977).

RESULTS AND DISCUSSION

Site Effects

Plants grown in Otsego Lake accumulated far greater dry mass than those in Orchard or Pickerel, which produced only 19% and 15%, respectively, of the dry mass of Otsego plants (Fig. 1). The overall trend was highly significant ($p<0.001$) according to one-way ANOVA, although dry mass did not differ significantly between Orchard and Pickerel plants. Interestingly, the large Otsego plants contained the lowest concentration of each nutrient examined, while the smaller Pickerel Pond plants contained the highest (Fig. 2 a-c). This trend was highly significant ($p<0.001$; one-way ANOVA) for all three nutrients, and each mean differed significantly ($p<0.05$; Tukey-Kramer procedure) from the other two. In contrast, the total N and P content, based on multiplying nutrient concentration by shoot dry mass, was highest for plants grown in Otsego, and not significantly different for those from Orchard and Pickerel (Fig. 3b). Total K content was not significantly different among treatments (Fig. 3c).

These data indicate that site conditions can have a marked effect on growth and tissue nutrient concentrations. As all plants were grown on the same sediment, one must attribute differences in growth to other physical or chemical aspects of each lake and its water. Two physical factors which may influence macrophyte growth are light and temperature (Barko and Smart 1981, Barko et al. 1982). While not monitored extensively, summer temperatures in Otsego and Orchard Lakes were similar. Pickerel Pond, the smallest of the three lakes, was as much as 4-5°C warmer than the other lakes. One would expect such an increase to lead to greater Vallisneria dry mass (Titus and Adams 1979, Barko et al. 1982), yet the Pickerel plants were the smallest (Fig. 1). Light levels may have a variable effect on Vallisneria depending on

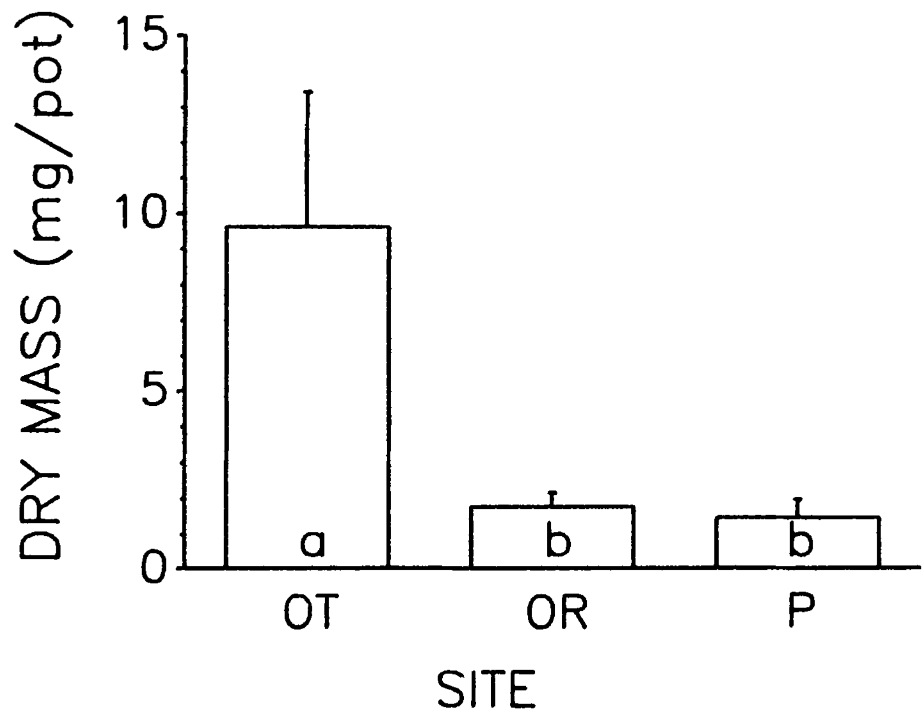

Figure 1. Shoot dry mass per pot (two plants each) for Vallisneria grown on Otsego sediment in three sites: Otsego (OT), Orchard (OR), and Pickerel (P). Means (shown with standard deviations) with different lowercase letters differ significantly ($p<0.05$) according to Tukey-Kramer procedure.

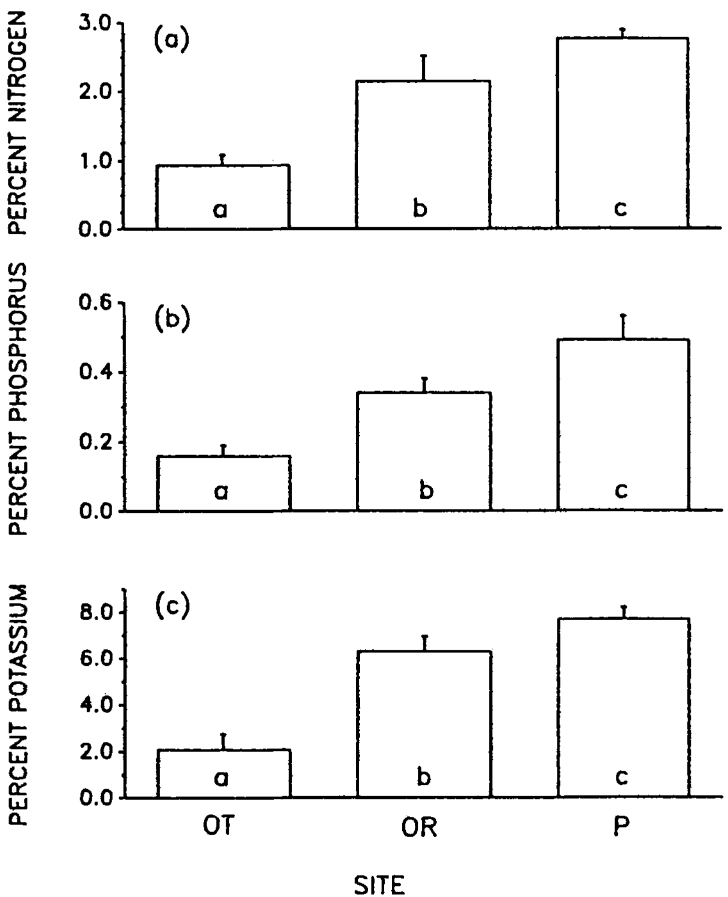

Figure 2. Tissue nutrients for shoots of Vallisneria grown on Otsego sediment in three sites (see Fig. 1 caption). (a-c): tissue concentrations of nitrogen (N), phosphorus (P), and potassium (K).

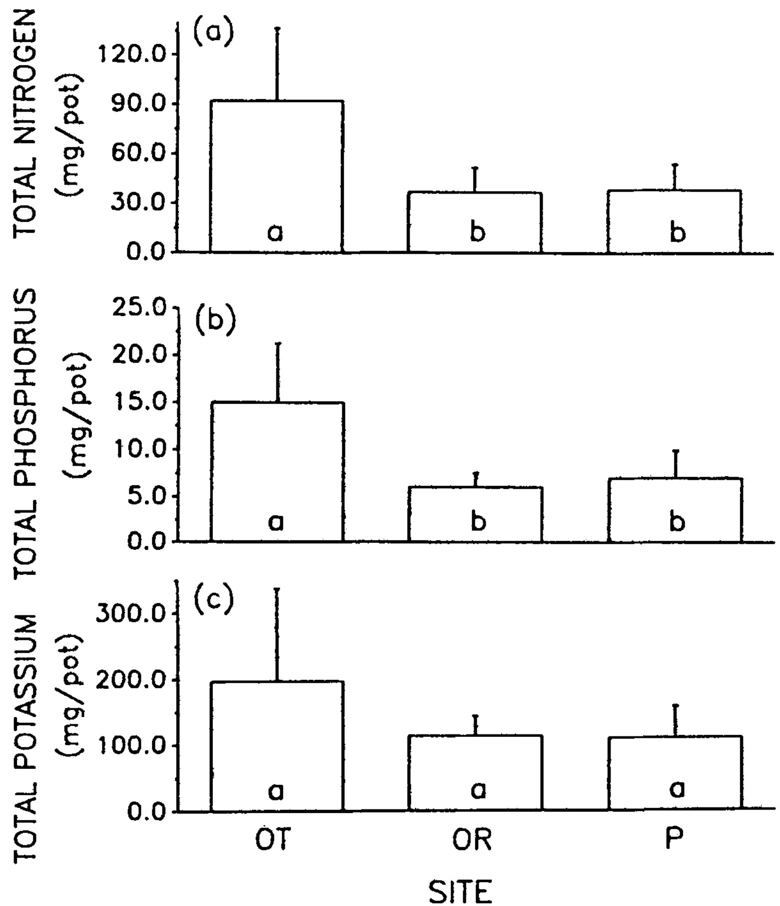

Figure 3. Tissue nutrients for shoots of Vallisneria grown on Otsego sediment in three sites (see Fig. 1 caption). (a-c): total content of N, P, and K per pot.

temperature (Barko et al. 1982); however, pots were placed at a different depth in each lake in order to obtain a similar fraction of subsurface PAR. Therefore, although they could not be controlled, differences in temperature and light do not appear to account for observed biomass differences.

One of the chemical features that differs among these lakes, and is known to influence both growth and tissue chemistry of Vallisneria, is pH (Grisé et al. 1986). Although the pH of Orchard and Pickerel was similar (low to mid 6's), it was lower than the pH of Otsego (mid 7's). This difference has been shown to cause substantial differences in growth (Grisé et al. 1986), although it may more likely be an effect of changing DIC availability than of pH per se (Titus et al. 1990).

An explanation consistent with our data is that differences in DIC availability may have altered biomass accumulation. Wetzel and Grace (1983) have argued that DIC availability can limit macrophyte growth; Hough and Fornwall (1988) and Hough et al. (1989) showed evidence that it is a major influence on macrophyte distribution. Titus and Stone (1982), Roelofs et al. (1984) and Wetzel et al. (1985) measured pronounced photosynthetic responses of submersed species to changes in DIC availability, and Titus et al. (1990) demonstrated a marked growth increase of Vallisneria on Otsego sediment with CO_2 enrichment in a controlled greenhouse experiment.

Table 1 shows that DIC concentration was 4-5 times greater in Otsego Lake than in Orchard or Pickerel. Otsego plants accumulated 5.4 times more shoot dry matter than Orchard plants and 6.5 times more than Pickerel plants. If DIC availability accounts for the sharply reduced plant growth in Orchard and Pickerel relative to Otsego, it may also explain the substantially lower tissue concentrations of N, P, and K in Otsego plants (Fig. 2 a-c); the relative ease of acquiring carbon in Otsego may have effectively diluted these mineral nutrients.

Whether greater DIC availability or some other site influence led to greater biomass accumulation in Otsego plants, it also led to greater nutrient accumulation in Vallisneria shoots there (Fig. 3 a-c). If these nutrients are derived primarily from the sediment (e.g., Carignan and Kalff 1980), the more favorable growth conditions of Otsego Lake resulted in greater mobilization of sediment nutrients into macrophyte shoots.

Sediment effects

Plants grown in Pickerel Pond showed more than twice as much dry matter accumulation (Fig. 4), higher N and P concentrations (Fig. 5 a,b), and greater total nutrient content (Fig. 6 a-c) on Otsego than on Pickerel sediment. These results clearly indicate that naturally occurring variations in sediment quality substantially influence Vallisneria growth. Thus, in a general way our findings provide a confirmation in situ of the extensive laboratory investigations of Barko and colleagues (e.g. Barko 1983, Barko and Smart 1986).

While the use of naturally occurring sediments allows the testing of ecologically meaningful variations in sediment quality, exactly which physical or chemical sediment traits cause differential growth may be difficult to determine with this approach. Pickerel sediment had significantly lower values for pore water ammonium and soluble reactive phosphate (SRP) concentrations than did Otsego sediment, and also had lower bulk density and greater loss on ignition (Table 2). Low bulk density and high organic content may limit macrophyte growth (Barko and Smart 1986). The sediment characteristics, coupled with the significantly lower tissue N and P concentrations (Fig. 5 a,b), suggest the possibility of N or P limitation of Vallisneria growth on Pickerel sediment.

Whatever the specific cause(s) of reduced growth on Pickerel sediment, we believe a different phenomenon accounts for differences in tissue chemistry than was noted among the sites. Plants grew side by side in the same lake,

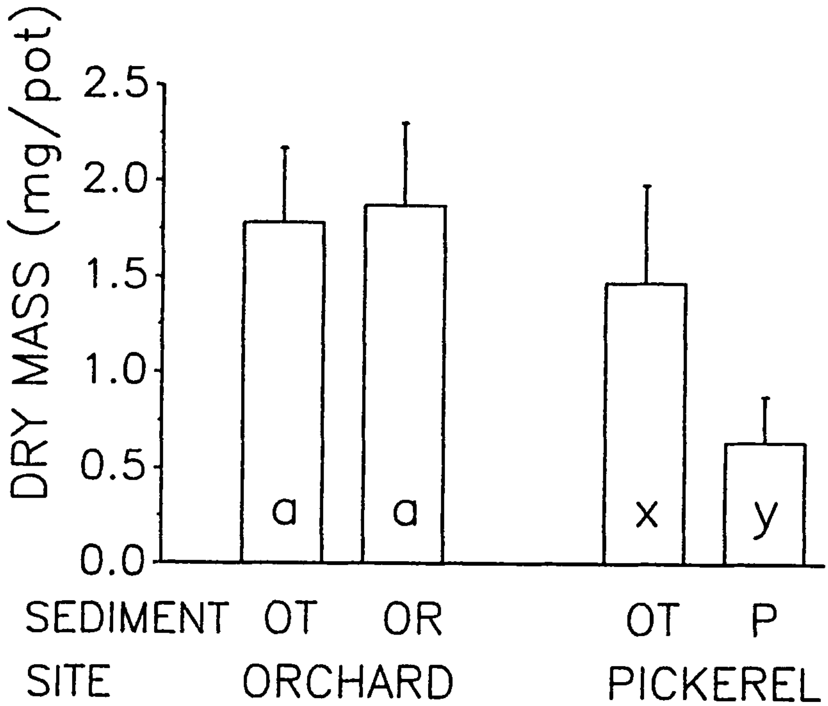

Figure 4. Shoot dry mass per pot for Vallisneria grown on Otsego (OT) or native sediment in two sites: Orchard (OR) and Pickerel (P). Means (with standard errors) with different lowercase letters within each site differ significantly ($p<0.05$; t-test).

Table 2. Selected characteristics of sediments from the three sites. Means with standard deviations shown for pore water concentrations of ammonium and soluble reactive phosphate (SRP). Values in each column with different lowercase letters differ highly significantly ($p<0.01$; Duncan's multiple range test).

sediment	$[NH_4^+]$ (mg liter^{-1})	[SRP] (µg liter^{-1})	bulk density (g ml^{-1})	loss on ignition (%)
OT	10.4±1.4 a	1290±70 a	844-1043	5
OR	4.6±0.7 b	160±20 b	248-258	26
P	0.8±0.1 c	130±40 b	142-158	36

and thus growth dilution due to greater DIC availability could not account for lower tissue nutrient concentrations. Indeed, these plants showed a pattern opposite to that noted above; the smaller plants had the lower tissue N and P levels. Further, these plants do not differ in tissue K concentration (Fig. 5c), which is consistent with Barko's (1982) finding that K nutrition is determined more by water than sediment chemistry.

Plants grown in Orchard Lake on Otsego and Orchard sediments showed

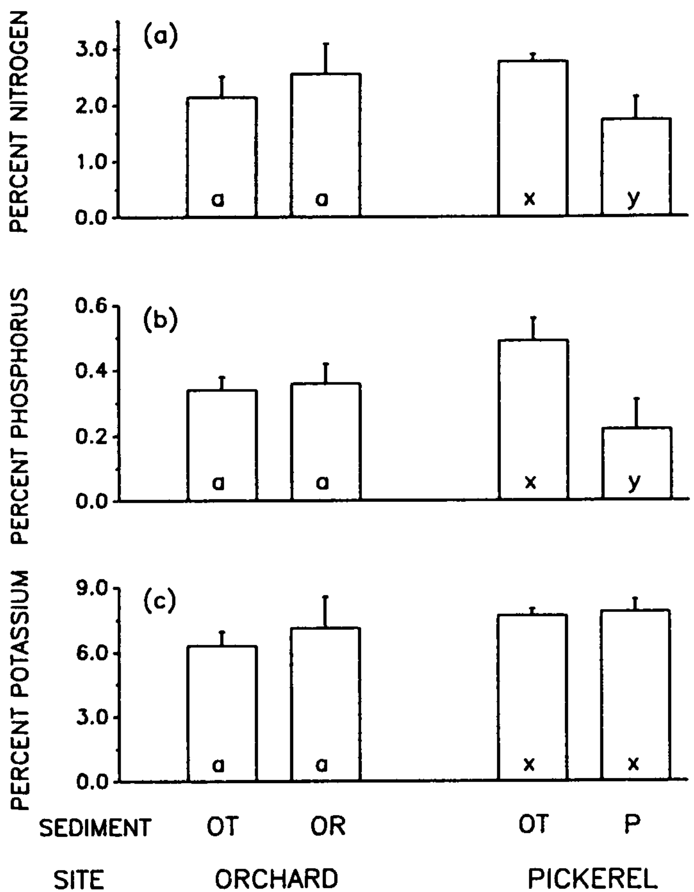

Figure 5. Tissue nutrients for shoots of Vallisneria grown on Otsego (OT) or native sediment in Orchard (OR) and Pickerel (P) (see Fig. 4 caption). (a-c): tissue concentrations of N, P, and K.

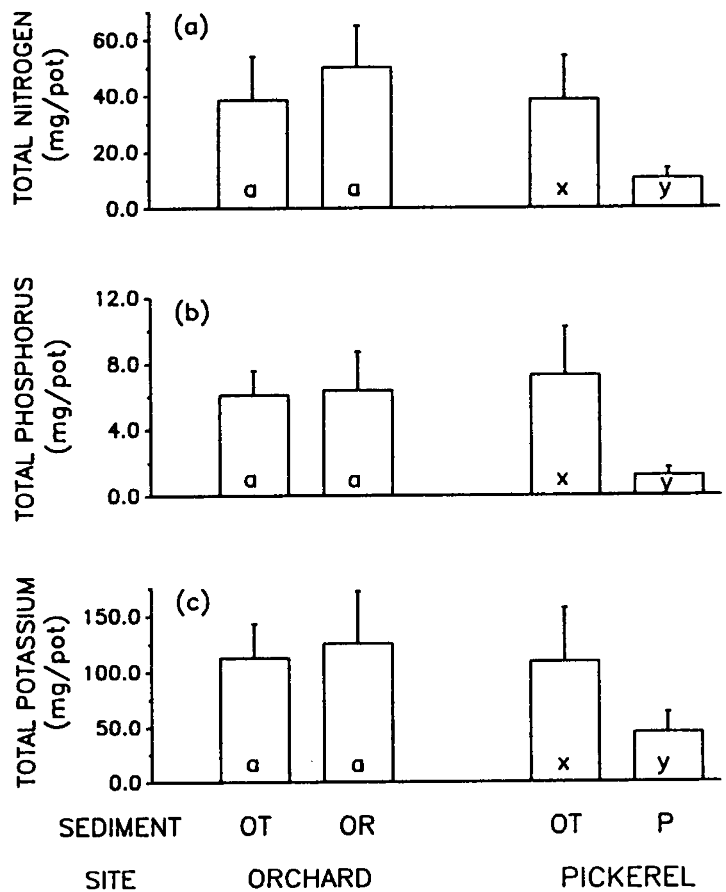

Figure 6. Tissue nutrients for shoots of Vallisneria grown on Otsego (OT) or native sediment in Orchard (OR) and Pickerel (P) (see Fig. 4 caption). (a-c): total content of N, P, and K per pot.

no significant differences in dry matter accumulation (Fig. 4), nutrient concentrations in shoots (Fig. 5 a-c), or total nutrient content (Fig. 6 a-c). These findings indicate that Otsego and Orchard sediments are comparable in supplying nutrients for growth, a result not easily reconciled with sediment characteristics (Table 2): Orchard sediment had significantly lower pore water ammonia and SRP concentrations. Bulk density was also lower and organic content higher for Orchard. These latter two features suggest that Orchard sediment may be less suitable for macrophyte growth than Otsego sediment (cf. Barko and Smart 1986); however, the rate of nutrient supply from these two sediments was evidently quite similar. Perhaps in a system with limited DIC availability, such as Orchard Lake, the supply of mineral nutrients in Orchard sediment is not depleted because plants grow slowly enough to preclude mineral nutrient limitation.

We conclude, as did Barko (1983) for lab-grown plants, that both site and sediment features are important determinants of submersed macrophyte growth in situ, although site effects were more pronounced in this study. Very few experimental studies using different naturally occurring sediments exist to test the relative importance of site and sediment in situ. We suggest that differing DIC availabilities may have played an important role as a "site effect," and contrasts in mineral nutrient availability may have been a key "sediment effect." Both site and sediment clearly influence dry matter and mineral nutrient accumulation.

The nutrient analysis results of both experiments also highlight the difficulties in interpreting tissue nutrient data. In the site experiment the most robust plants--those grown in Otsego Lake--had the lowest nutrient levels. We interpret this as an indication of growth dilution: the rate of mineral nutrient supply did not keep up with the relatively high rate of biomass accumulation. However, in Pickerel Pond the lower P and N concentrations in the smaller plants are interpreted as an indication of potential growth limitation by these nutrients. Therefore, low nutrient concentrations in plants may suggest different plant/environment relationships in different circumstances, and care must be taken in their interpretation.

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