Lacunal allocation and gas transport capacity in the salt marsh grass *Spartina alterniflora*

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Received June 12, 1991 / Accepted in revised form January 9, 1992

**Summary.** Lacunal allocation as the fraction of the total cross sectional area of leaves, stem bases, rhizomes, and roots was determined in both tall and short growth forms of *Spartina alterniflora* collected from natural monospecific stands. The results indicate that in both growth forms lacunal allocation is greater in stem bases and rhizomes than in leaves and roots and that tall form plants allocate more of their stem and rhizome to lacunae than short form plants.

Measurements made in natural stands of *Spartina alterniflora* suggest that total lacunal area of the stem base increases with increasing stem diameter and that stem diameter increases with increasing plant height and above-ground biomass. However, the fraction of cross section allocated to lacunae was relatively constant and increased only with the formation of a central lacuna.

Experimental manipulations of surface and subsurface water exchange were carried out to test the influence of flooding regime on aerenchyma formation. No significant differences in lacunal allocation were detected between plants grown in flooded (reduced) and drained (oxidized) sediments in either laboratory or field experiments. While aerenchyma formation in *Spartina alterniflora* may be an adaptation to soil waterlogging/anoxia, our results suggest that lacunal formation is maximized as a normal part of development with allocation constrained structurally by the size of plants in highly organic New England and Mid-Atlantic marshes.

The cross sectional area of aerenchyma for gas transport was found to be related to the growth of *Spartina alterniflora* with stands of short form *Spartina alterniflora* exhibiting a lower specific gas transport capacity (lacunal area per unit below ground biomass) than tall form plants despite having a similar below-ground biomass supported by a 10-fold higher culm density. The increased specific gas transport capacity in tall vs. short plants may provide a new mechanism to explain the better aeration, higher nutrient uptake rates and lower frequency of anaerobic respiration in roots of tall vs. short *Spartina alterniflora*.

**Key words:** Aerenchyma – Gas transport – Salt marsh – *Spartina alterniflora*

*Spartina alterniflora* Loisel. is the dominant macrophyte in salt marshes along the east and gulf coasts of North America and is generally responsible for the naturally high levels of primary production found in these ecosystems. Growing in nearly monospecific stands, *S. alterniflora* exhibits variations in productivity and morphology related to gradients in sediment redox characteristics influenced by surface and subsurface hydrologic features. A tall form (1–3 m) is typically found growing adjacent to creeks where porewater turnover is high and the sediments are relatively oxidized. A few meters inland from creekbanks, where porewater turnover is low and sediments are more reduced, a short growth form (10–45 cm) with diminished productivity predominates (Valiela et al. 1978).

Studies which have demonstrated an increase in plant production upon addition of nitrogen attribute the growth differences in natural stands of *S. alterniflora* to nitrogen limitation (Sullivan and Daiber 1974; Valiela and Teal 1974). Dissolved ammonium concentrations, however, are frequently higher in the root zone of short *S. alterniflora* than in the root zone of tall (Mendelssohn 1979). Moreover, laboratory culture studies show that plants grown in aerobic hydroponic systems are not nitrogen limited at field nutrient levels (Morris 1980). Instead, it has been suggested that growth is a function of nitrogen uptake which is strongly influenced by oxygen availability to the roots (Morris and Dacey 1984).

Sediments supporting stands of *S. alterniflora* are water-saturated like those in most regularly flooded wetlands. As a result, the sediments are anoxic a few millimeters below the surface (Teal and Kanwisher 1961). High levels of reduced chemical species accumulate in the
sediments as products of bacterial metabolism increasing the latent chemical oxygen demand in the sediments (Howes et al. 1984) and seen as highly negative oxidation-reduction potentials in the rhizosphere. Certain of these reduced compounds (e.g. H₂S, Fe⁺⁺) may also act as phytoxins, directly inhibiting nutrient uptake and plant growth (Mitsui 1965; Koch and Mendelssohn 1989). As aerobic root respiration is essential for plant growth and nutrient uptake (Vlamis and Davis 1944; Morris and Dacey 1984), many wetland adapted species have evolved internal gas transport systems to carry oxygen from photosynthesis and/or atmospheric exchange to below-ground roots and rhizomes. Gas transport in these plants occurs via a series of lacunae which form a continuous gas filled aerenchyma system extending from the leaves to the root tips (Williams and Barber 1961).

In S. alterniflora, lacunae appear to provide a diffusive pathway for exchange primarily of oxygen and carbon dioxide between above and below-ground portions (Teal and Kanwisher 1966). In either case, the volume of gas transported will be increased with increasing lacunal cross sectional area available for transport. Therefore, in salt marsh sediments nutrient uptake as controlled by root oxygen concentration is mediated by the interaction between oxygen delivery via the aerenchyma, and oxygen consumption through both plant respiration and the oxidation of reduced chemical species (Howes et al. 1986). The ability to transport O₂ to the root zone may then play an important role in controlling the productivity of this species.

Our goal was to test the hypothesis that the linkage between root oxygen status and productivity in S. alterniflora is in part mediated by the lacunal area of the plants relative to their root respiratory oxygen requirements. We first determined relationships of plant morphology, growth habit and lacunal allocation in natural stands of S. alterniflora. The ability of tall and short form plants to alter their lacunal allocation in response to sediment redox characteristics was then investigated in field and laboratory experiments. Finally, the relationship between specific gas transport capacity (lacunal area/below-ground tissue) of stands of S. alterniflora and above-ground biomass was investigated to assess the possible role of gas transport in controlling the growth form of S. alterniflora.

**Methods**

**Field survey 1**

To compare lacunal allocation among the various plant parts and between the different growth forms, plants were collected at peak biomass from monospecific stands of creekbank (tall) and inland (short) S. alterniflora in the Great Sippewissett and Mullica River-Great Bay (Tuckerton, NJ, USA) Marshes. Above-ground plant material was harvested at the sediment surface from replicate 0.1 m² quadrats, placed in plastic bags and held on ice for return to the laboratory, while below-ground biomass was determined by sorting live roots and rhizomes from replicate cores (6.5 cm i.d., 30 cm deep) collected at the same time. Cumul densities and stem diameters were determined from the harvested plants immediately upon return to the lab. The sample base represents the primary constriction in the diffusion pathway and serves as the final conduit through which all oxygen from aerial portions of the plant is transported to below-ground tissue, we focused on stem base lacunal allocation as a measure of overall plant gas transport capability. Immediately upon collection, 6–10 stems were randomly selected from each above-ground harvest and the lower 2 cm excised and preserved for lacunal analysis as described above.

**Field and laboratory experiments**

To test the ability of tall and short form plants to alter lacunal allocation in response to variations in flooding regime and related sediment redox characteristics, samples were collected from hydrologically manipulated experimental field plots located in the Mullica River-Great Bay Marsh at the Rutgers Marine Station near Tuckerton, NJ (Strakosch 1991) and from laboratory microcosms at the Woods Hole Oceanographic Institution. Above and below-ground biomass, cumul densities, cumul heights, stem diameters and lacunal allocation in stem bases were determined as in the survey studies (described above). Sediment redox (Eh) at 2 cm and 5 cm depth was measured by arrays of platinum electrodes using 3 electrodes per depth with external reference (+242 mV, Orion Research) (Procedure as in Howes et al. 1981; 1986). These measurements, while they represent nonequilibrium potentials and therefore not true Eh, are reproducible and are related to sulfide concentration in anoxic marine sediments (Berner 1963). Thus, they are useful in comparing relative oxidation status of marsh sediments.

The large scale hydrological manipulations (Strakosch 1992) were conducted in 10 m x 10 m plots of short S. alterniflora. Replicate plots under three treatments plus control unaltered marsh (under natural flooding regime) were hydrologically manipulated to either decrease or increase the oxidation of the sediments. Subsurface drainage was negligible in these inland sites and enhanced flooding leads to increased waterlogging and lowered sediment oxidation-reduction potentials in the flooded treatment. In the drained treatment, perforated drainage pipes placed 30 cm beneath the marsh accelerates water table drop and lead to increased sediment oxidation. The flooded and drained treatments were then combined in a “flood/drain” treatment which closely approximates the hydrologic regime of nearby creekbank areas and, like the drained treatment, leads to greater sediment oxidation. The treatments represent a gradient in sediment redox state from relatively oxidized (Drained Treatment) to very reduced (Flooded Treatment).

In the laboratory, two experiments were conducted in lysimeter microcosms (Howes et al. 1986) to test the ability of tall and short S. alterniflora to generate aerenchyma in response to increased or