Photosynthesis and root growth in *Spartina alterniflora* in relation to root zone aeration

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Abstract

Spartina alterniflora Lois. is a dominant species growing in intermediate and saline marshes of the US Gulf coast and Atlantic coastal marshes. *S. alterniflora* plants were subjected to a range of soil redox potential (Eh) conditions representing a well aerated to reduced conditions in a rhizotron system under controlled environmental conditions. The low soil Eh resulted in inhibition of root elongation shortly after treatment initiation. Root elongation was reduced as soil Eh approached values below *ca.* +350 mV. Substantial decrease in root elongation was noted when soil Eh fell below +200 mV. Generally, net photosynthetic rate (P_N) decreased as soil Eh was reduced, with substantial reductions in P_N found when Eh approached negative values. Average P_N was reduced to 87, 64, and 44 % of control under +340, +245, and -180 mV treatments, respectively. The reductions in root elongation and P_N in response to low soil Eh indicated the adverse effects of low soil Eh on plant functioning and the need for periods of soil aeration that allow plants to resume normal functioning. Thus periods of drainage allowing soil aeration during the growing season appear to be critical to *S. alterniflora* by providing favorable conditions for root growth and gas exchange with important implications for plant carbon fixation.

Introduction

Soil oxygen deficiency is a prevailing edaphic factor in wetland ecosystems imposing substantial stress on plants. For instance, a close correlation between productivity of wetland macrophytes and soil oxygen availability (quantified as soil redox potential, Eh) has been found in several studies (Linthurst 1979, Pezeshki *et al.* 1989, Pezeshki

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and DeLaune 1990). The decrease in productivity has been attributed to the adverse effects of poor aeration on critical plant functions such as carbon assimilation. In addition, low soil Eh may result in substantial reductions in root growth as found for other wetland species (Pezeshki and DeLaune 1990, Pezeshki 1994, and the references therein). The decrease in root growth reduces sink size as roots are major sinks for assimilates leading to the potential for feed-back inhibition of photosynthesis (Carmi et al. 1983).

S. alterniflora Lois. is a dominant species growing in intermediate and saline marshes of the US Gulf coast and Atlantic coastal marshes. Change in productivity of this species has been attributed to many factors including soil Eh (Howes et al. 1981, DeLaune et al. 1983). Field observation from the Atlantic coastal marshes indicated that soil Eh was higher in the tall form stands than soil Eh in the short form stands of S. alterniflora (Howes et al. 1981). Similarly, sediment Eh was higher for more productive streamside S. alterniflora stands than less productive inland sites in US Gulf Coast marshes (DeLaune et al. 1983). The present study was conducted to examine root growth and gas exchange responses of S. alterniflora to low soil Eh. The specific questions asked were: What is the effects of low soil Eh on root elongation of S. alterniflora? Is there a threshold Eh at which root elongation ceases? Does such threshold correspond to the Eh level at which P_N is reduced significantly? A controlled root environment system designed to maintain a range of soil redox conditions was utilized for the experiment.

Materials and methods

S. alterniflora plants were collected from salt marshes of US Gulf coast and were transferred to a greenhouse. Newly germinated shoots and associated roots were planted in nursery pots filled with commercial potting soil (Jiffy Mix Plus, Jiffy Products of America, Chicago. U.S.A.). The pots were watered to excess and were fertilized with a commercial water-soluble plant food (23-19-17 N, P, K, respective %) once per week.

In the laboratory. twelve rhizotrons constructed of Plexiglas similar to those described in detail by Pezeshki and DeLaune (1990) were used for growing plants and control of Eh conditions. Each rhizotron had dimensions of 50.0×30.0×1.7 cm. Gas mixture entry was provided by installation of a 3 mm diameter Plexiglas tube inserted into each rhizotron and sealed at the entry. Each rhizotron contained two Eh electrodes installed at 10 and 40 cm depth, a calomel reference electrode, a gas purge valve and three holes for growing plants located at the top.

Three-week old plants uniform in size, 12.6±2.3 cm in height, were placed through holes in each rhizotron (3 plants per rhizotron). Each rhizotron was filled with Mississippi alluvial sediment and was placed at 30° angle to promote root growth at the front window. Plants were sealed into the rhizotrons using non-toxic RTV Rubber Sealant (General Electric, Waterford, New York, U.S.A.). The study comprised four treatments, three rhizotrons per treatment. Treatment I was initiated by flooding the designated rhizotrons using tap water. In other treatments, soil Eh was controlled

using different gas mixtures (*Liquid Carbonics*) entering each rhizotron to provide a range of soil Eh (Pezeshki and DeLaune 1990). Gas mixtures were air (control), N_2 (treatment *II*), and 50 cm^3 m^{-3} H_2 in N_2 (treatment *III*). The treatments imposed in the present study were designed to test plant responses under conditions where rhizosphere oxidation in immediate root zone and the associated Eh gradient is likely to occur as is the case in natural environment (treatment *I*). Other treatments simulated conditions where rhizosphere Eh gradient is minimized by continuous pressurized gas flow containing no oxygen (treatments *II* and *III*).

The environmental conditions inside the growth chamber (where rhizotrons were located) were: 25±2 °C temperature, photosynthetic photon flux density (PPFD) around 900±100 µmol m^{-2} s^{-1}, 14/10 h light/dark periods. Measurements of PPFD, leaf temperature, leaf conductance (g_w) and P_N were made on one leaf per replication per treatment at 3 and 6 h into the photoperiod on days 6, 9, 11, and 13 following treatment initiation. An open gas-exchange system similar to that described in detail by Pezeshki (1987) was used for g_w and P_N measurements.

Root growth was measured on both branched and non-branched basal and lateral roots. Root growth was followed daily by drawings of roots on the transparency papers attached to the window of each rhizotron. The General Linear Models (GLM) procedures were employed using the Statistical Analysis System (*SAS Institute*, Cary, NC, U.S.A.) to compare means of variables across treatments. Due to logistical limitations only three rhizotrons were used for each treatment (total of 9 plants per treatment), and the experiment was conducted over a two weeks period. The stomatal and photosynthetic values were analyzed by using a repeated-measures design described by Moser *et al.* (1990).

Results

The Eh measurements conducted over the experimental period indicated an aerated condition in control (+430±26 mV), hypoxic conditions for treatment *I* (+340±20 mV), treatment *II* (+245±30 mV), and treatment *III* (-180±30 mV). The treatments imposed in the present study were designed to test plant responses under conditions where rhizosphere oxidation by roots was likely to result in a Eh gradient to immediate rhizosphere (treatment *I*). The treatments *II* and *III* simulated conditions where rhizosphere oxidation was countered by continuous flow of pressurized gas that contained no oxygen. When roots are flooded, wetland plants rely on transport of oxygen from aerial parts to the roots to maintain root aeration and to oxidize the reduced rhizosphere. This mechanism is an important adaptation allowing survival of wetland plants under oxygen-deficient conditions in flooded soils. The time-course changes in soil Eh (Fig. 1, *bottom*) indicated that the continuous flow of N_2 gas (treatment *II*) and H_2/N_2 gas mixture (treatment *III*) resulted in Eh lower than obtained in the flooded treatment (treatment *I*). The Eh difference between *I* and *II* or *III* may be partially attributed to the ability of plant roots for rhizosphere oxidation in the flooded treatment and the limited soil volume in the rhizotron. In such conditions, plant roots modify Eh conditions in the immediate rhizosphere. In the gas flow

treatments, the continuous flow of pressurized gases would reduce the ability of roots for rhizosphere oxidation. In such conditions, the Eh condition is likely to be more uniform around the root system than under flooded conditions.
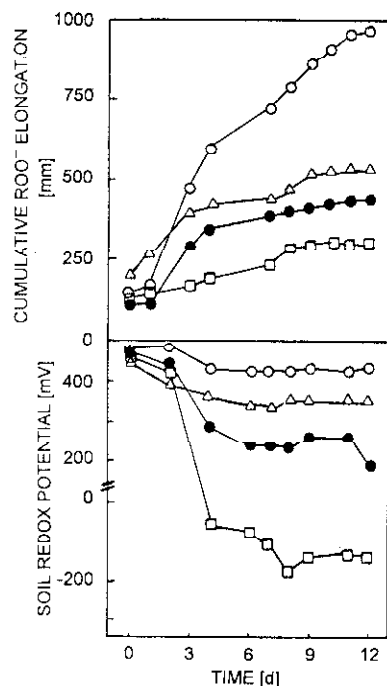

Fig. 1. Time course of cumulative root elongation (*top*) of *Spartina alterniflora* in response to soil redox potential, Eh (*bottom*). Treatments are represented by: control (O), treatment *I* (△), treatment *II* (●), and treatment *III* (□). Mean for 9 plants (*top*) or for 8 measurements (*bottom*).

Root elongation was inhibited in response to low soil Eh shortly after treatment initiation (Fig. 1, *top*). There was a close relationship between soil Eh and root elongation, with root elongation being reduced as soil Eh approached values below approximately +350 mV (Fig. 1). Substantial decreases in root elongation were noted when soil Eh fell below +200 mV (Fig. 2). Such Eh appeared to be the threshold at which reduction in root elongation was significant in *S. alterniflora* under our experimental conditions. The response may be attributed to plant's ability for
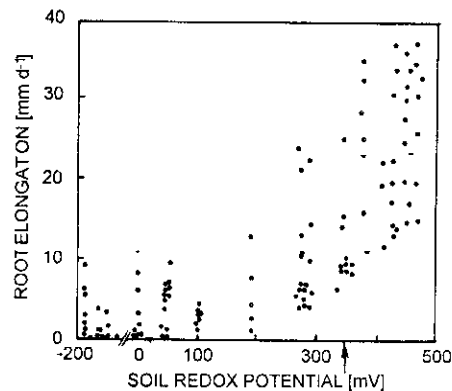

Fig. 2. The relationship between root elongation [mm d^{-1}] in *Spartina alterniflora* and soil redox potential (Eh) [mV]. *Arrow* signifies Eh level at which soil oxygen disappears.

rhizosphere oxidation under flooded conditions (treatment *I*). In this treatment plants influenced root zone substantially *via* root oxygenation mechanism. On the other hand, in treatments *II* and *III*, the continuous gas flow may have minimized rhizosphere oxidation. Under such conditions, plants performed poorly.
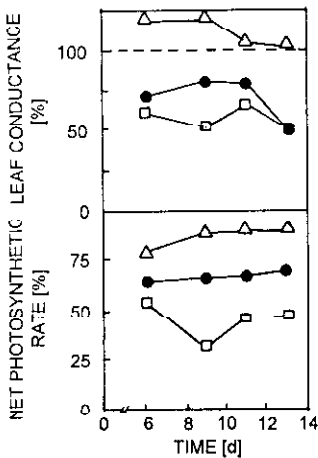

Fig. 3. Time-course responses of net photosynthetic rate (P_N) and leaf conductance (g_w) to various soil treatments [*I* (△), *II* (●), and *III* (□)] presented as % of control.

The time-course response of g_w to the treatments (Fig. 3, *top*) showed no significant changes in plants under treatment *I* but significant reductions in g_w were noted under treatments *II* and *III* ($p<0.05$) throughout the experimental period. In treatment *I*, average g_w over the experiment was 116 % of control. However, g_w averaged 77 and 63 % of control in treatments *II* and *III*, respectively. The P_N responses (Fig. 3, *bottom*) also showed similar patterns. Average P_N reduced to 87, 64, and 44 % of control in treatment I, II, and III, respectively. Significant P_N reductions were found in treatments *II* and *III* (Table 1). The patterns of gas exchange in treatment *I* suggest that under flooded conditions and the level of reduction imposed, *S. alterniflora* was able to maintain its gas exchange. The relationship between P_N and Eh showed a general pattern of decreasing P_N as Eh was reduced (Fig. 4). Low P_N values were associated with reduced Eh.
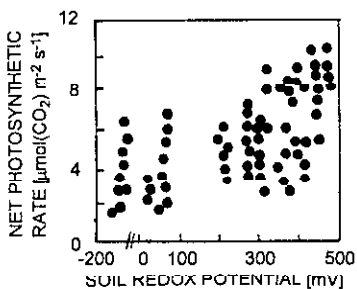

Fig. 4. The relationship between net photosynthetic rate (P_N) in *Spartina alterniflora* and soil redox potential (Eh).

Discussion

Low soil Eh resulted in severe inhibition of root growth in *S. alterniflora* (Fig. 1). Such response has been previously reported in flood-sensitive crop species, *Zea mays* (Stepniewski *et al.* 1991), in flood-tolerant marsh species, *S. patens* (Gleason and Zieman 1981, Pezeshki and DeLaune 1990) and in tree species, *e.g.*, in *Erythrina variegata* (Muthuchelian *et al.* 1995). The status of soil aeration influences root O_2 supply due to changes in O_2 concentration gradient between foliage and rhizosphere (Yamasaki 1952, 1987, Linthurst 1979). Oxygen supply is essential for root growth in flood-tolerant and flood-sensitive plants (Yamasaki 1952, Everard *et al.* 1991).

Table 1. Response of net photosynthetic rate (P_N) [μmol(CO_2) m^{-2} s^{-1}] and leaf conductance (g_w) [mmol(H_2O) m^{-2} s^{-1}] of *Spartina alterniflora* to various soil redox potentials (Eh) [mV]. Treatment *I* = flooded, treatment *II* = N_2, treatment *III* = 50 cm^3 m^{-3} H_2 in N_2. Values within rows followed by different letters are significantly different ($p = 0.05$) as determined by the Duncan's multiple range test.

Variable	Control (air)	*I* (flooded)	*II* (N_2)	*III* (H_2 in N_2)
Soil Eh	430	340	245	-180
P_N	7.81 a	6.80 a	4.99 b	3.42 c
g_w	57 a	66 a	44 b	36 c

Atwell *et al.* (1985) demonstrated that roots of flood-sensitive *Z. mays* require high O_2 pressures for growth. Similarly, root growth in flood-tolerant *Oryza sativa* is O_2 dependent (Alpi and Beevers 1983, Cobb and Kennedy 1987). In addition, normal growth and functioning of roots requires more oxygen than is needed for root respiration processes (Jackson and Drew 1984, Atwell and Greenway 1987). The relationship between root elongation and soil Eh (Fig. 2) further indicated that whereas inhibition of root elongation at soil Eh condition below +350 mV was evident, at soil Eh below +200 mV root elongation was severely inhibited. This Eh value was below the +350 mV, the Eh considered to signify the onset of soil oxygen disappearance (DeLaune *et al.* 1990). The responses suggest that root oxygenation mechanism can be efficient up to certain soil reduction intensity, after which the soil oxygen demand (microbial, chemical) becomes overwhelmingly competitive with the root oxygen demand. The oxygen that is much needed by the roots is likely to be lost to the rhizosphere due to the external sinks (Armstrong *et al.* 1994). In addition, the efficiency and/or utilization of various growth regulators involved in root elongation is oxygen dependent (Atwell *et al.* 1985). The reduced root elongation in *S. alterniflora*, however, is likely to be reversible once aerated conditions are resumed as found in other flood-tolerant species (Pezeshki and DeLaune 1990).

Restricted root elongation results in a smaller root system (at least during the initial period of stress), which no longer supports the shoot adequately. This change also affects roots as major sink for assimilates causing a potential for feed-back inhibition of photosynthesis (Carmi *et al.* 1983). In addition, low soil Eh may result in physiological stresses leading to limitation of active uptake of essential elements

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such as nitrogen. Plant nitrogen status in turn can affect photosynthetic activity in plants because a certain organic nitrogen content in leaves is necessary for CO_2 fixation (Makino *et al.* 1984). The response of roots in *S. alterniflora* indicated the importance of sediment aeration to root elongation in this species. *S. alterniflora* grows under flooded conditions in wetland environments dominated by low sediment Eh. Under field conditions, Linthurst and Seneca (1980, 1981) reported decreased growth in *S. alterniflora* in response to low sediment Eh.

Soil oxygen-deficiency results in stress-induced symptoms including stomatal closure and reduction in P_N (Kozlowski 1984). The significant reductions in P_N found in treatments *II* and *III* may be attributed to several physiological effects of hypoxia. For example, the substantial decrease in g_w found in treatments *II* and *III* is a reflection of partial stomatal closure. Stomatal closure can impose diffusional limitation of photosynthesis due to limitations on gas exchange (Kozlowski 1984). Flood-tolerant plants, however, show limited initial response and a speedy recovery (Pezeshki 1994). As found in treatment *I*, P_N recovers following the initial reduction contributing to *S. alterniflora* ability to withstand such adverse conditions. The recovery was pronounced in treatment *I* that was more comparable with the natural environment than the continuous gas flow treatments. Nevertheless, the results indicated that short periods of reduced carbon fixation occurred in response to low soil Eh. Such conditions occur frequently in coastal wetlands due to many factors including tidal actions. Stomatal closure may also adversely affect oxygen transport to the roots in wetland plants, due to the restriction imposed upon gas exchange with the atmosphere. The present results indicate that low sediment Eh may adversely affect both root (elongation) and shoot (P_N) in *S. alterniflora* depending on the intensity of reduction. Thus periods of drainage (low tides) during the growing season are critical to *S. alterniflora* functioning and growth by providing the means for soil aeration (high Eh) creating favorable environment for root growth with important implications for plant carbon fixation and functioning.

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