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TEMPERATURE-DRIVEN VARIATION IN SUBSTRATE OXYGENATION AND THE BALANCE OF COMPETITION AND FACILITATION¹

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Abstract. Emergent wetland plants often alleviate the effects of anaerobic soils on root respiration by passively transporting oxygen belowground through continuous air spaces (aerenchyma) in leaves and roots. Oxygen leaked from the roots into the rhizosphere may oxidize minerals in the soil or become available to other plants. Some spatial patterns in marsh plant communities suggest interspecific facilitative interactions, but there is little experimental evidence for interplant facilitation via soil oxygenation. We investigated the capability of the widespread, highly aerenchymous wetland plant, *Typha latifolia*, to aerate sediments and affect the growth of two non-aerenchymous neighbors, *Salix exigua* and *Myosotis laxa*, both in greenhouse experiments and in a natural pothole pond in western Montana. At soil temperatures of 11°–12°C in the greenhouse, mean dissolved oxygen (DO) ranged from 2.75 ± 0.41 to 4.43 ± 1.11 mg/L (mean $\pm$ 1 SE) in pots with *Typha*, whereas in pots without *Typha* DO content ranged from 0.40 ± 0.06 to 0.65 ± 0.06 mg/L. At soil temperatures of 18°–20°C, DO in the *Typha* treatment was lower than in the low-temperature experiment and did not differ significantly from DO in the pots without *Typha*. At substrate temperatures of 11°–12°C, all rooted *Salix* cuttings survived when planted with *Typha*, whereas none survived when planted alone. At the same substrate temperature, *Myosotis* transplants grew significantly larger when planted with *Typha* than when alone, also indicating that facilitation occurred. When grown with *Typha* at soil temperatures of 18°–20°C, however, *Myosotis* root mass was significantly less than when grown alone, suggesting that competition occurred. At the pond margins where *Typha* and *Myosotis* coexist in water-saturated soils, naturally occurring *Myosotis* plants adjacent to transplanted *Typha* had significantly larger shoot and fruit mass than did control *Myosotis* without nearby *Typha*. In this experiment DO levels in soil water and available soil nitrogen did not differ among treatments. These experiments indicate that aerenchymous wetland plants have the potential to facilitate neighbors via soil oxygenation, and that facilitation and competition may shift in importance with changes in the physical environment.

Key words: aerenchyma; cattails; competition; facilitation; interference; nitrogen; oxygen; roots; soil temperature; *Typha*; Montana; wetlands.

INTRODUCTION

Interference among emergent freshwater plants has been well documented with experimental manipulations in natural environments (Grace and Wetzel 1981, Grace 1987, 1988, Gopal and Goel 1993). Light and nitrogen have been identified as primary limiting resources, but substrate oxygen may also limit plant growth in wetlands (Drew 1983). To alleviate oxygen limitation in their roots, many wetland emergent plants passively transport oxygen from leaves to roots through aerenchymous tissue (Armstrong 1964, 1979). In some cases oxygen may leak out of submerged roots and oxidize toxic substances and nutrients in the rhizosphere and oxygenate marsh sediments (Green and Etherington 1977, Carlson and Forrest 1982, Howes et al. 1981, Dunbabin et al. 1988, Armstrong et al. 1992) although the extent and importance of rhizosphere oxidation is controversial (Morris and Dacey 1984, Brix 1988, Bedford et al. 1991). Schat and Van Beckhoven

(1991) reported that *Plantago coronopus* and *Samolus valerandi* were tightly clumped around tussocks of the aerenchymous *Juncus maritimus* in dune slacks on the coast of Holland, where survival rates appeared to be enhanced by soil oxygenation and oxidation of iron, manganese, and sulfide. These, and similar spatial patterns in saltmarshes (Castellanos et al. 1994, Bertness and Yeh 1994), and bogs (Berendse and Aerts 1984), and field experiments conducted by Hacker and Bertness (1995) in saltmarshes suggest that positive interactions involving transported oxygen may occur between highly aerenchymous and less-aerenchymous plants.

We studied facilitation and rhizosphere oxidation in a “pothole” pond in the Swan Valley of western Montana. These glacially derived ponds support a diverse array of emergent macrophytes, including the highly aerenchymous *Typha latifolia* L. (cattail). *Typha latifolia* occurs in dense, virtually monospecific stands in deep water, and in diverse stands in shallow water at the pond margins, which include species that are much less aerenchymous. Although facilitation has been studied experimentally in many natural systems and

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operates via many mechanisms (Attsat and O'Dowd 1976, Hunter and Aarssen 1990, Callaway 1992, 1994, 1995, Bertness and Shumway 1993, Bertness and Callaway 1994), facilitation via soil aeration has never been experimentally studied in natural freshwater systems. Here we focus on the following questions: (1) Does *Typha* oxygenate sediments in which it grows? (2) Does *Typha* facilitate less aerenchymous neighbors? and (3) Do facilitative effects change with variation in the physical environment? We pursued answers to these questions by conducting experiments both in the field and in the greenhouse.

STUDY AREA

We conducted field experiments and collected plants for greenhouse experiments from a single pond in the Swan Valley, Montana (47°44' N, 113°48' W, 950 m elevation). *Typha latifolia* is widely distributed throughout North America and has exceptionally aerenchymous shoots and roots. The effects of *Typha* were tested on *Salix exigua* Nutt. (narrow-leaved willow) and *Myosotis laxa* Lehm. (small-flowered forget-me-not). *Salix exigua* is commonly found at the upper edges of wetlands and riparian zones in western Montana and has completely woody, nonaerenchymous stems. *Myosotis* stems have a small central air chamber, but the leaves are not aerenchymous. *Myosotis* typically is found intermixed with *Typha* lower on the pond margins, and *S. exigua* often grows at the upper edge of the *Typha*-dominated vegetation.

METHODS

In September, 1993, mature *Typha* individuals were transplanted from the pond into 2.25-L undrained plastic pots. Soil in the pots consisted of 80% natural pond soil and 20% peat. The soil mixture was also placed in 2.25-L undrained pots without cattails. Distilled water was added as required to maintain a depth of 1–2 cm above the soil surface. Algae were controlled with copper sulfate added in equal amounts to all pots in both treatments. Experiments were conducted at two different soil temperatures. The pots were kept in wading pools through which tap water continually flowed in order to maintain cool soil temperatures (range during experiment was 11°–12°C). Water from the wading pools was not allowed to flow into the pots. For the high soil temperature experiment, flow was cut off and standing water was left in the pools to buffer daily fluctuations in temperature (which ranged from 18° to 20°C during the experiment) in the 2.5-L pots. A 70-d establishment and acclimation period and the experiments were conducted under a combination of natural and supplemental high-pressure sodium light (photon flux density $\approx 500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) set for a 12:12 light:dark photoperiod. Midday air temperature in the greenhouse ranged from 18° to 22°C in both high and low substrate temperature experiments.

Dissolved oxygen (DO) was measured between 0800

and 1000 on all days, with a Cole-Parmer Model 5513-55 meter. The probes cannot be pushed directly into soil so DO was measured in water that percolated into perforated plastic tubes pushed into the waterlogged soil and left at permanent locations in the pots. Tubes were located midway between the *Typha* shoot and the edge of the pot and DO was measured at a depth of 12 cm. Calibrations were performed at the temperatures of the experiment. DO was measured while the probe was gently agitated and after the readout had stabilized. A single *Typha* root-rhizome mass was transplanted to each of 16 randomly selected pots, and 8 control pots were established without *Typha*. Following the 70-d establishment period, during which new leaves developed, DO was measured on four different days over a 9-d period. Afterwards, the flow of water through the pools was stopped and the pots were allowed to warm. Beginning 4 d later, DO was measured four times during a 7-d period.

After the completion of the preceding experiment, flow was resumed in the pools to cool the pots back to 11°–12°C and *Salix exigua* clones, prepared from cuttings of a single shrub, were planted in the treatment and control pots. These clones were also collected in September, 1993, and grown together in moist but not saturated soil during the 70-d establishment period. All clones were between 10 and 15 cm in height and produced substantial root systems during the establishment period. *Salix* clones were grown and checked for mortality over a 17-d period. A *Salix* clone was presumed dead when all leaves were either yellow or brown.

All *Salix* clones then were removed, and similarly sized *Myosotis laxa* rosettes that also had been collected in September were transplanted into the treatment and control pots. After 40 d at soil temperatures of 11°–12°C, *Myosotis* were harvested, and maximum root length was measured. Plants were divided into roots and shoots, then dried at 60°C for 5 d and weighed. Flow of the coolant water was then stopped, warming the pots to 18°–20°C, and a second cohort of *Myosotis* were planted. After 40 d these plants were harvested and measured as in the low-temperature experiment. At the times of all transplantings, soil in the control pots was similarly disturbed to control for changes due to the transplanting process. Control and treatment pots were randomly located under the lights and rotated so that *Salix* and *Myosotis* in both treatments experienced similar shade conditions.

To test the effects of rhizosphere oxidation and facilitation in the field, *Typha* transplant experiments were conducted in the summer of 1994 at the same pond in the Swan Valley from which the greenhouse plants had been collected. In June, root-rhizome balls and shoots of 20 mature *Typha* were excavated, and each was relocated 10 cm from a *Myosotis* rosette along the margin of the pond where soils were saturated but not continuously submerged throughout the summer. Twenty additional *Myosotis* rosettes that were at least

FIG. 1. Dissolved oxygen in soil water in pots with and without *Typha latifolia* when plants were grown at different substrate temperatures in greenhouse conditions. Data are means $\pm$ 2 SE. All daily comparisons showed significant differences between treatments (Student's *t* tests, n_{control} = 8 measurements, $n_{\text{treatment}}$ = 16, $P < 0.01$).

1 m away from the nearest *Typha* were marked and used for controls. All 40 *Myosotis* rosettes were initially between 5 and 8 cm in diameter.

Soil near control rosettes was excavated and refilled to simulate physical disturbance associated with transplanting. Dissolved oxygen was measured four times during the summer in perforated PVC (polyvinyl chloride plastic) tubes inserted into the soil next to each of the 40 experimental *Myosotis* plants. In late July, plant height was recorded and shoots of the 40 treatment and control *Myosotis* plants were harvested, divided into roots, shoots, and fruits, dried at 60°C for 5 d, and weighed. A single soil sample was collected at 7 cm in depth at the edge of each rosette. Available soil nitrogen (ammonium plus nitrate) were analyzed following Setaro and Jones (1989).

RESULTS

Over a 9-d period during which soil temperature was between 11° and 12°C, soil water in pots containing

Typha consistently had higher dissolved-oxygen (DO) content than in pots without *Typha* (Fig. 1). Mean soil DO values in pots with *Typha* ranged from 2.75 ± 0.41 to 4.43 ± 1.11 mg/L (mean $\pm$ 1 SE); these were significantly higher than means in pots without *Typha*, which ranged from 0.40 ± 0.06 to 0.65 ± 0.06 mg/L. In experiments conducted at soil temperatures of 18°–20°C, however, DO decreased to an overall mean of 0.78 mg/L in pots with *Typha*, which did not differ significantly on any days from DO in pots without *Typha* (Fig. 2).

All *Salix* cuttings planted with *Typha* survived for the 17-d duration of the experiment (Fig. 3). However, when planted without *Typha*, 50% were dead within 7 d and all died by the 11th day of the experiment. Experiments with *Salix* were conducted only at 11°–12°C.

At cool soil temperatures (11°–12°C), no *Myosotis* died during the 40-d experiment whether or not they were planted with *Typha*. However, final root and shoot masses of *Myosotis* that shared pots with *Typha* were two and three times larger, respectively, than those grown without *Typha* (Fig. 4A). Likewise, mean root length of *Myosotis* grown with *Typha* was significantly greater. Although comparisons were confounded by different experimental periods, DO in soil water was substantially lower in pots with *Typha* during the co-planting experiments (mean DO ranged from 1.72 ± 0.88 to 2.24 ± 0.58 mg/L on three different days) than when *Typha* was grown alone (Fig. 1), suggesting that *Salix* and *Myosotis* roots may have decreased dissolved oxygen in the pots.

In the experiment conducted at high soil temperatures (18°–20°C), *Myosotis* planted with *Typha* were generally smaller than when grown alone (Fig. 4B). Root mass of *Myosotis* in the control was significantly lower with *Typha* (Student's *t* = 2.163, $P = 0.042$)

FIG. 2. Survival of cloned cuttings of *Salix exigua* when grown with and without *Typha latifolia* at substrate temperatures of 11°–12°C under greenhouse conditions. n_{control} = 8 cuttings, $n_{\text{treatment}}$ = 8 cuttings.

FIG. 3. Growth characteristics of *Myosotis laxa* when grown for 40 d with and without *Typha latifolia* under greenhouse conditions at two different substrate temperatures. Narrow bars represent ± 2 SE, and an * designates a significant difference between treatments at $P < 0.01$ (Student's t test, $n_{\text{control}} = 8$ rosettes, $n_{\text{treatment}} = 16$ rosettes).

than when alone, but shoot length ($t = 1.748$, $P = 0.094$) and shoot mass ($t = 0.890$, $P = 0.383$) did not differ significantly between treatments.

During the field experiment at the Swan Valley pond, the mean temperatures of the soil water ranged from 11.4° to 13.2°C. Soil solution DO and available soil nitrogen did not differ significantly between treatment and control in the field experiment (Fig. 4, Table 1); however, mean shoot mass and root mass of *Myosotis* rosettes were significantly greater when growing next to transplanted *Typha* than when growing alone (Table

FIG. 4. Dissolved oxygen in soils in a pothole pond in the Swan Valley, Montana. Measurements were made in situ near *Myosotis* plants either growing adjacent to *Typha latifolia* or ≥ 1 m away from the nearest *Typha* plant. Data are means ± 2 SE. No daily comparison showed a significant difference (Student's t tests, $n_{\text{control}} = 20$ measurements, $n_{\text{treatment}} = 20$, $P > 0.05$).

1). Plant height did not differ significantly between treatments, but *Myosotis* growing next to *Typha* produced more than twice as much fruit mass as those growing alone.

DISCUSSION

Greenhouse and field experiments indicated that the highly aerenchymous *Typha* can aerate soil near its roots and improve the growth and reproductive capacity of less aerenchymous neighbors under some conditions. Our greenhouse experiments also indicate that the interaction between *Typha* and its neighbors may be highly asymmetrical (see Connell 1983) and shift between facilitation and competition as the physical environment (substrate temperature) varies. We have not, however, provided a conclusive connection between rhizosphere oxygenation and either the positive or negative effects of *Typha* on the survival, growth, and reproduction of its neighbors.

Previous studies of oxygen transport through leaves

TABLE 1. Characteristics of *Myosotis laxa* individuals grown either next to planted *Typha latifolia*, or ≥ 1 m from the closest *T. latifolia*, in field experiments in Montana. Values shown are means ± 1 SE. $n = 20$ plants.

	Treatment		<i>t</i>	<i>P</i>
	With <i>T. latifolia</i>	Without <i>T. latifolia</i>		
<i>Myosotis</i> characteristics				
Shoot mass (mg)	93.6 ± 11.1	66.5 ± 7.9	2.07	0.045
Shoot height (mm)	72.4 ± 3.9	64.9 ± 5.2	1.16	0.255
Root mass (mg)	49.1 ± 4.1	34.1 ± 3.9	2.63	0.012
Fruit mass (mg)	0.56 ± 0.06	0.20 ± 0.03	5.15	<0.001
Soil characteristics				
Nitrate ± ammonium (µg/g soil)	3.82 ± 0.37	3.16 ± 0.45	1.12	0.271

and roots into the rhizosphere have produced conflicting results. Some aerenchymous emergent wetland plants transport enough oxygen belowground to sustain aerobic root respiration and to oxidize compounds near root surfaces, as demonstrated by the reddish streaks of oxidized iron that often develop on or near roots in anaerobic sediments (Green and Etherington 1977, Gambrell and Patrick 1978, Armstrong 1979). Emergent or submerged aquatic plants may increase sediment redox potentials or oxygen concentrations in some cases (Wium-Anderson and Anderson 1972, Howes et al. 1981, Sand-Jensen et al. 1982, Sand-Jensen and Prahl 1982, Jaynes and Carpenter 1986, Armstrong et al. 1992). Conversely, others have measured substantial oxygen transport from shoots to roots, but little net change of O_2 concentration in the rhizosphere (Morris and Dacey 1984, Brix 1988, Bedford et al. 1991). This controversy is featured in a current exchange between Sorrell and Armstrong (1994) and Bedford and Bouldin (1994).

Respiration rates vary greatly with temperature, therefore differences in the temperatures at which oxygen efflux was measured may explain the differences we found for the effect of *Typha* on substrate dissolved oxygen (DO) at high and low temperature, and may account for some of the discrepancies among previous studies (see Gries et al. 1990). In our experiment, there were no significant differences between DO in *Typha* and no-*Typha* controls when pots were maintained at 18°–20°C. However, when pots were maintained at 11°–12°C, differences in DO in soil water were substantial. It is possible that increased root respiration by roots or soil microbes at higher temperatures mitigated net oxygenation, but respiration was not measured in this study. Howes and Teal (1994) found that net oxygen loss from *Spartina alterniflora* roots did not occur at ambient chamber temperatures of 25°C and 9°C, but did occur at 6°C.

There are a number of other possible reasons for contradictory results reported in the literature on rhizosphere oxygenation by aerenchymous plants. Differences may arise from the use of different techniques to measure rhizosphere oxygenation. In some studies redox potential was used to infer oxygenation. However, redox potential is influenced by many factors, and provides only a qualitative measure of dissolved oxygen in sediment pore water. Other inconsistencies may occur because some estimates of oxygen efflux were made using excised plant parts and others were based on whole-plant gas balance (see Bedford et al. 1991). Another potential (and seldom reported) cause of conflicting results in sediment oxidation studies may be due to differences in biomass allocation of the plants being tested. The rate of oxygen transport to roots and the rhizosphere is partially dependent on shoot:root ratios as large leaf areas may provide a greater surface area for photosynthetic generation or stomatal conductance of oxygen than small leaf areas. For all treatments

combined in our greenhouse study, shoot:root mass ratios of *Typha* were 0.88 ± 0.23 in the cool-temperature experiment and 0.91 ± 0.24 in the warm-temperature experiment, and not significantly different. We did, however, find that shoot:root mass ratio of *Typha* was positively correlated with soil DO content ($r = 0.77$) in the cool-temperature experiment with *Typha* alone.

Intense competition has been measured between emergent wetland species that are highly aerenchymous (Grace 1987, 1988, Gopal and Goel 1993). However, in these cases effects were tested between highly aerenchymous species, and thus these species would be less likely to compete for soil oxygen. In other studies, highly aerenchymous plants with superior abilities to transport oxygen appeared to facilitate less-aerenchymous species. Castellanos et al. (1994) reported that *Spartina maritima* aerates surface sediments in southern Spain, creating conditions favorable for the invasion of *Arthrocnemum perenne*. In eastern saltmarshes in North America, Hacker and Bertness (1995) found that the aerenchymous *Juncus maritimus* increased the redox potential in its rhizosphere, which corresponded with increased growth of *Iva frutescens*, a woody-stemmed perennial. Spatial associations of *Plantago coronopus* and *Samolus valerandi* with tussocks of the aerenchymous *Juncus maritimus* in northern Europe were attributed to soil oxygenation (Schat 1984, Schat and Van Beckhoven 1991).

Neither *Salix* nor *Myosotis* is highly aerenchymous; thus the positive effects of soil oxygenation on these species, which are unlikely to oxygenate their own roots effectively, may have been more important than any concurrent competition for nutrients or light. Such complex combinations of competitive and facilitative mechanisms have been described in oak woodlands (Callaway et al. 1991), coastal salt marshes (Bertness and Shumway 1993, Bertness and Hacker 1994, Bertness and Yeh 1994, Callaway 1994), and intertidal seaweed communities (Hay 1986). In the greenhouse, interactions between *Typha* and *Myosotis* shifted between facilitation and competition depending on the temperature of the substrate. At cool temperatures, DO in pots increased with *Typha* and *Myosotis* were larger when grown with *Typha*. At warm sediment temperatures, oxygen was not higher in pots with *Typha* than in controls, and *Myosotis* root mass was smaller when plants were grown with *Typha*. This suggests that the interactions between aerenchymous plants and their neighbors may fluctuate in nature with changes in the physical environment. However, these interpretations of the differences between the high- and low-temperature experiments should be viewed with caution because they were not conducted concurrently. Factors that may have differed between the two experiments include depletion of nutrients in the substrate, differences in *Typha* or *Myosotis* lifestages, and different oxygen solubility.

In our field experiment, the net seasonal effect of *Typha* on *Myosotis* was positive; *Myosotis* attained

greater shoot, root, and fruit mass. Even though soil temperatures in the field were comparable to those in the low-temperature, greenhouse experiment, we found no net increase of DO in the *Typha* treatments. This may have been a result of many factors: oxygen may have been taken up by the nonaerenchymous plants near the *Typha*, more oxygen may have been consumed via respiration by plant roots or soil microorganisms, or sediments in the field may have been more reducing than those used in the greenhouse. On the other hand, these results may indicate that substantial sediment oxygenation did not occur in the field and positive effects were due to other factors such as shade.

Considered together, our experiments indicated that oxygen release from roots can be an important factor in interactions among freshwater marsh plants. The apparently transient nature of this mechanism and the potential for environmental variation to shift effects from facilitation to competition add to the expanding body of literature that suggests that our understanding of species interactions cannot be based strictly on competition for limiting resources, and that complex combinations of mechanisms must be explored to fully understand species interactions in nature.

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