

The effect of mowing on oxygen transport in *Spartina anglica* (Poaceae)

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ABSTRACT

Spartina anglica (English Cordgrass) is an estuarine cordgrass that develops an extensive aerenchyma system to lower metabolic demands and supply submerged portions of the plant with atmospheric and photosynthetic oxygen. These physiological benefits are crucial for growth in hypoxic sediments and therefore help make introduced *S. anglica* a formidable invasive species in North American Pacific Northwest estuaries. Removal of above-ground biomass by mowing is presently used as a means of *Spartina* control. This treatment may prevent oxygen transport and render underground tissues anaerobic. Physiological experiments were conducted on mowed *S. anglica* plants from Skagit Bay, Washington to determine the effect of mowing treatment on rates of oxygen transport and anaerobic enzyme expression. It was found that mowing has very little effect on oxygen transport within *S. anglica*. Mowing plants to mud level appears to be slightly more successful for control than mowing to stubble.

Porewater sulfide concentrations remain low, alcohol dehydrogenase activities are temporarily increased, and regrowth is slower than treatments mowed to stubble.

INTRODUCTION

Four species of *Spartina* cordgrass (Poaceae) have been introduced into estuaries on the West Coast of the United States. Two of the introduced species (*S. densiflora* and *S. patens*) are somewhat rare in Washington. *Spartina densiflora* Brong. is widespread in California (Spicher and Josselyn, 1985) but has only been recently discovered in Grays Harbor, WA (WSDA news release, 11 Jan 2002). *Spartina patens* (Aiton) Muhl. grows in isolated areas in California (Spicher and Josselyn, 1985), Oregon, and Washington (Frenkel, 1987). Invasive *Spartina alterniflora* Loisel. and *S. anglica* C. E. Hubbard are far more widespread in Pacific estuaries. The largest invasions of *S. alterniflora*, which is native to the East and Gulf Coasts of North America, are found in San Francisco Bay, CA (approximately 190 net ha; San Francisco Estuary Invasive *Spartina* Project data) and Willapa Bay, WA (approximately 16,000 affected ha; (Reeves, 2000)). *S. anglica* is a species of great interest. It is a fertile amphidiploid that formed in Southampton, U.K. around 1892 from infertile hybrids between introduced *S. alterniflora* and native *S. maritima* (Curtis) Fernald (Raybould et al., 1991b). *S. anglica* was noted for its ability to stabilize sediment and was extensively planted worldwide to prevent shoreline erosion and to reclaim mudflats (Gray et al., 1991). *S. anglica* was introduced at one location in northern Puget Sound, WA in 1961 but quickly spread via tidal currents and now affects over 3,300 ha in the Puget Sound area (Hacker et al., 2001).

Introduced *Spartina* species can affect estuarine ecology on multiple scales. *Spartina* can potentially out-compete native vegetation and alter estuary topography by sediment

accretion (Daehler and Strong, 1996; Sanchez et al., 2001). Conversion of estuarine mudflats to *Spartina* stands results in reduced mudflat area available for foraging by shorebirds (Daehler and Strong, 1996), mariculture of oysters and clams (Bishop, 1997), and potentially stimulates production of the toxin hydrogen sulfide (Wang and Chapman, 1999) through anaerobic decay of organic material that accumulates in *Spartina* stands.

Introduced *Spartina* can quickly overtake estuaries. Most of its success as an invader stems from the fact that *Spartina* lacks competitors in North American West Coast estuaries. *Spartina* invades low-level mudflats and tidal channels that were previously devoid of vascular plant life. These mudflats and tidal channels are characterized by highly reducing sediments ($E_h < -300\text{mV}$; DeLaune et al., 1990; Brix and Sorrell, 1996), providing a hostile environment for plant growth. Native West Coast estuarine vascular plants do not colonize these areas. Native species such as *Distichlis spicata* (L.) Greene, *Triglochin maritima* L., and *Salicornia virginica* L. are mostly confined to the mid- and upper-intertidal zones, leaving bare mudflats in the lower regions of the marsh (Emmett et al., 2000). *Spartina* can survive in these low-level areas because it has a suitable physiology to cope with anoxic mudflats and their associated toxins.

East Coast estuaries are dominated by monotypic stands of *Spartina alterniflora* and *S. patens*, often with a sharp elevational ecotone dividing the two species (Bertness, 1991). Similarly, it has been noted that *S. anglica* grows lower in the intertidal zone than either parent species (Raybould et al., 1991a; Raybould et al., 1991b). Sharp elevational zonation patterns are common in saltmarsh communities (Adam, 2002), suggesting differences between species in physiological tolerance limits. Plants that can endure more reducing conditions are able to grow lower in the intertidal range. Physiological differences between species may be important

in a case like *Spartina*, since plants that can colonize bare mudflats are a primary concern as invaders. Plants restricted to the upper marsh would be less threatening because few plants are able to establish themselves in communities dominated by natives such as *Distichlis spicata* (Chater and Jones, 1957).

Plants may adapt to hypoxic sediments by increasing capacity for anaerobic fermentation or through abilities to supply oxygen to affected tissues internally (Vartapetian and Jackson, 1997). Many estuarine and wetland plants counter oxygen deficiency by forming aerenchyma (Jackson and Armstrong, 1999). Aerenchyma has two important benefits for plants growing in reduced sediments (Armstrong et al., 1991). Aerenchyma may serve as a ventilation pathway to connect submerged tissues to atmospheric oxygen (Teal and Kanwisher, 1966; Arenovski and Howes, 1992) or it may simply function to reduce the number of respiring cells, thus lowering respiratory demands (Williams and Barber, 1961).

In emergent plants, the most important benefit of aerenchyma is thought to be facilitation of oxygen transport (Armstrong, 1979). A constant oxygen supply is required to all cells; permanent structural damage and organelle breakdown may quickly result in anoxic root cells (Linthurst, 1980). For these reasons, the ability to transport oxygen is paramount in wetland and estuarine settings and often regulates plant zonation in these areas (Howes et al., 1981; Yamasaki, 1984). Plants better adapted to growth in anoxic conditions are able to grow in lower areas of the intertidal range (Blom, 1999).

Cordgrasses of the genus *Spartina* develop extensive aerenchyma systems (Burdick, 1989; Pezeshki et al., 1991) and have been shown to transport substantial oxygen internally through these aerenchyma systems (Teal and Kanwisher, 1966; Howes and Teal, 1994; Maricle and Lee, 2002; Lee, in press). These abilities enable *Spartina* to colonize anoxic estuarine

mudflats and tidal channels, and help *Spartina* species to be aggressive invaders in areas of introduction (Daehler and Strong, 1996). *S. anglica* appears to be especially adept at colonizing intertidal mudflats. *S. anglica* exhibits accelerated rates of photosynthesis and oxygen transport despite waterlogged or saline soil conditions that limit many other species (Maricle et al., in preparation).

In Washington State, gas-powered brushcutters are one method currently being used to control *Spartina*. Mowing serves to remove above-ground biomass, and it may be beneficial for control efforts if physiological stress can be induced in *Spartina*. This study sought to determine the effect of mowing on oxygen-transport physiology in *S. anglica*. If oxygen-transport abilities can be inhibited by mowing, *Spartina* will not be able to survive in its current environment. Conversely, if current mowing practices cannot retard internal oxygen transport they may not be effective long-term control agents. However, mowing may still be beneficial in short-term control strategies for prevention of seed set in mature plants (Vickery et al., 2001) and controlling leaf area to reduce photosynthetic production (Sheley et al., 2003) and eventual below-ground storage of carbohydrates in root and rhizome systems. Additionally, if multiple control strategies are used sequentially, the reduction of above-ground biomass by mowing may reduce amounts of herbicide required to coat plants in a subsequent application (S.R. Riggs, personal communication).

MATERIALS AND METHODS

Study Site, Sampling, and Mowing Treatments

Study sites were selected within a large *Spartina anglica* meadow at English Boom (Camano Island, Island County), located in South Skagit Bay, WA (approximately 122° 25' W

longitude; 48° 15' N latitude). Replicate plots of *S. anglica* were selected for uniformity (approximate age of plants, height in tidal zone, and sediment characteristics) and were mowed with a gas-powered Stihl 120 brushcutter with nylon blades and line. Two 1.5 m x 1.5 m plots of *S. anglica* were mowed on 2 September 2001. One plot was mowed leaving a 2-5 cm stubble (“mowed to stubble”), which is typical of large-scale mowing operations on estuarine mudflats in Washington. The second plot was mowed to remove all above-ground biomass; shoots were mowed below the surface of the mud (“mowed to mud”). Ten additional 1.5 m x 1.5 m plots were mowed on 2 July 2002. These plots were similar to the original plots in terms of plant and tidal characteristics. Five of these plots were mowed to mud level and five were mowed to stubble. Therefore, three treatments resulted: (1) mowed to mud, (2) mowed to stubble, and (3) intact (unmowed) *Spartina*.

Immediately following mowing, clumps of plants were removed from each replicate plot. Clumps contained several *S. anglica* plants and were approximately 3 liters in volume. Care was taken to avoid damaging plant roots during removal from mudflats and transport. Additional clumps of plants were obtained from adjacent unmowed *Spartina*. Plants were then transported to the Washington State University campus in Pullman for laboratory testing. The mowed plots remained undisturbed for subsequent tests during the regrowth period following mowing. Plant regrowth was monitored during this period and percent cover estimates were recorded on 25 July 2002 using a 0.5 m x 0.5 m quadrat (Kent and Coker, 1992). Plant regrowth was observed and estimates were generated based on the amount of living plant material present. Additionally, the plots mowed in 2001 were monitored during the 2002 field season to assess long-term effects of mowing.

Several environmental physical factors were measured in each plot. Porewater sulfide concentrations, salinity, and sediment redox potential were monitored in each replicate plot during the post-mowing period. Similar measurements were made in stands of unmowed *Spartina*, on nearby empty mudflats, and in areas mowed to stubble the previous season (10 months prior to measurement). For sulfide and salinity measurements, porewater was extracted from a depth of 15 cm at each location by using a narrow plastic tube (0.16 cm OD, 0.08 cm ID) fitted to a syringe (McKee et al., 1988). Porewater was drawn up and filtered with Swinney filter cartridges containing paper filters (Howes et al., 1985). One mL of the filtered extracted water was then fixed with 20 μ L 22% zinc acetate and 20 μ L 6 N NaOH to precipitate dissolved sulfides. Sulfide concentrations were later measured spectrophotometrically using the methylene blue method of Cline (1969). At each site, porewater salinity was measured with a Leica temperature-compensated refractometer and redox potential was measured with a Thermo-Orion 290A plus portable pH/ISE meter.

Root Aerenchyma Development

Representative *S. anglica* roots from treatments mowed to stubble were sectioned serially and examined for aerenchyma development after Maricle and Lee (2002). It was difficult to distinguish between living and dead root tissue in treatments mowed to mud. Therefore, only roots from mowed to stubble treatments were measured and compared to roots from unmowed plants. Roots from unmowed *Spartina* were compared to roots from plants 20 and 30 days following a mowing to stubble treatment.

At harvest, plant roots were carefully separated from the sediment and thoroughly rinsed to remove all soil particles. Several roots from each plant were fixed for microscopy in

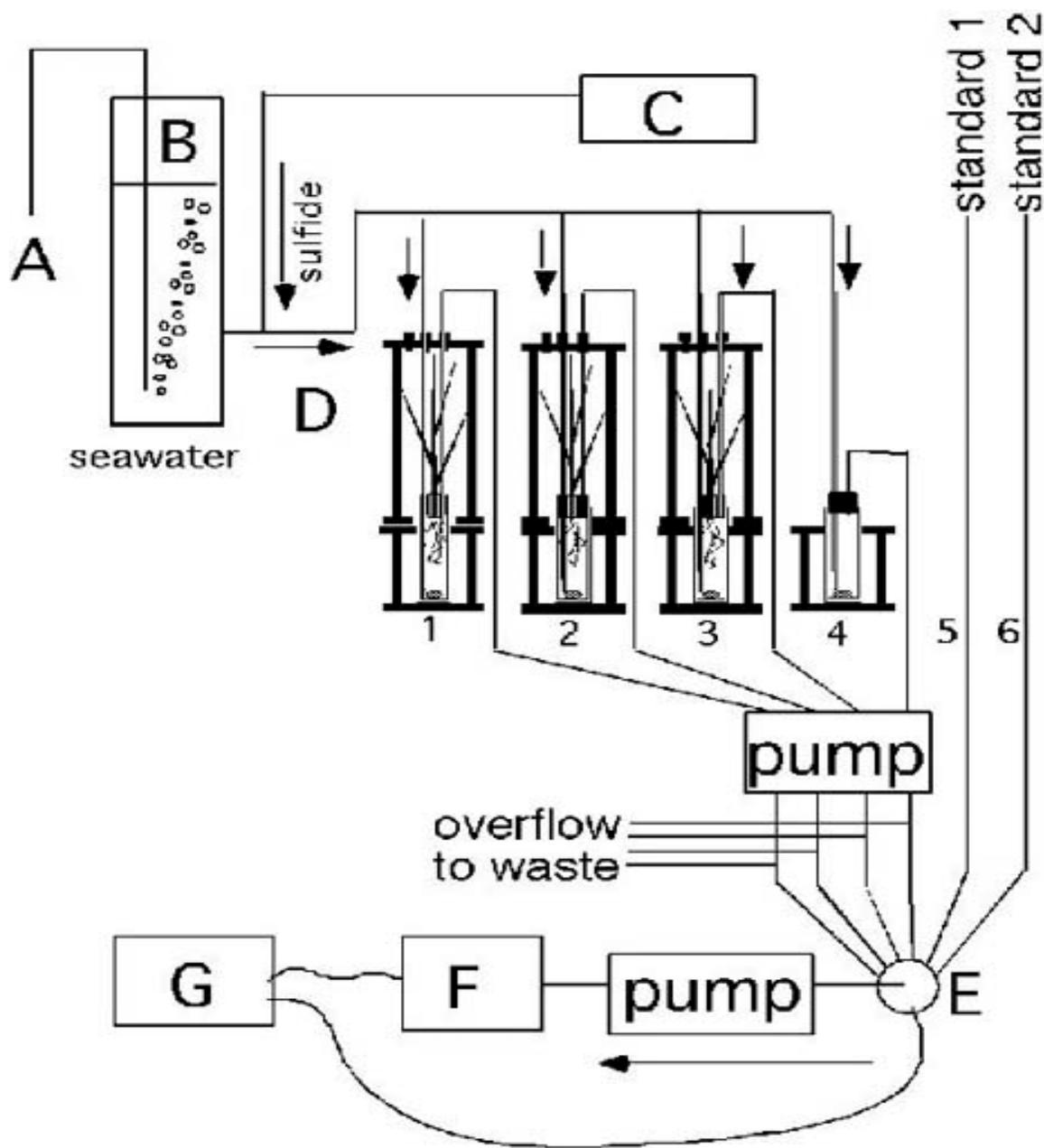
0.05 M PIPES buffer (pH 7.2) containing 2% glutaraldehyde and 2% paraformaldehyde. Fixed roots were later freehand sectioned to a thickness of 0.15-0.20 mm, immersed in distilled water, and examined with an Olympus BH-2 light microscope. Images were recorded with a Microimage Video Systems digital camera (model A209). Cross-sections were taken at 2-cm increments along the entire length of each root; three sections were measured and averaged at each representative position on a root. Total root lengths were also noted for each plant.

Digital images of root cross-sections were later analyzed using Scion Image 1.62a software (Scion Corporation; Frederick, MD) to measure the percentage of root area comprised of aerenchyma (Maricle and Lee, 2002). Scion Image software is able to count pixels in digital images; when serial cross-sections are examined, a highly accurate and direct measurement of root porosity is obtained for the entire root. Root porosity results were compared between treatments using analysis of covariance (ANCOVA, StatView 5, 1998 SAS Institute Inc., Cary, NC; $\alpha=0.05$).

Internal Oxygen Transport

Aerenchyma function was also quantified for unmowed plants and plants mowed to stubble. Individual plants were tested for their ability to transport oxygen internally after Lee (in press). A flow-through respirometry system was used to measure dissolved oxygen concentrations in sealed chambers containing plant roots suspended in water (Fig. 1). Oxygen concentrations were monitored for three to four days to observe consumption or release of oxygen by plants into the surrounding medium. Relative rates of oxygen flux (negative = consumption; positive = release) were calculated by finding the difference in dissolved oxygen concentration between empty chambers and those containing plants. Absolute rates of oxygen

Fig. 1. Schematic diagram of flow-through respirometry system used in experiments. A water source (B) is drawn through individual plant chambers (D) by pumps. A multi-way valve (E) samples one chamber at a time, directing flow into the appropriate sensor (F); in this case an oxygen-sensor was used. Relative oxygen consumption or release is found by comparing empty and occupied plant chambers. Absolute oxygen concentrations can be calculated by comparison with known standards. All flow ultimately is drained down a sink (G). Additional conditions may be brought about in the system, such as bubbling the source water with O_2 or N_2 (A), or pumping Na_2S into the system (C).



flux were found by comparing dissolved oxygen concentrations in experimental chambers with known standards. Plants mowed to mud did not have a stem long enough to successfully suspend the plant in a respiration chamber, so they were not included in this measurement. Intact (unmowed) plants and plants mowed to stubble were measured over time to assess oxygen-transport physiology in the period following a mowed to stubble treatment. Parallel measurements of oxygen consumption were conducted on individual plants where aerenchyma transport capabilities were blocked. Placing the shoot of the plant in a 100% N₂ atmosphere prevents the entry of oxygen into the aerenchyma system (Armstrong, 1964; Teal and Kanwisher, 1966). Chamber oxygen consumption was measured with plants under both a 21% O₂ atmosphere and a 100% N₂ atmosphere. The difference between the two consumption rates equals the amount of oxygen transported internally through the plant's aerenchyma system (Lee, in press). Rates of oxygen consumption under 100% N₂ equal total oxygen demand by plants, and represent rates of dark (i.e., mitochondrial) respiration. These consumption rates were recorded to see if mowing influences plant metabolic rates. Oxygen transport and dark respiration results were compared between treatments using one-way analysis of variance (ANOVA, StatView 5; $\alpha=0.05$).

Greenhouse *S. anglica* plants were also subjected to artificial mowing treatments while in the respirometry system. Intact plants were monitored in the flow-through system for two days, then the shoots of the plants were clipped to resemble a mowed to stubble treatment. The resulting plant stumps were monitored for another two days, allowing pre- and post-mowing observations of oxygen transport and respiration rates.

Alcohol Dehydrogenase Assays

Root samples were obtained from all treatments of field-collected plants and frozen immediately in liquid nitrogen. Alcohol dehydrogenase (ADH) assays were later performed using a protocol modified from John and Greenway (1976). Root samples stored at -80°C were ground in liquid nitrogen and cold extraction buffer was added at 5 mL g^{-1} . The resulting mixture was homogenized, filtered through Miracloth (Calbiochem; San Diego, CA), and centrifuged at $16,000\text{g}$ for 10 minutes at 4°C . The supernatant was assayed for ADH activity spectrophotometrically at 25°C . Enzyme activity was determined as the rate of NADH oxidation, measured as a decrease in absorbance at 340 nm. Rates of NADH oxidation in the presence of acetaldehyde were corrected for background rates, then standardized to g fresh weight. ADH activities were compared between treatments using one-way ANOVA ($\alpha=0.05$).

RESULTS AND DISCUSSION

Environmental Physical Factors

In this study, substrate chemistry was measured within intact stands of *S. anglica* prior to mowing and was then remeasured 22 days following mowing. Sediment redox potential measurements were highly variable so there were no significant differences between any treatments (ANOVA, $p=0.2703$). However, there were trends that appear real. Sediment redox potentials ranged from -183 mV in stands of intact *Spartina* down to -326 mV in treatments mowed to mud (Table 1). Redox measurements indicated that *S. anglica* may oxidize the soil, consistent with findings by Howes et al. (1981) for *S. alterniflora*. The results also show a slight decrease in sediment redox potential following treatments mowed to stubble. This may seem to be a result of decreased oxygen transport within plants mowed to stubble, but this was

not the case. Porewater sulfide levels varied greatly depending on the treatment and may be the cause of sediment redox potential changing without changes in plant oxygen transport.

Table 1. Physical characteristics of sediment across mowing treatments of *Spartina anglica* at the study site in English Boom (South Skagit Bay), Washington. Shown is the mean \pm SD (N) for each value.

Treatment/Habitat	Sediment Redox Potential (mV)	Porewater Salinity (‰)	Porewater Sulfide (μ M)
Intact <i>S. anglica</i>	-183.38 \pm 170.82 (8)	17.00 \pm 2.67 (6)	643.55 \pm 539.61 (10)
Bare Mudflat	-291.67 \pm 56.61 (3)	17.50 \pm 2.74 (6)	737.14 \pm 1296.50 (6)
Mowed to Mud	-326.00 \pm 68.07 (5)	17.75 \pm 2.61 (8)	747.58 \pm 473.03 (8)
Mowed to Stubble	-316.60 \pm 27.63 (5)	16.38 \pm 1.60 (8)	2205.80 \pm 975.20 (8)
Mowed Previous Year	-193.33 \pm 232.41 (3)	18.00 \pm 2.00 (3)	1114.37 \pm 766.46 (3)

Several physical parameters measured in this study showed that *S. anglica* altered the sediment chemistry at English Boom. Stands of live *S. anglica* appeared to raise sediment redox potential, probably due to internal transport and release of oxygen into the rhizosphere (Teal and Kanwisher, 1966; Howes and Teal, 1994). However, sediment redox potentials decreased markedly following both mowed to stubble and mowed to mud treatments in this study. Anaerobic decay of mowed *Spartina* wrack can lead to the production of sulfides (Koch and Mendelssohn, 1989) and is likely to be the reason sediment redox potentials decreased and porewater sulfides increased among some mowed stands of *Spartina*.

Mean porewater sulfide values measured in this study were variable and ranged from a minimum of 0.64 mM in intact *Spartina* to a maximum of 2.21 mM in mowed to stubble treatments (Table 1). Regions with large amounts of detritus accumulation in the absence of

live plants showed the highest sulfide levels. Whereas having intact *S. anglica* plants did not significantly increase sulfide concentrations over that of bare mudflats (ANOVA, $p=0.8276$), treatments mowed to stubble (ANOVA, $p=0.0025$) and treatments mowed the previous year (ANOVA, $p=0.0601$) had increased porewater sulfide concentrations over mudflat values. Interestingly, treatments mowed to mud did not show increased sulfide concentrations compared to bare mudflats (ANOVA, $p=0.9815$).

Plots mowed to mud (i.e., no stubble remaining) may not have shown increased sulfide concentrations because mowed wrack can freely wash away from these areas. In contrast, wrack resulting from mowing can easily become entangled on *Spartina* stubble where it then can become silted in and proceed to decay anaerobically to produce sulfides. Indeed, treatments mowed to stubble (current and previous year's mowing) showed a significant increase in porewater sulfide concentration. Wrack does not accumulate in treatments mowed to mud level, resulting in minimal sulfide levels. Below-ground biomass remaining in treatments mowed to mud did not result in increased sulfide levels, possibly due to chemical properties of the root tissue.

Stands of live *Spartina* do not show increased levels of porewater sulfides. This may result from oxygen release by plants into the sediment or sulfide oxidizing processes associated with *Spartina* roots. These processes may include sulfide oxidase enzymes, nonenzymatic or metal catalysts, or rhizosphere bacteria that function to oxidize sulfides (Lee et al., 1999). Non-enzymatic sulfide oxidizing processes involved with *Spartina* roots may function in intact as well as mowed plants, and may be the reason increased sulfide concentrations were not measured in treatments mowed to mud. Large amounts of wrack accumulating in treatments mowed to stubble probably overwhelm these processes, leading to high sulfide concentrations.

Physiological mechanisms of sulfide oxidation by various species of *Spartina* are currently under investigation.

Porewater salinity ranged from 16 to 18‰ across treatments (Table 1). There were no significant differences in salinity between any mowing treatments, intact *Spartina*, or empty mudflats at English Boom (ANOVA, $p=0.7644$). Soil salinity measurements may be more valuable in higher marsh regions, as transpiration of water might serve to elevate sediment salinity, but this was not observed in the low-marsh regions in this study. Low-intertidal sediments containing *Spartina* are submerged twice daily with tidal water that equalizes sediment salinity across the entire area.

Root Aerenchyma Development

S. anglica roots contained 0 to 25% aerenchyma by cross-sectional area (Fig. 2). Mean root porosities ranged from 14.78% aerenchyma (by total volume) in unmowed plant roots up

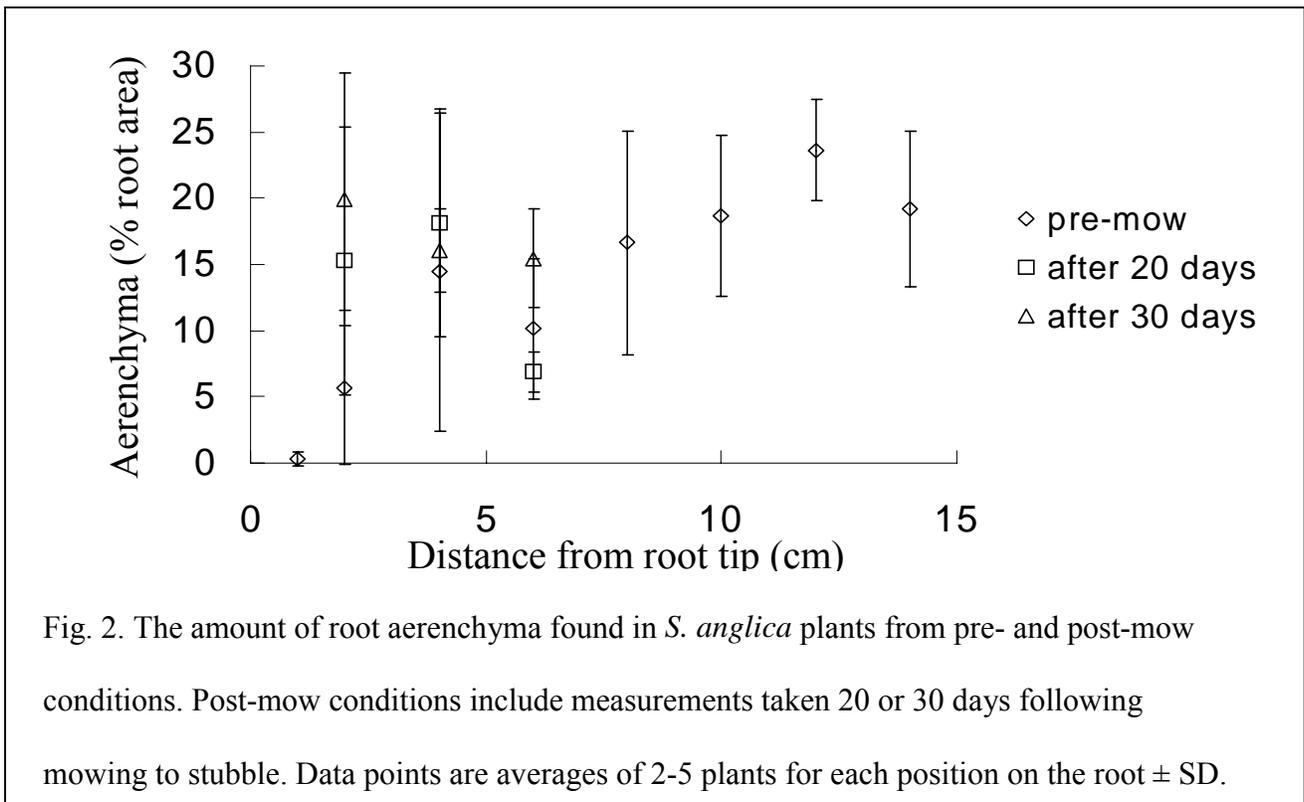


Fig. 2. The amount of root aerenchyma found in *S. anglica* plants from pre- and post-mow conditions. Post-mow conditions include measurements taken 20 or 30 days following mowing to stubble. Data points are averages of 2-5 plants for each position on the root \pm SD.

to 15.51% and 17.11% aerenchyma in roots 20 and 30 days after mowing, respectively.

Amounts of *S. anglica* root aerenchyma were not significantly affected by mowing to stubble 20 or 30 days prior to measurement (ANCOVA, $p=0.2544$). Roots from plants mowed to stubble tended to show slightly more aerenchyma per root area than unmowed plants, but this difference was not significant. Changes in aerenchyma may occur because plants are lowering energy demands by reducing tissue or perhaps mobilizing C and N for new growth.

Roots in field-collected plants were significantly shorter than roots in greenhouse-raised plants (ANOVA, $p<0.0001$; data not shown). Typically, roots in flooded plants tend to be shorter in length than corresponding non-flooded plants (Luxmoore et al., 1970; Drew et al., 1985). Diffusion and other transport processes (Armstrong, 1979; Dacey, 1980, 1981; Raskin and Kende, 1983, 1985; Armstrong et al., 1992) can supply oxygen more easily to short roots than long roots. As oxygen is transported through plant tissue, each successive region consumes the oxygen it needs. Tissues far removed from the oxygen source may not receive the needed amounts of oxygen. It is therefore in the interest of a waterlogged plant to keep its roots as short as possible. In this case, the roots from field-grown *S. anglica* would experience a much greater rhizosphere oxygen demand than greenhouse plants. Short roots would decrease the rhizosphere volume, and likely the amount of oxygen lost to it.

Collective amounts of root aerenchyma were significantly greater in field-collected plants compared to greenhouse plants (ANCOVA, $p<0.0001$). This difference suggests there are increased demands for aerenchyma function in highly reduced growth substrates. The results indicate that *S. anglica* develops additional aerenchyma when grown on mudflats compared to the more oxidized substrates used for greenhouse studies (see Maricle and Lee, 2002).

Internal Oxygen Transport

S. anglica plants mowed to stubble showed similar respiration and oxygen flux measurements when compared to intact (unmowed) plants in the respirometry experiments. Internal oxygen transport rates ranged from 0.00 to 0.38 $\mu\text{mol g}^{-1} \text{h}^{-1}$ in intact plants and from 0.00 to 0.78 $\mu\text{mol g}^{-1} \text{h}^{-1}$ in plants mowed to stubble (Fig. 3). Rates of oxygen flux and internal oxygen transport were not significantly different between the two treatments (ANOVA, $p=0.2575$). Similarly, greenhouse experiments involving artificial mowing showed no difference in internal oxygen transport between mowed and intact plants (ANOVA, $p=0.2720$; data not shown). Total oxygen consumption (measured under 100% N_2) averaged 0.364 $\mu\text{mol g}^{-1} \text{h}^{-1}$ in intact *S. anglica* and 0.952 $\mu\text{mol g}^{-1} \text{h}^{-1}$ in treatments mowed to stubble. Mowing had no effect on the overall oxygen consumption rate in *S. anglica* (ANOVA, $p=0.2266$).

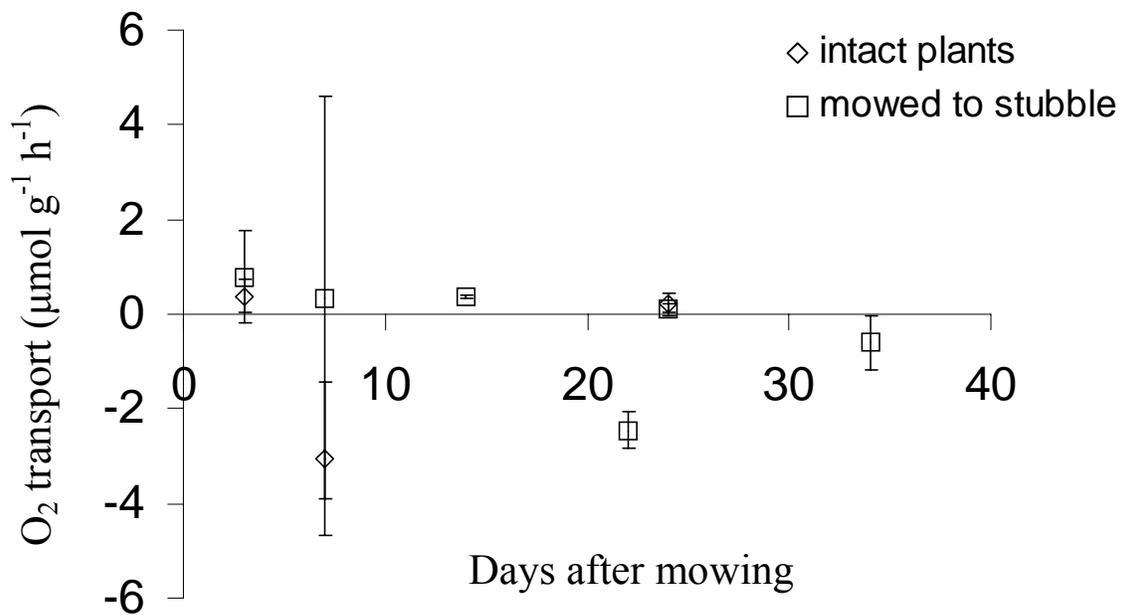


Fig. 3. Rates of internal oxygen transport in *Spartina anglica* plants. Shown are results from intact (unmowed) plants and plants mowed to stubble. Data points are averages of 2-4 plants \pm SD.

Alcohol Dehydrogenase Activities

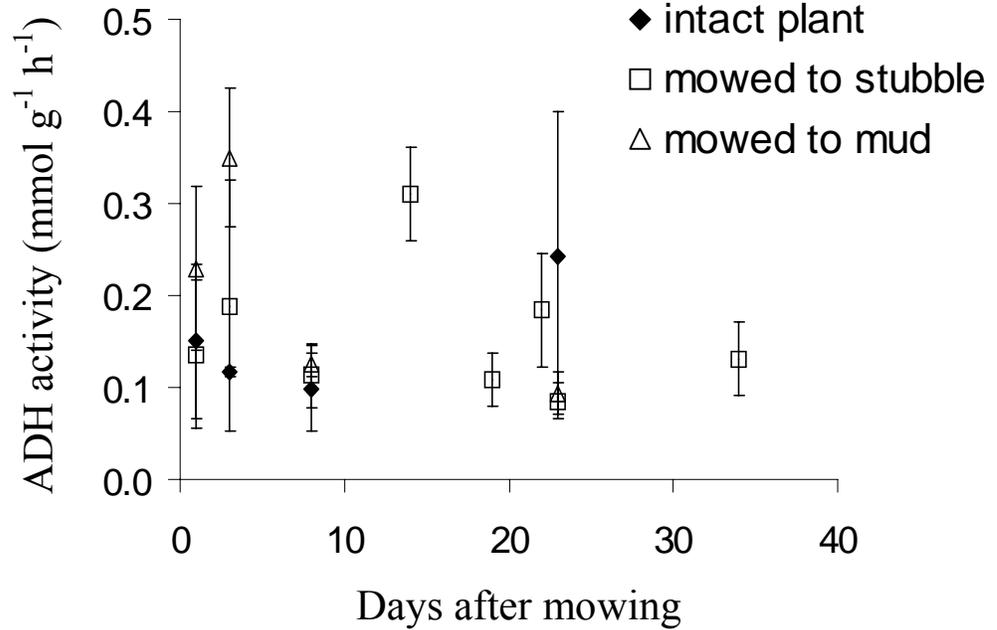
The enzyme alcohol dehydrogenase (ADH) converts acetaldehyde to ethanol, a reaction found in anaerobic fermentation (John and Greenway, 1976). ADH is only used in the absence of oxygen, so the presence of high ADH activities indicates oxygen deficiency in the tissue of interest (Mendelssohn et al., 1981). High ADH activities in mowed *S. anglica* roots would therefore indicate an interruption of oxygen transport from aerial tissues, and hence an effective control strategy.

In some cases *S. anglica* root ADH activities significantly increased following mowing (Fig.4). Mowing plants to stubble did not affect ADH activity, but mowing to mud significantly increased root ADH activity temporarily. Mean root ADH activities ranged from 0.0989 to 0.2418 mmol g⁻¹ h⁻¹ in intact plants, 0.0855 to 0.3102 mmol g⁻¹ h⁻¹ in plants mowed to stubble, and from 0.0941 to 0.3493 mmol g⁻¹ h⁻¹ in plants mowed to mud. Three days after mowing, roots mowed to mud showed significantly higher ADH activities than the intact plant roots or roots mowed to stubble (ANOVA, p=0.0410). The plants seemed able to recover quickly, however; ADH activities were indistinguishable between treatments after eight days (ANOVA, p=0.7666). Short-lived increases in ADH activity may have been alleviated by oxygen supplied by restoration of internal oxygen transport and/or photosynthesis.

Post-Mowing Regrowth

The different mowing strategies used in this study showed different success for the control of *Spartina* (Table 2). New tillers were observed growing 22 days after mowing in both mowed to mud and mowed to stubble treatments. However, the mowed to mud treatment had

Fig. 4. ADH activities of *Spartina anglica* roots following mowing. Data points represent intact (unmowed) plants as well as plants mowed to stubble and mud. Points are the means of 2-4 plants \pm SD.



significantly less regrowth than the mowed to stubble treatment at this time (ANOVA, $p=0.0250$). This suggests mowing down to mud level is a more effective killing strategy than mowing to stubble. However, mowing to stubble may be an effective control strategy in some cases. Areas of English Boom that had been mowed to stubble the previous year showed little or no regrowth in locations heavily inundated by tides (Table 2). If all above-ground biomass is submerged, oxygen cannot enter leaves and be transported to roots and rhizomes (similar to enclosing shoots in a 100% N₂ atmosphere in the respirometry system; see Materials and Methods). Therefore, mowing to stubble may be an effective control strategy in low-level intertidal areas that are submerged for long periods of time.

Table 2. The percent cover of *S. anglica* tillers regrowing following different mowing treatments. Ground-cover estimates were made 22 days following mowing. Shown is the mean \pm SD(n) for each. The significance level indicates differences based on a one-way analysis of variance ($\alpha=0.05$).

Treatment	% area covered by living plant material	Significance Level (ANOVA, $\alpha=0.05$)
Mowed to Stubble the Previous Year	0.000 \pm 0.000 (3)	c
Mowed to Mud	1.600 \pm 2.074 (5)	c
Open Mudflat	0.000 \pm 0.000 (3)	c
Mowed to Stubble	10.400 \pm 10.164 (5)	b
Intact (unmowed) <i>Spartina anglica</i>	100.000 \pm 0.000 (3)	a

CONCLUSIONS

In the Pacific Northwest, *Spartina* can proliferate in places native species cannot because it possesses adequate physiological mechanisms to transport oxygen and thus overcome highly reducing sediments. Survival in an anoxic environment is dependent on processes to supply oxygen to submerged tissues. Therefore, if oxygen-transport processes can be inhibited, *Spartina* would not be able to survive in its current areas of invasion. Control strategies that prevent oxygen transport to underground tissues would be very successful in managing unwanted *Spartina*.

It appears that mowing can affect some aspects of oxygen-transport physiology in *S. anglica*. Anaerobic metabolism increased in *S. anglica* root tissue following a “mowed to mud” treatment. However, these effects were quickly reversed as plants began to grow back.

ADH activities soon decreased back to pre-mowing levels following any mowing treatment. Mowing plants to stubble did not appear to have any effect on oxygen-transport physiology in *S. anglica*. No significant differences were detected in *S. anglica* root aerenchyma following mowing to stubble. Similarly, oxygen transport and ADH levels (dependent on internally-supplied oxygen) were not affected in treatments mowed to stubble.

Other factors could be important in studying the physiology of mowed plants. The removal of shoots will decrease photosynthesis, which in turn decreases the carbon supply, energy supplies, and nutrient uptake (Edwards and Walker, 1983). Plants must then expend energy to regrow tissues despite a shortage of carbon and energy resulting from decreased photosynthesis. These factors may be important to fully understand the effects of mowing and remain an area for future investigation.

Following either mowing to mud or mowing to stubble, *Spartina* regrowth was observed within 22 days (Table 2). Removal of above-ground *Spartina* tissues by a single mowing does not affect the plants enough to cause death. The ADH activities indicate oxygen can still reach submerged tissues after mowing, albeit at decreased amounts in treatments mowed to mud. Stored carbon is quickly used for regrowth and new tillers are soon present. Therefore in most cases, removal of above-ground biomass by mowing is not an effective long-term strategy for the control of unwanted *Spartina*. Mowing can be useful for controlling seed set (Vickery et al., 2001), and may be practical for controlling the growth of *Spartina* by reducing photosynthetically active tissues (Sheley et al., 2003). If *Spartina* is mowed, mowing plants down to mud level appears to be slightly more successful for control efforts. Porewater sulfide levels remain low, ADH levels are temporarily increased, and regrowth is much slower than treatments mowed to stubble.

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