ABSTRACT

Title of Document: PLANT PRODUCTIVITY AND COMPETITIVE RESPONSE TO PRESCRIBED FIRE IN MID-ATLANTIC BRACKISH MARSHES

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Prescribed fire may increase productivity of some brackish marsh species. An understanding of the mechanisms behind this stimulatory effect is important for land managers to maximize the benefits to the ecosystem. I found that canopy removal is the dominant mechanism through which fire stimulates biomass production in the marshes at the Blackwater National Wildlife Refuge in Dorchester County, Maryland. The stimulatory effect of canopy removal was stronger in sedge-dominated systems than grass-dominated systems. Faster sprouting sedge species may be able to take fuller advantage of light and soil temperature increases following canopy removal than later-sprouting grass species. Results of a greenhouse study indicated that canopy removal gives sedges a competitive advantage over grasses. These studies have numerous implications for land managers using anthropogenic disturbances as a management technique. Canopy-level disturbances, such as fire may increase productivity in sedge-dominated marshes *and* may suppress grass species in mixed compositions.

PLANT PRODUCTIVITY AND COMPETITIVE RESPONSE TO PRESCRIBED FIRE IN MID-ATLANTIC BRACKISH MARSHES

By

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Table of Contents

List of Tables

Chapter 1

Chapter 2

Chapter 3:

Appendix C:

List of Figures

Chapter 2

Chapter 3

Appendix A

Appendix C

Chapter 1: Literature Review

Contents of Literature Review

1. Introduction

This literature review will provide appropriate background information on the impetus for studying the vegetation response to prescribed fire in mid-Atlantic brackish marshes. In order to adequately tell the story, I will begin with the current state of coastal marsh loss in the United States and the main factors influencing marsh loss worldwide. From there, it is important to understand the biotic and abiotic processes taking place within the marsh that can guard the marsh against loss in the face of the suite of natural and anthropogenic factors causing losses. Marsh accretion will be described in detail as well as the impact that biomass production has on accretion. The goal of the background section is to provide the reader with sufficient information about the processes, plant communities, study sites, and current management practices to think critically about the more complicated interactions discussed in later portions of the review.

Later sections will discuss the current state of knowledge of fire’s impact on accretion rates as well as the dominant mechanisms behind those impacts. These are the sections of the review that this thesis will address directly. That will segue into the competitive interaction of marsh species and relationships between plant community compositions and environmental characteristics. Finally, I will review how plant species respond to disturbance and how plant competition is influenced by disturbance. This literature review will make the case that this thesis is the next logical step in our understanding of the processes involved in marsh loss and that the goals of the thesis are important to the broader topic of coastal marsh loss.

2. Background

2.1 Marsh Loss

Globally, it is estimated that 50 percent of wetlands have been lost due to anthropogenic or natural phenomena since 1780. In the United States, the loss is on the same order as the global loss (Mitsch and Gosselink 2007). Coastal wetland losses are primarily due to development of the coasts, pollution, hydrologic modification, and seawall construction (Mitsch and Gosselink 2007). Nearly 41 percent of the coastal wetlands in the lower United States are concentrated in Louisiana (Turner 1990). By the early 1980's Louisiana had already lost 46 percent of the wetlands that were estimated to be present in the 1780's (Dahl 1990). In Maryland, there has been a loss of 73 percent of wetlands since the 1780’s (Dahl 1990). Many of the wetlands of Maryland and the Chesapeake Bay region are tidal marshes. Even after the advent of stringent wetland protection laws, coastal tidal marshes remain especially affected because losses often result from indirect anthropogenic impacts (Mitsch and Gosselink 2007).

2.1.1 Sea Level Rise

Global climate change impacts nearly all habitats and ecosystems to various degrees. Of particular concern is an increase in the rate of sea level-rise (SLR) due to both the thermal expansion of the oceans and the melting of glaciers and ice sheets as temperatures rise (IPCC 2007). The latest Intergovernmental Panel on Climate Change (IPCC) report predicts that sea levels will rise 17 to 58 cm by 2090 (IPCC 2007). Land-based ice melting from Greenland and Antarctica was not included in the IPCC model, so many believe that the predicted rise is severely underestimated

(Overpeck *et al.* 2006, Rahmstorf 2007). One well-respected projection incorporates land-based ice melting and predicts 75 to 190 cm of rise by 2100 (Vermeer and Rahmstorf 2009). One critical outcome of SLR as a result of global climate change is its effect on coastal and estuarine marsh systems. Located at or just above mean sea level, estuarine marshes are extremely vulnerable to rising seas. The historically low rate of SLR since the last ice age is believed to be responsible for the formation of coastal marshes present today (Rabenhorst 1997, Warren and Nearing 1993). Rabenhorst (1997) asserts that SLR and the inundation of uplands gradually transforms soils from predominantly mineral, upland soils, to organic-rich marsh soils through increased flooding and slower rates of organic matter decomposition. In other words, sea level has risen slowly over time and coastal marshes were formed and have survived through a migration of the marsh/upland border (Titus 1991).

At an increased rate of SLR, the marsh/upland ecotone will need to migrate faster in order for coastal marshes to persist. Increased coastal development and the continued use of common shoreline armoring practices, such as bulkheads, however, inhibit marsh migration and play a role in determining whether marshes are able to keep up with SLR. As a result, marsh shorelines stand to be subject to retreat by erosion or drowning (Titus 1991, Schwimmer and Pizzuto 2000). An increased rate of SLR, in combination with other factors such as land subsidence, erosion, saltwater intrusion, and invasive species herbivory, is already contributing to significant marsh loss (Stevenson *et al.* 2000). The Sea-Level Rise Affecting Marshes Model (SLAMM) indicates that at a fairly conservative rate of 1 m of SLR, 88 percent of the brackish marshes of the Chesapeake Bay region could be converted to open water within the century (Glick *et al.* 2008).

2.1.2 Land Subsidence

Land subsidence refers to any loss of elevation or “sinking” of the land. To accurately distinguish the processes responsible for subsidence, this phenomenon should be thought of as a combination of both deep subsidence and shallow subsidence (Cahoon *et al.* 1995). Shallow subsidence (Cahoon *et al.* 1995) refers to the difference between vertical accretion and surface elevation as referenced by a deep subsurface datum. Processes such as mineral and organic matter deposition, compaction, shrink-swell, and decomposition can contribute to shallow subsidence (Cahoon *et al.* 1995). These shallow subsidence processes will be discussed at length in section 2.2 of this review.

Deep subsidence can be driven by a number of factors, both natural and anthropogenic (Kennish 2001). Isostatic subsidence, one means of deep subsidence, is a geologic process that occurs as the Earth’s crust sinks into the Athenosphere as a result of added mass to a region. This is an issue in the Mississippi River Delta region where huge sediment loads can influence the subsidence rate (Roberts 1997). Isostatic rebound can also have a significant effect on deep subsidence. During the initial growth and formation of glacial ice sheets, the mantle material beneath the glaciated area was displaced outward. After melting occured, these bulges that formed in unglaciated areas begin to subside (Lambeck and Chappell 2001). This is a concern in the mid-Atlantic region of the U.S. where deep subsidence occurs due to rebound in the formerly glaciated northeast. Other contributors to local deep subsidence are oil and gas and groundwater withdrawal. Groundwater withdrawal causes subsidence as the sedimentary layers between aquifers compress as the water pressure decreases (Johnson and Morris 1962). In areas with buried peat layers, organic materials are subject to oxidation as groundwater is withdrawn (Stevenson *et al.* 2000), leading to deep subsidence and loss of surface elevation. The impacts of resultant increased rates of deep subsidence on coastal marshes can be substantial. In coastal Louisiana, local subsidence of 2 cm has been attributed to oil and gas removal (Martin and Sedengecti 1984). A combination of oil, gas, and groundwater withdrawal has contributed to a loss of close to 11,000 ha of wetlands in the Galvaston Bay estuary (White and Tremblay 1995). In the Chesapeake Bay region, it has been suggested that groundwater withdrawal has significantly contributed to the rate of deep subsidence (Stevenson *et al.* 2000).

2.1.3 Erosion

Marsh shorelines are increasingly subject to erosion as wave action works in concurrence with other factors attributed to marsh loss, such as herbivory and saltwater intrusion. Erosion of marsh soils below the living root zone is an important consideration; while it may contribute little to plant stress, it may be a significant driver of marsh loss (Nyman *et al.* 1994). In this case, it is hypothesized that localized diebacks create small ponds in which the living root zone collapses. Nyman *et al.* (1994) suggest that as the marsh attempts to mend itself, the pace of accretion will be faster on the edges compared to the bottom of the pond. Over time, the living root zone migrates to a point above the pond bottom and erosion occurs, undercutting the marsh surface. Similarly, other mechanisms responsible for marsh loss due to pond formation have been documented. In such situations, wave action in the ponds in the direction of the prevailing winds elongates these ponds over time until complete marsh islands are lost (Stevenson *et al.* 1985, DeLaune *et al.* 1994).

2.1.4 Saltwater Intrusion

As sea levels continue to rise, waters of higher salinity will begin to inundate marshes further up stream than were previously affected. This is of particular concern in tidal areas. Many of these marshes are composed of species that are intolerant of saltwater or are evolutionarily adapted to a particular salinity regime. Saltwater intrusion can cause a significant amount of plant stress that influences plant primary production and can lead to diebacks and marsh erosion (Spalding and Hester 2007, Salinas *et al.* 1986). In a greenhouse mesocosm experiment where salinities were manipulated, Spalding and Hester (2007) found that increases in salinity of 4 parts per thousand (ppt) and 6 ppt led to significant declines in growth and eventual death of two common marsh plant species. They also found that increased flooding (an impact likely to couple with saltwater intrusion) exacerbated the stress and mortality.

2.1.5 Herbivory

Herbivory in marshes leaves affected areas devoid of vegetation and exposes them further to erosive forces. Grazing by mammals, such as muskrat (*Ondatra zibethicus*), nonnative nutria (*Myocastor coypus*), and waterfowl (e.g. snow goose, *Chen caerulescens*), is a major concern in coastal marshes (Willner *et al.* 1979, Pendleton and Stevenson 1983, Pendleton *et al.* 1985, Stevenson *et al.* 2000). Muskrats consume standing live and dead plant material as well as roots and rhizomes of many marsh plants. Based on analysis of stomach contents, Pendleton and Stevenson (1983) speculate that as plant stems become seasonally unavailable, the muskrat's diet shifts towards belowground material. Pendleton *et al.* (1985) implicate muskrat herbivory in the creation of interior ponds within thinning marsh that lead to increased erosion and complete marsh loss. Hunting and trapping of muskrats is one means by which populations have been abated.

It is estimated that around the 1930's or 40's, nutria were introduced to the marshes of the U.S. from South America (Willner *et al.* 1979). Nutria feed predominantly on roots and rhizomes of marsh plants. As many of these plants reproduce vegetatively, loss of rhizomes contributes to major plant diebacks (Willner *et al.* 1979, Stevenson *et al.* 2000). In the absence of natural predators, factors leading to nutria mortality are limited to extreme winter weather conditions and hunting and trapping. In Blackwater National Wildlife Refuge of the Chesapeake Bay region, an extensive nutria eradication programs was established with significant successes. The refuge reported successful eradication in 2005 (Cahoon *et al.* 2010). However, nutria herbivory continues to be a problem in other regions without the means to combat the problem.

2.2 Marsh Elevation and Accretion

For long-term viability, coastal marshes must remain at the same relative elevation as the tidal range (Reed and Cahoon 1999). Therefore, as the rate of SLR increases, survival of coastal marshes is dependent on their ability to accrete, or build vertically. Marsh vertical accretion has been defined as the vertical dimension of marsh soil formation (Cahoon *et al.* 1995) and is driven by a combination of the input of mineral sediment and organic matter (Cahoon *et al.* 1995, Neubauer *et al.* 2002, Redfield 1972, Rooth *et al.* 2003, Warren and Niering 1993). The buildup of materials through vertical accretion can be thought of as a source of natural capital that contributes to marsh resilience, or capacity of the system to respond to disturbance and maintain normal functionality (Cahoon and Guntenspergen 2010). To accurately depict marsh elevation dynamics, the term *relative sea level-rise* (RSLR) is often used, which refers to the eustatic SLR plus the local subsidence rate (Cahoon *et al.* 1995, Morris *et al.* 2002). Several researchers contend that as long as marsh accretion is greater than RSLR, a marsh will remain above water and survive (Cahoon *et al.* 1995, Stevenson *et al.* 1986, Nyman *et al.* 1990, 1993, 1995).

Vertical accretion rates alone should not be considered a surrogate for tracking surface elevation change because autocompaction, or the compression of peat beneath its own weight (Kaye and Barghoorn 1964), and a suite of other factors controlling shallow subsidence, such as shrink swell and decomposition (Cahoon *et al.* 1995), can cause the marsh surface to lose elevation regardless of positive vertical accretion rates. For this reason, accretion rates are traditionally calculated with respect to a marker soil horizon while surface elevation is calculated with respect to a deep subsurface benchmark. The most widely used method of measuring surface elevation and accretion is through the use of the Sedimentation-Erosion Table or the Surface Elevation Table (SET) (Boumans and Day 1993, Cahoon *et al.* 2002a,b). The SET model measures shallow subsidence by sinking a reference pipe 3-5 m deep into the marsh surface as a benchmark. Several rods are dropped from a crossbar on the SET to the marsh surface and the distance between the surface and the crossbar are recorded. Surface elevation is monitored by evaluating the change in this distance. At the same time, a marker horizon is present, and accretion is measured by evaluating the length of the new soil column above the marker (Boumans and Day 1993, Cahoon *et al.* 1995, 2002a). Shallow benchmarks are also commonly used to quantify changes in the living root zone (Cahoon *et al.* 2002b). These new methods take subsurface processes into account in an attempt to alleviate the problems that arise from assuming a 1:1 relationship between vertical accretion and surface elevation (Cahoon *et al.* 1995). Understanding these subsurface processes and the mechanisms that drive accretion can help land managers address coastal marsh loss.

2.2.1 Mineral inputs

Mineral sedimentation is a key component to coastal marsh vertical accretion. Particularly in tidal areas, accretion is aided by mineral sediment that falls out of suspension or is trapped and accumulates on the marsh surface. Some marshes near the river channels in the Mississippi River Delta region accrete due to the accumulation of mineral sediment that was once suspended in the flowing river. Recently, there has been a considerable decrease in the rate of this mineral sedimentation as the River is now forced down a reinforced channel, directing much of the sediment load to be deposited off the continental shelf (Stevenson *et al.* 1988, Delaune *et al.* 1990).

Regionally, mineral sedimentation rates are generally higher in salt marshes than in brackish and fresh marshes (Delaune *et al.* 1990, Nyman *et al.* 1990). Locally, mineral accretion rates vary with respect to distance from tidal creeks as well as tidal frequency and magnitude (Reed *et al.* 1999, Delaune *et al.* 1990). As one might expect, areas nearest to tidal creek channels see higher accretion rates than areas on the marsh interior (Delaune *et al.* 1990). Using Cs^{137} profiles, Delaune *et al.* (1978) found that the accretion rate near a tidal creek was almost twice that of the inland marsh. When surveying accretion rates of several marsh types, Hatton *et al.* (1983) found the average accretion rate of the streamside levees to be 1.3 cm yr^{-1} while adjacent marsh interiors accreted at just 0.31 cm yr^{-1}. However, in areas where tidal and channel velocities are high, sedimentation can occur at a greater rate in marsh interiors as heavy flows push more sediment to the interior (Reed *et al.* 1999). Higher tidal amplitude and velocity can also contribute to accumulation of coarser sediments that are less prone to compaction (Stevenson *et al.* 1986).

Vegetation can also play an important role in mineral accretion rates. A fibrous rhizome and root mat formed at the soil surface is important in trapping mineral sediments (Erwin *et al.* 2006, Stevenson *et al.* 1988, Rooth *et al.* 2003). Litter deposition can also encourage sediment accumulation from tidal flows (Frey and Basan 1978). Rooth *et al.* (2003) found that due to its high primary productivity, litter deposition, and stem density, the invasive *Phragmites australis* significantly increased sediment accumulation in tidal marshes.

Mineral input to marsh soils can also affect plant growth by introducing allochthonous nutrients such as nitrogen, calcium, potassium, and phosphorus to the substrate as well as, under the right conditions, provide cation exchange sites for sorption of orthophosphate (Patrick and Khalid 1974). The introduction of mineral sediment may also be important in reducing sulfide toxicity in salt marsh environments. Nyman *et al.* (1990) suggest that of the introduction of iron to the system through mineral sediment is necessary in salt marshes in order to precipitate sulfides that are toxic to plants and more prevalent at higher salinities under reducing conditions. Since reduction of sulfide from sulfate increases with increasing salinity, they argue that rates of mineral inputs must remain high in salt marshes in order to avoid vegetation die-back and ultimately marsh loss.

The relative contributions of mineral matter and organic matter to marsh vertical accretion have been a topic of interest to many researchers (Turner *et al.* 2000, Erwin *et al.* 2006, DeLaune *et al.* 1990, Nyman *et al.* 1990, 1993, 2006). In a meta-analysis of accretion rates along the East Coast and Gulf Coast of the U.S., Turner *et al.* (2000) found that while inorganic sedimentation is correlated strongly with soil bulk density (r^2=0.92), its correlation with overall accretion is very modest (r^2=0.22) while organic matter has a much stronger correlation with accretion (r^2=0.59). Others have suggested that higher rates of mineral sedimentation are necessary for survival of marshes of the Mississippi Delta region, as their formation was dependant on mineral inputs (Delaune *et al.* 1990). While many areas historically relied upon mineral inputs to drive accretion, changes in local hydrology and sediment loading in streams and rivers have impacted these marshes such that there is limited mineral sediment influx and accretion is now driven primarily by organic inputs (Kearney and Stevenson 1991, USDOI 2006).

2.2.2 Organic matter inputs

In many marsh systems, organic accumulation is the primary driver of vertical accretion. Nyman *et al.* (2006) found a strong correlation between organic matter accumulation and vertical accretion in a stable and deteriorating region of marsh (r^2=0.696 and r^2=0.876, respectively) but no relationship between sediment accumulation and vertical accretion in stable and deteriorating regions of marshes in coastal Louisiana. Additionally, using ^{137}Cs profiles, Nyman *et al.* (1993) found variations in vertical accretion to be explained only by variations in organic matter accumulation in marshes of coastal Louisiana.

Organic inputs can accumulate from aboveground and belowground sources. At the soil surface, senesced plant material and other plant litter are deposited; when inundated with water decomposition is slowed and organic material accumulates under anaerobic conditions (Pendleton and Stevenson 1983, Cahoon *et al.* 2006). In mangrove systems, Cahoon *et al.* (2006) report that vertical accretion is correlated (r^2=0.71) with standing stock of plant litter.

Accretion can occur aboveground through other processes, such as accumulation of algal mats or aerial roots (Cahoon *et al.* 2006). Nyman *et al.* (2006) cited the formation of aerial or aquatic roots just above the soil surface as the primary mechanism behind vertical accretion via vegetative growth. They hypothesize that as relative sea level rises, the belowground soil roots are subject to prolonged anoxic conditions, resulting in the growth of these aquatic roots in a thick mat just above the current soil surface where oxygen is more abundant. Over time, these roots become the soil roots as new aquatic roots form in later years (Nyman *et al.* 2006).

Another aboveground source of organic matter is allochthonous organic material carried in by mineral sediments. Cahoon and Reed (1995) found a small, but significant relationship between accumulation of organic matter and duration of flooding (r^2=0.33, P=0.0067) in a Mississippi salt marsh. They attributed this to allochthonous organic matter as they also saw a correlation between mineral sediment and duration of flooding (r^2=0.45, P=0.0009, Cahoon and Reed 1995).

Root and rhizome growth, death, and decomposition are also important inputs of organic matter to marsh soils. If root production is greater than decomposition, organic matter will accumulate sub-surface and this expansion of the root zone can lead to increases in surface elevation (Cahoon *et al.* 2006, Stevenson *et al.* 1985). Gross *et al.* (1991) found that live belowground biomass of *Spartina alterniflora* was correlated with growth of aboveground leaves and stems (R=0.93) and that live belowground biomass was concentrated in the top 10 cm while dead biomass extended to 15 cm deep in the soil.

The importance of organic additions to marsh systems may lie in the volumetric difference between organic matter and equivalent mass of mineral sediment. Turner *et al.* (2000) found a 10:1 volumetric leverage of organic matter over mineral sediment in a meta-analysis of organic and inorganic contributions to accretion. This increased volume helps marsh soils to gain elevation. Root growth may contribute directly to surface elevation of marshes. Cahoon *et al.* (2006) found a small, but significant correlation between root production and surface elevation (r^2=0.44, P=0.0038). Conversely, reductions in sub-surface growth can cause declines in elevation (Cahoon *et al.* 2006). Stressors such as increased flooding can potentially induce declines in root growth. This can create a positive feedback loop in which low accretion leads to more flooding which, consequently, further decreases plant production and vertical accretion (Nyman *et al.* 1993). Delaune *et al.* (1990) estimate that if belowground organic matter was not replaced yearly, there would be an increase of 0.5 to 1.0 cm yr^{-1} to the rate of RSLR.

Due to differences in primary productivity between of coastal marsh plant species, their relative contribution to accretion may differ (Roman and Daiber 1984). In a study of underground biomass profiles, Gallagher and Plumley (1979) found strong differences in increment and turnover time of belowground carbon inputs of several coastal marsh species, suggesting that the belowground input and contribution to soil organic matter is dependent upon the species present. Warren and Niering (1993) suggest that shifts in plant species zonation could affect accretion as the influence of organic matter to accretion may depend on the plant species present. Communities of *S. alterniflora* and forbs, for example, have lower stem, root, and rhizome densities than high-marsh communities, which would both directly and indirectly decrease accretion rates.

Marshes must produce peat in a thickness greater than the subsidence rate for elevation to build and keep pace with rising sea level (Cahoon *et al.* 1995). This section has outlined several mechanisms by which these organic additions can occur. Management techniques that can increase aboveground and belowground biomass production and in turn increase the rate of accretion could be extremely important to land managers in order to reduce marsh declines. Research should focus, therefore, on ways to maximize organic additions (increasing above and belowground production), or reduce organic declines (decrease decomposition and fight peat collapse) for these marshes to remain viable.

2.3 Brackish Marsh Vegetation

Brackish and salt marsh vegetation must be able to tolerate saline stress and, consequently, these areas are typically dominated by only a few grasses, sedges, rushes, and succulent dicotyledons (Adams 1963). In brackish marshes, *S. americanus, S. patens,* and *D. spicata* commonly co-occur where salinities range from 5-10 ppt (Gabrey and Afton 2001, Allan 1950, Sipple 1979, Broome *et al.* 1995) and water table depth ranges from about -10 to +10 cm (Broome *et al.* 1995, Allan 1950, Palmisano and Newsom 1967, Sipple 1979). Despite the relative lack of diversity, these species vary in photosynthetic pathways (Saunders *et al.* 2006), plant canopy architecture (Turiztin and Drake 1981), and growing season length (Sipple 1979). Given the relative low species diversity of these systems, a brief background of four of these species is reasonable and warranted in this review. **Section 6** of this review will cover the effects of fire on brackish marsh vegetation.

2.3.1 *Schoenoplectus americanus*

Schoenoplectus americanus (Olney's threesquare, threesquare bulrush, chairmaker's bulrush) is a perennial, rhizomatous, C_3 sedge (Family: Cyperaceae) that is abundant in brackish marshes and commonly associated with *S. patens, D. spicata, S. alterniflora,* and *Schoenoplectus robustus* (saltmarsh bulrush). It commonly grows along the Atlantic and Gulf Coasts but is also found in the arid west (Sipple 1979). *S. americanus* is a valuable food source for muskrat, Canada geese, and snow geese. The rhizomes are the preferred forage for each of these species. It is also a prime wintering grounds for snow geese in marshes of the Gulf Coast, making up about 90% of its diet over winter months (Sipple 1979). *S. americanus* can be 0.5-

3.0 m tall (Fernald 1950) and primarily spreads by rhizomes and rootstocks (Martin and Uhler 1951, Sculthorpe 1967). It grows in poorly and very poorly drained organic soils typically at water levels of 5-10 cm above the soil surface (Ross and Chabreck 1972). *S. americanus* typically grows in salinities of 0-15 ppt (Sipple 1979). *S. americanus* flowers from late June to September in the mid-Atlantic region (Tatnall 1946) and by early July in Louisiana (Palmisano and Newsom 1967). New sprouts from rhizomes typically occur when soil temperatures exceed 60°F (15.5°C; Sipple 1979), but have been noted to occur in the winter in the Gulf coast (Allan 1950). *S. americanus* is considered a highly productive species. Darmondy (1975) found it to be a better organic matter producer than *Typha latifolia* (broadleaf cattail) as soils of *S. americanus* had an average of 68 percent organic matter. According to Palmisano and Newsom (1967), 97 percent of the roots of *S. americanus* occur in the top 15 cm of the soil. *S. americanus* is considered co-dominant with grass species such as *S. patens* and *D. spicata*; however, it may assume temporary dominance because these grasses have slower growth rates (Lynch 1947). Other factors influencing the successional dynamics of *S. americanus* and its response to disturbances (e.g. fire) will be discussed in **Section 6** of this review.

2.3.2 *Spartina patens* and *Distichlis spicata*

Spartina patens (saltmeadow cordgrass) and *Distichlis spicata* (saltgrass) are perennial, warm-season, C_4 grasses (Family: Poaceae) commonly found in salt and brackish marshes of the East and Gulf Coast of the United States. *S. patens* is considered the most prevalent species in the vast wetlands of the Mississippi River Delta, accounting for roughly 50 percent of the total marsh vegetation (Walkup

1991). *D. spicata* also has a range that extends into inland salt marshes, saline flats, deserts, and grasslands of the western U.S. (Hauser 2006). It is considered ubiquitous in New England salt marshes (Niering and Warren 1980). *S. patens* is an important species for wildlife as it is used for forage or den habitat for many species, but under climax conditions can become too dense for waterfowl (Allan 1950). *S. patens* ranges in height from 0.3 to 1.5 m and primarily grows vegetatively from slender rhizomes (Duncan and Duncan 1987). *S. patens* can grow in salinities of 1.2 to 39.1 ppt but thrives in low salinity and water level (Palmisano and Newsom 1968). *D. spicata* ranges in height from 0.15 to 0.45 m and is extremely dense in pure stands. Growth occurs in tidal marshes at salinity of 0.3 to 39 ppt with the optimum reported as 11.8 to 17.1 ppt (Adams 1963). *D. spicata* generally grows in poorly to very drained soils (Cooke *et al.* 1993) but can withstand periodic drought and complete inundation of all aboveground biomass for up to 30 days (Walkup 1991). The roots of *S. patens* and *D. spicata* are aerenchymatous, allowing sufficient oxygen to the rhizosphere for mycorrhizal fungi associations to exist, and were found to reach a depth of 42 cm in a Connecticut salt marsh (Cooke *et al.* 1993). However, Bertness (1991) suggests that *S. patens* is not as adept at oxidizing it's rhizospere than other salt marsh species. So it often declines in prolonged high water. Walkup (1991) reported that 88.9 percent of roots and 99.9 percent of rhizomes of *D. spicata* in the top 12 cm of tidal marsh soils in Louisiana. *D. spicata* is a shade-intolerant species (USDA 2006) and is effective at colonization after disturbance in tidal marsh environments (Allan 1950, Allison 1995). Hansen *et al.* (1976) found that in western grasslands, *D. spicata* growth rate is highest in early spring when air temperature is cool and soil moisture is high. *S.*

patens has historically been grazed as it is a highly productive forage, however, if disturbance increases, *D. spicata,* an undesirable forage species, will increase (Allan 1950). Adams (1963) found a significant association (α=0.01) between *S. patens* and *D. spicata* in salt marshes of the Atlantic Coast. Photosynthetic rate in *D. spicata* has been shown to be higher at higher light intensities in a controlled growth chamber experiment (Kemp and Cunningham 1981). On the other hand, Warren and Brockelman (1989) found a negative correlation between salinity and photosynthesis in a field and a greenhouse study (R=0.68 P=0.001 and R=0.90 P=0.001, respectively). This means that net primary production and growth is lower in *D. spicata* growing at high salinities.

2.3.3 *Spartina alterniflora*

Spartina alterniflora (smooth cordgrass) is a large, perennial, warm season, C_4 grass which is physiologically adapted to coastal salt marshes. It is considered important cover for waterfowl, wading birds, shorebirds, and muskrats (Webb *et al.* 1985) and an important food source for West Indian Manatees (*Trichechus manatus*) and snow geese (Allan 1950, Walkup 1991). *S. alterniflora* can reach a height of 8 feet (2.5 m), but is often only 16 inches (40 cm) in high salt marshes (Duncan and Duncun 1987, Niering and Warren 1980). In fact, *S. alterniflora* has two distinct height forms: a tall form, occurring along creek fronts, and a short form, occurring in inland areas. These two forms are thought to be associated with differential tidal flushing (Niering and Warren 1978). *S. alterniflora* typically dominates the “low marsh” vegetational zone (below mean high water) because it is adapted to conditions of high water and high salinity that many other species (*S. patens* and *D. spicata*) cannot tolerate (Bertness and Ellison 1987, Bertness 1991). It forms dense, monotypic stands in salt and brackish marshes in mid to high tide level (Bertness 1991). It spreads prominently by rhizomatous growth. Gallagher *et al.* (1984) found 74 percent of the rhizomes occurred in the top 15 cm of the soil.

As *S. alterniflora* can occupy up to 98 percent of the plant cover in many Louisiana marshes (Edwards and Proffitt 2003), primary productivity of this species is of great importance to the health and maintenance of these marshes. Net aboveground productivity of S. alterniflora marshes in Louisiana ranges from 750 g m^{-2} yr^{-1} to 2600 g m^{-2} yr^{-1} depending on the method used (Edwards and Mills 2005) Edwards and Mills (2005) also found root to shoot ratios of 6.85 and 2.10 in two natural marshes of Louisiana. This high biomass production aboveground and belowground underscores its importance to accretion as a biomass producer. *S. alterniflora* will not grow in soils of bulk density less than 0.20 g cm^{-2} (DeLaune *et al.* 1978). Assuming all aboveground biomass is incorporated into the surface soils (0-5 cm) of at least 0.20 g cm^{-2}, accretion rates should equal roughly 3.75 to 14 mm in the marshes reported by Edwards and Mills (2005). In a meta-analysis of accretion rates, Hatton *et al.* (1983) found that accretion rates in *S. alterniflora* marshes range from 3 to 18 mm yr^{-1} (mean=7.7, median=5.6) along the Atlantic seaboard, in agreement with the rough calculation performed above. Therefore, aboveground productivity is very important to accretion in *S. alterniflora* marshes. Erwin *et al.* (2006) found that *S. alterniflora* marshes also form a dense, fibrous root mat that helps to trap and stabilize sediments important for marsh vertical accretion.

Table 1: Summary of characteristics of brackish marsh plants. Cites Sipple 1979, Duncan and Duncan 1987, Bertness and Ellison 1987, Bertness 1991, Broome et al. 1995.

	Common Name	**Photosynthetic Pathway**	**Family**	**Height Range (m)**	**Salinity tolerance**	**Water table tolerance**
S. americanus	threesquare bulrush	C3	Cyperaceae	0.5-3.0	Tolerance declines with increasing salinity	Moderate to high tolerance
S. patens	saltmarsh cordgrass	C4	Poaceae	0.3-1.5	Moderate tolerance	Low tolerance
D. spicata	saltgrass	C4	Poaceae	0.15-0.45	Moderate to high tolerance	Low to moderate tolerance
S. alterniflora	smooth cordgrass	C4	Poaceae	$\leq$0.4 short $\leq$2.5 tall	High tolerance	High tolerance

2.4 Blackwater National Wildlife Refuge

Brackish marsh loss is particularly troubling in the 25,000 acres of wildlife habitat in lower Dorchester County, MD that comprise Blackwater National Wildlife Refuge (Blackwater). Dorchester County contains 40 percent of Maryland's wetlands (Pendleton and Stevenson 1983) and is considered home to the largest concentration of breeding bald eagles (*Haliaeetus leucocephalus*) on the East Coast north of Florida (USDOI 2006). Since the 1930's, Blackwater has lost over 2000 hectares of marshland (Cahoon *et al.* 2010). With use of the SLAMM model, Glick *et al.* (2008) projected that 68-98 percent of the marshes of Dorchester County, MD will be lost by 2100. Though managers have taken an aggressive approach to eradicate invasive herbivores (e.g. nutria) and have experimented with restoration using salvaged dredge materials, the physical and biological processes involved in marsh elevation dynamics are at the heart of the marsh loss problem at Blackwater and should be the focus of management practices (Cahoon *et al.* 2010).

The first documentation of marsh loss came in the 1938, when the first aerial photograph of the refuge was taken, indicating break-up and deterioration of inland areas. Following this revelation and with the use of subsequent aerial photographs, the USGS determined that some 5700 acres (2300 ha) had been lost between 1938 and 1979 (Pendleton and Stevenson 1983). Stevenson *et al.* (1985) assert that much of the open water at Blackwater, referred to as "Lake Blackwater," began as small ponds within the marsh. They hypothesize that, over time, wave action in the ponds in the direction of the prevailing winds elongated these ponds until complete marsh islands were lost. In addition, a road was constructed in the early 1900's that bisects the marshes of Blackwater without any culverts for 10 km. As a result, flow is restricted and the upper and lower portions of the marsh are essentially isolated from one another. Some suggest that this limits sediment input and contributes significantly to marsh loss at Blackwater (Pendleton and Stevenson 1983, Stevenson *et al.* 2000). Pendleton and Stevenson (1983) found that marsh loss increased upstream of the road after raising and paving was completed in the 1960’s. They also found that increased sedimentation might have contributed to gains in marsh areas downstream from the road. Stevenson *et al.* (2000) suggest that the road construction led to increased flow rates in the channels resulting in increased bank erosion and sediment loads leaving the upstream portion of the marsh. This and the lack of a strong tidal creek network support the assertion that Blackwater is a “sediment starved” system (Stevenson *et al.* 2000). Lack of mineral sedimentation in Blackwater marshes underscores the importance of organic matter inputs to allow vertical accretion to keep pace with RSLR.

2.5 Prescribed Fire in wetlands

Prescribed fire is an inexpensive means of land clearing and is a widely used land management technique utilized to promote wildlife habitat, reduce fuel loads, and facilitate hunting and trapping. Fires ignited by lightning were historically fairly common in many marsh communities (Pyne 1995). However, Cohen (1974) found that historically, fire was restricted to a few “fire prone” plant communities. In coastal Louisiana, the use of fire as a management tool is noted as far back as 1719 in an effort to facilitate travel (Pratz 1758). In terms of current marsh management efforts, fire can be used to maintain wetland graminoids, at the expense of woody shrubs that would otherwise begin to dominate, or to set back aggressive plant and animal species and allow more desirable species to propagate (Auclair *et al.* 1973, Buele 1979). Bradbury (1938) suggests that prescribed fire helps to suppress mosquito populations by opening the plant canopy and allowing birds to prey on larval stages. In tundra wetlands, fire has been seen as a way to increase the depth of active soil layers by localized permafrost melting (Bliss and Wein 1972, Buckley 1958). In coastal marshes, the main historical role of fire was to facilitate hunting and trapping (Cartwright 1942, Allan 1950, Hoffpauer 1968).

In coastal marshes, there are three basic types of burns: peat burns, root burns, and cover burns (Lynch 1941, Hoffpauer 1968, Nyman and Chabreck 1995). Peat burns are generally accidental or lightning-induced, as they have no positive benefits to the marsh. They occur when the soil is dry and can cause significant damage to marsh soils, resulting in declines in elevation. Root burns occur when a fire is hot enough, or the water table is low enough for plant roots to be damaged. Root burns are sometimes conducted intentionally as a technique for eradicating unwanted species but they can also occur in marshes where fire is uncommon and roots have grown up into litter that gets consumed during the burn. Cover burns are the most common form of prescribed fire. A cover burn is performed when the water table is just above the surface and removes only senescent plant material and litter (Hoffpauer 1968, Nyman and Chabreck 1995). Prescribed fire can benefit wildlife by encouraging species that comprise important sources of food (Lynch 1941, Hoffpauer 1968) and improving habitat (Schlichtemeier 1967, Vogl 1967). Perkins (1968) suggests that the type of wildlife encouraged by fire is dependent upon the season of the burn. In the marshes of the Gulf coast and the mid-Atlantic, prescribed fire is said to encourage the growth of *S. americanus*, a plant favored by muskrat. Continued application of fire shifts *S. americanus* to dominance over species such as *S. patens* and *D. spicata* (O'Neil 1949, Chabreck 1981, Sipple 1979, Pendleton and Stevenson 1983). Hoffpauer (1968) stated that in a system where *S. patens* dominates over a low density of *S. americanus* or *Schoenoplectus robustus*, a complete reversal in wildlife species dominance is probable. The mechanisms that may cause these types of species composition changes will be discussed in **Section 6** of this review. Because of differences among requirements of wildlife in marshes, Hackney and de la Cruz (1981) suggest a management approach of rotationally burning sections of a marsh to encourage diversity in cover and wildlife.

Though prescribed fire is an inexpensive management practice that offers many benefits to wildlife and habitat, there are some downsides to burning. The carbon emissions from burning organic-rich wetlands can be quite high (Poutler 2006). Coastal brackish marshes, under normal conditions, are usually carbon sinks. Churma *et al.* (2003) found that tidal saline wetlands remove an average of 210 g C $m^{-2}yr^{-1}$. Combustion of plant materials would not only introduce a significant source of carbon dioxide to the atmosphere, it may decrease the ability of wetlands to sequester carbon by removing the aboveground organic input that sustains these systems. Poulter *et al.* (2006) found that, globally, peatland wildfires emit 0.32 petagrams (one peta gram is equal to 10^{15} g) of carbon during drought years. They also calculated that individual fires emit between 1 and 3.8 teragrams (one teragram is equal to 10^{12} g) or 200 to 11000 g C m^{-2}, far offsetting the sequestration potential.

While these fires are likely unintentional and difficult to extinguish, it underscores the potential for fires in organic systems to emit large amounts of carbon to the atmosphere. In forests, prescribed burning was found to decrease the carbon emissions by reducing the buildup of detrital material that would make wildfires more intense (Houghton *et al.* 2000). Such a budget for prescribed fire in wetlands has not yet been preformed but, due to the increasing interest in the role of wetlands as greenhouse gas sources and sinks, it is warranted.

3. Fire effects on accretion and elevation

Rising sea levels and rapid coastal marsh loss has brought much attention to the topic of the effect of fire on marsh elevation and accretion. As described previously, the combination of standing dead plant litter and plant roots is a major driver of vertical accretion. Since prescribed fire consumes much of the standing dead biomass that would otherwise be deposited on the surface and contribute to accretion (Gabrey *et al.* 2001, Pendleton and Stevenson 1983), it is reasonable to question whether accretion rates may slow in marshes under fire management (Daiber 1974, Nyman and Chabreack 1995).

Pendleton and Stevenson (1983) attempted to estimate the loss of aboveground biomass to fire by harvesting vegetation before and immediately after burning a brackish marsh in Dorchester County, MD. They found that burning removes an average of 379 g m^{-2} (66.8 percent) and 459.5 g m^{-2} (62.4 percent) of the standing dead biomass from the system in two consecutive years of burning. Assuming burial and complete incorporation of all of the biomass lost by burning, this would result in an increase of approximately 3.28 mm to the marsh surface via accretion. These assumptions neglect losses due to decomposition, leaching, and export from the system due to storms, among other losses. Therefore, this number is a severe overestimate, but demonstrates the potential for aboveground material to be a significant contributor to vertical accretion (Pendleton and Stevenson 1983).

Ford and Grace (1998) conducted a study where 10 by 10 m plots were arbitrarily established in a marsh in Louisiana. Plots were either burned or not burned in the fall for two consecutive years. After the second year, biomass was harvested from all plots and compared between burned and unburned. They found that after two years of fire management, total (live + dead) biomass was significantly (P=0.003) decreased across several plant community types. However, the inclusion of dead aboveground biomass and lack of attention given to belowground inputs in this study may have obscured any stimulatory effect of fire on new growth. Shay *et al.* (1987) found that fall and spring burns increased stem density of *Phramites australis*, but the weight of each stem was less than half pre-burn levels, indicating no net gain in biomass following burning.

Fire can also be potentially harmful to marsh roots and rhizomes since roots may migrate into accumulated dead material on the surface and be damaged during a burn (Lynch 1941, Nyman and Chabreck 1995). Even when damage to the root zone is avoided during a burn, if water levels rise above the height of the remaining plant stubble for a sufficient period of time after a burn, the flow of oxygen will be cut off from the root zone and can lead to root mortality (Hoffpauer 1968). Given these concerns, the effect of fire on accretion rates has been questioned (Nyman and Chabreck 1995).

In a study examining the effects of hydrological management on coastal *S. patens*-dominated marshes of Louisiana, Flynn *et al.* (1999) compared managed marsh units to unmanaged units with respect to soil and plant characteristics. In addition to hydrological management, the units were also under fire management. The authors found significant differences amongst many of the soil and nutrient characteristics (see **Section 4** of this review), and although there was a significant increase in total aboveground biomass resulting from hydrologic management, burning resulted in a 51 percent decrease in total biomass (P=0.0002). Belowground production was not measured in this study, so any potential fire effects belowground were not realized. These studies underscore the concerns that fire can decrease litter accumulation and soil organic matter accumulation thereby having potentially negative effects of vertical accretion.

However, studies have also shown that fire can increase plant primary productivity and biomass production of several species (Christianson and Wilbur 1993, Gabrey *et al.* 2001, Hackney and de la Cruz 1981, 1992, Nyman and Chabreck 1995, Pendleton and Stevenson 1983). The extent of biomass production stimulation is largely a factor of burn season and plant species composition (Chabreck 1981, Laubhan 1995). De la Cruz and Hackney (1981) found that burning and harvesting of a needle rush (*Juncus roemerianus*) marsh increased aboveground primary productivity 21 to 48 percent in the following growing season.

Despite increases in biomass associated with burning, it has been suggested that increased soil temperatures and nutrient availability following fire may increase the rate of organic matter decomposition which could partially or totally negate the positive biomass effects of prescribed fire (Cahoon *et al.* 2004). However, some studies have found no increase in soil macronutrients following burning in moist-soil impoundments (Laubhan 1995) and others have suggested that since fungal colonization of soil ultimately leading to decomposition occurs via plant stems, removing the aboveground material could limit colonization and decrease decomposition rates (Cahoon *et al.* 2004). Therefore, the effect of fire on decomposition rates is likely related to site-specific characteristics.

Although increases to primary productivity alone are presumed to have positive elevation and accretion effects, the full picture of fire’s effects on elevation can only be obtained by using a direct measure of surface elevation. Cahoon *et al.* (2004) used SET's to determine differences in elevation between one burned and one unburned 50 by 50 m plot. Prior to establishment, the study site was impacted by continuous flood waters from a tropical storm. Vegetation mortality was high and the site was in danger of experiencing peat collapse as a result. Following the controlled burn, surface elevation, mineral sediment accretion, soil organic matter volume, soil bulk density, percent organic matter, and vegetative cover were measured. Both treatments saw declines in elevation for the first five months after the prolonged flooding (deemed the "collapse phase"). However, the burned treatment declined at a significantly slower rate than the unburned treatment. Following the collapse phase, both treatments began to recover. The burned treatment gained elevation at a faster rate than the unburned treatment. Soil organic matter volume of the burned treatment was more strongly correlated with elevation (r^2=0.40, P=0.0001) than the unburned treatment (r^2=0.32, P=0.001) during the recovery phase. The authors hypothesized that fire indirectly increased soil organic matter by stimulating root growth, slowing decomposition, or both.

In an ongoing study at Blackwater, Cahoon *et al.* (2010) are using SET's to evaluate the effect of the refuge's fire program and burn frequency on surface elevation. Treatments are (1) control, not burned; (2) burned annually; (3) 3-5 year burn frequency; (4) 7-10 year burn frequency. SET measurements are taken three times each year and incorporate a marker horizon and shallow benchmarks to evaluate shallow and deep subsurface processes. Standing crop biomass is harvested from subplots and stem density, plant height, and C:N ratio is obtained from the aboveground biomass. Belowground production is estimated using the ingrowth core method. The cores are harvested annually to obtain an estimate of root production.

Since the 1970’s Blackwater has implemented annual burning on most of the marsh area. Therefore, treatments of 3-5 year, 7-10 year, and no burns represent a release from annual burning pressure. They found slight positive trends in surface accretion in all treatments, but there were negative trends shallow subsidence leading to elevation declines in all treatments. Although elevation declines were present at all treatments, there were some interesting trends associated with the annual burn treatment. They found annual burning to increase vegetation growth aboveground and belowground helping to slow root zone collapse; the annual burn treatment also had the lowest elevation deficit of all of the treatments. However, annual burning significantly decreased standing dead biomass and litter production ($P<0.0001$) leading to lower surface accretion rates, so the positive root zone effects on marsh elevation were statistically insignificant. Their conclusion was that there were trends toward positive effects of annual burning; therefore, this management technique was not contributing to, and actually may slow, marsh declines at Blackwater (Cahoon *et al.* 2010).

These studies outline the importance of vegetation growth and, in particular, belowground biomass production in influencing elevation dynamics. Despite the positive biomass effects seen following prescribed fire, no significant elevation gains have been attributed to fire. Therefore, fair questions can be raised about the importance of further research into a management technique that has not proven to significantly affect elevation in rapidly subsiding marshes. In other words, if these marshes will be lost either way, why does fire matter? Given the results presented in Table 2, it is reasonable to suggest that over time, while these marshes will eventually be lost to open water, the stimulatory effect of fire may slow the pace of loss. In fact, these data suggest that the rate of shallow subsidence will be slower in the burned marsh than the unburned. This has the potential to extend the life of these marshes slightly.

Increasing the life of the interior marsh could have far reaching effects on wildlife if it allows for increased connectivity as marshes migrate into upland zones. Titus (1991) predicts that increased tidal flooding will shift entire wetland ecosystems landward. Specifically, dry land will convert to transitional wetland, transitional wetland will convert to high marsh, high marsh to low marsh, low marsh to mud flats, and mud flats to open water. This evolution of plant communities and soil characteristics would likely take many years. Hussein (2009) used a model that incorporated soil data related to rates of marsh migration to find that the time required

Table 2: Marsh elevation dynamics in burned and unburned marshes of Blackwater National Wildlife Refuge. From Cahoon *et al*. 2010.

	Burned	**Unburned**	**Significance**
Surface Accretion	5.9 ± 1.5 mm·yr^{-1}	9.7 ± 1.8 mm·yr^{-1}	NS
Elevation Gain (from SET)	4.0 ±1.5 mm·yr^{-1}	3.8 ± 0.6 mm·yr^{-1}	NS
Root Zone Subsidence	-0.4 ± 1.2 mm·yr^{-1}	-6.2 ± 1.0 mm·yr^{-1}	NS
Total Shallow Subsidence	1.7 ± 1.2 mm·yr^{-1}	5.9 ± 1.2 mm·yr^{-1}	NS
Aboveground Biomass	443 ± 24 g·m^{-2}	290 ± 31 g·m^{-2}	NS, P=0.06
Stem Density	3518 ± 357 stems·m^{-2}	1589 ± 236 stems·m^{-2}	P=0.02
Belowground Production (roots only)	122 ± 10 g·m^{-2}	58 ± 8 g·m^{-2}	P=0.0002

to convert coastal Ultisols (soils common in forested uplands of the mid-Atlantic and Southern U.S.) to Histosols (wetland soils with >40 cm of organic material at the surface) was 180 ± 35 years at the current rate of SLR in Dorchester County, MD. Although the time required was reduced by 63 percent when modeled at a predicted rate of SLR (0.6 cm yr^{-1}), the ecosystem services provided by these mature, albeit dying, interior marshes could be valuable as the marsh transitions upland. Therefore, management techniques that can even modestly extend the life of these systems by influencing elevation dynamics, specifically organic inputs, may be of tremendous net value to the future existence of these systems.

4. Fire and Plant Productivity

Many studies have noted that fire has a stimulatory effect on plant production (Cahoon *et al.* 2004, Christianson and Wilbur 1993, Gabrey *et al.* 2001, Hackney and de la Cruz 1981, 1992, Nyman and Chabreck 1995, Pendleton and Stevenson 1983). The mechanisms behind this stimulatory effect are not as well understood. Immediately following a cover burn, the plant canopy is absent, the bare ground is blackened and there is a release of nitrogen, phosphorus, calcium, magnesium, potassium, and chloride by ash deposition on the canopy floor (Hoffpauer 1968). These potential mechanisms, canopy removal, ash deposition, and increased soil albedo, and to what extent these mechanisms interactively affect biomass production are not well understood and worth further review.

4.1 Canopy Removal

Lynch (1941) associates the removal of the dense canopy of *S. patens* following a burn as a factor in the increased production of *S. americanus*. In a study investigating the mechanisms behind increases in biomass production following fire, Pendleton and Stevenson (1983, report) tagged culms of new growth of *S. americanus* in burned and unburned tracts of a brackish marsh in Dorchester County, MD. They found growth rates to be similar in each treatment, but the stems of *S. americanus* in the burned plots grew taller than those in the unburned plots. They hypothesize that if nutrient inputs were responsible for these differences in biomass production, one would expect that growth rate would differ between the treatments. Therefore, they hypothesized that canopy removal was responsible for increasing plant height in the burned plots because plants in the unburned plots have a slightly shorter growing season than those where the canopy has been removed.

To further test this hypothesis, during the next burn season, they included two 2 m^2 plots at each unburned site that was clipped at the time of a burn to remove the canopy. They noted that sprouting occurred two weeks earlier in the burned and clipped plots than in the unburned/unclipped plots. When new shoots came up in the unburned/unclipped plots, the growth rates were equal to or greater than the clipped and burned plots. Aboveground plant growth continued longer in the unburned/unclipped plots resulting in a statistically insignificant difference in plant height between all treatments. Samples of belowground biomass showed that production was higher in the burn plots than the clipped and unburned/unclipped plots. However, there was slightly more belowground biomass in the clipped compared to the unburned/unclipped plots suggesting that although aboveground growth in clipped plots was not different from unburned/unclipped plots, clipped plots may have produced more total biomass.

Canopy removal could affect biomass production by increasing soil temperature or by increasing light availability to new shoots. When standing dead plant material is left on an unburned marsh, new shoots must grow tall enough to penetrate the canopy before they can reach photosynthetically active radiation (PAR) for photosynthesis. Removing this canopy only requires new shoots to penetrate the soil surface to gain access to PAR. In a study on how changes in canopy structure affect photosynthetic efficiency, Turitzin and Drake (1981) found that as time passes, plants of brackish marshes shift from an erectophile (vertical leaves predominate) to a planophile (horizontal leaves predominate) architecture. Erectophile structure is known to be the more productive canopy structure (Turitzin and Drake 1981). They found that changes in canopy structure from erectophile to planophile structure can lead to declines in photosynthetic efficiencies. Therefore, marsh plants that do not need to penetrate a canopy of dead plant materials and can immediately take advantage of higher photosynthetic rates of an erectophile structure may produce more biomass than plants that may exhibit a more planophile structure as a result of the necessity to grow through the dead litter and sensesced canopy.

In a study of fire effects on microclimates and plant production in prairie grasses, Old (1969) set up treatments of (1) canopy clipped and removed, or “Clear cut,” (2) canopy clipped, removed, ashed in an incinerator, and reapplied, “Clear cut + Ash,” (3) canopy clipped and left in place, or “Cut and left,” (4) Vegetation undisturbed, “Undisturbed,” (5) clipped vegetation from clear cut treatment was ashed and spread onto surface, “Undisturbed + Ash,” and (6) vegetation burned, “Burn.” Root and shoot production, microclimatic data, and nutrient analysis data were collected. Based on shoot production and usable solar radiation of each treatment, percent efficiency was calculated for each treatment. Areas that were clear cut or burned maintained higher efficiency (0.85% and 0.89%, respectively) than undisturbed plots (0.65%). Burn treatments were shown to influence the solar radiation distribution. Solar radiation at 50 cm above the surface of the burned area more closely approached the 200 cm radiation levels (ambient) than did the undisturbed plots. Since burning also appeared to increase the 0 to 50 cm light intensity, Old (1969) suggests that photosynthetic efficiency of burned prairie grasses is increased. This could account for the increased productivity of burned vegetation.

As canopy removal allows more solar radiation to the soil surface (Old 1969), soil warming may occur in the upper part of soil following canopy removal (Sharrow and Wright 1977, Old 1969). Old (1969) found that burning increased temperatures from 50 cm aboveground to 5 cm belowground for much of the growing season. She found this to have a favorable effect on flowering response and also speculates that this increase in belowground temperature may stimulate microbial release of nitrogen and phosphorus by favoring the growth of nitrifying bacteria.

In a study of the temperature response of grasslands to prescribed fire, Sharrow and Wright (1977) used treatments of canopy removal (clipping), burning, and control and found that removing the litter (by either burning or clipping) significantly ($P<0.05$) increased soil temperatures by an average of 3.9°C at a depth of 8 cm. Soil temperatures from clipped plots did not vary significantly from burned plots. They measured soil properties in zones of root exclusion and areas occupied by plant roots. In root excluded areas they found accumulated soil nitrate to be significantly (a=0.05) higher in plots with no litter versus plots where litter remained (24.2 ppm with no litter, 18.1 ppm with litter). They also found that while soil nitrate in root occupied zones was significantly lower in burned plots than control (47, 25, and 17 ppm dry weight in burned vs. 94, 37, and 25 ppm dry weight for control at 0-2.5, 2.5-5.0, and 5.0-12.5 cm depths respectively), it did not differ significantly from the clipped plots (50, 21, and 17 ppm dry weight at 0-2.5, 2.5-5.0, and 5.0-12.5 cm depths respectively). This suggests rapid uptake of more available soil nitrate by vigorously growing plants in burned and clipped plots. This may be related to the soil temperature increase providing optimal conditions for both nitrifying bacteria and plant growth. DeLucia *et al.* (1992) found that increases in soil temperatures caused a nearly linear significant ($P<0.05$) increase in the specific utilization rate of soil nitrogen, a measure of efficiency of nitrogen usage up to a temperature of 30°C.

Canopy removal has been found to increase soil temperatures in the upper part of the soil (Sharrow and Wright 1977). This is the region (oxidized zone) where nitrifying bacteria are expected to occupy in wetlands (Mitsch and Gosselink 2007). The increase in soil temperatures and resulting increase nitrate availability may create optimal growth conditions for plants (Sharrow and Wright 1977, Old 1969, DeLucia *et al.* 1992). Once new shoots establish, they can take advantage of increase photosynthetic efficiency due to their erectophile architecture (Turitzin and Drake 1981, Old 1969). These processes related to canopy removal may be responsible for the increases in production recognized in burned plots.

4.2 Ash Deposition

Hoffpauer (1968) implicates ash deposition in an increase in aboveground biomass production following fire. Schmalzer *et al.* (1992) found increased nutrient availability in Florida marshes following burning. Ash deposition could also potentially affect soil temperatures by decreasing the surface albedo and absorbing more solar energy (Hoffpauer 1968). By comparing soil temperatures at burned sites to clipped sites and control sites, Sharrow and Wright (1977) found evidence that increased temperatures at the surface may have been minimally influenced by albedo, but was mostly affected by canopy removal since both clipped and burned plots had significantly higher temperatures. Temperatures of burned plots were only slightly higher than clipped plots for a short portion of the growing season.

In a study of irregularly flooded marshes of the Gulf coast, Faulkner and de la Cruz (1982) performed a nutrient analysis of marsh dominated by *J. roemerianus* and *Spartina cynosuroides* (big cordgrass) before and after a prescribed burn was conducted. Chemical composition of ash compared to plant tissue samples showed that nitrogen losses from burning were very high (over 90%) in both plant communities. This was likely caused by volatilization due to high burn temperatures (Qian *et al.* 2009). Potassium behaved similarly in both communities, losing approximately 50 percent fine particulates. Soil nutrient availability increased following burning, but only in the top 2 cm of the soil. The initial release of base cations had a transient effect on soil pH, raising it (from 5.9 ± 0.1 to 6.7 ± 0.4) following burning in the *S. cynosuroides* marsh. Soil calcium, magnesium, and phosphorus all increased following burning. Soil calcium increased 37 and 34 percent following fire in the *J. roemerianus* and *Spartina cynosuroides* marshes, respectively. Soil magnesium increased following fire in both marshes, but this increase was not realized until much later. After 29 days, there was a 15.2 percent increase from preburn conditions in the *J. roemerianus* marsh. In the *S. cynosuroides* marsh, a 3.3 percent decrease was found after 26 days, but a 28.5 percent increase from preburn levels was found after 68 days. Soil Phosphorus increased by 260 and 385 percent following fire in the *J. roemerianus* and *Spartina cynosuroides* marshes, respectively. Tissue samples of both communities showed higher levels of N, P, K, Ca, Mg, and Mn in the burned plots when compared to tissue samples of a reference unburned site. Flynn *et al.* (1999) also noticed differences in soil macro and micronutrients between burned and unburned management areas. Increases in nutrient availability from ash deposition were thought to be related to the relative earliness of spring growth when compared to unburned sites as well as the higher tissue nutrient concentrations of standing stock (Faulkner and de la Cruz 1982).

Nutrient input from ash deposition is likely a function of plant species composition, habitat nutrient availability, and ratio of live/dead biomass in the burned area (Debano and Conrad 1978, Gray and Dighton 2006). Another factor that could influence the nutrient availability in ash is the temperature of the burn. Qian *et al.* (2009) combusted marsh plant materials from the Florida Everglades at various temperatures to examine the changes in nutrient contents of the ash. Consistent with what was reported by Faulkner and de la Cruz (1981), Qian *et al.* found that ash burned at 150^{o}C is still yellowish in color and has retained most of its organic matter. From 150^{o}C to 250^{o}C, there is a significant loss of total nitrogen and ash turns a reddish-black color. At 350^{o}C, ash become black as organic matter begins to combust. Ash becomes white and total organic N was not detectable after burning at temperature of 450-550^{o}C. At this point, there was almost complete loss of all organic matter, total nitrogen, and total carbon from the ash via volatilization. Total phosphorus and total calcium are likely unaffected by temperature due to their high heat of vaporization. They reported that the effect of burn temperature on nutrient distribution in the ash varied with respect to plant species, nutrients in the soil, and leaf type (live/dead). The moisture content of the vegetation has also been found to significantly (α=0.01) affect burn intensity (Smith and Bowes 1974), implying that the moisture content of the plants will play an important role in the composition of nutrients deposited in the ash.

While nutrient losses from volatilization are dependent upon burn intensity, nutrients can also be lost from ash through fly ash deposition away from the burned site. Smith and Bowes (1974) attempted to quantify these losses by setting up an experiment in which plots were burned while a series of ash catching dishes were set up in transects ranging from 1 to 200 m from the edge of the burned site in the direction of the prevailing wind. Analysis of ground ash samples indicated nutrient losses of 40-50 percent – too high for volatilization considering the relatively low burn intensity (< ca. 500° C). Fly ash collection from the transects recovered 30.2% of the Ca, 28.0% of the P, 29.1% of the K, and 30.3% of the Mg lost from the ash. These data indicate that a significant proportion of the nutrients from the ash was incorporated into fine particulate fly ash and carried further than 200 m from the edge of the burn site.

Ash deposition has been found to increase nutrient availability in the upper part of the soil (Faulkner and de la Cruz 1982, Flynn *et al.* 1999). The increase in the abundance of these soil micro and macronutrients may be related to increased biomass production following burning. However, the species composition and intensity of the fire play a very important role in the relative abundance of these nutrients (Qian *et al.* 2009). In addition, site specific environmental characteristics (e.g. ratio of live to dead litter, Debano and Conrad 1978, Gray and Dighton 2006) or even weather conditions during a burn could influence the soil nutrient content as many nutrients are incorporated into fine particulates and carried offsite (Smith and Bowes 1974). Therefore, the effect of ash deposition on primary production is likely to be variable and site specific.

4.3 Other Factors

The ephemeral increase in soil temperature from the heat of the fire has been implicated in another common occurrence following fire in coastal marshes. Following continued application of fire, researchers have noted a shift in dominance from *S. patens* to *S. americanus* (O'Neil 1949, Chabreck 1981, Lynch 1941, Nyman and Chabreck 1995, Pendleton and Stevenson 1983, Ford and Grace 1998, Hackney and de la Cruz 1981). This phenomenon will be discussed in **Section 6** of this review. Hoffpauer (1968) hypothesized that this species shift is due to the shallower roots of *S. patens* compared to *S. americanus*, which may be damaged by the heat of the fire.

5. Tidal marsh vegetation zonation, successional dynamics, and competition

Specific vegetation patterns exist in wetland plant communities. Sometimes the boundaries can be quite sharp between community types or monotypic species stands. These patterns, or zonation, of marsh species are thought to be a function of a combination of topography, salinity, nutrients, and Eh. These patterns in vegetation have also been described as related to succession. As a result of overlap in many species' tolerances to environmental conditions (salinity, water table, etc.), competition between species ultimately drives plant zonation (Bertness and Ellison 1987, Niering and Warren 1980, Emery *et al*. 2000).

5.1 Vegetation zonation

Conditions in coastal tidal marshes require that species be adapted to salinity and periodic high water. As a result, there are relatively few species adapted to inhabit coastal marshes. Species vary in their tolerances to saline and or high water conditions and are therefore fairly predictably grouped into zones of species with common tolerances (Emery *et al.* 2000, Bertness and Ellison 1987, Niering and Warren 1980). This zonal structure is governed by resource stressors, competitive exclusion, and non-resource stressors like tidal flooding (Emerey *et al.* 2000, Tilman 1997, Bertness and Ellison 1987, Niering and Warren 1980). The general understanding of salt marsh zonation follows a conventional pattern of vegetation banding.

Many researchers document this pattern in the following way: *S. alterniflora*, a tolerator of high salinity and high water (Niering and Warren 1980, Adams 1963, Ungar 1998, Warren and Niering 1993, Bertness and Ellison 1987, Bertness 1991, Emerey *et al.* 2001), occupies the fringe or "low marsh" near tidal creaks channels subject to frequent inundation. This zone continues from the mean low water point (MLW) to the point of mean high water (MHW). At MHW, the vegetation shifts distinctly to *S. patens* dominance. *S. patens* is less salt tolerant and less tolerant to frequent inundation (Niering and Warren 1980, Adams 1963, Ungar 1998, Warren and Niering 1993, Bertness and Ellison 1987, Bertness 1991, Emerey *et al.* 2001). This zone is known as the “high marsh.” Within this high marsh zone, there are frequent changes in microtopography that may cause shifts in vegetation. For instance, minor depressions may shift to dominance by short form *S. alterniflora* since inundation may be more frequent in a depression (Niering and Warren 1980). Additionally, disturbed areas may be colonized by *D. spicata*, a species that coexists with *S. patens*, but is an efficient colonizer of disturbed areas (Allan 1950, Adams 1963, Niering and Warren 1980, Bertness and Ellison 1987). At the upper border, characterized by infrequent inundation and higher elevation, *Iva frutescens*, *Panicum virginatum*, and *Phragmites australis* may colonize. These species are relatively intolerant of salinity and inundation (Niering and Warren 1980).

This characterization of saltmarsh zonation is well accepted and documented in the literature. The distinct banding has been described as an observation of plant succession from emergent grasses to shrub ecotone (Allan 1950). However, because this assessment assumes ecosystem development will ultimately lead to a ‘climax’ regime, many have disputed this claim and consign more influence to environmental and biotic causes (Niering and Warren 1980, Bertness 1991, Bertness and Ellison 1987, Ungar 1998). Other species common to brackish marshes (*S. americanus*) are not considered as ubiquitous as those mentioned in the previous section and are therefore not included in the general model. Because of its importance to brackish marsh ecosystems and our experimental study, the tolerences and range of *S. americanus* will be discussed in this chapter.

The dominant factors affecting zonation are thought to be environmental: salinity and flooding depth. Bertness and Ellison (1987) found that the occurance of *S. patens* and *D. spicata* was rare below the point of MHW. They set up a series of transplant experiments to test each high marsh species' tolerance to low marsh conditions. Both *S. patens* and *D. spicata* experience reduced aboveground production following transplantation to the low marsh. They concluded that these species were not adapted to the high water, high salinity environment of the low marsh. Taking this one step further, Bertness (1991) used the same transplantation technique to discover that when placed into low marsh, *S. patens*' production was an order of magnitude lower for two years and the species did not survive the third year. He hypothesized that *S. patens* was not as adept at oxidizing its rhizosphere as *S. alterniflora* and thus cannot inhabit the low marsh.

In a brackish marsh of Quebec, Dechênes and Sérodes (1985) found that *S. americanus* has a very particular range of growth relative to submergence and salinity. A series of vegetation assessments indicated that, like *S. patens, S. americanus* cannot thrive in low marsh conditions. There, salinity in conjunction with submergence acts as a liming factor for its growth. In freshwater marshes, they document *S. americanus* tolerating submergence of 65 to 87%, while in brackish marshes, 33 to 37% submergence causes significant stress to the plant. They contend that if salinity were zero, *S. americanus* may be able to tolerate nearly 100%

submergence, but if salinity is raised to 15 or 20 ppt, the species may tolerate only 30% submergence, after which, mortality may occur.

Broome *et al.* (1998) tested the salinity and flooding tolerances of *S. americanus* and *S. patens* in a controlled greenhouse study. They used a factorial arrangement with three flooding levels (-10, +10, and +30 cm) and five salinity levels (0, 5, 10, 15, and 20 ppt). They then measured stem density, height, and biomass production response to the treatments. Contrary to the contention of Dechênes and Sérodes (1985), they found no significant salinity X depth interaction indicating that salinity and flooding depth were acting independently on production. Their results indicated that *S. americanus* biomass production declined with increasing salinity. While there was little change from 0, 5, and 10 ppt, production declined sharply above 10 ppt. Production of *S. americanus* was optimum at 10 cm, while -10 and 30 cm production was modestly lower.

S. patens showed modest decreases in production with increased salinity, although change was not significant. However, there were significant declines in stem length with increasing salinity. *S. patens* production showed sharp declines following increases in flooding depth. They note that *S. patens* “barely survived” the 30 cm depth treatment. They conclude that in the field, increases in salinity would likely decrease production of both species, but *S. americanus* would be more severely impacted. Increases in flooding depth would favor growth of *S. americanus* over *S. patens*.

Other factors such as nutrient availability, soil Eh, light availability, and interspecific competition also influence zonation. Bertness (1984, 1985) found that zonation patterns could be influenced by facultative animal associations. He found tall form *S. alterniflora* to be associated with ribbed mussels (Geukensia demissa) and that the mussel beds increased soil nitrogen, stimulating plant production. Fiddler crabs (Uca pugnax) have been found to be associated with increased production in *S. alterniflora* as well (Bertness 1985). He found that their burrows increased soil drainage, redox potential, and decomposition. When fiddler crab populations declined in that area, there was a 47% reduction in *S. americanus* biomass production.

5.2 Competition

Interspecific competition is an important factor controlling zonation in tidal salt marshes. Many researchers have pointed out that plant tolerances exhibit wide and variable ranges, but while zonation is governed by those tolerances, it is often expressed in the form of sharp boundaries. So what causes these boundaries to exist in zones where more than one species could theoretically tolerate? These upper and lower boundaries are often determined by interspecific competition between species adapted to high or low marsh conditions (Bertness 1991, Bertness and Ellison 1987, Ungar 1998 Emery *et al.* 2001). Plants adapted to saline environments are usually not competitive in freshwater environments, but as salinity increases, so does their competitive ability (Ungar 1998).

Bertness (1991) found that *S. patens* and *D. spicata* were rare in low marsh areas (below MHW) and that transplants also did not survive low marsh comditions. He also transplanted *S. alterniflora* to high marsh regions. These results were more complex. He found that transplants thrived in high marsh conditions when *S. patens* was clipped from the surrounding area. However, when *S. patens* was present, it eventually outcompeted *S. alterniflora* in the high marsh. He also found that many rhizomes of *S. alterniflora* extended past the MHW boundary, but no aboveground material grew due to competitive interactions with *S. patens*.

Some researchers have pointed to the ability of certain species to compete for resources such as light or nutrients as the reason for development of monotypic stands. Tilman (1986) suggests that its superior ability to compete for soil nitrogen and light allows *S. alterniflora* to florish in low marsh areas. Pidwirny 1990 found that *S. americanus* coexisted with Carex lyngbei in a narrow band representing the upper and lower elevational limits of the two species. However, in this zone, both species produced less biomass in this zone. He hypothesized that the two species were competing for light and soil nitrogen in this zone. He goes on to predict that in areas of low nitrogen and high light, *S. americanus* is competitively superior whereas high nitrogen, low light conditions favor C. lyngbei. In high light, moderate nitrogen conditions, both species coexist.

6. Disturbance and competition in brackish marshes

Disturbance is another factor that can control the composition of tidal marsh vegetation. Disturbances have the potential to suppress species, or in some cases, give certain species a competitive advantage. Disturbances can be catastrophic (killing all residents) or non-catastrophic (not a complete kill, but residents affected) such as many plant canopy disturbances (Platt and Connell 2003). Canopy disturbances could come in the form of herbivory, fire, or severe weather, for instance. Muskrat (*Ondatra zibethicus*) are known to consume standing live and dead plant material as well as roots and rhizomes of many marsh plants. Based on analysis of stomach contents, Pendleton and Stevenson (1983) speculate that as plant stems become seasonally unavailable, the muskrat's diet shifts towards belowground material. Thus, muskrat herbivory can be non-catastrophic (affecting only the plant canopy) or catastrophic (affecting roots and rhizomes; killing the vegetation). Other herbivores such as non-native nutria (*Myocastor coypus*) or lesser snow geese (*Chen caerulescens*) are heavy consumers of belowground material and account for more catastrophic disturbances (Willner *et al.* 1979, Miller *et al.* 2005). This level of disturbance in coastal marshes has been shown to result in re-colonization by grass species in the short-term (Miller *et al.* 2005, Bhattacharjee *et al.* 2007). Allison (1995) found that *D. spicata* was also especially adept at re-colonizing areas after small-scale sediment spoil disturbances that killed underlying vegetation. However, Bhattacharjee *et al.* (2007) noted that while grasses re-colonized in the short term, there was a shift from a grass-dominated to a sedge-dominated community several years after extreme muskrat herbivory.

Some species are understood to be better at tolerating disturbance or better equipped to invade disturbed areas. Bertness and Ellison (1987) report that dead plant materials (or wrack) rafted in by tides causes a disturbance by covering and killing underlying vegetation. In an assessment of plant communities, they found *D. spicata* was twice as common in disturbed areas than in randomly chosen areas ($P<0.0001$). They found that this species is especially adept at sending runners into areas of disturbance. The found it to dominate these areas for two year, after which it succumbed to competition from *S. patens*. They also found that *D. spicata* could survive under wrack for up to 10 weeks, far longer than other species such as *S. patens* and S. alteriflora.

Bertness (1991) found that artificial removal of dominant species from high marsh communities (*S. patens* and *D. spicata*) allowed some species normally associated with low marsh (*S. alterniflora*) to invade. The removal of these dominant species gave others with the ability to survive, but poor competitive ability, a chance to invade in the absence of competitive pressures. As time passed, these areas began to yield to competitive pressures and were eventually replaced with *S. patens* and *D. spicata* once again. This study has many parallels to disturbance used as a management technique to encourage the establishment of species with lesser competitive abilities.

6.1 Fire's influence on plant community composition

Platt and Connell (2003) modeled the effects of disturbances on directional replacement of plant species. They found that non-catastrophic disturbance affecting two or more species has the potential to change the rates of replacement ongoing at the time of disturbance if one species is less affected or recovers more quickly than another. In brackish marshes, *S. americanus*, *S. patens*, and *D. spicata* commonly co-occur where salinities range from 5-10 ppt (Gabrey and Afton 2001, Allan 1950, Sipple 1979, Broome *et al.* 1995) and water table depth ranges from about -10 to +10 cm (Broome *et al.* 1995, Allan 1950, Palmisano and Newsom 1967, Sipple 1979). Despite the relative lack of diversity, these species vary in photosynthetic pathways (Saunders *et al.* 2006), plant canopy architecture (Turiztin and Drake 1981), and growing season length (Sipple 1979). These differences in physiology have the potential to influence competitive interactions in the presence of canopy disturbances. *S. americanus* is thought of as a sub-climax species under normal conditions while *S. patens* and *D. spicata* are normally dominant (Sipple 1979). *S. patens* and *D. spicata* are known to create a dense canopy which shades out *S. americanus* and keeps it from establishing dominance (Hoffpauer 1968, Sipple 1979). However, under fire management, *S. americanus*, which grows better in cooler temperatures, is relieved from competitive pressure and is able to outcompete *S. patens* (Sipple 1979), a species normally suppressed by fire (Ford and Grace 1998).

The disturbance caused by prescribed fire is non-catastrophic and mainly confined to the canopy level. Cover burns are the most common form of prescribed fire; they are performed when the water table is just above the surface and remove only senesced plant material and litter (Hoffpauer 1968, Nyman and Chabreck 1995). Studies have shown that cover fires can increase plant primary productivity and biomass production of several species (Hackney and de la Cruz 1981, Pendelton and Stevenson 1983, Nyman and Chabreck 1995, Gabrey *et al.* 2001, Cahoon *et al.* 2010). This stimulatory effect may be associated with the mechanisms discussed in **Section 4** of this review**.** Pidwirny 1990 found *S. americanus* to be competitively superior to surrounding vegetation in conditions of high light, low soil nitrogen. This may indicate that competition for light is the dominant force affecting the growth of *S. americanus*. If this is true, canopy level disturbances that remove *S. patens* and *D. spicata* will relieve the species from competitive pressure and allow it to increase in production. This is consistent with the well-documented assumption that continued application of fire gives the marsh species *S. americanus* a competitive advantage over grass species (O'Neil 1949).

Additionally, *S. americanus* is known to exhibit the "phalanx and guerilla" strategies of clonal plant growth (Ikegami *et al* 2007, Lovett Doust 1981). Guerilla strategy occurs in areas of low resource availability such as when *S. americanus* is co-occurring with *S. patens* and *D. spicata*. It involves less branching of ramets and longer spacers to explore adjacent areas (Lovett Doust 1981, de Kroon and Knops 1990). When a disturbance removes the plant canopy, for instance, increasing the availability of resources (i.e. light), *S. americanus* can produce frequently branched ramets with shorter spacers to occupy local resource patches resulting in higher stem density, aboveground, and belowground production in the species (Lovett Doust 1981, de Kroon and Knops 1990, Ikegami *et al* 2007). *S. patens* and *D. spicata* have been found to increase in biomass following burning or mowing when faster growing species are not present (de Szalay and Resh 1997). To what extent plant canopy disturbances affect biomass production may differ as species composition varies.

Water level may also play a critical role in determining the way in which plants respond to canopy disturbances. Previous section of this review mentioned that *S. patens* is not well adapted for growth in high water (Bertness and Ellison 1987, Bertness 1991). Gabrey and Afton (2001) found that structural marsh management (or use of impoundments and water control structures to stabilize water levels and prevent salt water intrusion) used in combination with prescribed fire negatively affected *S. patens* production while burns in areas that were not impounded actually stimulated *S. patens* productivity. Other researchers have seen similar trends in grass species where canopy disturbances (burning, mowing) followed by prolonged periods of high water affect grass species negatively (de Szalay and Resh 1997, Smith and Kadlec 1985). Under high water conditions, these grasses either cannot survive (Smith and Kadlec 1985) or succumb to competitive pressures from faster growing plants that can handle high water such as *S. americanus* (Gabrey and Afton 2001). These grass species while impounded, but not burned, did not show declines in production (Gabrey and Afton 2001). These observations suggest that water level and disturbance may interactively affect productivity in marsh systems.

7. Summary

Prescribed fire is a common coastal marsh management technique in the Mid-Atlantic region. While this management strategy has many benefits (e.g. habitat maintenance, fuel load reduction, increased plant productivity), if it makes these heavily impacted coastal marshes more vulnerable to rising sea level, its future usage cannot be justified. While fire is known to have a stimulatory effect on some plant species which could lead to increased organic matter inputs, removing litter and senesced plant material will also decrease surface accretion. For fire to have a net positive effect on surface elevation, the organic matter increase must be greater than the losses to direct volatilization.

Understanding the mechanisms behind fire’s stimulatory effect on productivity will help managers maximize the biomass input and, in turn, maximize the benefits to the ecosystem. Canopy removal may allow more light to the surface warming the soil early in the growing season. This increased temperature could stimulate microbial activity increasing the rate of nitrification, benefitting the plants through increased nutrient availability. Plants may also benefit directly from the increased light at the surface. Ash deposition my deposit many plant available nutrients onto the marsh surface that plants can take advantage of. Because the nutritive quality of ash is highly dependent on the heat of the fire and species composition of the burned material, the influence of ash deposition on plant productivity is likely variable.

There is evidence that the brackish marsh sedge species, *S. americanus*, responds more favorably to fire than many grass species, *S. patens* and *D. spicata*. The disturbance caused by fire may influence the “normal” competitive interactions of these species. In the absence of canopy disturbances, grass species form a dense canopy that shades out the new shoots of the sedge species. This results in the grasses maintaining dominance over the sedges. However, when the canopy is removed, the sedges are released from competitive pressure with increased light availability at the surface. Under fire management, *S. americanus* is able to assume dominance over *S. patens* and *D. spicata*. Grasses may also respond favorably to canopy removal in pure stands. However, they tend to be sensitive to high water following canopy level disturbances which may further lead to declines in grasses if flooding depth remains high following fire.

Facing the threat of sea-level rise, marsh managers are concerned with increasing the adaptive capacity of these systems through increased inputs to elevation. Without increases in surface elevation to keep up with rising sea level, these coastal marshes could face a critical tipping point. Increased sea level will likely increase salinity which has been shown to decrease the growth rate of *S. americanus*.

If elevation cannot keep up and the flooding depth also increases, this decline in *S. americanus* could be coupled with a loss of flood-sensitive grasses. Such losses in the major species could cripple these marshes and could lead to significant losses to open water. However, if done properly, prescribed fire has the potential to increase belowground inputs and decrease the rate of shallow subsidence in marshes. If the rates of decline are slowed, these marshes may be able to maintain connectivity while migration to uplands occurs. Therefore, prescribed fire may subtly increase the adaptive capacity of these fragile systems.

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Chapter 2: Vegetation response to prescribed fire in Mid-Atlantic brackish marshes

Abstract

Prescribed fire is an effective and inexpensive means of land clearing that can provide many benefits to the management of coastal marsh ecosystems. Fire can have a stimulatory effect on biomass production that could stem from canopy removal, ash deposition, or a combination of these mechanisms during burning. This study was conducted to better understand the interactive effects of the mechanisms of fire on aboveground and belowground biomass production. The effects of canopy removal and ash deposition on biomass production were investigated in two manipulative experiments at Blackwater National Wildlife Refuge, Dorchester County, MD. Canopy removal increased biomass production above and belowground on non-burned sites, while canopy replacement of burned sites decreased biomass production above and belowground. Ash deposition showed no effect on biomass production. Sites dominated by *Schoenoplectus americanus* had a stronger biomass production response to canopy removal than those dominated by *Spartina patens* and *Distichlis spicata*. Aboveground biomass increased 40 % ($P<0.0001$) in plots with canopy removal than plots without. Belowground biomass was 2.6 times higher in plots with canopy removal than those without ($P=0.0044$). Following canopy removal, stem density of *S. americanus* increased by nearly 100% ($P<0.0001$) and *S. americanus* stems height decreased ($P=0.0414$) by 12 %. Canopy removal appears to be the dominant mechanism affecting biomass production response to prescribed fire at

these sites. Our results indicate that fires that maximize canopy removal in *S. americanus*-dominated, brackish marsh systems will maximize biomass production.

Introduction

Prescribed fire is a management technique utilized by land managers to promote wildlife habitat, reduce fuel loads, and facilitate hunting and trapping. Although burning coastal marshes has been a common practice in the U.S. since European settlement (Cartwright 1942, Allan 1950, Hoffpauer 1968, Nyman and Chabreck 1995), the effect of prescribed fire on marsh loss has come into question as total area of deteriorating or collapsing coastal marsh increases (Nyman and Chabreck 1995). Significant marsh loss and conversion to open water are occurring due to factors such as sea-level rise, land subsidence, erosion, saltwater intrusion, and invasive species herbivory (Stevenson et al. 2000). Faced with these threats, the long-term persistence of coastal marshes will be dependent on their ability to accrete, or build vertically. Understanding the effects of fire on vertical accretion is therefore important to coastal marsh sustainability.

Marsh accretion has been defined as the vertical dimension of marsh soil formation (Cahoon et al. 1995) and is driven by a combination of the input of mineral sediment and organic matter (Redfield 1972, Warren and Niering 1993, Cahoon et al. 1995, Neubauer et al. 2002, Rooth et al. 2003). As long as marsh accretion is greater than relative sea-level rise (the eustatic sea-level rise plus the local subsidence rate, Cahoon et al. 1995, Morris et al. 2002), a marsh will remain above water and persist (Stevenson et al. 1986, Nyman et al. 1990, 1993, 1994, Cahoon et al. 1995). Organic inputs can accumulate from aboveground and belowground sources. At the soil surface, senesced plant material and other plant litter are deposited and accumulate under anaerobic conditions (Pendleton and Stevenson 1983, Cahoon et al. 2006). Similarly, if root production is greater than decomposition, organic matter will accumulate sub-surface and this expansion of the root zone can lead to increases in surface elevation (Stevenson et al. 1985, Cahoon et al. 2006). Management techniques that can increase aboveground and belowground biomass production and, in turn, increase the rate of accretion could be extremely important to land managers in order to reduce marsh decline.

Cover burns are the most common form of prescribed fire; they are performed when the water table is just above the surface and remove only senesced plant material and litter (Hoffpauer 1968, Nyman and Chabreck 1995). Since prescribed fire consumes much of the standing dead biomass that would otherwise be deposited on the surface and contribute to accretion (Pendleton and Stevenson 1983, Gabrey et al. 2001), it is reasonable to question whether accretion rates may slow in marshes under fire management (Daiber 1974, Nyman and Chabreck 1995). Additionally, fire can be directly harmful to marsh roots and rhizomes that migrate into accumulated dead material on the surface (Lynch 1941, Nyman and Chabreck 1995) or indirectly harmful if water levels rise above the height of the remaining plant stubble after a burn and cut off the flow of oxygen from the root zone (Hoffpauer 1968).

However, studies have also shown that cover fires can increase plant primary productivity and biomass production of several species (Hackney and de la Cruz 1981, Pendelton and Stevenson 1983, Nyman and Chabreck 1995, Gabrey et al. 2001). Fire has been found to indirectly increase soil organic matter by stimulating root growth, slowing decomposition, or both, significantly slowing the pace of collapse and increasing the pace of recovery following tropical storm damage (Cahoon et al. 2004). Cahoon et al. (2010) found that annual burning significantly increases belowground production of roots compared to longer burning intervals and not burning altogether. They also noted trends toward decreased shallow and root zone subsidence in annual burn sites when compared to not burning.

While many studies have noted that fire has a stimulatory effect on plant production (Hackney and de la Cruz 1981, Pendleton and Stevenson 1983, Nyman and Chabreck 1995, Gabrey et al. 2001, Cahoon et al. 2004), the mechanisms behind this stimulatory effect are not as well understood. Immediately following a cover burn, the plant canopy is absent, the bare ground is blackened and there may be a release of nitrogen, phosphorus, calcium, magnesium, potassium, and chloride by ash deposition on the canopy floor (Hoffpauer 1968). These processes (i.e. canopy removal, ash deposition, and increased soil albedo), and to what extent they interactively affect biomass production, are not well understood and worth further review.

Ash deposition has been found to increase nutrient availability in the upper part of the soil following fire (Faulkner and de la Cruz 1982, Flynn et al. 1999). This increase in abundance of soil micro and macronutrients may be implicated in increased biomass production following burning. However, species composition and fire intensity play important roles in the relative abundance of these nutrients (Qian et al. 2009). In addition, site specific characteristics (e.g. ratio of live to dead litter, Debano and Conrad 1978, Gray and Dighton 2006) and weather conditions during a burn could influence the soil nutrient content, as many nutrients are incorporated into fine particulates and may be carried offsite (Smith and Bowes 1974). Therefore, the effect of ash deposition on primary production is likely to be variable and site specific.

Canopy removal has been found to increase soil temperatures in the upper part of the soil (Sharrow and Wright 1977). Because this region (oxidized zone) is expected to be occupied by nitrifying bacteria (Mitsch and Gosselink 2007), the increase in soil temperatures and resulting increase in nitrate availability may create optimal growth conditions for plants (Old 1969, Sharrow and Wright 1977, DeLucia et al. 1992). Removing the plant canopy may also allow plants to allocate new growth to roots and rhizomes instead of devoting resources to longer stems necessary to penetrate the senesced plant canopy to gain access to light. This could change the canopy architecture leading to differences in photosynthetic efficiency (Old 1969, Turitzin and Drake 1981). Additionally, in the absence of this dense canopy, plant species may have increased access to light, increasing in production (Sipple 1979, Ford and Grace 1998). These processes associated with canopy removal may be responsible for the increases in plant productivity.

Continued application of fire gives the marsh species *Schoenoplectus americanus* (three-square bulrush) a competitive advantage over slower growing species (O’Neil 1949, Lynch 1941, Chabreck 1981, Pendelton and Stevenson 1983, Nyman and Chabreck 1995). *S. americanus* is thought of as a sub-climax species under normal conditions while *Spartina patens* (saltmeadow cordgrass) is normally dominant (Sipple 1979). However, under fire management, *S. americanus,* which grows better in cooler temperatures, is relieved from competitive pressure and is able to outcompete *S. patens* (Sipple 1979), a species normally suppressed by fire (Ford and Grace 1998). Other findings indicate that fire may suppress *S. americanus* and increase *S. patens* and *Distichlis spicata* (Flores et al. 2011). Thus, to what extent canopy removal and ash deposition interactively affect biomass production may differ as species composition varies.

We conducted two manipulative experiments to determine to what extent two mechanisms, canopy removal and ash deposition, interactively affect aboveground and belowground biomass production in brackish marshes of Dorchester County, MD. The objectives were to find whether plots with ash deposition had greater biomass production than plots without, plots with canopy removal had greater biomass production than plots without, or whether there was an interaction between canopy removal and ash deposition in their effects on biomass production. The second experiment was employed to find whether burned plots with replaced artificial canopies had lower biomass production than control burned plots. The main response variables were aboveground biomass and belowground production.

Materials and Methods

Study Location

The Blackwater National Wildlife Refuge (Blackwater) consists of about 10,000 ha of tidal marsh, open water, and forest habitat in Dorchester County, MD, USA (38° 27′ 0″ N, 76° 7′ 12″ W). The dominant soil series are Bestpitch and Transquaking soils (Terric or Typic Sulfihemists) in the tidal marsh and Honga peat (Terric Sulfihemists) and Sunken silt loams (Typic Endoaqualfs) in the submerged upland areas (Soil Survey Staff 2010). Tides can range from roughly 30 cm above and below the surface, but typically are maintained in the range of 10 cm above and below the surface (Sipple 1979). Tides at Blackwater are primarily driven by wind. Because of regional hydrological modifications and the lack of a strong tidal creek network, Blackwater is considered a "sediment starved" system; in other words, accretion is primarily driven by organic inputs (Stevenson et al. 2000). Salinities range from roughly 5 to 15 ppt and the plant communities in the area of study dominantly consist of the salt marsh species *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller, *Spartina patens* (Aiton) Muhl., and *Distichlis spicata* (L.) Greene, with lower dominance of *Spartina alterniflora* Loisel. and *Juncus roemerianus* Scheele (USDA 2011). The study took place in interior tidal marsh under fire management. Blackwater currently has management blocks under differential fire regimes including annual burns and no burns. Because Blackwater has been conducting annual burns since the 1970's, the No Burn units represent a release from annual burning pressure.

Site selection

In early January 2009, two separate experiments were established. The first experiment was conducted at four sites in the 'No Burn' management regime. The second experiment was conducted on four sites within the 'Annual Burn' regime. Due to improper conditions, fire managers were unable to burn one of the sites during the study; so it was removed from the annual burn experiment. Plot establishment and data collection were identical in each experiment. On each site, 3 x 4 m plots were selected based on marsh surficial conditions and plant species composition. Areas

Table 1: Characteristics of each site in Annual burn and No burn experiments. Salinity and pH are averaged over the duration of the studies.

Annual Burn Sites				
Site	pH	Salinity (ppt)	Dominant Soil Series	Dominant plant species
1A	6.4	12.7	Honga	*S. americanus*
2A	6.4	10.2	Bestpitch & Transquaking	*S. americanus*
3A	6.4	9.7	Bestpitch & Transquaking	*S. americanus*
No Burn Sites				
Site	pH	Salinity (ppt)	Dominant Soil Series	Species Composition
1D	6.6	8.9	Sunken	*S. patens / D. spicata*
2D	6.5	7.6	Bestpitch & Transquaking	*S. americanus*
3D	6.6	8.8	Bestpitch & Transquaking	*S. patens / D. spicata*
7D	6.5	8.7	Bestpitch & Transquaking	*S. americanus*

with large holes, bare ground, or wildlife trails and dens were avoided. Plots were selected to have plant species compositions consisting of a mixed community of *S. americanus*, *S. patens*, and *D. spicata* though actual percent cover of each species varied greatly from site to site.

Each plot had a temperature logger installed at a depth of 5 cm in the soil. One of the three replicate plots per site was also equipped with a second logger at 20 cm. Pretreatment aboveground biomass was sampled from two 0.25 m^2 quadrats from an area adjacent to each plot that shared a similar species composition and percent aerial cover. Within each plot, we established a non-destructive sampling area (Fig. 1) where all non-invasive data collection, such as the species composition assessment, was performed. For the duration of the study, all of the invasive data collection, such as biomass harvest or installing instruments into the soil, was performed outside of the non-destructive zone. There was a 50-cm buffer around the perimeter where no sampling occurred. A well was established at each plot where water chemistry and water table height data were collected.

No Burn Experiment

Four treatments were established at the no burn sites: Control (no disturbance), Canopy Removal, Ash Deposition, and Canopy Removal + Ash Deposition. Treatments were randomized and replicated three times for a total sample size of n=12 on each of the four no burn sites. Canopy Removal was implemented 17 March 2009 by clipping the aboveground biomass of the entire plot. After clipping, there was roughly 3 cm of stubble remaining on the surface, resembling the condition after a controlled burn. Biomass from the clipped plots was used to make ash for plots

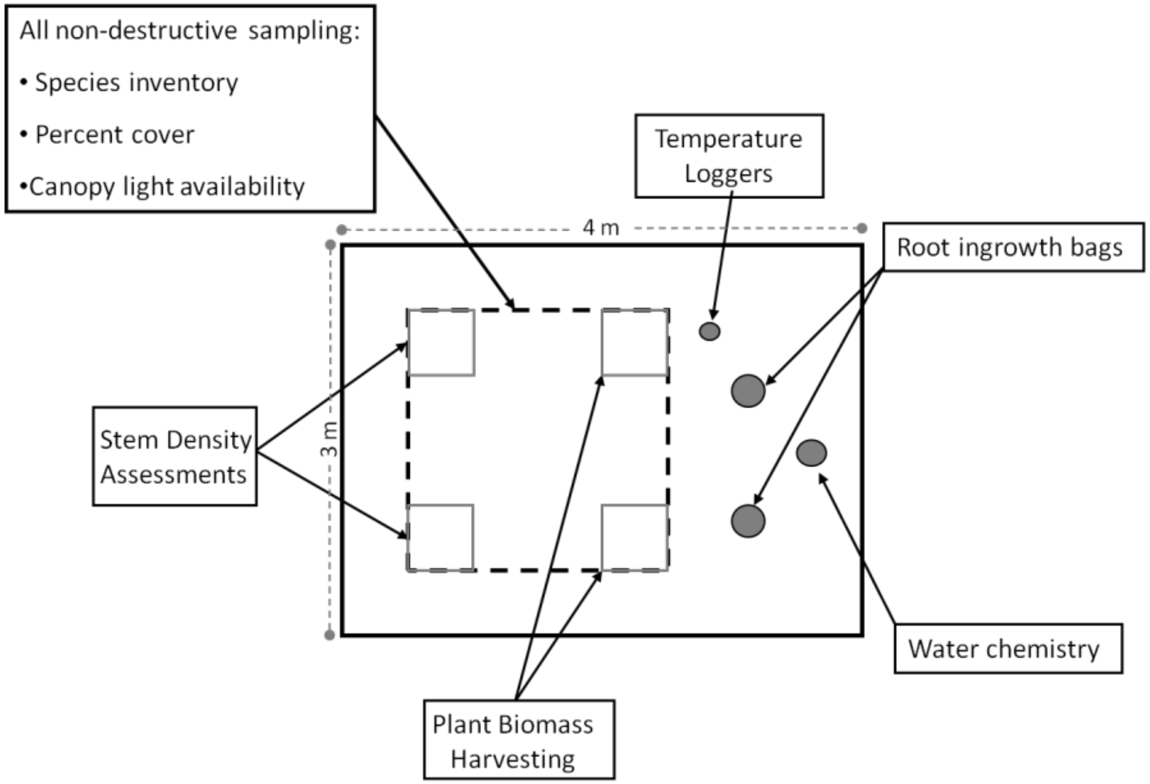

Fig. 1 Schematic of plot set-up. All plots were identical in Annual burn experiment and No burn experiment

treated with ash. Biomass was dried in an oven at 40°C. The clipped biomass from each plot was burned offsite in metal bins and the ash was collected. The ash of each site was homogenized and divided evenly, ensuring that each treatment received ash composed of the same species. The ash was deposited onto the surface of the Ash Deposition and Canopy Removal + Ash plots in April 2009. The ash was deposited when the water was below the marsh surface to prevent immediate dissolution and flushing away from the plot. It was distributed evenly using a 1 mm sieve.

Annual Burn Experiment

Plots were established prior to burning. Two treatments were established in the annual burn sites: Control (burned) and Canopy Replacement (burned with artificial canopy installed). Treatments were replicated three times for total sample size of n=6 at each of the three sites. After the fire managers conducted a burn, we created artificial plant canopies to cover the entire plot. Wood frames were constructed to cover the entire plot and hardware cloth was stretched across and fastened. The frames had legs that kept them approximately 15 cm off the ground. Canopies were assembled using plant material clipped from un-burned adjacent areas of the marsh that had similar species compositions to the burned sites. This material was transported to the treatment sites and inserted into the mesh of the cloth to resemble a natural canopy (Fig. 2). The goal was to establish similar species composition and percent aerial cover as was present pre-burn, however, after completion, light availability measurements indicated that the replaced canopies were slightly denser and allowed less light to reach the surface than a natural canopy (Miller et al. in prep).

Fig. 2 Photos of replaced canopy construction over burned marsh

Data Collection

Data collection was identical for both (annual burn and no burn) experiments. Throughout the study period, there were several variables that were measured on a regular basis. Water chemistry data (pH, temperature, salinity, conductivity) were obtained periodically throughout the study. Species composition, species percent cover and height, and photon flux above and below the canopy were measured regularly throughout the growing season. Solar photon flux was measured with a line quantum sensor to obtain an estimate of photosynthetically active radiation (PAR) above and below the plant canopy. Peak aboveground biomass was harvested in late July 2009 when plants were showing signs of senescence. Aboveground biomass from two 0.25 m^2 quadrats was harvested from each plot in July 2009. Stem density counts were performed by counting all stems of each species within two 0.25 m^2 quadrats in each plot. Biomass harvests and stem density counts only included growth from the current season. We installed two mesh root ingrowth bags (similar to the methods of Gallagher et al. 1984, Cahoon et al. 2003, and McKee et al. 2007) to estimate belowground production. The ingrowth bags were 5 cm diameter, 30 cm deep, and made of 2 mm nylon mesh. They were filled in the laboratory with super-fine sphagnum peat prior to deployment in April 2009. Native peat could not be used because it contained fine roots that would be indistinguishable from those established post-deployment. Root ingrowth bags were harvested in November and December 2009, presumably after root growth had ceased. Temperature loggers were removed and downloaded at the conclusion of the study in winter 2009/2010.

Laboratory analyses

Biomass was dried at 60°C and weighed to obtain total aboveground biomass ($g \cdot m^{-2}$) for each plot. The specimens were separated into categories of Grass or Sedge. *S. americanus* was the only species included in the Sedges while Grasses included *S. patens, D. spicata*, and *S. alterniflora*. Other species (e.g. *Juncus roemerianus* and some annual forbs) occurred in less than 2 percent of the plots and were placed into a separate "other" category and not included in analysis. Each category was reweighed to determine its contribution to the total biomass. Root ingrowth bags were harvested and stored at 5°C for processing. Ingrowth cores were cut into 10 cm segments; the contents were washed through a 1-mm sieve to separate the fine sphagnum peat from the belowground plant growth and washed. Contents were washed and separated into four classes: (1) rhizomes, (2) coarse roots (>2 mm), (3) fine roots (<2 mm), and (4) belowground plant tissue. Belowground material was dried at 60°C for 72 hours and weighed to obtain an estimate of belowground production for each plot.

Data Analysis and Hypothesis testing

An ordination analysis of species composition, soil bulk density, salinity, percent carbon, and percent moisture was performed using PC-ORD 5 for Windows (McCune and Mefford 1999). Main matrix variables were percent cover of *S. americanus, S. patens*, and *D. spicata*. The secondary matrix variables were salinity (averaged over the study period), soil bulk density (0-30 cm), and soil percent carbon at each plot. A two-dimensional NMS (Non-metric Multidimensional Scaling) ordination was run using the data in the two matrices.

There were two separate randomized complete block experiments within this study. The No Burn experiment was a two-way factorial arrangement consisting of 4 blocks with 3 replications per block. The Annual Burn experiment was a one-way arrangement consisting of 3 blocks with 3 replications per block. Variables were tested using analysis of variance (ANOVA). The inference space for this analysis was brackish, emergent marshes within the geomorphic landscape (drowned river valley) of lower Dorchester County, MD. Variations in marsh conditions were analyzed statistically as the block variable. Statistically significant block by main effect and block by interaction terms indicated that these processes operate differently across marsh conditions.

Results

No Burn Experiment

The No Burn experiment illustrated that aboveground and belowground biomass production increased following canopy removal. Belowground production was most affected in the 0-10 cm zone. There was no effect of ash deposition on biomass production.

Biomass Production. Aboveground biomass was 40 % higher ($P<0.0001$) in plots with canopy removal than plots without (Fig. 3a). Plots receiving canopy removal had 2.6 times more belowground production than plots that did not ($P=0.0044$; Fig. 3b). A significant site X canopy interaction ($P=0.0043$) in aboveground biomass production indicated that although the canopy effect was significant over the entire study, these effects were not uniform across sites. There was no effect of ash deposition when deposited onto undisturbed plots ($P=0.33$) or in

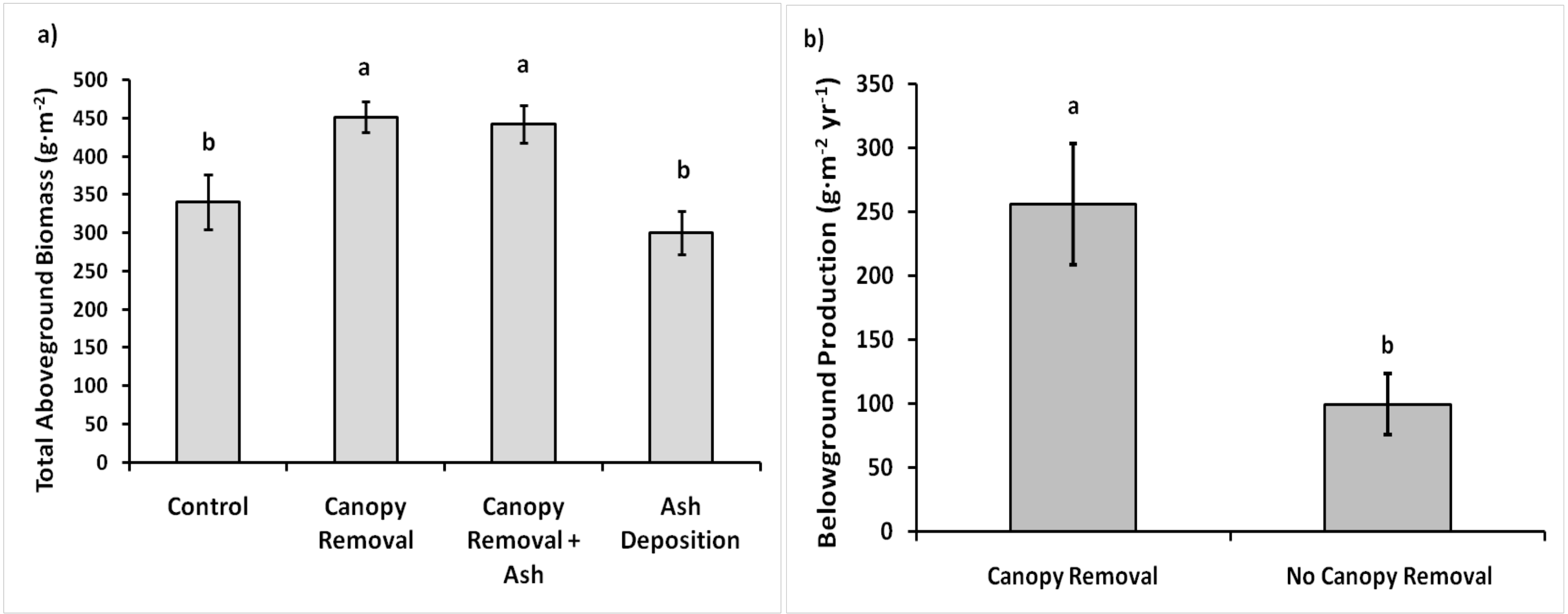

Fig. 3 Biomass production from all sites. **a)** Total aboveground biomass production, values represent the mean of 24 replicates (± standard error of the mean). Letters indicate the results of a Tukey Test; means with the same letter are not significantly different from each other (α=0.05). **b)** Belowground production, values represent the mean production to a depth of 30 cm of 48 replicates (± standard error of the mean) Letters indicate the results of an ANOVA; means with the same letter are not significantly different from each other (α=0.05)

interaction with canopy removal (P=0.54). Ash deposition did not affect belowground production (P=0.92). Additionally, there was no significant site X ash interaction, so ash deposition will not be included in further analyses.

Across all sites, total belowground production was 3.2 times higher in the 0-10 cm depth in plots with canopy removal than in plots without (P=0.0039, Fig. 4a). Canopy removal resulted in a 3.6 fold increase in rhizome biomass production in the 0-10 cm depth (P=0.0073, Fig. 4b), which accounted for most of the increase in total production. There was also a threefold increase in fine root production following canopy removal in the 0-10 cm depth (P=0.0039, Fig. 4c).

Species composition analysis. The ordination analysis (Bickford 2011) made clear what may have caused individual sites to respond differently to the treatments. Species composition of sites 2D and 7D was related to high *S. americanus* (sedge) percent cover. Sites 1D and 3D were variable, but more related to the percent cover of the grasses, *S. patens* and *D. spicata* than *S. americanus*. We therefore refer to sites 2D and 7D as sedge-dominated sites and 1D and 3D as grass-dominated sites. This ordination explained 92 % of the variability between our sampling sites. The ordination analysis is evidence that species composition was different between sites and may be related to the site X canopy interaction observed in biomass production. Therefore, to obtain a better understanding of the subtleties involved in the response to canopy removal, we grouped sites by species composition for further analysis.

At the grass-dominated sites (1D and 3D), total aboveground biomass did not differ with respect to canopy removal (P=0.40; Fig. 5a). Belowground production was 96% higher in plots with canopy removal than plots without; however, this trend was

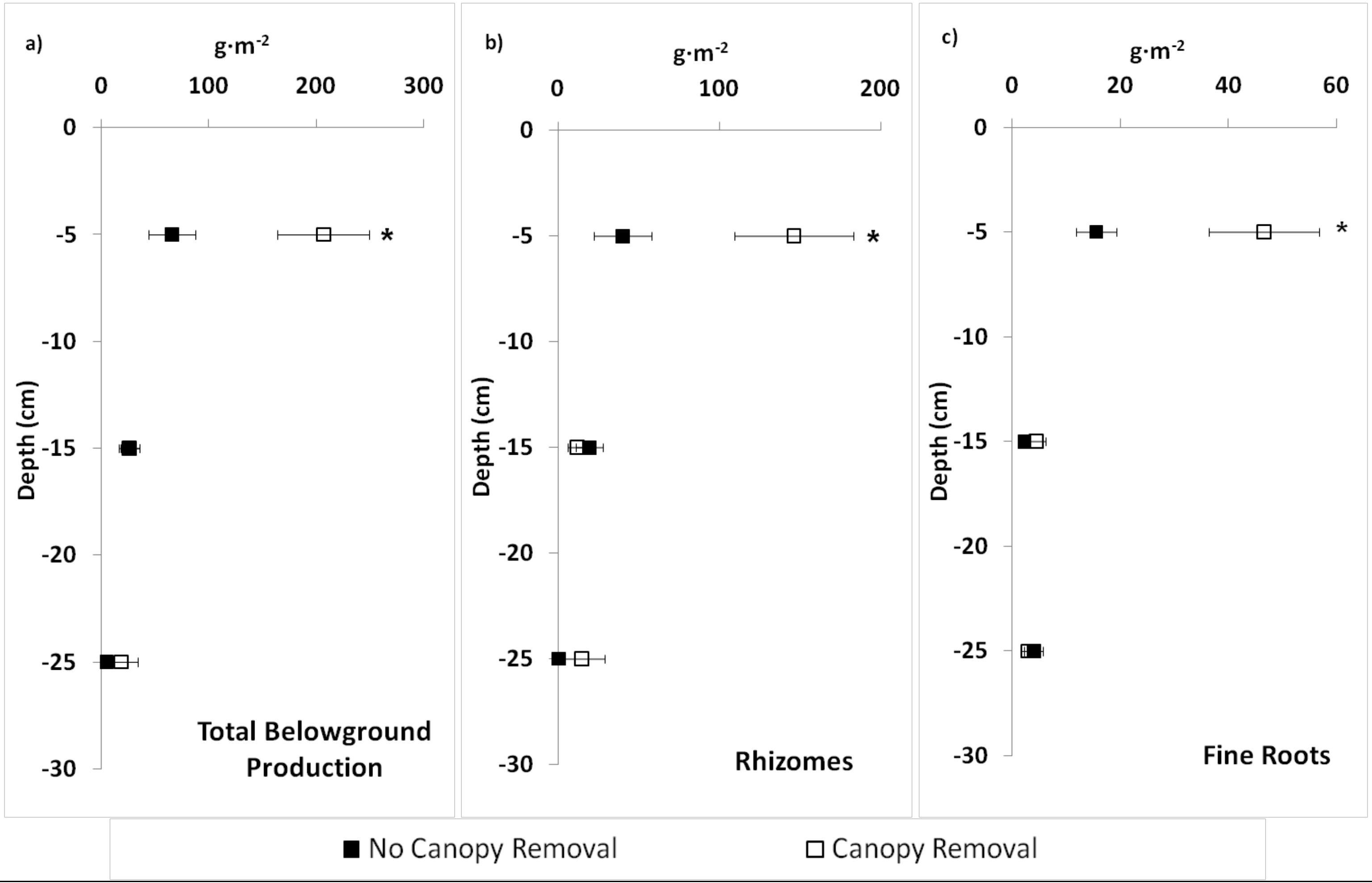

Fig. 4 Belowground depth profiles averaged across all No Burn sites**. a)** Total belowground production, **b)** rhizomes, and **c)** fine root production averaged across all sites. Each point represents the average of 48 replicates (± standard error of the mean). Each point was arbitrarily positioned in the center of its 10 cm depth zone. Single asterisks represent a significant canopy effect (α=0.05)

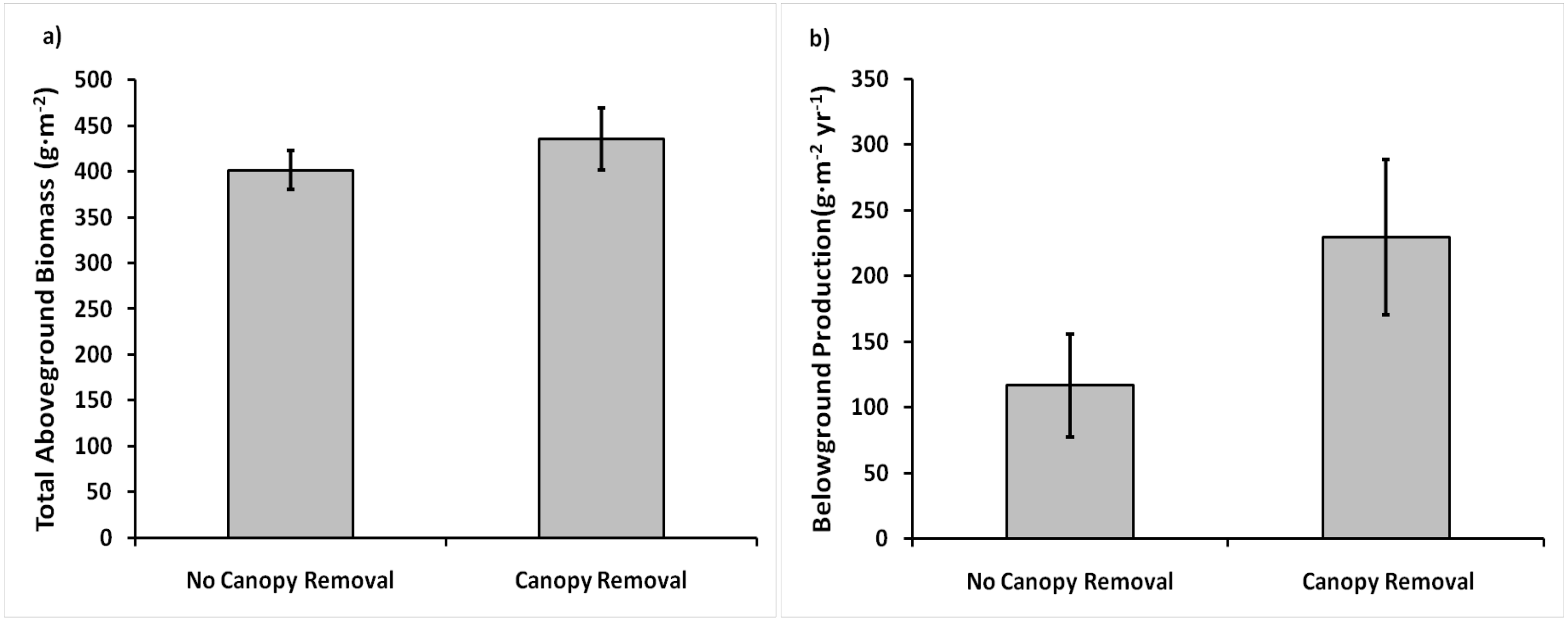

Fig. 5 Biomass production from sites grass dominated sites (1D and 3D). **a)** Total aboveground biomass production, values represent the mean of 24 replicates (± standard error of the mean). Results of an ANOVA indicate there is no significant difference amongst the treatments. **b)** Belowground production, values represent the mean production to a depth of 30 cm of 24 replicates (± standard error of the mean). The results of an ANOVA indicate that there is no significant difference (α=0.05) between the treatments

not statistically significant (P=0.13; Fig. 5b). Total belowground production and rhizome growth also were not significant (P=0.13 and P=0.28, respectively), but showed trends toward increase following canopy removal in the 0-10 cm zone (Fig. 6). Fine root production increased by 2.7 times in the 0-10 cm zone in plots receiving canopy removal compared to those without (P=0.03, Fig. 6c). However, the increase in fine root production was not enough to significantly increase the total production in the 0-10 cm zone.

In sedge-dominated sites (sites 2D and 7D), plots receiving canopy removal produced an average of 92 % more aboveground biomass (459±24 $g{\cdot}m^{-2}$) than plots without (239±19 $g{\cdot}m^{-2}$, P<0.0001, Fig. 7a). Plots in which the canopy was removed had an average of 3.6 times higher belowground production (287±76 $g{\cdot}m^{-2}yr^{-1}$) than plots in which it was not (81±26 $g{\cdot}m^{-2}yr^{-1}$, P=0.015, Fig. 7b). The depth profiles indicate that canopy removal resulted in a nearly 7-fold increase in total belowground production in the 0-10 cm zone (P=0.014, Fig. 8a). This increase in total production corresponded to an increase in both rhizome (P=0.0084, Fig. 8b) and fine root production (P=0.040, Fig. 8c) in the 0-10 cm zone following canopy removal. Belowground production was minimal below 10 cm and did not change following canopy removal.

When aboveground biomass harvested from each site was categorized into gras and sedge, trends in the results were similar to those in which sites were grouped according to species composition (Table 2). Averaged over all no burn sites, *S. americanus* produced 81 % more aboveground biomass in plots with canopy removal

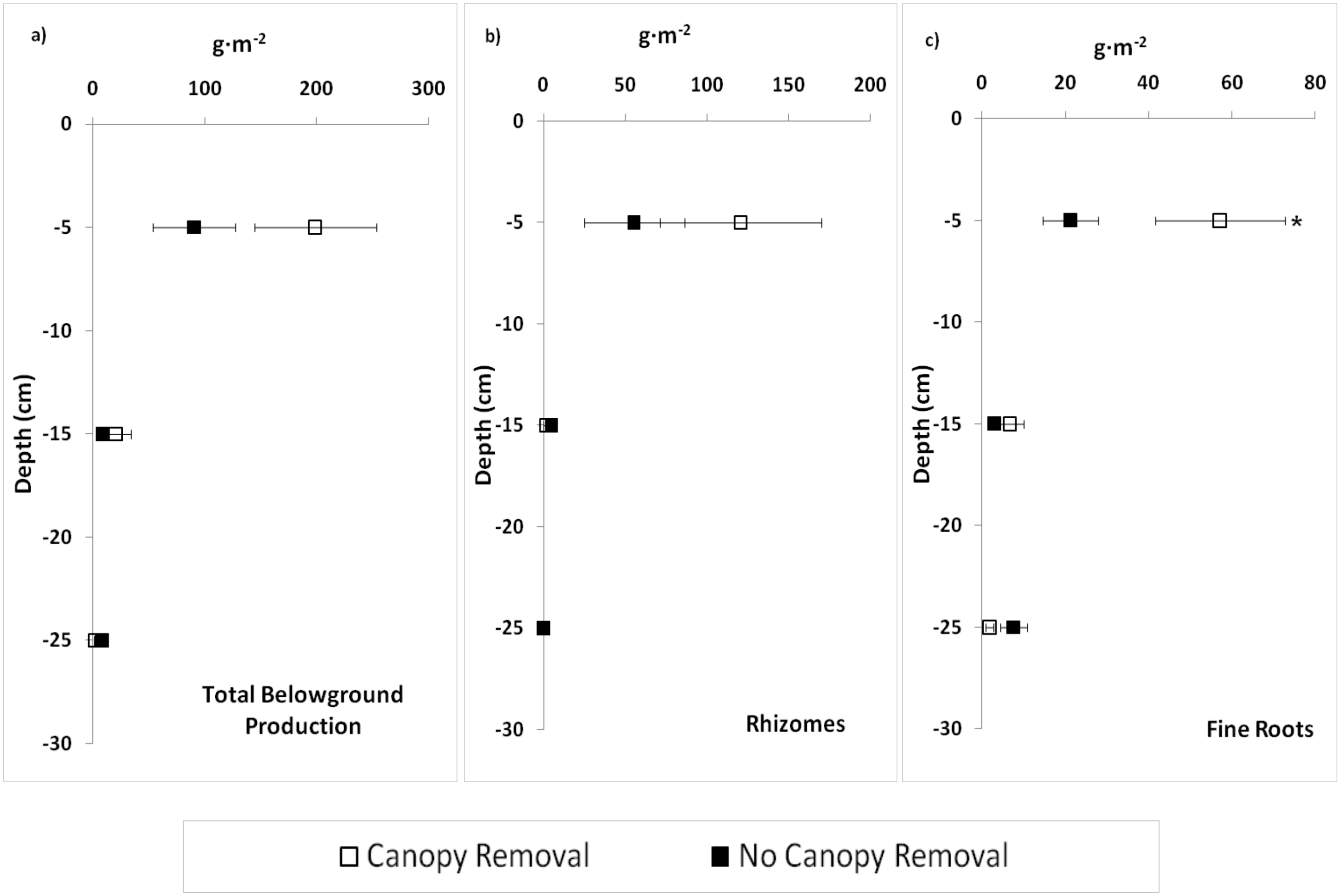

Fig. 6 Belowground depth profiles from sites grass-dominated sites (1D and 3D)**. a)** Total belowground production, **b)** rhizomes, and **c)** fine root production. Each point represents the average of 24 replicates (± standard error of the mean). Each point was arbitrarily positioned in the center of its 10 cm depth zone. Single asterisks represent a significant canopy effect (α=0.05)

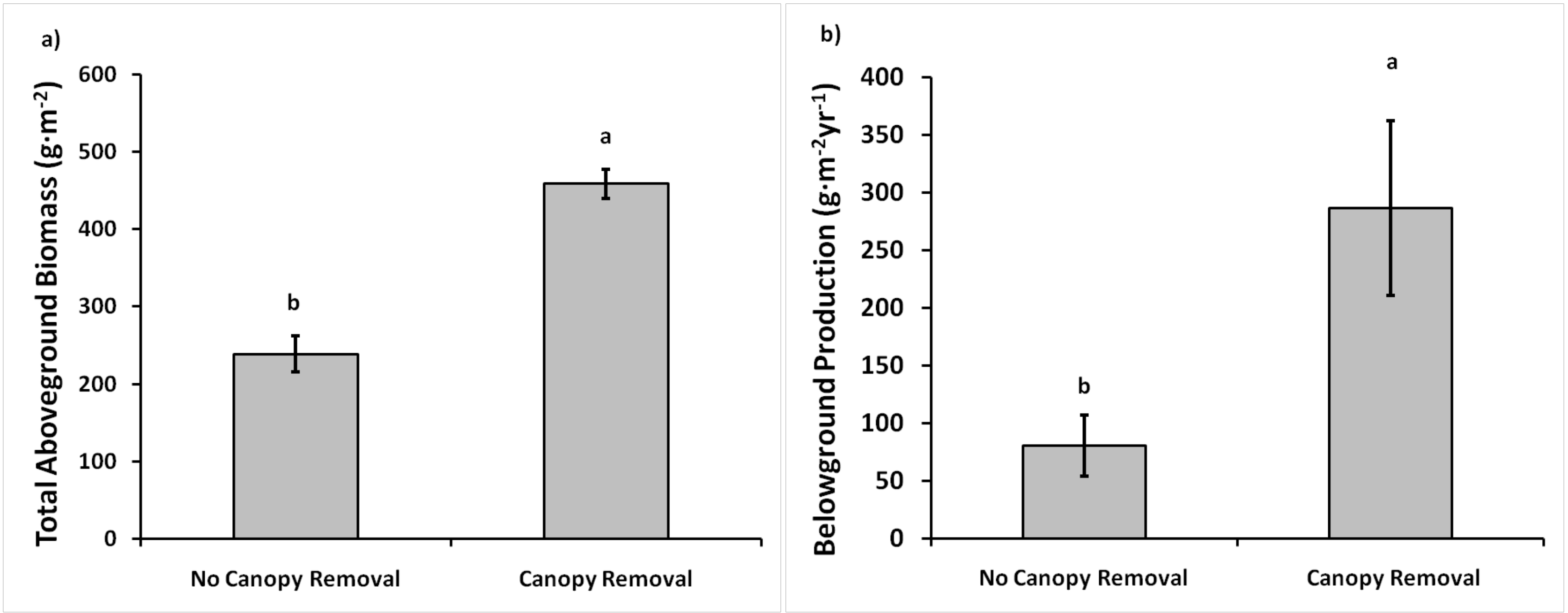

Fig. 7 Biomass production from sites sedge dominated sites (2D and 7D). **a)** Total aboveground biomass production, values represent the mean of 24 replicates (± standard error of the mean). Letters indicate the results of an ANOVA; means with the same letter are not significantly different from each other (α=0.05). **b)** Belowground production, values represent the mean production to a depth of 30 cm of 24 replicates (± standard error of the mean) Letters indicate the results of an ANOVA; means with the same letter are not significantly different from each other (α=0.05)

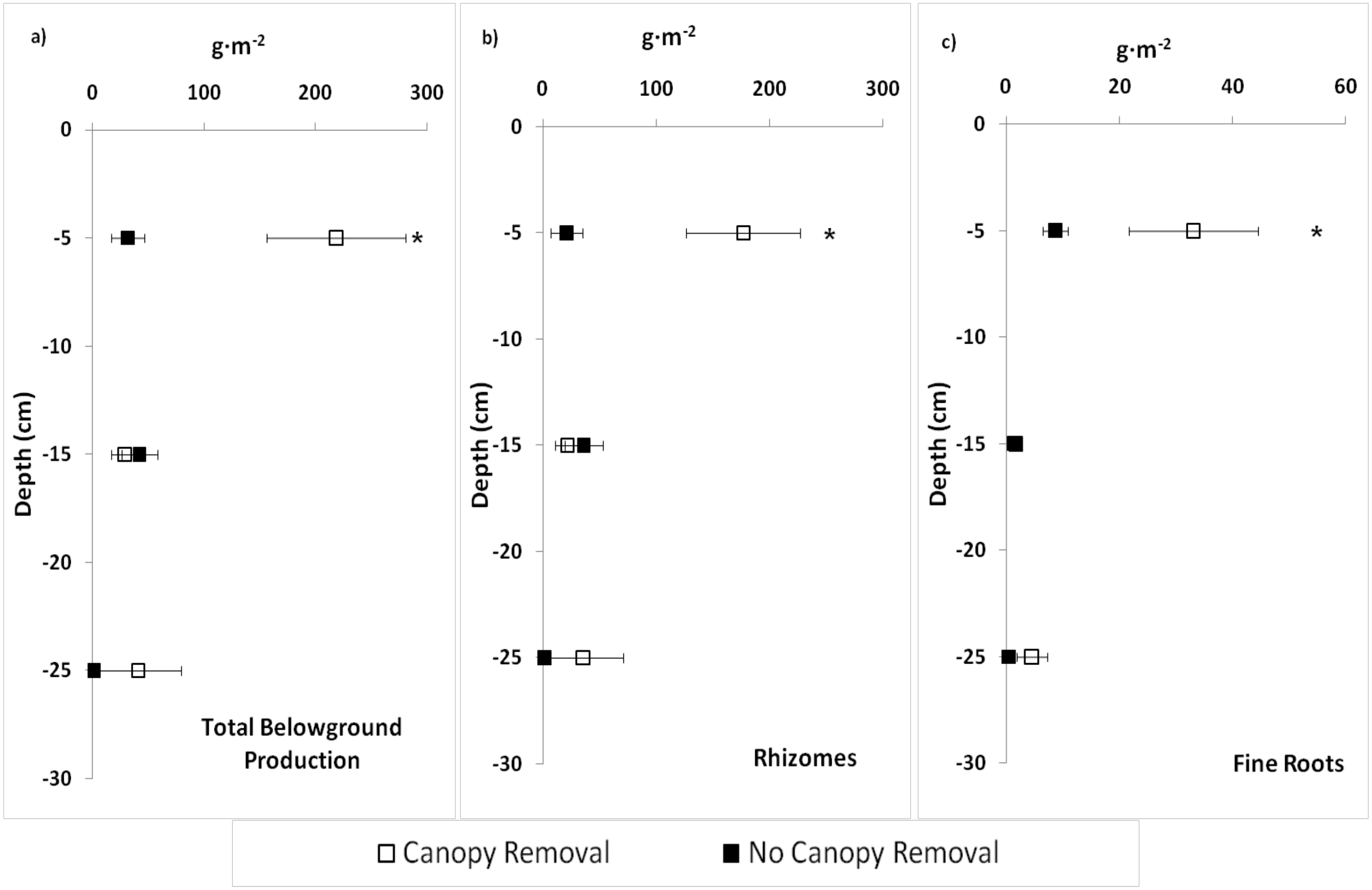

Fig. 8 Belowground depth profiles from sites sedge-dominated sites (2D and 7D)**. a)** Total belowground production, **b)** rhizomes, and **c)** fine root production. Each point represents the average of 24 replicates (± standard error of the mean). Each point was arbitrarily positioned in the center of its 10 cm depth zone. Single asterisks represent a significant canopy effect (α=0.05)

Table 2: Aboveground biomass production separated by plant type. Sedge refers to biomass of *S. americanus*. Grass includes *S. patens*, *D. spicata*, and *S. alterniflora*. Numbers indicate mean number aboveground biomass by species per square meter plus or minus the standard error. Comparisons with significant (α=0.05) canopy effects include P-values.

	a. mean aboveground biomass $g \cdot m^{-2}$ at grass-dominated sites		
	Canopy Removal	No Canopy Removal	Significance
Sedge	76 ± 15	32 ± 13	P=0.046
Grasses	398 ± 55	410 ± 59	NS
	b. mean aboveground biomass $g \cdot m^{-2}$ at sedge-dominated sites		
	Canopy Removal	No Canopy Removal	Significance
Sedge	339 ± 40	187 ± 26	P=0.0004
Grasses	90 ± 27	17 ± 8	P=0.014

than plots without. The grass biomass did not differ with respect to canopy removal when averaged across the entire study.

At the grass-dominated sites, biomass of *S. americanus* increased by 2.4 times following canopy removal (Table 2a), but *S. patens* and *D. spicata* biomass showed no response to canopy removal. At the sedge-dominated islands, *S. americanus* biomass increased by 1.8 times (P=0.0004) and, although they made up only about 17% of the total biomass at these sites, *S. patens* and *D. spicata* also increased by 5 times (P=0.014) following canopy removal (Table 2b).

Stem Density and Height. The results of the stem density assessments roughly mirrored those seen in aboveground biomass (Fig. 9). Averaged over all sites, removing the canopy resulted in a nearly 100 % increase (P<0.0001) in *S. americanus* stems$\cdot$m^{-2} but a trend toward a decrease in *S. americanus* stem height (P=0.13). There was no effect of canopy removal on grass stem density (P=0.89) or height (P=0.60; Table 3). There was no effect of ash deposition on stem density of any species. There was a significant site X canopy interaction in *S. americanus* stem density (P=0.0035), so the results were again grouped by species composition.

At the grass-dominated sites (1D & 3D), canopy removal resulted in 93 % more sedge stems per square meter than those without (Fig. 9a). However, this effect was not statistically significant (P= 0.059). Canopy removal had no effect on grass stem density (P=0.94) at sites where grass dominated. At the sedge-dominated sites (2D and 7D), the plots receiving canopy removal had 69 % more total stems per square meter than those that did not (P=0.0002). Removing the canopy resulted in a 76 % increase in stems of *S. americanus* at sites 2D and 7D (P<0.0001; Fig. 9b).

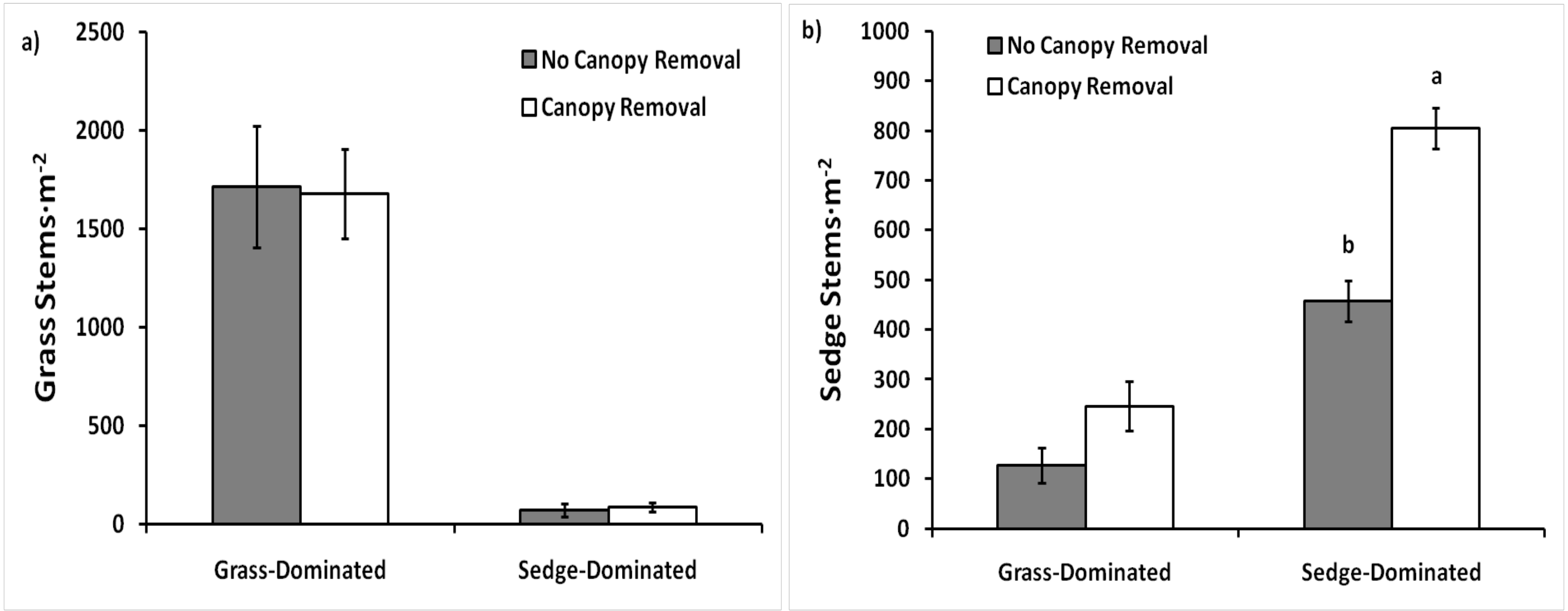

Fig. 9: Results of stem density assessment. Numbers indicate mean number of stems of **a.** *S. patens*, *D. spicata*, and *S. alterniflora* and **b.** *S. americanus* per square meter plus or minus the standard error at grass-dominated (1D & 3D) and sedge-dominated (2D & 7D) sites. Letters indicate the results of a pre-planned contrast; means with the same letter are not significantly different from each other (α=0.05).

Table 3: Average Stem Height. Numbers indicate mean stem height of **a.** *S. americanus* and **b.** *S. patens*/*D. spicata* plus or minus the standard error. Comparisons with a significant (α=0.05) canopy effects include P-values.

	a. average sedge stem height (cm)		
	Canopy Removal	No Canopy Removal	Significance
1D&3D	80 ± 3	78 ± 6	NS
2D&7D	107 ± 4	121 ± 5	P=0.0414
	b. average grass stem height (cm)		
	Canopy Removal	No Canopy Removal	Significance
1D&3D	45 ± 4	49 ± 2	NS
2D&7D	42 ± 3	35 ± 5	NS

However, those stems were an average of 12 % shorter than those where the canopy remained (P=0.041; Table 3a). Canopy removal increased stem density of *S. americanus* at all no burn sites and decreased stem height in the sedge-dominated sites.

Annual Burn Experiment

The annual burn experiment found biomass production of burned sites to decrease when a plant canopy was replaced over the burned area. Aboveground and belowground production decreased as well as stem density, while stem height increased following canopy replacement.

Biomass Production. Aboveground biomass was 68 % higher (P<0.0001) in control plots than in plots with replaced canopy (Fig. 10a). Plots in which the canopy was replaced post burn produced an average of 40 % less belowground production than control (Fig. 10b). However, this trend was not statistically significant (P=0.19). Harvested biomass separated by species indicated a 100 % decrease in sedge biomass when the canopy was replaced, but no significant change in the grass biomass (Table 4a; P=0.0047).

Following canopy replacement, there was a trend toward decreased total belowground production in the 0-10 cm zone (P=0.36; Fig. 11a). Rhizome growth did not decrease, but fine root production was 59 % lower when the canopy was artificially replaced than when it was not (P=0.0078, Fig. 11c). Fine root growth also modestly decreased in the 10-20 cm zone following canopy replacement (P=0.046; Fig. 11c).

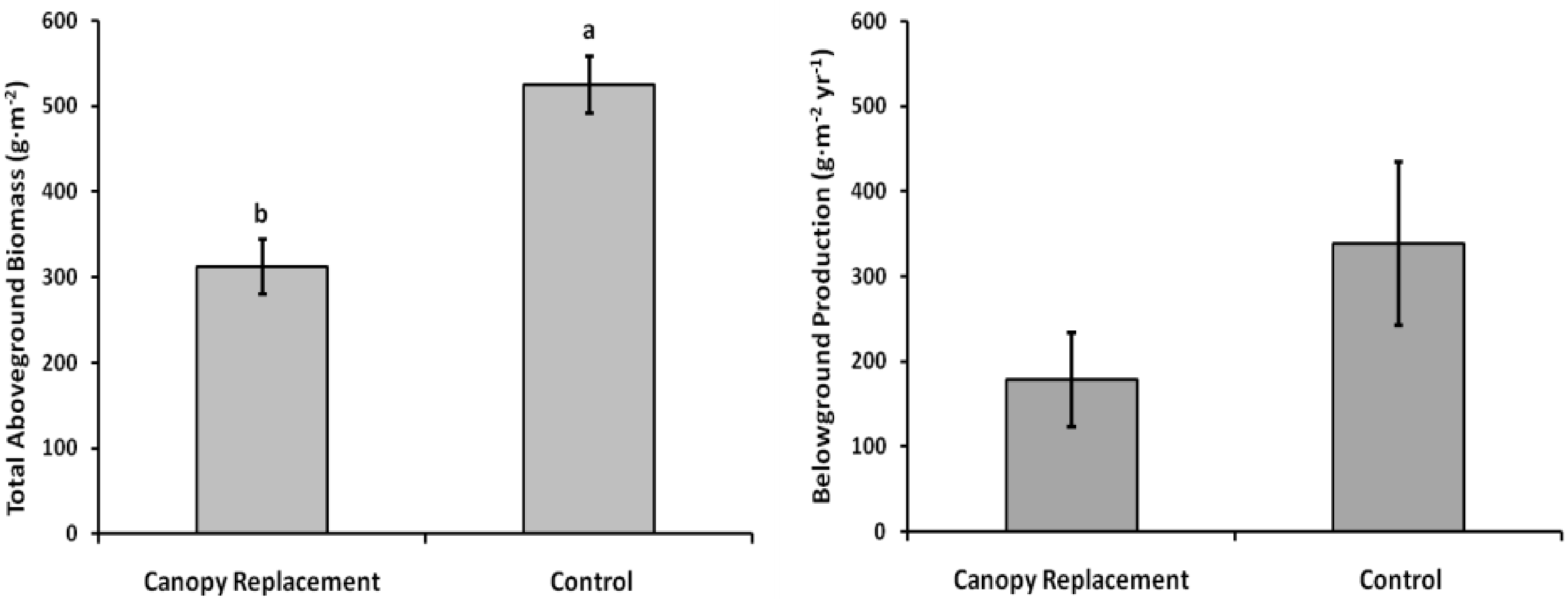

Fig. 10 Biomass production from all burn sites. **a)** Total aboveground biomass production, values represent the mean of 18 replicates (± standard error of the mean). Letters indicate the results of a T-Test; means with the same letter are not significantly different from each other (α=0.05). **b)** Belowground production, values represent the mean to a depth of 30 cm of 18 replicates (± standard error of the mean) According to the results of a T-test, the means are not significantly different from each other (α=0.05)

Table 4: Aboveground data from Annual Burn Experiment. **a)** Aboveground biomass production separated by plant type. **b)** Results of stem density assessment. **c)** Average stem height. Sedge refers to biomass of *S. americanus*. Grasses includes *S. patens*, *D. spicata*, and *S. alterniflora*. Numbers indicate mean number aboveground biomass by species per square meter plus or minus the standard error. Comparisons with significant (α=0.05) difference include P-values.

	a. total aboveground biomass g·m^{-2}		
	Canopy Replacement	Control	Significance
Sedge	106 ± 33	218 ± 24	P=0.0047
Grasses	228 ± 58	323 ± 63	NS
	b. mean stems·m^{-2}		
	Canopy Replacement	Control	Significance
Sedge	404 ± 58	694 ± 112	P=0.0044
Grasses	1456 ± 314	1868 ± 304	NS
	c. average plant height (cm)		
	Canopy Replacement	Control	Significance
Sedge	88 ± 3	79 ± 2	P=0.0110
Grasses	52 ± 5	37 ± 4	NS

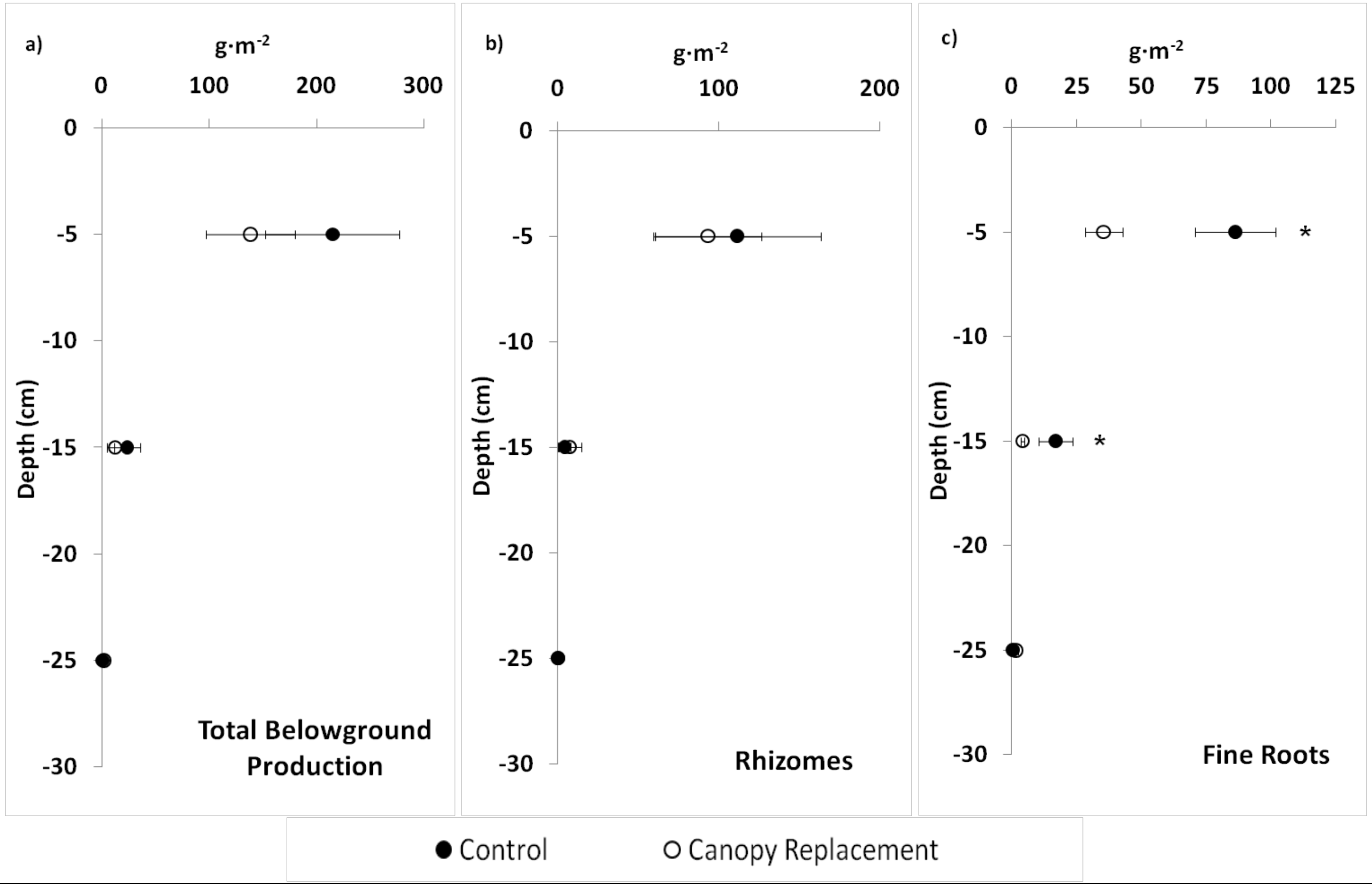

Fig. 11 Belowground depth profiles averaged across all Annual Burn sites**. a)** Total belowground production, **b)** rhizomes, and **c)** fine root production averaged across all sites. Each point represents the average of 18 replicates (± standard error of the mean). Each point was arbitrarily positioned in the center of its 10 cm depth zone. Asterisks represent a significant difference resulting from a t-test (α=0.05)

Stem Density and Height. The results of the stem density assessments were similar to those seen in aboveground biomass (Table 4b). Replacing the canopy resulted in a 42 % decrease in *S. americanus* stems·m^{-2} (Table 4b), but also resulted in a 10 % increase in stem height (Table 4c). There was no effect of canopy replacement on grass stem density (P=0.31) or height (P=0.20).

Discussion

The results of the No Burn experiment indicated that canopy removal increased *S. americanus* stem density and aboveground and belowground biomass production. There was also a trend towards an increase in belowground production in areas where grasses dominated. Ash deposition had no effect on aboveground or belowground biomass production. Additionally, the Annual Burn study indicated that replacing the plant canopy post-burn can negate the positive biomass effects of burning, as aboveground and belowground production both decreased when the plant canopy was replaced immediately after burning. If ash deposition was playing an integral role in biomass production at these sites, one might expect the differences in biomass production to be less pronounced among the treatments in the annual burn study.

To adequately interpret canopy removal as the dominant mechanism affecting biomass response to fire, it is helpful to corroborate our data with that of a study focusing on surface elevation and biomass response to fire at Blackwater. Cahoon et al. (2010) found that areas under annual burn management had increased aboveground and belowground biomass when compared to those with no burning

(Table 5). A comparison of the two studies indicates that canopy removal in our study was able to elicit a similar aboveground biomass response as fire. The magnitude of the fine root production response following fire (Cahoon et al. 2010) was also similar to the response following canopy removal in our study. Canopy removal is therefore the dominant mechanism affecting biomass production in these systems because it elicited the same response as fire on biomass production.

The biomass response to canopy removal likely results from changes in canopy light availability and/or soil temperature (Miller et al. in prep). When the canopy was not removed, *S. americanus* plant height was greater, but stem density was lower than with canopy removal. In the annual burn experiment, the height of *S. americanus* stems was greater but stem density was lower in plots with the artificial canopy. This relationship suggests increased productivity may be a result of the following scenario involving plant canopy, canopy light availability, and soil temperature. When the senesced plant canopy of the previous year's growth is present, *S. americanus* may devote reserve energy stored in rhizomes to increasing new shoot height in order to penetrate the canopy and gain access to light in the early part of the growing season. When the plant canopy was removed, more light and solar radiation was present at the soil surface, warming the upper part of the soil (Miller et al. in prep). Then, because the plant canopy was absent, reserve resources may not have been allocated to stems to penetrate the senesced canopy, so new culm growth increased. We speculate that this resulted in higher stem density and the increased light availability continued to lead to higher productivity in those stems, rhizomes, and roots.

Table 5: A comparison of biomass response to fire from Cahoon *et al*. (2010) and response to Canopy Removal in our study.

	Cahoon et al. (2010)		This Study	
	Annual Burn	No Burn	Canopy Removal	No Canopy Removal
Aboveground Biomass	443 ± 24 $g{\cdot}m^{-2}$	290 ± 31 $g{\cdot}m^{-2}$	447 ± 16 $g{\cdot}m^{-2}$	320 ± 23 $g{\cdot}m^{-2}$
Fine Root Production	122 ± 10 $g{\cdot}m^{-2}$	58 ± 8 $g{\cdot}m^{-2}$	59± 12 $g{\cdot}m^{-2}$	20 ± 4 $g{\cdot}m^{-2}$

This relationship between light availability, stem density, and stem height is consistent with the “phalanx and guerilla” strategies of clonal plant growth (Lovett Doust 1981). Phalanx strategy assumes that, in the presence of high resources, clonal plants produce frequently branched ramets with shorter spacers to occupy local resource patches. On the other hand, guerilla strategy occurs in areas of low resource availability and involves less branching of ramets and longer spacers to explore adjacent areas (Lovett Doust 1981, de Kroon and Knops 1990). Ikegami *et al* (2007) found *S. americanus* grown in higher light availability to produce more stems than those grown in shaded areas. They also found stem height to be lowest in the areas of highest light availability.

An increase in soil temperatures in the early part of the year could increase root and rhizome activity. Temperature and canopy light availability were expected to increase as a result of canopy removal. Over the course of this study, Miller et al. (in prep) documented an increase in canopy light availability in the plots with canopy removal. Data also indicated an increase (up to 2°C) in soil temperature at 5 cm depth in plots with canopy removal versus plots without (Fig. 12). Soil temperature was buffered by high water table height, but showed significant differences from week four to eight following canopy removal. Soil temperatures began to equilibrate later in the season as the rising water table and new growth shading the surface eliminated the temperature difference. In the annual burn experiment, canopy light availability and soil temperature were also affected at annual burn sites following canopy replacement. Soil temperatures at 5 cm were lower (up to 1.5°C) in canopy

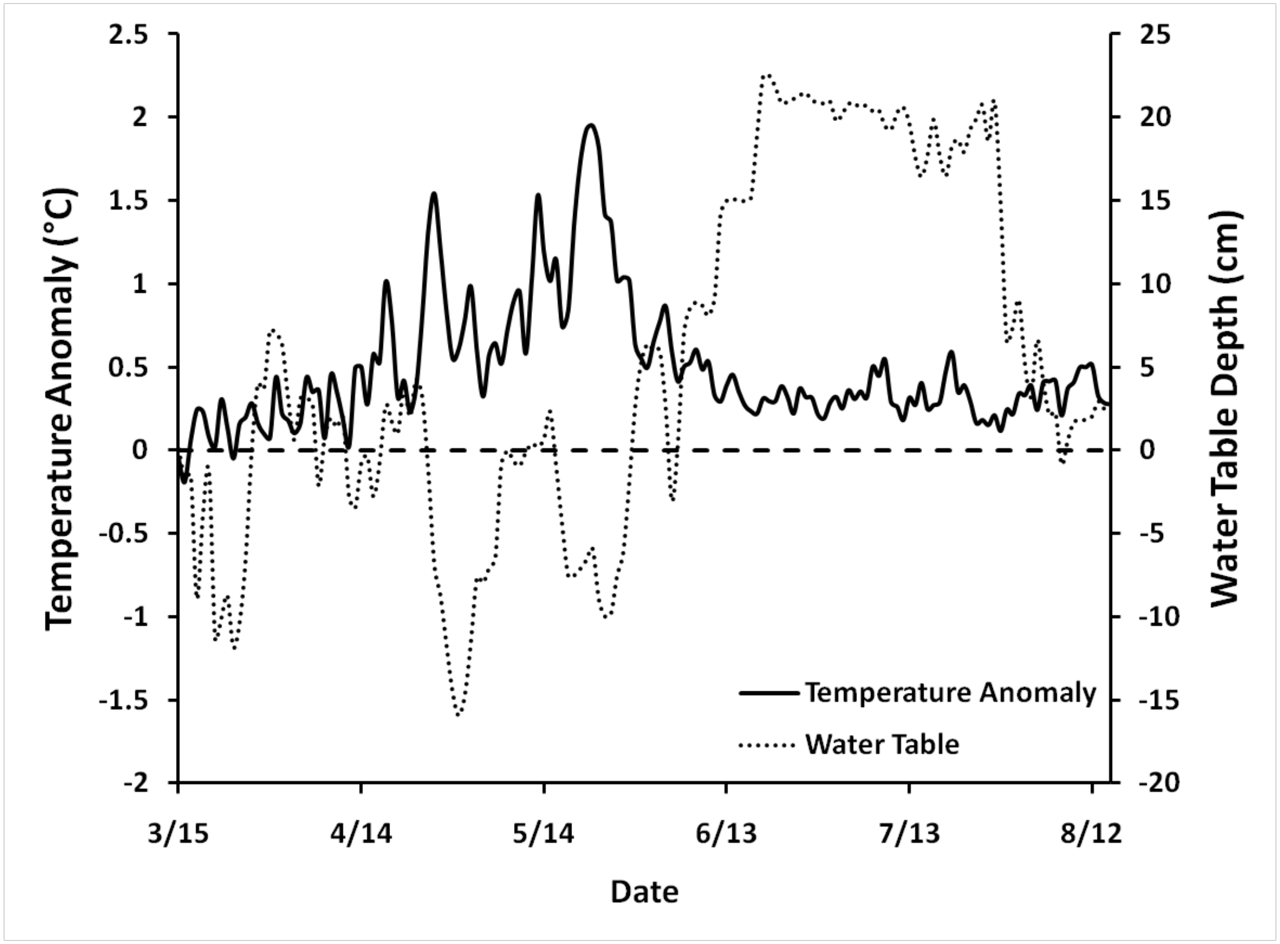

Fig. 12 Daily mean soil temperature at a depth of 5 cm averaged across all no-burn sites. Temperature anomaly the difference in temperature at the Canopy Removal plots from the temperature in the Non-Canopy Removal plots. Water table from a nearby auto recording well is plotted over the same time period. From Miller et al. (in prep)

replacement plots versus control early in the growing season. These temperature differences in both experiments may have had a significant impact on root and rhizome activity and on triggering plants to break dormancy earlier in the season.

In addition to increasing biomass production, Geatz et al. (in prep) found evidence that the rate of organic matter decomposition also decreases following canopy removal in sedge-dominated sites. They speculate that this is a result of high plant uptake of soil N by rapidly growing *S. americanus* vegetation following canopy removal. This leads to high tissue N in the plants, but may decrease the pool of soil N that is required for decomposition to occur (Geatz et al. in prep). This suggests that although fire leads to direct loss of organic matter from volatilization, it may increase soil organic matter inputs *and* decrease soil organic matter losses from these systems.

Ash deposition was predicted to increase biomass production by creating a pulse of plant-available nutrients akin to fertilization. These effects may not have been observed because the temperature of the fire was such that most of the nitrogen was likely volatilized. Based on analysis of the ash used in the study, Geatz et al. (in prep) found that the nutrient “pulse” consisted mostly of base cations that have little effect on productivity. Another explanation is that because of frequent tidal flushing at the study sites, the nutrients deposited by the ash were flushed away from plots before the plants could take them up. In an actual burn, although some flushing and translocation would occur, soluble nutrients deposited by ash would be ubiquitous across the management block. Assuming lateral tidal flow, translocation away from a given site should equal transfer into the area. Once again, however, if ash deposition was stimulating biomass production, the biomass response to canopy removal alone would not be enough to account for the response found by Cahoon et al. (2010).

Or results indicate that a species-specific response may be occurring. There was increased productivity aboveground and belowground following canopy removal at sites dominated by *S. americanus*. Additionally, sites dominated by *S. patens* and *D. spicata* did not respond to canopy removal aboveground, and showed only trends toward increased belowground production. Evolutionary triggers could be responsible for the differential effect of canopy removal on different plant communities. Land managers have long noted the trend toward *S. americanus* dominance following continued burning (Lynch 1941, Chabreck 1981, Pendelton and Stevenson 1983, Nyman and Chabreck 1995). *S. patens* and *D. spicata* are competitively superior to *S. americanus* under normal conditions, but burning has been found to help *S. americanus* assume dominance. In Louisiana, a study found that *S. americanus* growth is triggered by soil temperatures greater than 16°C (Sipple 1979). *S. patens* and *D. spicata* are warm season C4 species that may require warmer temperatures for growth to commence. Studies have indicated that because *S. americanus* grows better in cooler temperatures it has the ability to gain dominance over slower growing species (Sipple 1979).

Early in the growing season, *S. americanus* would have a competitive advantage over *S. patens* and *D. spicata* because it grows better in cool temperatures, but the senesced material normally creates a dense canopy that does not allow light to the surface, suppressing growth of new shoots from *S. americanus* rhizomes (Sipple 1979). Therefore, when the canopy is removed, *S. americanus* can take advantage of increased light availability for a longer portion of the growing season than a later sprouting species can and gain dominance. This leads to a competitive advantage for *S. americanus* in mixed stands and increased production due to a longer growing season length in pure stands. In areas where *S. patens* and *D. spicata* dominate the growing season is not functionally lengthened following canopy removal because these species are still dormant. This may explain the relatively modest gains in belowground production and absence of aboveground production response in grass-dominated sites following canopy removal.

Another hypothesis that has been proposed is that fire damages the roots of *S. patens* and *D. spicata*, but leaves *S. americanus* roots unscathed due to differential depths of rooting between the species (Hoffpauer 1968). Saunders et al. (2006) found that there are three to five times more roots in the top 5 cm in *S. patens*-dominated communities than *S. americanus*-dominated communities. The design of this study did not account for the heat generated by fire, but because above and belowground biomass response from canopy removal was so similar to the response seen from burning in Cahoon *et al*. (2010) ephemeral heat from the fire did not likely affect production. If heat from the fire had an effect on production, belowground production would have been lower in burned areas than in sites with canopy removal alone (Table 5).

While our results indicate strong evidence of a species-specific response, it is important to note that the differential response could also be correlated to marsh physical conditions. Because each site was not a controlled environment, it is impossible to determine statistically that increased response to canopy removal at the sedge-dominated sites was due to species composition alone. Sites varied by soil bulk density, soil organic matter content, and soil water content, so it would be impossible to assign complete culpability to only one factor.

Water table height and salinity may also impact species-specific responses to canopy removal. For instance, researchers have noted that production of *S. patens* can be stimulated by burning or mowing. However, when followed by periods of high water, removal of the plant canopy decreased production (de Szalay and Resh 1997, Gabrey and Afton 2001). *S. patens* is known to be relatively intolerant of high water (Bertness and Ellison 1987, Bertness 1991, Broome et al. 1995) perhaps because it is less adept at oxidizing its rhizosphere than other species such as *S. alterniflora* and *S. americanus* (Bertness 1991, Broome et al. 1995). This may be exacerbated by removing the plant canopy and effectively cutting off the flow of oxygen to the root zone.

Conversely Flores et al. (2011) found fire to increase production of *S. patens* and *D. spicata* and *not S. americanus* in a study at Blackwater. However, because there was a hurricane in the Mid-Atlantic during their study, these sites had higher salinities than they ordinarily would (Flores 2011). Because *S. americanus* declines in increasing salinity (Broome et al. 1995), saltwater intrusion may have been a factor in influencing their results. It is possible that canopy removal at no burn sites was influenced by an interaction between canopy removal, elevation, salinity, and species composition on biomass production.

Implications

This study outlines the importance of the canopy removal aspect of prescribed fire in increasing biomass production. If our data is representative of other systems, land managers could conduct fires in a way that maximizes removal of the plant canopy in order to encourage increased production of *S. americanus*. Patchy fires where much of the plant canopy is left standing may not have the desirable plant response and may not increase organic inputs to marsh accretion. This study also has parallels to other plant canopy disturbances. For instance, herbivory in the winter months may increase production in *S. americanus*-dominated systems as long as the roots and rhizomes remain unaffected. Winter storms where heavy snow is produced may also impact plant canopy dynamics. If more light is allowed to the surface in the spring as a result of this snowpack, it may have positive biomass effects as well.

Because many coastal marshes are declining as sea-level rises, it is important to think of this research in the larger context of marsh accretion, surface elevation, and the prolonged survival of these ecosystems. Although we found that canopy removal increased aboveground production by 92% and belowground production 3.6 times versus no canopy removal in *S. americanus*-dominated sites, Cahoon et al. (2010) found that increases in productivity of this magnitude do not translate into significant increases in surface elevation in burned vs. unburned marsh. In fact, since burning removes the plant canopy, surface accretion was much lower (5.9 ± 1.5 mm yr^{-1} vs. 9.7 ± 1.8 mm yr^{-1}, Cahoon et al. 2010) in burned vs. unburned plots. However, the increase in belowground production (potentially in combination with a decline in organic matter decomposition, Geatz et al. in prep) helped to slow root zone collapse and decrease the elevation deficit in annual burn sites. Their conclusion was that since there are trends toward positive effects of annual burning, this management technique is not contributing to, and may be slowing, marsh declines at Blackwater (Cahoon et al. 2010). Their study did not separate sites by species composition, so it is possible that there may have been differences in elevation following burning in sites dominated by *S. americanus*, but not those dominated by *S. patens* and *D. spicata*.

The results of Cahoon et al. (2010) and our study outline the subtle importance of vegetation growth and, in particular, belowground biomass production in influencing elevation dynamics. Despite the positive biomass effects seen following canopy removal, no significant elevation gains have been attributed to fire. Therefore, fair questions can be raised about the importance of further use of a management technique that has not proven to significantly affect elevation in rapidly subsiding marshes. Given the results presented by Cahoon et al. (2010), it is reasonable to suggest that over time, while these marshes will eventually be lost to open water, the stimulatory effect of fire may slow the pace of loss. Thus, we speculate that if fires are conducted with emphasis on complete canopy removal in *S. americanus*-dominated marshes, they may slow the pace of shallow subsidence and extend the life of these marshes, and the ecosystem services associated with them, slightly. A slightly longer lifespan in the marsh interiors may be particularly important to maintain the connectivity of the ecosystem as the marsh-upland border migrates inland with sea-level rise.

Conclusions

Prescribed fire increases aboveground and belowground biomass production in these systems through canopy removal, the dominant mechanism. Biomass increases were greatest following canopy removal in *S. americanus*-dominated communities. If our results are accurate, managers concerned with enhancing accretion rates in marsh systems should focus on maximizing canopy removal in *S. americanus* communities. Evidence suggests that even in grass-dominated communities, canopy removal resulted in a trend toward increased belowground production of *S. patens* and *D. spicata*. Canopy removal also increased aboveground biomass of *S. americanus* in grass-dominated sites, which may lead to an eventual shift to *S. americanus* dominance. So, fire need not be confined to only *S. americanus*-dominated marshes to experience the positive biomass effects. Burning in areas with areas where *S. americanus* is co-dominant or subsidiary to grasses, may increase *S. americanus* cover and lead to eventual dominance.

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Chapter 3: Competition and disturbance in vegetation of Mid-Atlantic brackish marshes

Abstract

Variations in plant species composition can dictate the response of a coastal tidal marsh to disturbance. Disturbances may cause certain species to decline while increasing production of other species. These interactions are largely governed by interspecific competition. Disturbances have the ability give a species a competitive advantage over another. This study was conducted to understand the competitive interactions between two common brackish marsh species, *Schoenoplectus americanus* and *Distichlis spicata*, and the ways that disturbance affects those interactions. The effects of a non-catastrophic disturbance, canopy removal, were investigated through a manipulative greenhouse replacement series competition experiment. In mixed compositions, production of *S. americanus* was significantly higher than production of *D. spicata* aboveground (P=0.0033) and belowground (P=0.047) following canopy removal. However, when the canopy was not removed, there was no significant difference between the yields of the two species. Comparisons of relative yields of the two species indicated that *S. americanus* was suppressing *D. spicata* when the plant canopy was removed. However, when it was not removed, belowground production may have been experiencing competitive interference. This is evidence that the canopy disturbance gives *S. americanus* a competitive advantage over *D. spicata* in mixed compositions. As anthropogenic disturbance continues to be used as a land management technique, these competitive interactions could play a role in plant productivity response.

Introduction

Human induced disturbances can have a significant effect on interspecific competition in coastal marshes. There are relatively few species adapted to inhabit coastal marshes due to the necessary tolerance to salinity and periodic high water. Species vary in their ability to exist in saline and or high water conditions and are therefore fairly predictably grouped into zones of species with common tolerances (Emery et al. 2000, Bertness and Ellison 1987, Niering and Warren 1980). This zonal structure is governed by resource stressors, competitive exclusion, and non-resource stressors like tidal flooding (Emerey et al. 2000, Bertness and Ellison 1987, Niering and Warren 1980). The general understanding of salt marsh zonation follows a conventional pattern of vegetation banding.

Many researchers have pointed out that zonation is governed by plant tolerances that exhibit wide and variable ranges, but is often expressed in the form of sharp boundaries. These upper and lower boundaries are often determined by interspecific competition between species adapted to high or low marsh conditions (Bertness 1991, Bertness and Ellison 1987, Pidwirney 1990, Ungar 1998, Emery et al. 2001). Plants adapted to saline environments are usually not competitive in freshwater environments, but as salinity increases, fresh adapted species cannot compete as well, so salt-tolerators increase (Ungar 1998). Therefore, interspecific competition is an important factor controlling zonation in tidal salt marshes.

In brackish marshes of North America, *Shoenoplectus americanus*, *Spartina patens*, and *Distichlis spicata* commonly co-occur where salinities range from 5-10 ppt (Gabrey and Afton 2001, Allan 1950, Sipple 1979, Broome et al. 1995) and water table depth ranges from about -10 to +10 cm (Broome et al. 1995, Allan 1950, Palmisano and Newsom 1967, Sipple 1979). Despite the relative lack of diversity, these species vary in photosynthetic pathways (Saunders et al. 2006), plant canopy architecture (Turiztin and Drake 1981), and growing season length (Sipple 1979). These differences in physiology have the potential to influence competitive interactions in the presence of canopy disturbances.

Disturbances also have the ability to influence coastal marsh vegetation patterns (Baldwin and Mendelssohn 1998a,b). Disturbances can be catastrophic (killing all residents) or non-catastrophic (not a complete kill, but residents affected) such as many plant canopy disturbances (Platt and Connell 2003). Canopy disturbances may result from herbivory, fire, or severe weather. Muskrat (*Ondatra zibethicus*) herbivory can be non-catastrophic (affecting only the plant canopy) or catastrophic (affecting roots and rhizomes; killing the vegetation). Other herbivores such as non-native nutria (*Myocastor coypus*) or lesser snow geese (*Chen caerulescens*) are heavy consumers of belowground material and account for more catastrophic disturbances (Willner et al. 1979, Miller et al. 2005). This level of disturbance in coastal marshes has been shown to result in re-colonization by grass species in the short-term (Miller et al. 2005, Bhattacharjee et al. 2007). Allison (1995) found that *D. spicata* was also especially adept at re-colonizing areas after small-scale sediment spoil disturbances that killed underlying vegetation. However, Bhattacharjee et al (2007) noted that while grasses re-colonized in the short term, there was a shift from a grass-dominated to a sedge-dominated community several years after extreme muskrat herbivory.

The disturbance caused by prescribed fire is non-catastrophic and usually confined to the canopy level. Cover burns are the most common form of prescribed fire; they are performed when the water table is just above the surface and remove only senesced plant material and litter (Hoffpauer 1968, Nyman and Chabreck 1995). Studies have shown that cover fires can increase plant primary productivity and biomass production of several species (Hackney and de la Cruz 1981, Pendelton and Stevenson 1983, Nyman and Chabreck 1995, Gabrey et al. 2001, Cahoon et al. 2010). This stimulatory effect may be associated with increased light availability and soil temperatures following the removal of the plant canopy (Bickford et al. in prep). Canopy removal has been found to increase soil temperatures in the upper part of the soil (Sharrow and Wright 1977, Miller et al. in prep). Increased soil temperatures may increase plant growth rates. Additionally, this is the region of the soil (oxidized zone) is likely occupied by nitrifying bacteria in wetlands (Mitsch and Gosselink 2007). The increase in soil temperatures and resulting increase in nitrate availability may create optimal growth conditions for plants (Old 1969, Sharrow and Wright 1977, DeLucia et al. 1992). Another explanation is that increased light availability following the removal of the plant canopy functionally increases the growing season for faster sprouting plant species (Hackney and de la Cruz 1983, Bickford et al. in prep).

Plant canopy disturbances such as fire may increase the competitive ability of certain species. Platt and Connell (2003) found that non-catastrophic disturbance affecting two or more species has the potential to change the rates of replacement ongoing at the time of disturbance if one species is less affected or recovers more quickly than another. Continued application of fire has been found to give the marsh species *S. americanus* a competitive advantage over slower growing species (O'Neil 1949). *S. americanus* is thought of as a sub-climax species under normal conditions while *S. patens* and *D. spicata* are normally dominant (Sipple 1979). However, under fire management, *S. americanus*, which begins its growth early in the season and grows better in cooler temperatures, is relieved from competitive pressure and is able to outcompete *S. patens* (Sipple 1979), a species normally suppressed by fire (Ford and Grace 1998).

Bickford et al. (in prep) found that canopy removal from prescribed fire was the dominant mechanism increasing biomass production. They found the stimulatory effect to be stronger in areas dominated by sedge species than in areas dominated by grasses. Because they grow better in cooler temperatures, the sedges may have been able to take advantage of increased light availability for a longer portion of the growing season than the warm season grass species, resulting in greater belowground production and stem density (Bickford *et al*. in prep). *S. patens* and *D. spicata* have been found to increase in biomass following burning or mowing when faster growing species are not present (de Szalay and Resh 1997). To what extent plant canopy disturbances affect biomass production may differ as species composition varies. Coastal marshes are heavily impacted systems experiencing extreme land losses that threaten wildlife habitat and other essential ecosystem services provided by wetlands. Significant marsh loss and conversion to open water are occurring due to factors such as sea-level rise, land subsidence, erosion, and saltwater intrusion (Stevenson et al. 2000). In addition, marshes are frequently impacted by localized natural and anthropogenic disturbances (e.g. herbivory, fire, inclement weather). Faced with these threats, the long-term persistence of coastal marshes will be dependent on their ability to accrete, or build vertically. The buildup of materials through aboveground and belowground organic matter accumulation can be thought of as a source of natural capital that contributes to marsh resilience, or capacity of the system to respond to disturbance and maintain normal functionality (Cahoon and Guntenspergen 2010). Understanding the effects of plant canopy disturbance on competition in various species compositions can influence vertical accretion and is therefore important for assessing the adaptive capacity of these systems.

We conducted a manipulative experiment to determine to what extent plant canopy removal affects aboveground and belowground biomass production of two dominant brackish marsh species, *S.americanus* and *D. spicata*, in pure and mixed species compositions. This study utilized a Replacement Series design (De Wit 1960, Jolliffe 2000). There were three species densities established: 100:0, 50:50, and 0:100. The main response variables were aboveground biomass and belowground production.

Methods

Plant Harvest

In December 2009, plugs of approximately 30-cm diameter were harvested from a tidal marsh located off of Maple Dam Road at Blackwater National Wildlife Refuge, Dorchester County, MD (approx. 38°24’31”N 76°03’03”W). The soils of the harvest area are mapped as Bestpitch and Transquaking Soils (terric or typic sulfihemists) or Sunken mucky silt loams (typic ochraqualfs; Soil Survey Staff 2010).

The tidal range is roughly 30 cm, but is not a regular, diurnal tide, but is rather driven primarily by wind. The average salinity in the area was 8 ppt based on field data collected by Bickford et al. (in prep). Plugs were exhumed from the marsh in relatively pure stands of either *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller or *Dischtlis spicata* (L.) Greene (USDA 2011). Plugs were placed in 30-cm diameter pots for transport to the University of Maryland Research Greenhouse Complex, College Park, MD.

Pot Establishment

Plugs of each species were kept in a greenhouse room with no heat to keep plants from breaking senescence during preparation. The 30-cm diameter plugs were cut into smaller plugs (approximately 5 X 5 cm). The small plugs were used to assemble pots of pure sedge (four *S. americanus* plugs), pure grass (four *D. spicata* plugs), or mixed species (two of each plug). Pots were 30 cm in diameter and 30 cm tall. Each pot contained two 30-cm long, 5-cm diameter mesh root ingrowth bags (similar to the methods of Gallagher et al. 1984, Cahoon et al. 2003, and McKee et al. 2007) to estimate belowground production. They were filled in the laboratory with super-fine sphagnum peat prior to deployment. Native peat could not be used because it contained fine roots that would be indistinguishable from those established post-deployment. Each pot also contained one temperature logger buried at 5 cm logging every two hours (Fig. 1). Void space was filled with fine ground commercial sphagnum peat saturated and packed to a density that mirrored that of the small plugs. Holes were punched in the side of the pots after they were assembled to allow water to flow through. Each pot was placed inside of a 12-gallon bin and saturated to the

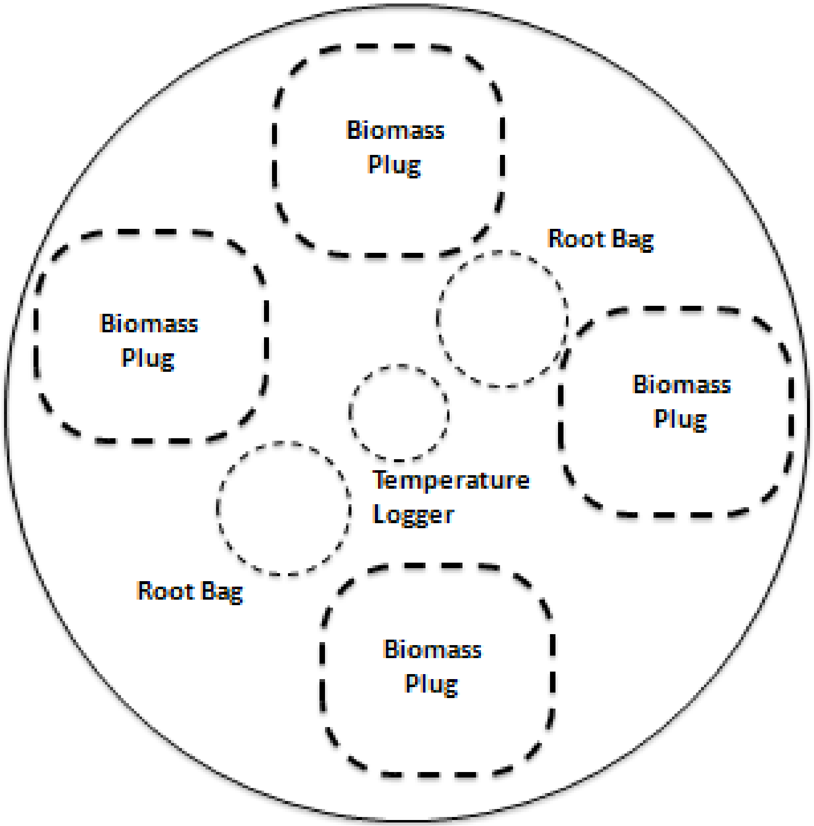

Figure 1: Schematic diagram of the components of each pot. Pot depth was approximately 30 cm. Void space filled with sphagnum peat.

soil surface with water of 8 ppt salinity. Saltwater was prepared by adding Instant Ocean (Spectrum Brands, Inc.) seasalt mix to tap water. The mixing ratio was approximately ½ cup of salt mix to 5 gal water. The salinity was verified at 8.0 (±0.2) ppt using a salinity probe before saturating the pots. Twelve pots of each species composition were assembled (n=36). Bins were placed on racks in a greenhouse room where the conditions were set to emulate the outdoor temperature and humidity, however, this was difficult as heat became trapped in the room and the temperature in the room remained much warmer than outdoors. The room was not irrigated.

Experimental Set-up

Bins of each species composition were numbered and each number was randomly assigned a spot on one of six rows. Within each row, bins of each species were randomly assigned to either a Canopy Removal or Control treatment. On 18 Mar 2010, pots assigned to the Canopy Removal treatment had all vegetation clipped, leaving about 1 cm of stubble on the soil surface. Due to heightened temperatures in the greenhouse, some plants had already begun to break dormancy when they were clipped. Therefore, some new growth was clipped along with senesced biomass. Pots were drained and refilled weekly with new saltwater. All pots were drained, flushed with freshwater, and refilled with saltwater biweekly to avoid buildup of salts in the soil from evaporation.

Data Collection

Light availability was monitored throughout the study using a quantum line point sensor. The average of three readings was taken above the canopy and at the soil surface of each pot a total of six times over the course of the growing season. At peak growth, on 28 July 2010, stem density was assessed by counting all stems of each species in each pot. Average plant height of each species in every pot was also recorded. Vegetation was then clipped, leaving only about 1 cm of stubble at the surface, and collected. Biomass harvests and stem density counts only included growth from the current season. Root ingrowth bags were extracted using a serrated knife to cut around the bag in order to avoid pulling roots from the bag. Ingrowth bags were stored in a refrigerator (5°C) for no more than two weeks prior to processing. Temperature loggers were removed and downloaded.

Laboratory Analyses

All harvested biomass was sorted by species, dried at 60°C for 48 hours, and weighed to obtain aboveground biomass. Ingrowth cores were cut into 10 cm segments; the contents were passed through a 1-mm sieve to separate the fine sphagnum peat from the belowground plant growth and washed. Contents were floated in water and dead material was removed. To identify roots by species, we used two methods described in Saunders *et al* (2006). Roots were first categorized visually by color. Because roots of *S. americanus* are typically orange, red, dark red, with only a small proportion of white roots (Saunders et al. 2006), and roots of *D. spicata* and *S. patens* are generally white or grey, we established a set of color standard classes to match to belowground materials. All live belowground materials were separated into four classes based on which standards they most closely matched: (1) red rhizomes, (2) white rhizomes, (3) red roots, and (4) white roots. Rhizomes of these two species can be distinguished by their color; red indicates *S. americanus* and white indicates *D. spicata*. However, because both species produce white roots, determination of species of the white roots required a more sophisticated analysis of the carbon isotopic signatures. Because *S. americanus* is a C_3 species and *D. spicata* is a C_4 species, the carbon isotopic signatures are measurably different. A comparison of carbon isotopic signatures in roots that were visually indistinguishable was used to determine whether the root is of a C_3 or C_4 species, and therefore, if it comes from *S. americanus* or *D. spicata*.

Each class of belowground material was dried at 60°C for 72 hours and weighed to obtain an estimate of belowground production in each pot. Roots were then finely ground using a table top ball mill. Approximately 4 mg of ground plant tissue was weighed using a microbalance and packed into tin capsules. Weights were recorded to 4 decimal places. All samples were run on a Thermo Delta V Advantage mass spectrometer in continuous flow mode coupled to a Costech 4010 Elemental Analyzer (EA) via a Thermo Conflo IV. A set of standards was included for every 10-12 samples. Standards included Costech Acetanilide and a urea standard, both of which were calibrated to USGS40 (L-glutamic acid) and USGS41 (L-glutamic acid). All standards were run with the same parameters and procedures as samples. Reproducibility of standards is ≤ 0.2 ‰ (1σ) for $\delta^{13}C$. The error associated with all sample data points is therefore reported as ±0.2‰. $\delta^{13}C$ analyses were determined by Christine France at the Smithsonian OUSS/MCI Stable Isotope Mass Spectrometry Laboratory of the Smithsonian Museum Conservation Institute in Suitland, MD.

Isotopic signatures were used to calculate the percent of root biomass belonging to the C_3 species. $\%C_3$ was calculated by the dual end-member equation (from Saunders et al. 2006):

$$\%C_3 = 100 \times (\delta^{13}C_{sample} - \delta^{13}C_{C4}) / (\delta^{13}C_{C3} - \delta^{13}C_{C4}),$$

where $\delta^{13}C_{sample}$ is the isotopic signature of a given sample of biomass, $\delta^{13}C_{C3}$ is the isotopic signature of samples taken from the pure *S. americanus* pots and $\delta^{13}C_{C4}$ is the isotopic signature of samples taken from the pure *D. spicata* pots. These percentages were then multiplied by the total biomass of the sample and red and white roots were combined to determine each species' contribution to the root production in each pot. Each species' contribution to total production was determined by the following equations:

$$\textit{total belowground S. americanus} = [(\%C3_{\text{red roots}}/100) \times \textit{red roots}] + [(\%C3_{\text{white roots}}/100) \times \textit{white roots}] + \textit{red rhizomes}$$

$$\textit{total belowground D. spicata} = [(\%C4_{\text{red roots}}/100) \times \textit{red roots}] + [(\%C4_{\text{white roots}}/100) \times \textit{white roots}] + \textit{white rhizomes}$$

where rhizome $\%C_4$ was assumed to be equal to 100 minus $\%C_3$. All belowground production values were scaled to $g\cdot m^{-2}$ to a depth of 30 cm.

Data Analysis

Replacement Diagrams were created to show trends in dry mass production aboveground and belowground (as described in Hill and Simamoto 1973, Jolliffe 2000). Relative Yield (RY) was calculated by dividing each species' mean yield in 50/50 mixture by half of the species' mean yield in monoculture (De Wit 1960, Williams and McCarthy 2001). A Relative Yield value of 1 indicates that a species grows just as well in mixture as in monoculture, or intra- and interspecific completion are equal. Values less than 1 indicate that interspecific competition is greater than intraspecific competition for the given species in mixture, or that the yield of a given species is reduced by the presence of another species. On the other hand, RY values greater than 1 indicate that given species does better competing against another species than it does in monoculture (Williams and McCarthy 2001).

This study utilized a complete randomized block design with six blocks. This was a two-way factorial arrangement. Discrete variables (biomass, stem density, plant height) were tested using analysis of variance (ANOVA). Repeated variable (temperature, light availability) were tested using repeated measures ANOVA. Comparisons of grass and sedge yield in mixed stands were analyzed using paired t-tests. Statistical analysis of relative yield utilized paired comparisons the yield in mixture vs. half of the yield in monoculture.

Results

Disturbance and Competition

Aboveground biomass. Replacement diagrams indicate that, in mixed compositions, aboveground *S. americanus* yield was 2.6 times greater than aboveground *D. spicata* yield when the canopy was removed (P=0.0033; Fig. 2a). However, when the canopy was not removed, although there was still a trend toward a 78 % increase in *S. americanus* yield over that of *D. spicata*, the difference was not significant (P=0.07; Fig. 2b). Similarly, the relative yield of *S. americanus* in mixture was significantly greater than 1 (P=0.016), indicating competitive superiority, when the canopy was removed. When the canopy was not removed, the relative yield of *S. americanus* in mixture was not different from 1 (P=0.095). Relative yields of *D. spicata* showed a trend of values less than 1, indicating competitive pressure, both

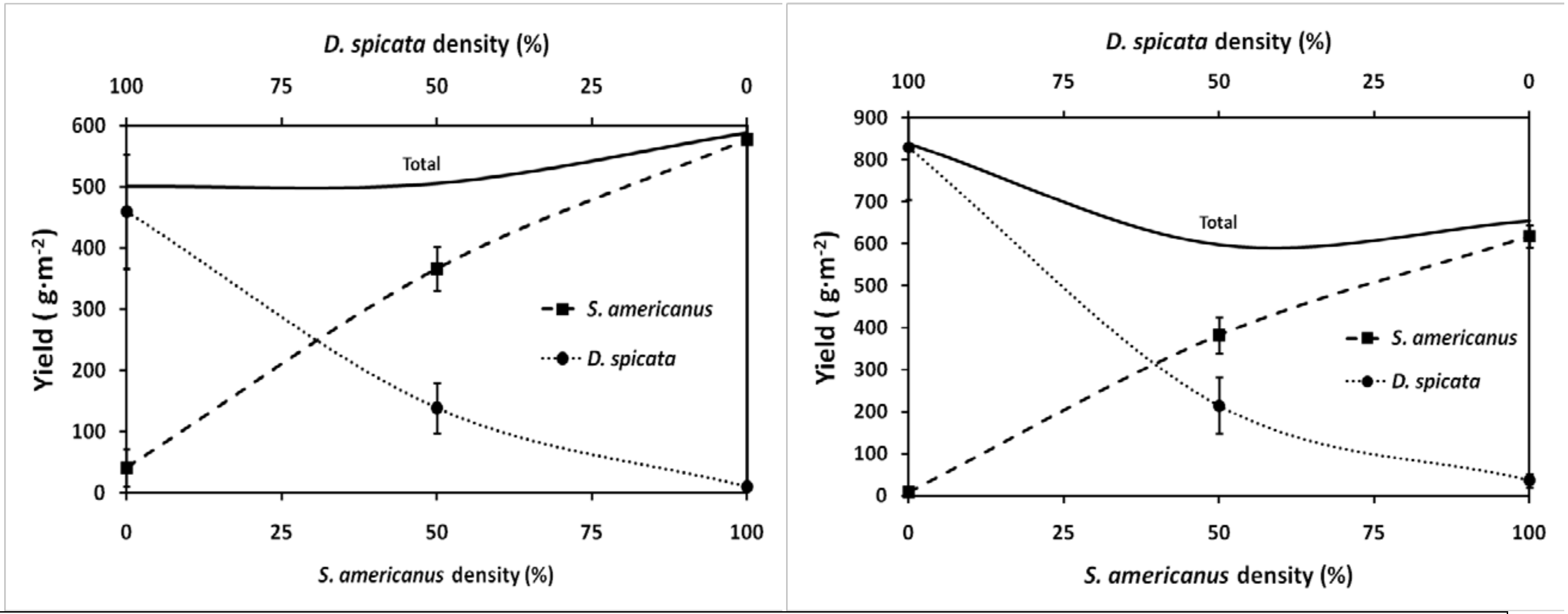

Figure 2: Replacement diagrams of aboveground biomass of each species in each species composition under **a)** canopy removal and **b)** no canopy removal. Values represent the mean of 6 replicates (± standard error of the mean). Asterisk indicates results of paired t-test; Asterisk indicated means are significantly different from each other (α=0.05).

when the canopy was and was not removed. These trends were not statistically significant (Table 1; P=0.092 and P=0.056, respectively).

Stem RY in mixture of *S. americanus* was significantly greater than 1 both when the canopy was, and was not removed (Table 1; P=0.0025 and P=0.027, respectively). The relative yield of stems of *D. spicata* in mixture was less than 1 in both canopy removal and no canopy removal treatments. These were only statistically different from 1 in the no canopy removal treatment (P=0.0079).

Belowground biomass. In mixed compositions, mean *S. americanus* total belowground production (root + rhizome) yield was 2 times greater than *D. spicata* yield when the canopy was removed (P=0.047; Fig. 3a). However, when the canopy was not removed, there was no significant difference between the yield of *S. americanus* and *D. spicata* (P=0.24; Fig. 3b). If analysis is focused on fine roots only, this effect is even stronger. In mixed compositions, *S. americanus* fine root production was 2.9 times greater than *D. spicata* yield when the canopy was removed (P=0.010; Fig. 4a). However, when the canopy was not removed, although there was no significant difference between the yield of *S. americanus* and *D. spicata* (P=0.080; Fig. 4b).

While Relative yields in mixture of total belowground production and fine root production of *S. americanus* were not significantly different from 1 across all treatments, when the canopy was removed, a trend towards higher values existed (Table 1; P=0.057 in fine roots). When the canopy was not removed, relative yields of total belowground and fine root production were not different from one (P=0.20 and P=0.11, respectively). Relative yield of total belowground and fine root production of

Table 1: Relative yields in mixture of each species under canopy removal and no canopy removal treatments. Asterisk indicates relative yield is significantly different from 1 (α=0.05).

	Relative Yield in Mixture			
	S. americanus		*D. spicata*	
	Canopy Removal	No Canopy Removal	Canopy Removal	No Canopy Removal
Aboveground Biomass	1.27*	1.24	0.61	0.52
Stem Density	1.77*	1.57*	0.46	0.58*
Belowground Production	1.20	0.88	0.75	0.69
Fine Root Production	1.53	0.88	0.74	0.71

Table 2: Breakdown of belowground production from each species composition. All values in g·m^{-2} (plus or minus the standard error of the mean.

	Sedge Pots	Grass Pots	Mixed Pots
Roots			
C_3-white roots			2.11 ± 0.48
C_4-white roots			20.48 ± 6.96
total white roots	0.84 ± 0.47	69.49 ± 9.46	23.54 ± 6.94
C_3-red roots			53.85 ± 6.56
C_4-red roots			6.52 ± 1.50
total red roots	111.34 ± 10.51	1.56 ± 0.90	60.37 ± 6.98
total roots	112.19 ± 10.42	71.06 ± 9.47	86.63 ± 11.16
Rhizomes			
White Rhizomes	0.18 ± 0.18	61.59 ± 10.56	29.4 ± 9.8
Red Rhizomes	79.75 ± 21.77	0.17 ± 0.17	25.5 ± 11.3
Total Rhizomes	73.27 ± 20.51	75.47 ± 14.89	54.75 ± 15.96
Roots + Rhizomes	180.81 ± 27.49	151.0 ± 23.29	150.36 ± 23.27

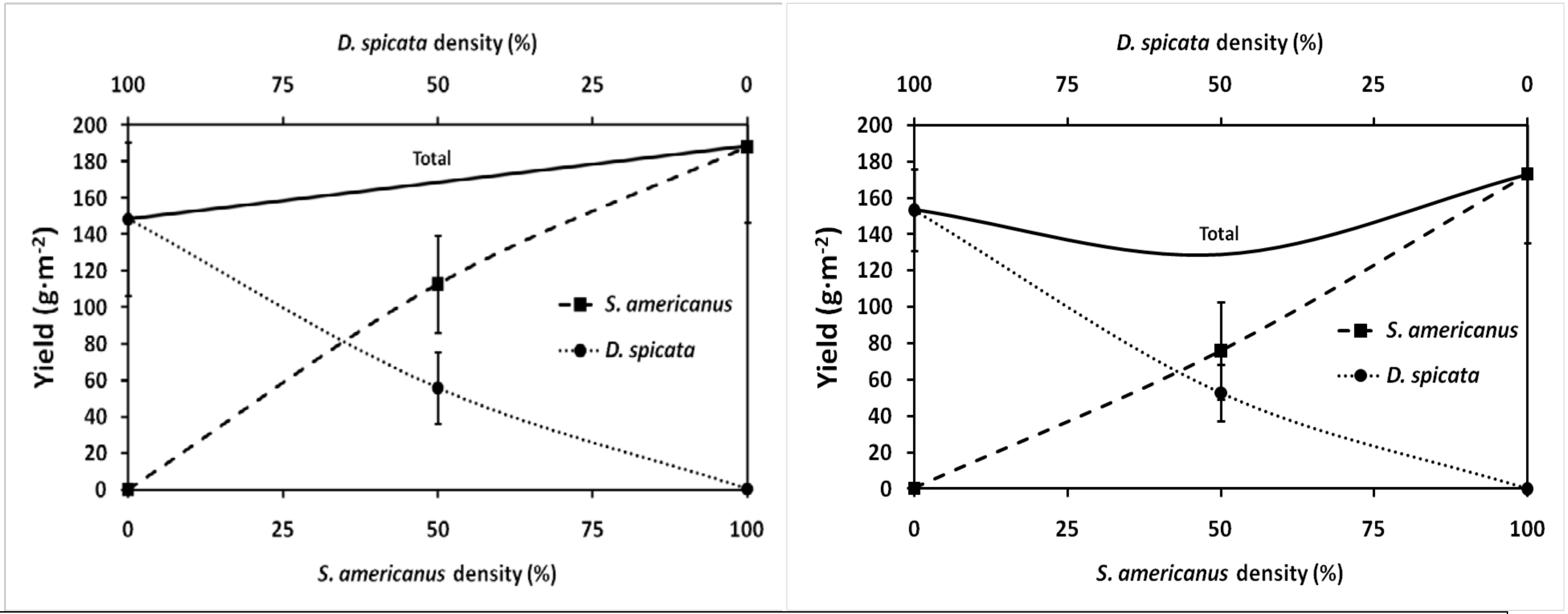

Figure 3: Replacement diagrams of total belowground production (roots + rhizomes) of each species in each species composition under **a)** canopy removal and **b)** no canopy removal. Values represent the mean of 12 replicates (± standard error of the mean). Asterisk indicates results of paired t-test; Asterisk indicated means are significantly different from each other (α=0.05).

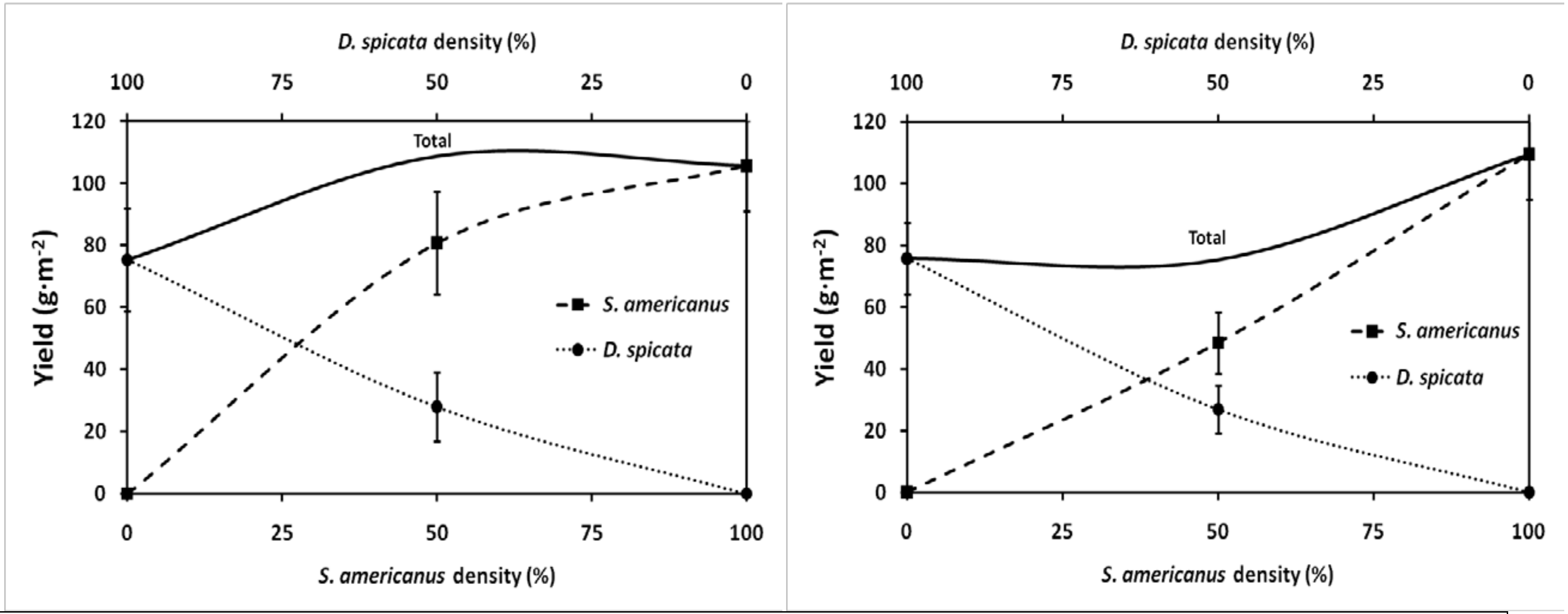

Figure 4: Replacement diagrams of fine root production of each species in each species composition under **a)** canopy removal and **b)** no canopy removal. Values represent the mean of 12 replicates (± standard error of the mean). Asterisk indicates results of paired t-test; Asterisk indicated means are significantly different from each other (α=0.05).

D. spicata was not significantly different from 1 in any treatment, but all showed a trend towards values less than 1 (Table 1, Fig. 5).

Light availability and Soil Temperature

Removing the plant canopy allowed more light to the soil surface in all species compositions throughout the study period (Fig. 6a; P=0.0045). There was also a significant species composition effect on light availability (P=0.0178). Over the course of the study, while there was some variability by date that was possibly attributable to canopy architecture changes as plants grow taller (no significant species X date interaction), sedge pots received more light to the surface than grass pots while mixed composition pots received more light than both (Fig. 6b). When averaged across all species compositions, soil temperature at 5 cm did not significantly increase following canopy removal (Fig. 7a). There was also no difference in soil temperature in each species composition. Overall, temperatures were slightly higher following canopy removal, but increased less than 1°C (Fig. 7b).

Discussion

Competitive dynamics in mixed compositions seemed to be influenced by canopy level disturbances. For instance, the amount of the total yield made up by *S. americanus* in mixed compositions was significantly greater than that made up by *D. spicata* when the canopy was removed, but was not different when the canopy was not removed. This is evidence of a competitive advantage in *S. americanus* following canopy removal. Examining the relative yield of aboveground biomass and stem density in mixture indicates that *S. americanus* was out competing *D. spicata* in mixture when the canopy was removed (Fig. 5). Similarly, *D. spicata* showed a trend

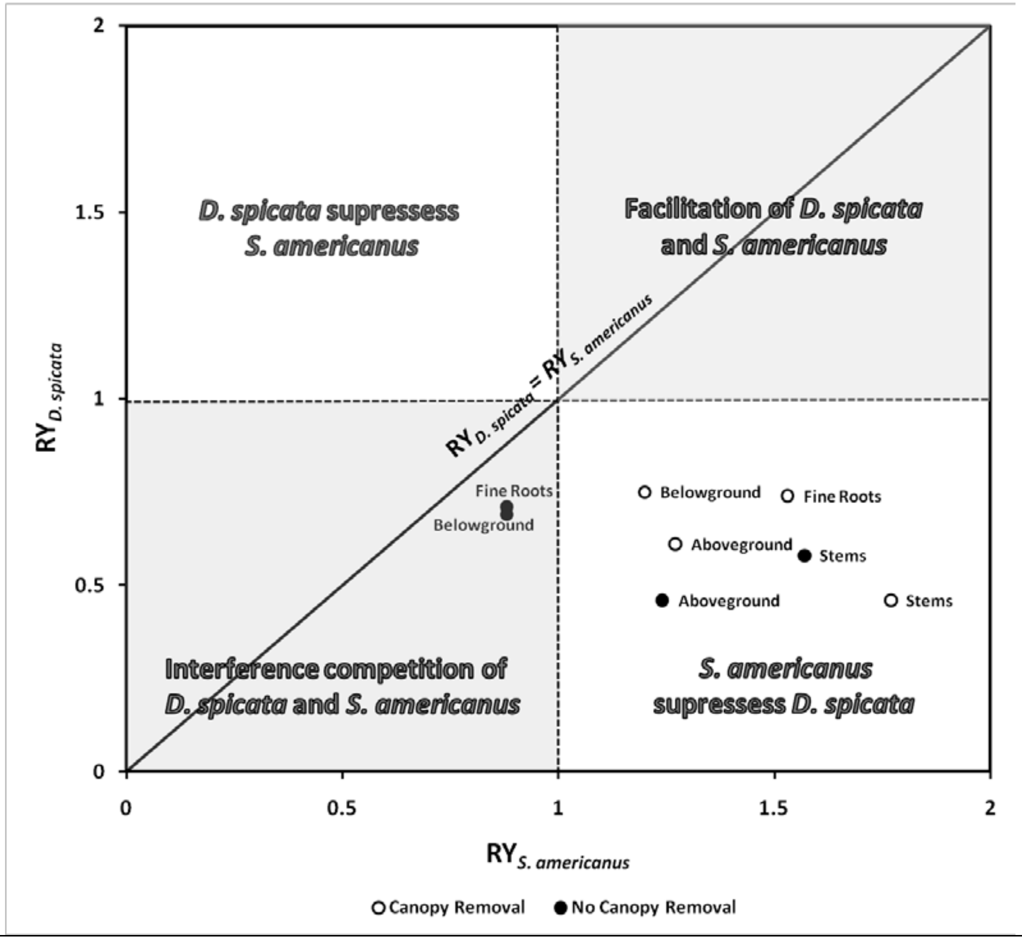

Figure 5: Relative Yield of *S. americanus* plotted against Relative Yield of *D. spicata* on a chart indicating all possible competitive outcomes (modified from Williams and McCarthy 2001). Each point is accompanied by its corresponding parameter from which the RY was calculated.

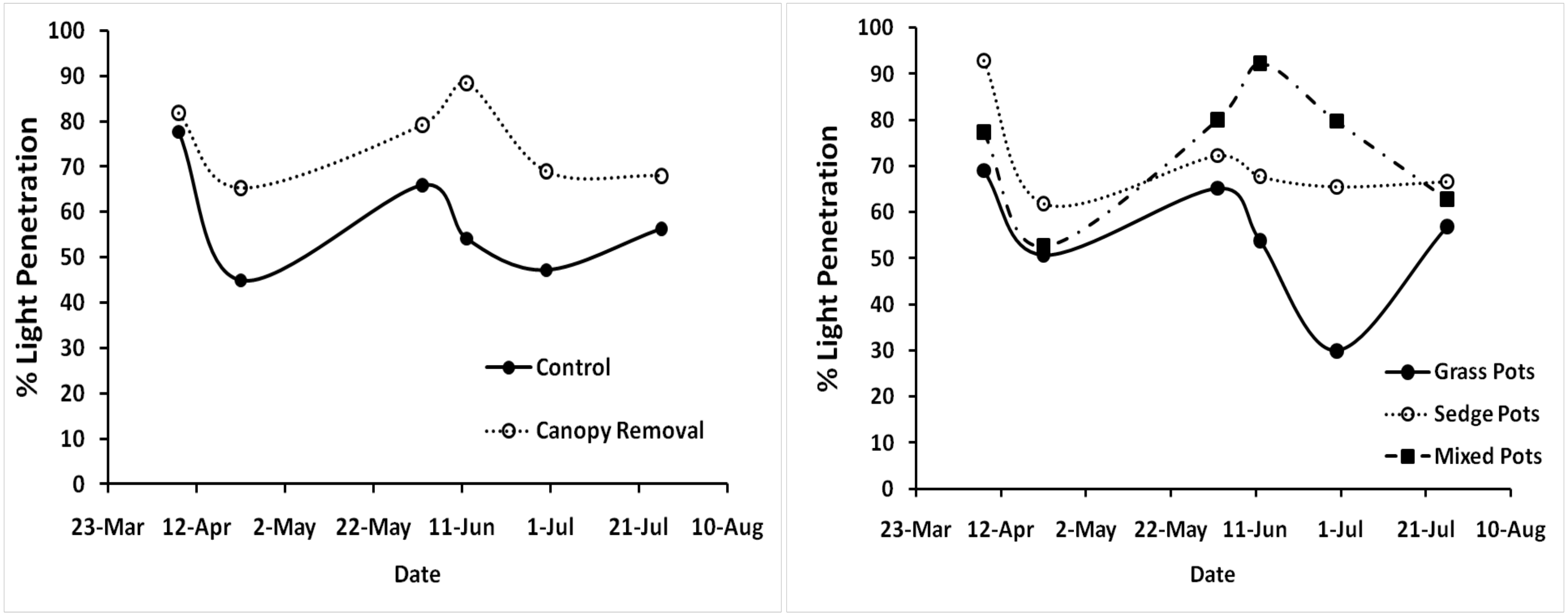

Figure 6: Percent light penetration (PAR below canopy / PAR above canopy) **a)** averaged across all species compositions (values represent the mean of 18 replicates) and **b)** averaged overall both canopy treatments (values represent the mean of 12 replicates).

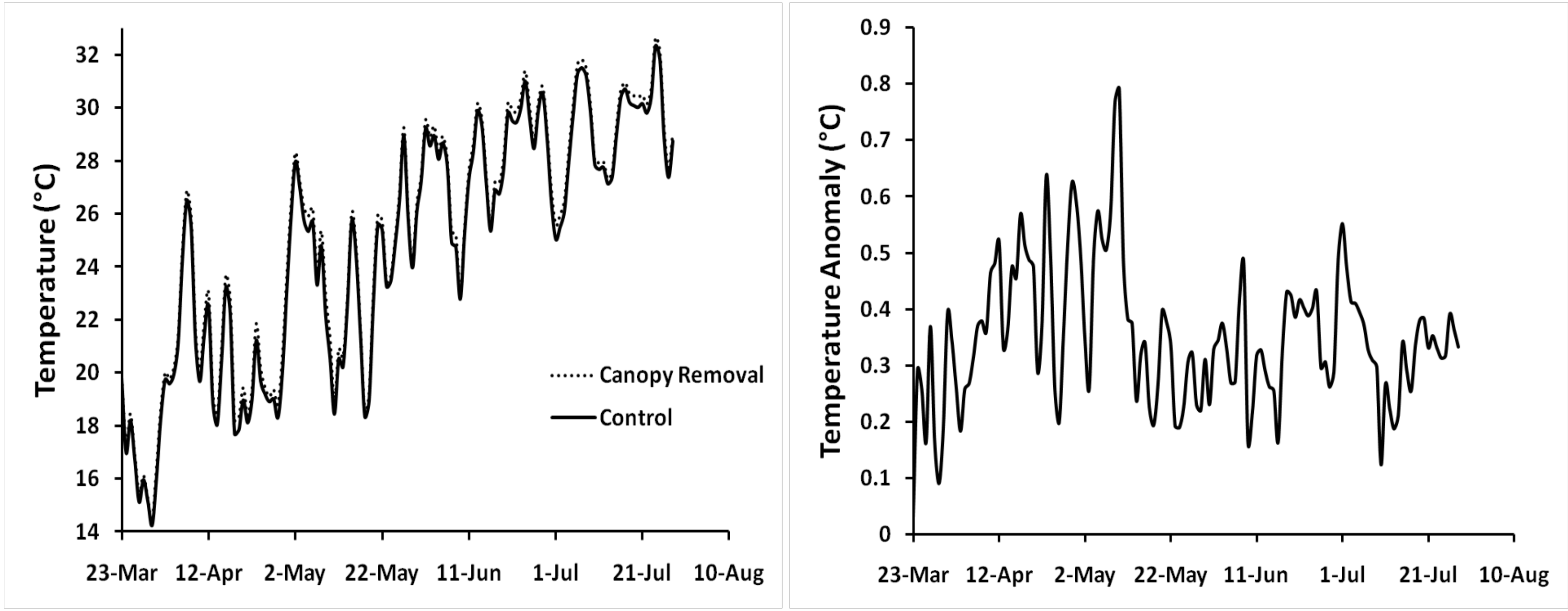

Figure 7: a) Soil temperature at 5 cm averaged across all species compositions (each data point represents the mean of 18 replicates) **b)** Temperature anomaly (difference from control) averaged across all species compositions.

toward competitive suppression in mixture as its relative yield was consistently less than 1 (Fig. 5; Williams and McCarthy 2001). The same relationship was present in belowground production. These competitive interactions are consistent with data indicating that under fire management, *S. americanus* is able to outcompete *S. patens* and *D. spicata* (Sipple 1979). Our data indicate that *D. spicata* trended towards competitive inferiority whether or not the canopy was removed (Fig. 5), but was suppressed (significantly) by *S. americanus* when the canopy was removed. It is possible therefore, that while the temperature and light increases were very modest, they still gave *S. americanus* a competitive advantage over *D. spicata* when grown in mixed compositions.

Additionally, Figure 5 indicates that *S. americanus* is competitively superior in all treatments. However, when the canopy was not removed, the belowground production may be experiencing interference competition, or a decrease in production of both species when put in mixture (Williams and McCarthy 2001). When the canopy is removed, the dynamic changes to one in which *S. americanus* suppresses *D. spicata*. Bickford et al. (in prep) suggested that *S. americanus* responded to canopy removal more strongly than did *S. patens* and *D. spicata* because *S. americanus* breaks dormancy in cooler temperatures earlier in the season than *S. patens* and *D. spicata*. This earlier evolutionary plant trigger of *S. americanus* may allow the species to take advantage of increased soil temperatures and light availability for a longer portion of its growing season than warm season species like *S. patens* and *D. spicata*. When the canopy is removed, resources stored in rhizomes can be allocated to increasing stem density and belowground production rather than to penetrating the plant canopy through aboveground growth to gain access to light. These additional resources may allow earlier-sprouting species to gain a competitive advantage over later-sprouting species. Our data suggests, therefore, that canopy level disturbance may be particularly important in influencing the competitive dynamics of belowground growth.

This study suggested that anthropogenic disturbance may influence competitive dynamics in brackish marsh species. Plant productivity following disturbance continues to be a topic worthy of further study. The impacts of disturbance on different species compositions will be important for land managers to recognize as they attempt to predict adaptive capacity of these heavily impacted coastal marsh systems. Management tools such as prescribed fire can be used to increase organic matter inputs to the system. However, species composition plays a very important role in determining productivity and competitive interactions following disturbances like prescribed fire. Therefore, managers should consider how disturbance will alter conditions (such as light availability, soil temperature, and water level) and how those conditions can influence competitive interactions.

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Chapter 4: Summary and Conclusions

Prescribed fire is a widely used management technique that is known to benefit wildlife habitat, reduce fuel loading, and aid hunting and trapping efforts in coastal marshes. Fire is also known to stimulate plant productivity of certain species, but it also directly volatilizes litter and senesced plant material that would otherwise be deposited and incorporated into soil organic matter and help marshes accrete. Faced with a suite of challenges such as sea-level rise, erosion, salt-water intrusion, herbivory, and land subsidence, management techniques in coastal marshes must be focused on increasing elevation to help marshes remain above water. Although fire has also been shown to increase root production and decrease the rate of shallow subsidence in coastal marshes, because it consumes much of the aboveground organic matter inputs, its merits as a management technique have come into question. For this management technique to be used effectively in highly impacted systems, an understanding of the mechanisms behind the stimulatory effect of fire is important for managers to maximize the benefits to the ecosystem.

The first chapter of this thesis assessed the impacts of two potential mechanisms by which fire affects biomass production, canopy removal and ash deposition. Two manipulative experiments were set up within current fire management blocks at Blackwater National Wildlife Refuge in Dorchester County, MD. The first experiment was run in the No Burn management block. Treatments were (1) Control, (2) Canopy Removal, (3) Canopy Removal + Ash Deposition, and (4) Ash Deposition. The second experiment was conducted within the annual burn management blocks. Treatments included a control (burned by fire managers) and a

Canopy Replacement Treatment where an artificial plant canopy was installed over the marsh after a burn. At the peak of the growing season (Late July) plots were sampled for aboveground biomass, stem density, species percent cover, and plant height. Belowground biomass was harvested in December 2009.

Canopy removal was found to significantly increase aboveground and belowground production and stem density when averaged across all No Burn sites. Ash deposition showed no affect on biomass production or stem density. Additionally, sites with artificial canopies had lower biomass production and stem density than control sites. This indicated that canopy removal has the ability to increase biomass production and stem density and that installing an artificial canopy can potentially negate the positive biomass effects of a burn.

The effect of canopy removal on productivity was stronger at sites dominated by *Schoenoplectus americanus* than those dominated by *Spartina patens* and *Distchlis spicata*. Canopy removal likely benefited *S. americanus* by allowing more light to the soil surface early in the growing season. Because *S. americanus* is a C_3, cool season species which begins its growth in cool temperatures, it may have been able to take advantage of this increased light availability and slightly warmer soil temperature for a longer portion of its growing season than *S. patens* or *D. spicata*, both warm season, C_4 grasses. While the grass species may have benefited slightly from canopy removal, they are also known to be sensitive to high water following canopy disturbances. It is possible that water levels impeded the production of grass species following fire, but did not affect *S. americanus* because it is more flood-tolerant.

Species composition, therefore, plays a very important role in determining productivity and competitive interactions following disturbances like prescribed fire. To further explore these interactions, we tested the effects of canopy removal and species composition on plant productivity in a controlled greenhouse study. Species compositions consisted of 100% *S. americanus*, 100% *D. spicata*, and 50/50 of each. Disturbance treatments consisted of canopy removal or control. At the peak of the growing season, we harvested aboveground and belowground biomass and measured stem density.

In mixed stands, *S. americanus* production was significantly greater than that of *D. spicata* when the canopy was removed, but under control conditions, yields of *S. americanus* and *D. spicata* were not significantly different. Additionally, relative yield of *S. americanus* aboveground was significantly greater than 1 when the canopy was removed, but not different from 1 under no canopy removal. This was evidence that the canopy disturbance gave *S. americanus* a competitive advantage over *D. spicata* which is normally allowed to create a dense canopy and shade out *S. americanus* in mixed compositions.

Light availability and soil temperature were only modestly increased from canopy removal in the greenhouse when compared to the field study. However, *S. americanus* still gained a competitive advantage over *D. spicata*. It is likely, then that if the light and temperature response is greater in the field, so too is the competitive response of *S. americanus* over *D. spicata*.

Facing the threat of sea-level rise, marsh managers are concerned with increasing the adaptive capacity of these systems through increased inputs to elevation. Without increases in surface elevation to keep up with rising sea level, these coastal marshes could face a critical tipping point. Increased sea level will likely increase salinity which has been shown to decrease the growth rate of *S. americanus*. If elevation cannot keep up and the flooding depth also increases, this decline in *S. americanus* could be coupled with a loss of flood-sensitive grasses. Such losses in the major species could cripple these marshes and could lead to significant losses to open water. However, if done properly by maximizing canopy removal, our results suggest that prescribed fire has the potential to increase belowground inputs and decrease the rate of shallow subsidence in marshes. If the rates of elevation decline are slowed, less flood tolerant species like *S. americanus* may remain productive, decreasing losses to open water. If significant losses to open water can be avoided, these marshes may be able to maintain connectivity while migration to uplands occurs. Therefore, prescribed fire may subtly increase the adaptive capacity of these vulnerable systems.

Appendix A: Additional Figures for Chapter 2

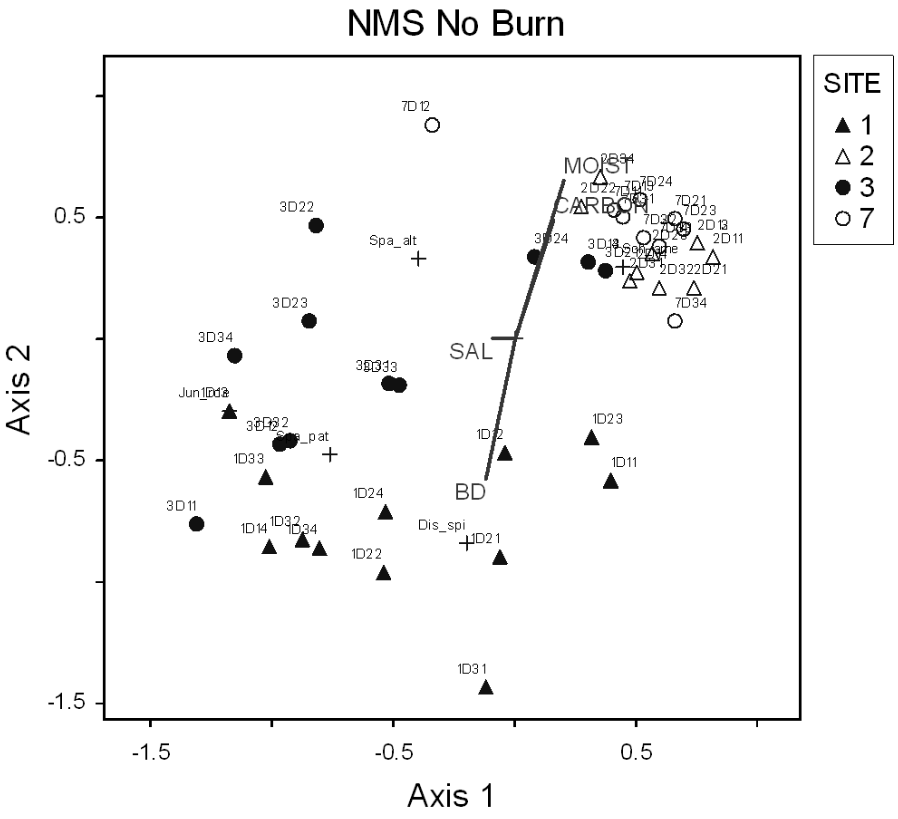

Figure 1: NMS ordination analysis of all No Burn Sites. Primary data were percent cover estimates of species in plots; secondary data included soil bulk density, soil percent carbon, soil moisture, and salinity. Points that are nearer to each other are share more in common than those that are far apart. Variables increase in the direction of the lines they are connected to. Sch_am: *S. americanus*, Spa_pat: *S. patens*, Dis_spi: *D. spicata*, Spa_alt: *S. alterniflora*, Jun_ro: *J. roemerianus*. BD: Bulk density, SAL: Salinity, CARBON: percent soil carbon, MOIST: percent soil moisture.

Appendix B. Statistical Models and Analysis for Chapter 2

This appendix provides statistical models and outputs from SAS for all data presented in tables and figures within chapter II. Each Program code is preceded by a title indicating the data it will analyze and the table or figure it corresponds with. To save space, parts of the out puts have been omitted. Generally, only the main effects are included unless further analyses (e.g. Tukey test) were used.

No Burn

Aboveground biomass all sites (Figure 3a)

Program:

```
title 'aboveground all islands';

proc mixed data=biomass;
       class island canopy ash;
       model total_above= canopy|ash;
       random island;
       lsmeans canopy ash canopy*ash / adjust=tukey;
       run;
```

Output:

```
                          aboveground all islands                         2
                                             12:10 Friday, September 3, 2010

                            The Mixed Procedure

                        Type 3 Tests of Fixed Effects

                              Num     Den
              Effect           DF      DF    F Value    Pr > F

              Canopy            1      89      21.79    <.0001
              Ash               1      89       0.83    0.3643
              Canopy*Ash        1      89       0.32    0.5708


                     Differences of Least Squares Means

    Effect      Canopy    Ash    Canopy    Ash    Adjustment      Adj P

    Canopy      Canopy           NoCanopy         Tukey-Kramer   <.0001
    Ash                   Ash              NoAsh  Tukey-Kramer   0.3643
    Canopy*Ash  Canopy    Ash    Canopy    NoAsh  Tukey-Kramer   0.7222
    Canopy*Ash  Canopy    Ash    NoCanopy  Ash    Tukey-Kramer   0.0021
    Canopy*Ash  Canopy    Ash    NoCanopy  NoAsh  Tukey-Kramer   0.0009
    Canopy*Ash  Canopy    NoAsh  NoCanopy  Ash    Tukey-Kramer   0.0454
    Canopy*Ash  Canopy    NoAsh  NoCanopy  NoAsh  Tukey-Kramer   0.0240
    Canopy*Ash  NoCanopy  Ash    NoCanopy  NoAsh  Tukey-Kramer   0.9950
```

Total Belowground Biomass (Figure 3b)

Program:

```
title 'belowground all islands';

proc mixed data=biomassbelow;
       class island canopy ash;
       model total_below= canopy|ash;
       random island;
       lsmeans canopy ash canopy*ash / adjust=tukey;
       run;
```

Output:

```
                         belowground all islands                         5
                                           12:10 Friday, September 3, 2010

                           The Mixed Procedure

                             Fit Statistics

                  -2 Res Log Likelihood         1208.4
                  AIC (smaller is better)       1210.4
                  AICC (smaller is better)      1210.5
                  BIC (smaller is better)       1209.8


                      Type 3 Tests of Fixed Effects

                             Num     Den
             Effect           DF      DF    F Value    Pr > F

             Canopy            1      83       8.58    0.0044
             Ash               1      83       0.01    0.9195
             Canopy*Ash        1      83       0.31    0.5807

                     Differences of Least Squares Means

   Effect      Canopy    Ash    Canopy    Ash    Adjustment      Adj P

   Canopy      Canopy           NoCanopy         Tukey          0.0044
   Ash                   Ash              NoAsh  Tukey          0.9195
   Canopy*Ash  Canopy    Ash    Canopy    NoAsh  Tukey-Kramer   0.9667
   Canopy*Ash  Canopy    Ash    NoCanopy  Ash    Tukey-Kramer   0.3413
   Canopy*Ash  Canopy    Ash    NoCanopy  NoAsh  Tukey-Kramer   0.1883
   Canopy*Ash  Canopy    NoAsh  NoCanopy  Ash    Tukey-Kramer   0.1555
   Canopy*Ash  Canopy    NoAsh  NoCanopy  NoAsh  Tukey-Kramer   0.0734
   Canopy*Ash  NoCanopy  Ash    NoCanopy  NoAsh  Tukey-Kramer   0.9885
```

Total belowground biomass in 0-10 cm zone (Figure 4a)

Program:

```
title 'Total all islands 0-10';

proc mixed data=totalbelowprofile;
      class island canopy ash;
      model zero_to_ten=canopy|ash|island;
      lsmeans canopy|ash / adjust=tukey;
run;
```

Output:

```
                        Total all islands 0-10                          2
                                       11:09 Tuesday, September 21, 2010

                          The Mixed Procedure

                    Type 3 Tests of Fixed Effects

                             Num     Den
        Effect                DF      DF    F Value    Pr > F

        Canopy                 1      72       8.89    0.0039
        Ash                    1      72       0.52    0.4746
        Canopy*Ash             1      72       0.08    0.7799
        Island                 3      72       0.49    0.6906
        Island*Canopy          3      72       0.57    0.6356
        Island*Ash             3      72       0.50    0.6801
        Island*Canopy*Ash      3      72       0.73    0.5390


                  Differences of Least Squares Means

  Effect      Canopy    Ash    Canopy    Ash    Adjustment      Adj P

  Canopy*Ash  Canopy    Ash    Canopy    NoAsh  Tukey-Kramer   0.9900
  Canopy*Ash  Canopy    Ash    NoCanopy  Ash    Tukey-Kramer   0.1134
  Canopy*Ash  Canopy    Ash    NoCanopy  NoAsh  Tukey-Kramer   0.3824
  Canopy*Ash  Canopy    NoAsh  NoCanopy  Ash    Tukey-Kramer   0.0526
  Canopy*Ash  Canopy    NoAsh  NoCanopy  NoAsh  Tukey-Kramer   0.2217
  Canopy*Ash  NoCanopy  Ash    NoCanopy  NoAsh  Tukey-Kramer   0.8901
```

Rhizome production 0-10 cm (Figure 4b)

Program:

```
title 'rhizome all islands 0-10';

proc mixed data=totalrzprofile;
      class island canopy ash;
      model zero_to_ten=canopy|ash|island;
      lsmeans canopy|ash / adjust=tukey;
run;
```

Output:

```
                         rhizome all islands 0-10                        29
                                          11:09 Tuesday, September 21, 2010

                            The Mixed Procedure

                       Type 3 Tests of Fixed Effects

                                 Num     Den
          Effect                  DF      DF    F Value    Pr > F

          Canopy                   1      73       7.61    0.0073
          Ash                      1      73       0.38    0.5393
          Canopy*Ash               1      73       0.22    0.6368
          Island                   3      73       1.62    0.1913
          Island*Canopy            3      73       1.02    0.3901
          Island*Ash               3      73       0.44    0.7278
          Island*Canopy*Ash        3      73       0.48    0.6965


                     Differences of Least Squares Means

    Effect      Canopy    Ash    Canopy    Ash    Adjustment      Adj P

    Canopy*Ash  Canopy    Ash    Canopy    NoAsh  Tukey-Kramer   0.9996
    Canopy*Ash  Canopy    Ash    NoCanopy  Ash    Tukey-Kramer   0.1139
    Canopy*Ash  Canopy    Ash    NoCanopy  NoAsh  Tukey-Kramer   0.4239
    Canopy*Ash  Canopy    NoAsh  NoCanopy  Ash    Tukey-Kramer   0.0941
    Canopy*Ash  Canopy    NoAsh  NoCanopy  NoAsh  Tukey-Kramer   0.3713
    Canopy*Ash  NoCanopy  Ash    NoCanopy  NoAsh  Tukey-Kramer   0.8651
```

Fine roots 0-10 cm (Figure 4c)

Program:

```
title 'ROOTS all islands 0-10';

proc mixed data=totalRTprofile;
      class island canopy ash;
      model zero_to_ten=canopy|ash|island;
      lsmeans canopy|ash / adjust=tukey;
run;
```

Output:

```
                           ROOTS all islands 0-10                          53
                                          11:09 Tuesday, September 21, 2010

                             The Mixed Procedure

                       Type 3 Tests of Fixed Effects

                               Num     Den
          Effect                DF      DF    F Value    Pr > F

          Canopy                 1      74       8.86    0.0039
          Ash                    1      74       0.51    0.4755
          Canopy*Ash             1      74       0.06    0.8132
          Island                 3      74       3.87    0.0126
          Island*Canopy          3      74       0.69    0.5585
          Island*Ash             3      74       0.99    0.4002
          Island*Canopy*Ash      3      74       0.86    0.4662



                      Differences of Least Squares Means

    Effect      Canopy    Ash    Canopy    Ash    Adjustment      Adj P

    Canopy*Ash  Canopy    Ash    Canopy    NoAsh  Tukey-Kramer   0.9864
    Canopy*Ash  Canopy    Ash    NoCanopy  Ash    Tukey-Kramer   0.1138
    Canopy*Ash  Canopy    Ash    NoCanopy  NoAsh  Tukey-Kramer   0.3705
    Canopy*Ash  Canopy    NoAsh  NoCanopy  Ash    Tukey-Kramer   0.0579
    Canopy*Ash  Canopy    NoAsh  NoCanopy  NoAsh  Tukey-Kramer   0.2216
    Canopy*Ash  NoCanopy  Ash    NoCanopy  NoAsh  Tukey-Kramer   0.9063
```

Aboveground Biomass Grass-Dominated Sites (Figure 6a)

Program:

```
title 'aboveground grass islands';

proc mixed data=onedthreed;
       class island canopy ash;
       model aboveground= canopy ash canopy*ash;
       random island;
       lsmeans canopy ash canopy*ash / adjust=tukey;
       run;
```

Output:

```
                        aboveground grass islands                         2
                                           12:10 Friday, September 3, 2010

                           The Mixed Procedure

                             Fit Statistics

                   -2 Res Log Likelihood           568.4
                   AIC (smaller is better)         570.4
                   AICC (smaller is better)        570.5
                   BIC (smaller is better)         569.1


                      Type 3 Tests of Fixed Effects

                          Num     Den
              Effect       DF      DF    F Value    Pr > F

              Canopy        1      43       0.73    0.3986
              Ash           1      43       0.03    0.8606
              Canopy*Ash    1      43       2.74    0.1051
```

Belowground production grass-dominated sites (Figure 6b)

Program:

```
proc mixed data=onedthreed;
      class island canopy ash;
      model total_below= canopy ash canopy*ash;
      random island;
      lsmeans canopy ash canopy*ash / adjust=tukey;
      run;
```

Output:

```
                      belowground grass islands                         5
                                        12:10 Friday, September 3, 2010

                         The Mixed Procedure

                           Fit Statistics

                -2 Res Log Likelihood           620.6
                AIC (smaller is better)         622.6
                AICC (smaller is better)        622.7
                BIC (smaller is better)         621.3


                     Type 3 Tests of Fixed Effects

                         Num     Den
           Effect         DF      DF    F Value    Pr > F

           Canopy          1      43       2.44    0.1256
           Ash             1      43       0.12    0.7317
           Canopy*Ash      1      43       0.59    0.4483
```

Belowground Production 0-10 cm (Figure 7)

Program:

```
title 'Total 1D3D 0-10';

proc mixed data=grassbelowprofile;
      class island canopy ash;
      model zero_to_ten=canopy|ash|island;
      lsmeans canopy|ash / adjust=tukey;
run;


title 'rhizome 1D3D 0-10';

proc mixed data=grassrzprofile;
      class island canopy ash;
      model zero_to_ten=canopy|ash|island;
      lsmeans canopy|ash / adjust=tukey;
run;


title 'ROOTS 1D3D 0-10';

proc mixed data=grassRTprofile;
      class island canopy ash;
      model zero_to_ten=canopy|ash|island;
      lsmeans canopy|ash / adjust=tukey;
run;
```

Output:

```
                          Total 1D3D 0-10                              20
                                     11:09 Tuesday, September 21, 2010

                        The Mixed Procedure

                  Type 3 Tests of Fixed Effects

                          Num     Den
Effect                     DF      DF    F Value    Pr > F

Canopy                      1      40       2.44    0.1260
Ash                         1      40       0.00    0.9718
Canopy*Ash                  1      40       0.25    0.6168
```

```
                   rhizome 1D3D 0-10                           47
                                11:09 Tuesday, September 21, 2010

                  The Mixed Procedure

            Type 3 Tests of Fixed Effects

                      Num     Den
Effect                 DF      DF    F Value    Pr > F

Canopy                  1      40       1.22    0.2763
Ash                     1      40       0.00    0.9609
Canopy*Ash              1      40       0.05    0.8249

                    ROOTS 1D3D 0-10                            71
                                11:09 Tuesday, September 21, 2010

                  The Mixed Procedure

            Type 3 Tests of Fixed Effects

                      Num     Den
Effect                 DF      DF    F Value    Pr > F

Canopy                  1      40       4.86    0.0332
Ash                     1      40       0.25    0.6170
Canopy*Ash              1      40       0.00    0.9999
```

Aboveground Biomass Sedge-dominated Sites (Figure 8a)

Program:

```
title 'aboveground sedge islands';

proc mixed data=twodsevend;
      class island canopy ash;
      model aboveground= canopy ash canopy*ash;
      random island;
      lsmeans canopy ash canopy*ash / adjust=tukey;
      run;
```

Output:

```
                      aboveground sedge islands                         2
                                        12:10 Friday, September 3, 2010

                         The Mixed Procedure

                           Fit Statistics

                 -2 Res Log Likelihood           542.8
                 AIC (smaller is better)         544.8
                 AICC (smaller is better)        544.9
                 BIC (smaller is better)         543.5


                     Type 3 Tests of Fixed Effects

                          Num     Den
            Effect         DF      DF    F Value    Pr > F

            Canopy          1      43      54.52    <.0001
            Ash             1      43       2.04    0.1603
            Canopy*Ash      1      43       1.38    0.2460
```

Belowground production Sedge-dominated Sites (Figure 8b)

Program:

```
title 'belowground sedge islands';

proc mixed data=twodsevend;
      class island canopy ash;
      model total_below= canopy ash canopy*ash;
      random island;
      lsmeans canopy ash canopy*ash / adjust=tukey;
      run;
```

Output:

```
                        belowground sedge islands                         5
                                         12:10 Friday, September 3, 2010

                           The Mixed Procedure

                             Fit Statistics

                   -2 Res Log Likelihood           541.4
                   AIC (smaller is better)         543.4
                   AICC (smaller is better)        543.5
                   BIC (smaller is better)         542.1


                      Type 3 Tests of Fixed Effects

                              Num     Den
              Effect           DF      DF    F Value    Pr > F

              Canopy            1      37       6.45    0.0154
              Ash               1      37       0.27    0.6073
              Canopy*Ash        1      37       0.00    0.9984
```

Belowground Production 0-10 cm Sedge-dominated Sites (Figure 9)

Program:

```
title 'Total 2D7D 0-10';

proc mixed data=sedgebelowprofile;
       class island canopy ash;
       model zero_to_ten=canopy|ash|island;
       lsmeans canopy|ash / adjust=tukey;
run;


title 'rhizome 2D7D 0-10';

proc mixed data=sedgerzprofile;
       class island canopy ash;
       model zero_to_ten=canopy|ash|island;
       lsmeans canopy|ash / adjust=tukey;
run;


title 'ROOTS 2D7D 0-10';

proc mixed data=sedgeRTprofile;
       class island canopy ash;
       model zero_to_ten=canopy|ash|island;
       lsmeans canopy|ash / adjust=tukey;
run;
```

Output:

```
                           Total 2D7D 0-10                              11
                                        11:09 Tuesday, September 21, 2010

                         The Mixed Procedure

                   Type 3 Tests of Fixed Effects

                          Num     Den
         Effect            DF      DF    F Value    Pr > F

         Canopy             1      32       6.82    0.0136
         Ash                1      32       0.88    0.3550
         Canopy*Ash         1      32       0.70    0.4095
```

```
                    rhizome 2D7D 0-10                             38
                                11:09 Tuesday, September 21, 2010

                   The Mixed Procedure

             Type 3 Tests of Fixed Effects

                      Num     Den
Effect                 DF      DF    F Value    Pr > F

Canopy                  1      33       7.85    0.0084
Ash                     1      33       0.84    0.3666
Canopy*Ash              1      33       0.78    0.3831
```

```
                     ROOTS 2D7D 0-10                              62
                                11:09 Tuesday, September 21, 2010

                   The Mixed Procedure

             Type 3 Tests of Fixed Effects

                      Num     Den
Effect                 DF      DF    F Value    Pr > F

Canopy                  1      34       4.57    0.0398
Ash                     1      34       0.30    0.5858
Canopy*Ash              1      34       0.16    0.6952
```

Aboveground Biomass harvested and separated by species (Grass-Dominated Sites; Table 2a)

Program:

```
title 'aboveground grass 1D3D';

proc mixed data=onedthreedsep;
      class island canopy ash;
      model total_grass= canopy ash canopy*ash;
      random island;
      lsmeans canopy ash canopy*ash / adjust=tukey;
      run;


title 'aboveground sedge 1D3D';

proc mixed data=onedthreedsep;
      class island canopy ash;
      model total_sedge= canopy ash canopy*ash;
      random island;
      lsmeans canopy ash canopy*ash / adjust=tukey;
      run;
```

Output:

```
                       aboveground grass 1D3D                          2
                                     15:20 Sunday, February 27, 2011

                         The Mixed Procedure

                           Fit Statistics

                 -2 Res Log Likelihood          496.5
                 AIC (smaller is better)        500.5
                 AICC (smaller is better)       500.8
                 BIC (smaller is better)        497.9


                     Type 3 Tests of Fixed Effects

                      Num     Den
            Effect          DF      DF    F Value    Pr > F

            Canopy           1      34       0.00    0.9559
            Ash              1      34       0.01    0.9308
            Canopy*Ash       1      34       0.08    0.7773
```

```
            The Mixed Procedure

              Fit Statistics

     -2 Res Log Likelihood           399.9
     AIC (smaller is better)         403.9
     AICC (smaller is better)        404.3
     BIC (smaller is better)         401.3


         Type 3 Tests of Fixed Effects

               Num     Den
Effect          DF      DF    F Value    Pr > F

Canopy           1      34       4.28    0.0461
Ash              1      34       0.01    0.9222
Canopy*Ash       1      34       0.72    0.4006
```

Aboveground Biomass harvested and separated by species (Sedge-Dominated Sites; Table 2b)

Program:

```
title 'aboveground grass 2D7D';

proc mixed data=twodsevendsep;
       class island canopy ash;
       model total_grass= canopy ash canopy*ash;
       random island;
       lsmeans canopy ash canopy*ash / adjust=tukey;
       run;


title 'aboveground sedge 2D7D';

proc mixed data=twodsevendsep;
       class island canopy ash;
       model total_sedge= canopy ash canopy*ash;
       random island;
       lsmeans canopy ash canopy*ash / adjust=tukey;
       run;
```

Output:

```
                         aboveground grass 2D7D                           8
                                           15:20 Sunday, February 27, 2011

                           The Mixed Procedure

                             Fit Statistics

                  -2 Res Log Likelihood           382.0
                  AIC (smaller is better)         386.0
                  AICC (smaller is better)        386.4
                  BIC (smaller is better)         383.3


                       Type 3 Tests of Fixed Effects

                          Num     Den
             Effect        DF      DF    F Value    Pr > F

             Canopy         1      31       6.82    0.0138
             Ash            1      31       2.60    0.1169
             Canopy*Ash     1      31       0.00    0.9713
```

```
                The Mixed Procedure

                  Fit Statistics

      -2 Res Log Likelihood           392.9
      AIC (smaller is better)         396.9
      AICC (smaller is better)        397.3
      BIC (smaller is better)         394.3


            Type 3 Tests of Fixed Effects

                  Num     Den
 Effect            DF      DF    F Value    Pr > F

 Canopy             1      30      15.71    0.0004
 Ash                1      30       8.87    0.0057
 Canopy*Ash         1      30       0.05    0.8333
```

Grass Stem Density (Figure 10a)

Program:

```
title 'grass 2D7D';

proc mixed data=twodsevendstems;
       class canopy ash;
       model grass_density=canopy ash canopy*ash;
       lsmeans canopy ash canopy*ash / adjust=tukey;
       run

title 'grass 1D3D';

proc mixed data=onedthreedstems;
       class canopy ash;
       model grass_density=canopy ash canopy*ash;
       lsmeans canopy ash canopy*ash / adjust=tukey;
       run;
```

Output:

```
                                grass 1D3D                              17
                                           15:20 Sunday, February 27, 2011

                            The Mixed Procedure

                       Type 3 Tests of Fixed Effects

                             Num     Den
              Effect          DF      DF    F Value    Pr > F

              Canopy           1      43       0.01    0.9379
              Ash              1      43       0.02    0.9013
              Canopy*Ash       1      43       0.54    0.4678


                                   grass 2D7D                              8
                                           15:20 Sunday, February 27, 2011

                            The Mixed Procedure

                       Type 3 Tests of Fixed Effects

                             Num     Den
              Effect          DF      DF    F Value    Pr > F

              Canopy           1      44       0.14    0.7141
              Ash              1      44       0.32    0.5751
              Canopy*Ash       1      44       0.19    0.6682
```

Sedge Stem Density (Figure 10b)

Program:

```
title 's. americanus 1D3D';

proc mixed data=onedthreedstems;
      class canopy ash;
      model sam_density=canopy ash canopy*ash;
      lsmeans canopy ash canopy*ash / adjust=tukey;
      run;


title 's. americanus 2D7D';

proc mixed data=twodsevendstems;
      class canopy ash;
      model sam_density=canopy ash canopy*ash;
      lsmeans canopy ash canopy*ash / adjust=tukey;
      run;
```

Output:

```
                           s. americanus 1D3D                           14
                                           15:20 Sunday, February 27, 2011

                           The Mixed Procedure

                      Type 3 Tests of Fixed Effects

                            Num     Den
              Effect         DF      DF    F Value    Pr > F

              Canopy          1      43       3.74    0.0596
              Ash             1      43       0.47    0.4984
              Canopy*Ash      1      43       1.85    0.1812



                            s. americanus 2D7D                            5
                                           15:20 Sunday, February 27, 2011

                           The Mixed Procedure

                      Type 3 Tests of Fixed Effects

                            Num     Den
              Effect         DF      DF    F Value    Pr > F

              Canopy          1      44      35.77    <.0001
              Ash             1      44       0.35    0.5578
              Canopy*Ash      1      44       0.69    0.4102
```

Sedge Stem Height (Table 3a)

Program:

```
title 'height sedge sites';

proc mixed data=heightsedge;
      class site canopy ash;
      model sedgeheight= canopy|ash|site;
      lsmeans canopy ash canopy*ash / adjust=tukey;
run;
```

Output:

```
                          height sedge sites                            2
                                         15:20 Sunday, February 27, 2011

                          The Mixed Procedure

                    Type 3 Tests of Fixed Effects

                            Num     Den
           Effect            DF      DF    F Value    Pr > F

           canopy             1      16       4.92    0.0414
           ash                1      16       1.14    0.3016
           canopy*ash         1      16       0.33    0.5734
```

Annual Burn Experiment

Aboveground Biomass (Figure 11a)

Program:

```
title 'aboveground all burn islands';

proc mixed data=biomass;
       class site treatment;
       model total_above= treatment|site;
       run;
```

Output:

```
                      aboveground all burn islands                          2
                                          15:20 Sunday, February 27, 2011

                           The Mixed Procedure

                      Type 3 Tests of Fixed Effects

                             Num     Den
           Effect             DF      DF    F Value    Pr > F

           Treatment           1      30      32.78    <.0001
           Site                2      30       7.23    0.0027
           Site*Treatment      2      30       3.83    0.0330
```

Belowground production (Figure 11b)

Program:

```
title 'belowground all islands';

proc mixed data=biomass;
      class site treatment;
      model total_below= treatment|site;
      run;
```

Output:

```
                         belowground all islands                         4
                                          15:20 Sunday, February 27, 2011

                           The Mixed Procedure

                      Type 3 Tests of Fixed Effects

                             Num     Den
            Effect            DF      DF    F Value    Pr > F

            Treatment          1      28       1.84    0.1861
            Site               2      28       1.34    0.2792
            Site*Treatment     2      28       0.05    0.9492
```

Belowground Production 0-10 cm (Figure 12)

Program:

```
title 'Total all islands 0-10';

proc mixed data=burnbelowprofile;
       class island treatment;
       model zero_to_ten=treatment|island;
       lsmeans treatment / adjust=tukey;
run;


title 'Total rhizome 0-10';

proc mixed data=burnrzprofile;
       class island treatment;
       model zero_to_ten=treatment|island;
       lsmeans treatment / adjust=tukey;
run;


title 'Total root 0-10';

proc mixed data=burnrtprofile;
       class island treatment;
       model zero_to_ten=treatment|island;
       lsmeans treatment / adjust=tukey;
run;
```

Output:

```
                       Total all islands 0-10                          2
                                         15:20 Sunday, February 27, 2011

                         The Mixed Procedure

                    Type 3 Tests of Fixed Effects

                             Num     Den
           Effect             DF      DF    F Value    Pr > F

           Treatment           1      28       0.90    0.3512
           Island              2      28       1.73    0.1954
           Island*Treatment    2      28       0.01    0.9929
```

```
                 Total rhizome 0-10                            6
                                 15:20 Sunday, February 27, 2011

                 The Mixed Procedure

            Type 3 Tests of Fixed Effects

                     Num     Den
Effect                DF      DF    F Value    Pr > F

Treatment              1      29       0.05    0.8232
Island                 2      29       2.25    0.1231
Island*Treatment       2      29       0.01    0.9886
```

```
                   Total root 0-10                            10
                                 15:20 Sunday, February 27, 2011

                 The Mixed Procedure

            Type 3 Tests of Fixed Effects

                     Num     Den
Effect                DF      DF    F Value    Pr > F

Treatment              1      29       8.18    0.0078
Island                 2      29       0.94    0.4028
Island*Treatment       2      29       0.01    0.9866
```

Belowground Production 10-20 cm (Figure 12)

Program:

```
title 'Total all islands 10-20';

proc mixed data=burnbelowprofile;
       class island treatment;
       model ten_to_twenty=treatment|island;
       lsmeans treatment / adjust=tukey;
run;


title 'Total all islands 10-20';

proc mixed data=burnbelowprofile;
       class island treatment;
       model ten_to_twenty=treatment|island;
       lsmeans treatment / adjust=tukey;
run;


title 'Total root 10-20';

proc mixed data=burnrtprofile;
       class island treatment;
       model ten_to_twenty=treatment|island;
       lsmeans treatment / adjust=tukey;
run;
```

Output:

```
                       Total all islands 10-20                          4
                                         15:20 Sunday, February 27, 2011

                         The Mixed Procedure

                    Type 3 Tests of Fixed Effects

                          Num     Den
          Effect           DF      DF    F Value    Pr > F

          Treatment         1      28       0.69    0.4124
          Island            2      28       0.57    0.5736
          Island*Treatment  2      28       1.99    0.1558
```

```
                 Total rhizome 10-20                            8
                                 15:20 Sunday, February 27, 2011

                 The Mixed Procedure

            Type 3 Tests of Fixed Effects

                      Num     Den
Effect                 DF      DF    F Value    Pr > F

Treatment               1      29       0.08    0.7734
Island                  2      29       0.63    0.5380
Island*Treatment        2      29       1.66    0.2077
```

```
                  Total root 10-20                             12
                                 15:20 Sunday, February 27, 2011

                 The Mixed Procedure

            Type 3 Tests of Fixed Effects

                      Num     Den
Effect                 DF      DF    F Value    Pr > F

Treatment               1      29       4.33    0.0463
Island                  2      29       0.64    0.5365
Island*Treatment        2      29       1.00    0.3793
```

Aboveground Biomass harvested and separated by species (Table 4)

Program:

```
title 'aboveground sedge';

proc mixed data=burnsep;
      class island treatment;
      model total_sedge= island|treatment;
      run;


title 'aboveground grass';

proc mixed data=burnsep;
      class island treatment;
      model total_grass= treatment|island;
      run;
```

Output:

```
                          aboveground sedge                                4
                                       15:20 Sunday, February 27, 2011

                         The Mixed Procedure

                    Type 3 Tests of Fixed Effects

                              Num     Den
          Effect               DF      DF    F Value    Pr > F

          Island                2      16      18.04    <.0001
          Treatment             1      16      10.76    0.0047
          Island*Treatment      2      16       1.80    0.1979


                          aboveground grass                                2
                                       15:20 Sunday, February 27, 2011

                         The Mixed Procedure

                    Type 3 Tests of Fixed Effects

                              Num     Den
          Effect               DF      DF    F Value    Pr > F

          Treatment             1      16       3.73    0.0712
          Island                2      16      11.95    0.0007
          Island*Treatment      2      16       1.26    0.3113
```

Stem Density (Table 5)

Program:

```
title 'sedge stems';

proc mixed data=burnstems;
      class island treatment;
      model sam_density = treatment;
      run;


title 'grass stems';

proc mixed data=burnstems;
      class island treatment;
      model grass_density = treatment;
      run;
```

Output:

```
                            sedge stems                                  4
                                      12:10 Friday, September 3, 2010

                   Type 3 Tests of Fixed Effects

                         Num      Den
            Effect        DF       DF    F Value    Pr > F

            Treatment      1       32       9.38    0.0044



                            grass stems                                  6
                                      12:10 Friday, September 3, 2010


                   Type 3 Tests of Fixed Effects

                         Num      Den
            Effect        DF       DF    F Value    Pr > F

            Treatment      1       32       1.08    0.3067
```

Stem Height (Table 6)

Program:

```
title 'sedge height annual burn sites';

proc mixed data=heightab;
      class site treatment;
      model sedgeheight= treatment|site;
      lsmeans treatment / adjust=tukey;
run;

title 'grass height annual burn sites';

proc mixed data=heightab;
      class site treatment;
      model grassheight= treatment|site;
      lsmeans treatment / adjust=tukey;
run;
```

Output:

```
                     sedge height annual burn sites                        8
                                        15:20 Sunday, February 27, 2011

                          The Mixed Procedure

                     Type 3 Tests of Fixed Effects

                            Num     Den
           Effect            DF      DF    F Value    Pr > F

           treatment          1      12       9.03    0.0110
           Site               2      12       2.84    0.0975
           Site*treatment     2      12       1.16    0.3474




                      grass height annual burn sites                       10
                                        15:20 Sunday, February 27, 2011

                          The Mixed Procedure

                     Type 3 Tests of Fixed Effects

                            Num     Den
           Effect            DF      DF    F Value    Pr > F

           treatment          1      10       1.87    0.2009
           Site               2      10       6.19    0.0178
           Site*treatment     1      10       1.87    0.2009
```

Appendix C: Additional tables, figures, and observations from Chapter 3

This appendix includes results of main effect analysis (Canopy, Species Composition) that were not deemed useful for publication. It also includes suggestions for improvement of greenhouse pot studies.

Results

Response to Disturbance

Aboveground biomass. Following removal of the plant canopy, aboveground biomass decreased significantly (P=0.0093) across all species compositions. There was no significant interaction between species composition and canopy. *D. spicata* seemed to be more negatively affected by canopy removal than *S. americanus* in pure stands and in mixed composition pots. Following canopy removal, *D. spicata* aboveground biomass decreased by 44 % averaged across all species compositions (P=0.0123; Fig. 1a).There was a significant interaction between species composition and canopy in grass biomass (P=0.0493). In the pure *D. spicata* stands, biomass decreased by 46 % following canopy removal (P=0.0130) while other species compositions showed trends toward decrease, but no significant difference following canopy removal (Fig. 1b).

Belowground Biomass. Isotope analysis indicated that most of the roots labeled as “red roots” were C_3 while “white roots” were more likely to be C_4 (Table 1). There was no significant difference in total belowground production (roots + rhizomes, Fig. 2a) or in fine root production (Fig. 2b) following canopy removal when averaged across all species compositions. Both *S. americanus* and *D. spicata* were affected similarly.

Stem density and height. Density of *S. americanus* stems showed no difference in pots with canopy removal versus pots without (Fig. 3a). Across all species compositions, stem density of *D. spicata* decreased by 28 % but this trend was not significant (P=0.2425). There was no significant difference in stem height of S. americanus or D. spicata following canopy removal when averaged across all species compositions (Fig. 3b).

Response to species composition

There was no significant effect of species composition on aboveground (Fig. 4) or belowground (Fig. 5) production. There was a trend toward greater production in grass pots aboveground and in sedge pots belowground. However, these differences were not significant (P=0.2735 and P=0.5929, respectively). The trend toward greater sedge production was stronger in fine roots (Fig. 5b) but still not significant (P=0.1188).

Discussion

Disturbance

Over the course of the study, we did not see significant differences in soil temperatures and belowground production following canopy removal. We also experienced some unexpected effects of canopy removal on biomass production. When averaged over all species compositions, aboveground biomass of *D. spicata* decreased following canopy removal while it showed no difference in *S. americanus*.

There are numerous explanations for the results found in this study that relate to experimental design in a greenhouse setting. Bickford et al (in prep) hypothesized that increased light availability in the early part of the growing season led to increased productivity in sedges following canopy removal. A comparison of the data from that study and this one shows that the change in canopy light availability was much greater in their study (Fig. 6) and that it led to a greater increase in soil temperature (Miller et al in prep). Because our canopy disturbance did not generate the same light and temperature effects, the biomass production response was not apparent.

It is also worth noting that soil temperatures were much warmer in the greenhouse in 2010 than they were in the field at the same time during the year in 2009 (Fig. 7). The soil temperatures were up to 15˚C warmer in the greenhouse than they were in the field the previous year during the same time period. Chabreck (1981) found that while early season prescribed burns can give *S. americanus* a competitive advantage over slower growing grasses, later burning may result in more similar production between *S. americanus* and co-dominant grasses and may result in stands dominated by grasses. These warmer temperatures in the greenhouse may have created conditions akin to a later season disturbance.

Canopy removal significantly decreased aboveground biomass of *D. spicata* when grown in pure stands. This may have occurred because clipping the aboveground biomass injured some of the new growth, but because stem density also decreased in grasses following canopy removal, it is likely that injury of new growth alone was not the cause. Production of C_4 marsh grasses has been found to decline if burning or mowing is followed by continued flooding (Gabrey and Afton 2001, de Szalay and Resh 1997, Smith and Kadlec 1985). It is possible that keeping the water table steady at the soil surface following the clipping treatment caused a decline in productivity in the grass pots.

The conditions in the greenhouse however were not ideal for mimicking field conditions. Future studies may focus in creating a light penetration effect was more similar to that found in Bickford et al. (in prep) in the field. Shade cloth may be used effectively in greenhouse mesocosms to keep light from penetrating from the sides of the plant canopy. This would make a greenhouse set-up closer to the conditions found in the field. It may also be possible to place the pots outdoors to eliminate a greenhouse effect as shown in Fig. 13. It may also be wise to insulate the pots so that the soil temperatures are less likely to be influenced by ambient temperatures. These improvements to a similar experimental design may increase response to disturbance and produce less ambiguous results.

Table 1: Stable isotopic signature (δ^{13}C) and calculated species compositions (%C3) of fine roots in the mixed species pots. %C3 is calculated using the dual end member equation [$\%C_3 = 100 \times (\delta^{13}C_{sample} - \delta^{13}C_{C4}) / (\delta^{13}C_{C3} - \delta^{13}C_{C4})$]. $\delta^{13}C_{C3}$ (-27.75) was found by averaging the δ^{13}C of all roots in pure *S. americanus* pots. $\delta^{13}C_{C4}$ (-15.84) was calculated by averaging δ13C of all roots in the pure *D. spicata* pots.

Pot	**Canopy**	**Rep**	**δ^{13}C red**	**%C3 red**	**%C4 red**	**δ^{13}C white**	**%C3 white**	**%C4 white**
E1	Removed	A	**-28.90**	100.00	0.00	**-15.78**	0.00	100.00
E1	Removed	B	**-26.57**	90.08	9.91	**-15.78**	0.00	100.00
E2	Removed	A	**-25.66**	82.47	17.53	**-18.59**	23.11	76.89
E2	Removed	B	**-24.10**	69.34	30.66	**-18.59**	23.11	76.89
E4	Removed	A	**-26.84**	92.36	7.64	**-20.47**	38.83	61.17
E4	Removed	B	**-26.55**	89.95	10.05	**-17.61**	14.84	85.16
E6	Removed	A	**-27.65**	99.21	0.79	**-15.77**	0.00	100.00
E6	Removed	B	**-25.21**	78.71	21.29	**-15.77**	0.00	100.00
E7	Removed	A	**-27.38**	96.93	3.07	**-15.96**	1.00	99.00
E7	Removed	B	**-27.02**	93.87	6.13	**-15.96**	1.00	99.00
E11	Removed	A	**-27.50**	97.94	2.06	**-27.63**	98.96	1.04
E11	Removed	B	**-27.46**	97.60	2.40	**-27.63**	98.96	1.04
F3	Control	A	**-24.29**	70.95	29.05	**-20.30**	37.46	62.54
F3	Control	B	**-26.59**	90.32	9.68	**-20.30**	37.46	62.54
F8	Control	A	**-27.74**	99.97	0.03	**-16.75**	7.66	92.34
F8	Control	B	**-24.23**	70.48	29.52	**-16.75**	7.66	92.34
F9	Control	A	**-26.96**	93.38	6.62	**-16.55**	5.96	94.04
F9	Control	B	**-26.60**	90.37	9.63	**-16.55**	5.96	94.04
F10	Control	A	**-26.70**	91.19	8.81	**-16.69**	7.13	92.87
F10	Control	B	**-27.24**	95.78	4.22	**-16.69**	7.12	92.88
F12	Control	A	**-26.44**	89.05	10.95	**-19.00**	26.52	73.48
F12	Control	B	**-26.41**	88.74	11.26	**-21.43**	46.94	53.06

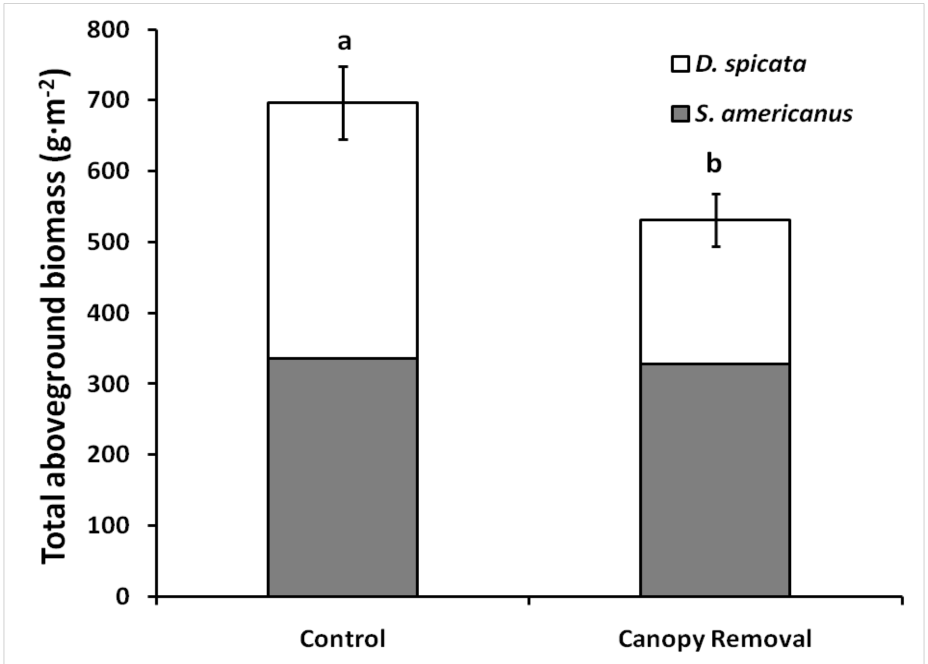

Figure 1: Total aboveground biomass production from all pots. Values represent the mean of 18 replicates (± standard error of the mean). Letters indicate the results of an ANOVA; means with the same letter are not significantly different from each other (α=0.05)

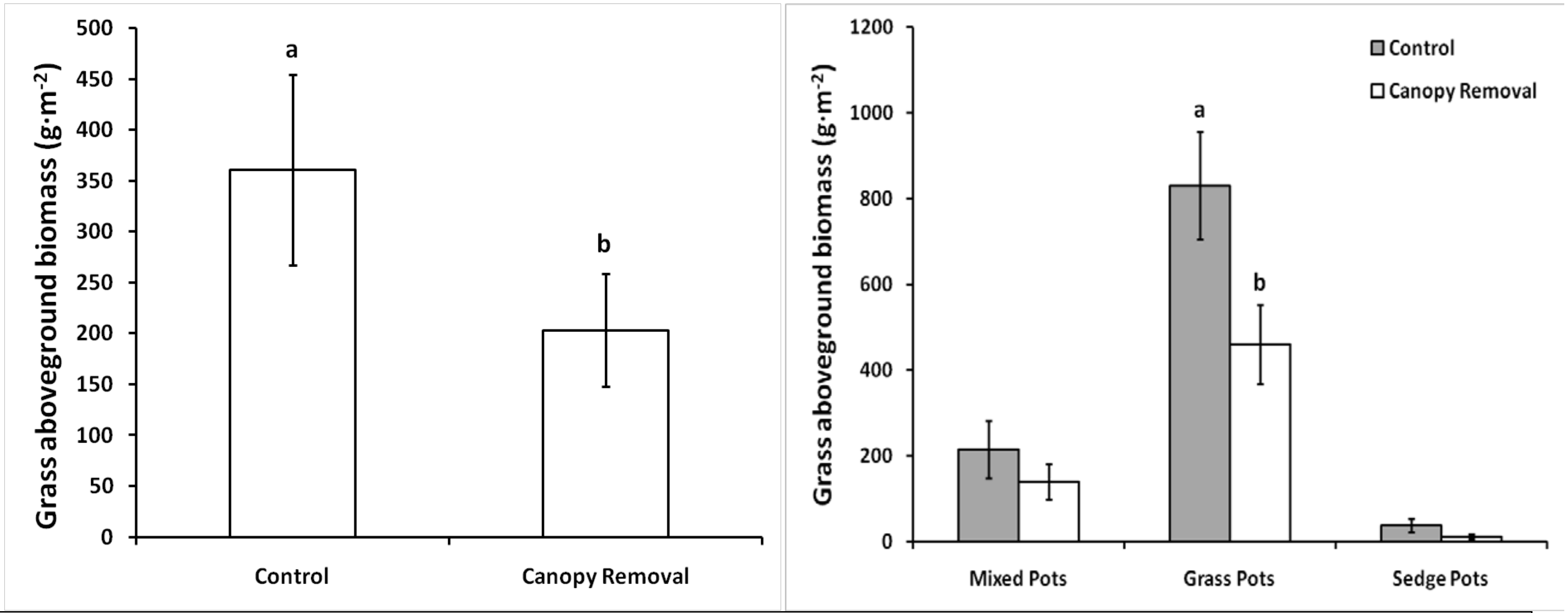

Figure 2: Aboveground biomass production of *D. spicata* from all pots. **a)** Aboveground biomass production of *D. spicata* averaged across all species compositions; values represent the mean of 18 replicates (± standard error of the mean). Letters indicate the results of an ANOVA; means with the same letter are not significantly different from each other (α=0.05). **b)** Aboveground biomass production of *D. spicata* in each species composition; values represent the mean of 6 replicates (± standard error of the mean). Letters indicate the results of a Tukey test; means with the same letter are not significantly different from each other (α=0.05).

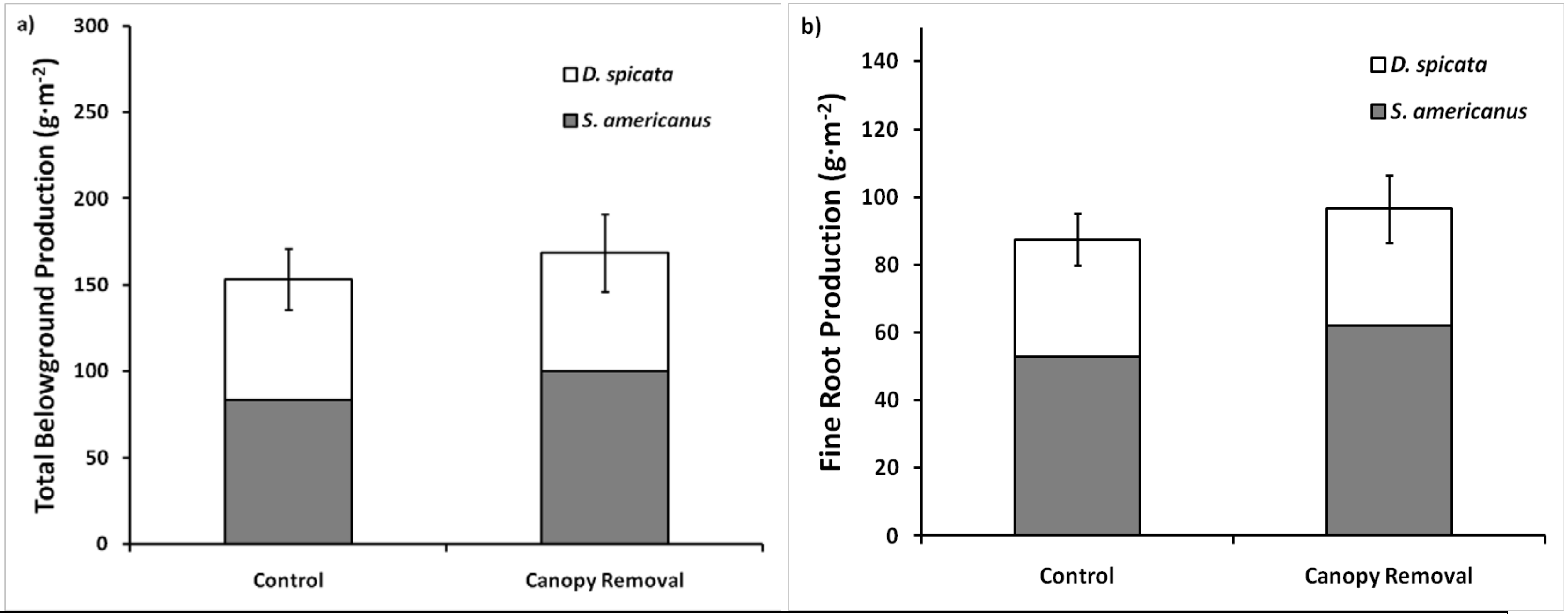

Figure 3: Belowground production of each species from all pots. **a)** Total belowground production (roots + rhizomes) averaged across all species compositions; values represent the mean of 36 replicates (± standard error of the mean). Means were not significantly different from each other (α=0.05). **b)** Fine root production averaged across all species compositions; values represent the mean of 36 replicates (± standard error of the mean). Means were not significantly different from each other (α=0.05).

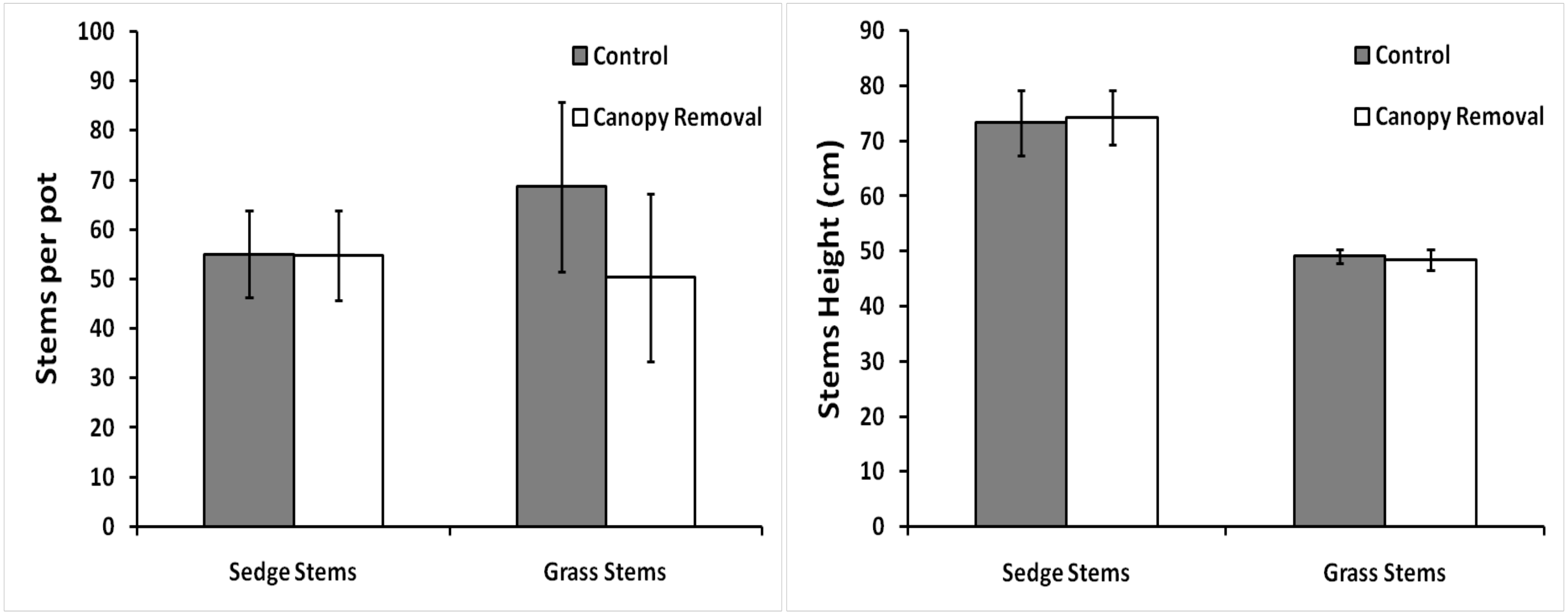

Figure 4: Stem density and height of each species from all pots. **a)** Stem density of each species averaged across all species compositions; values represent the mean of 18 replicates (± standard error of the mean). Means were not significantly different from each other (α=0.05). **b)** Stem height of each species averaged across all species compositions; values represent the mean of 18 replicates (± standard error of the mean). Means were not significantly different from each other (α=0.05).

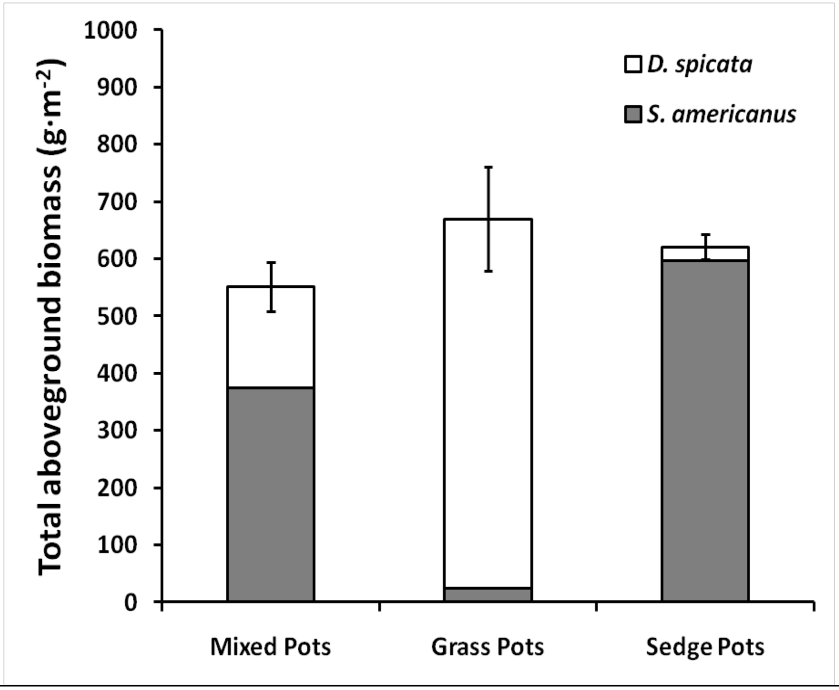

Figure 5: Total aboveground biomass from each species composition; values represent the mean of 6 replicates (± standard error of the mean). Means were not significantly different from each other (α=0.05)

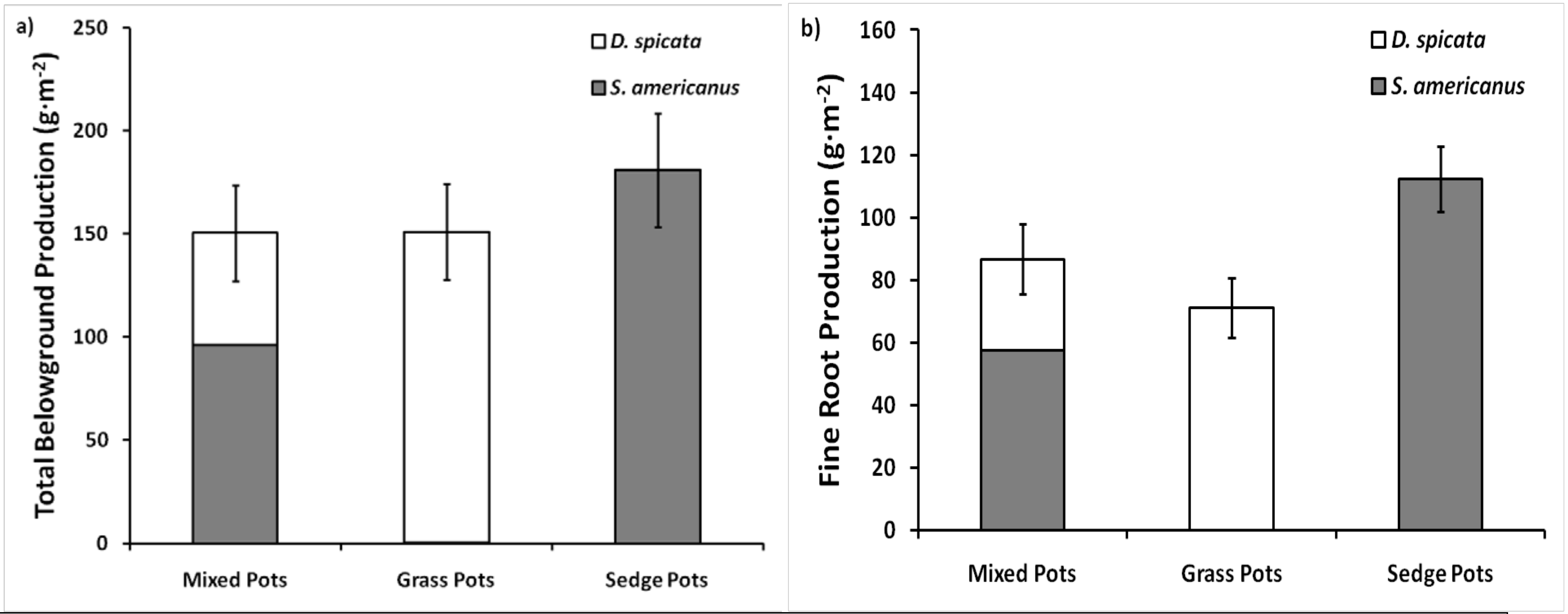

Figure 6: Belowground production of each species shown in each species composition **a)** Total belowground production (roots + rhizomes) shown in all species compositions; values represent the mean of 12 replicates (± standard error of the mean). Means were not significantly different from each other (α=0.05). **b)** Fine root production shown in all species compositions; values represent the mean of 12 replicates (± standard error of the mean). Means were not significantly different from each other (α=0.05).

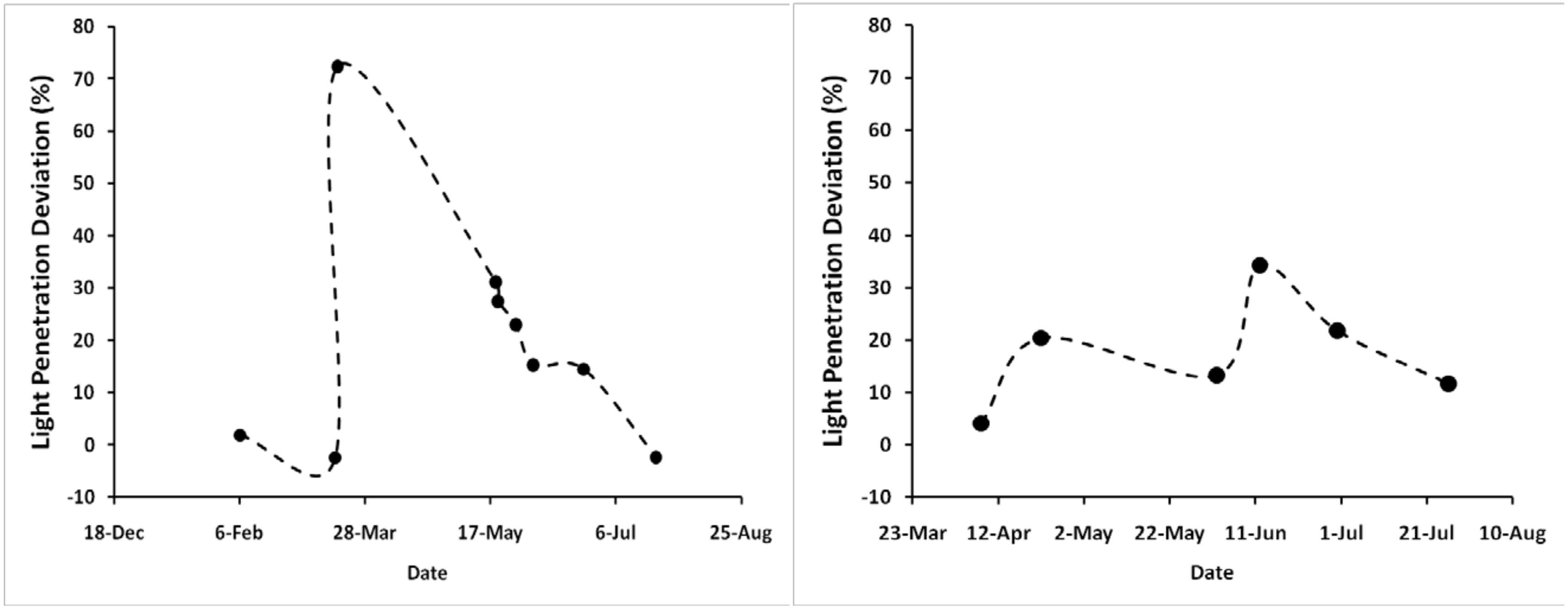

Figure 7: Difference in light penetration of canopy removal and control sites from **a)** Miller et al (in prep) field study 2009 **b)** Greenhouse study 2010.

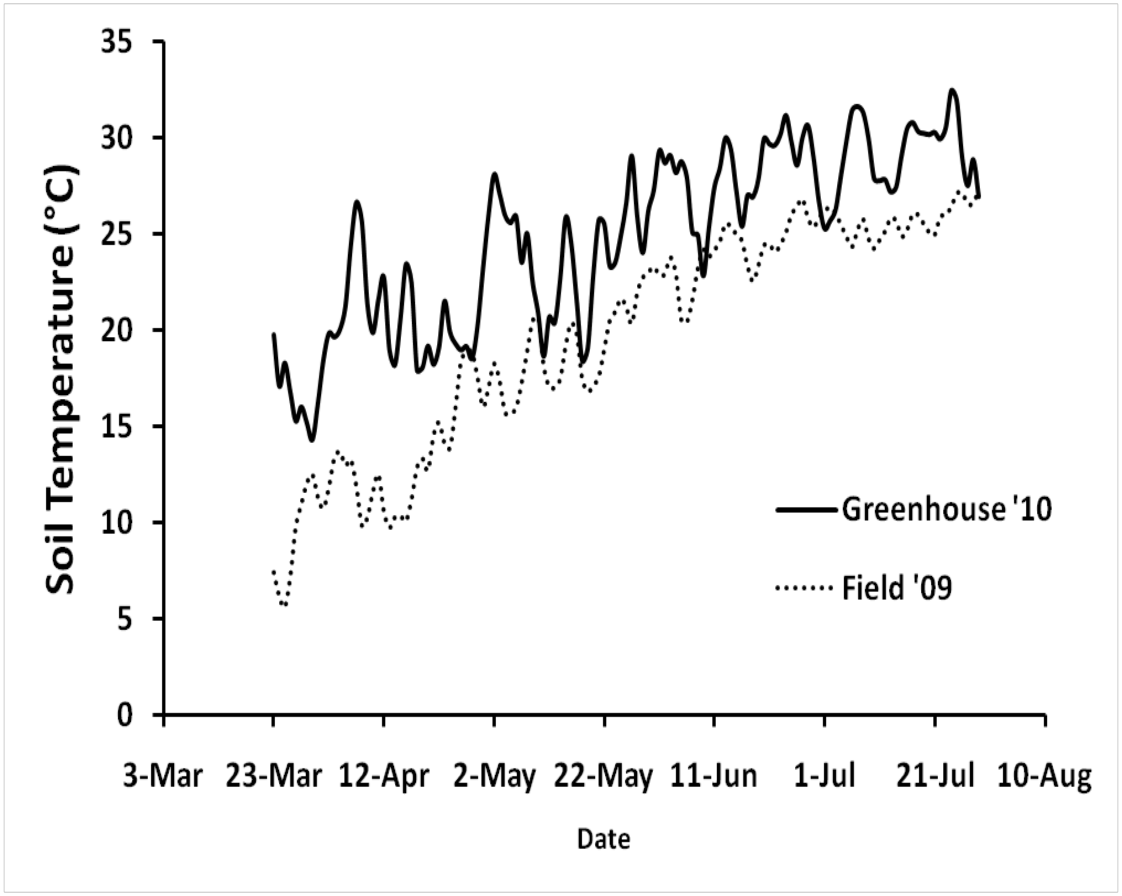

Figure 8: Difference in absolute soil temperature between Bickford et al (in prep) field study 2009 and this greenhouse study in 2010.

Statistical Models and Analysis for Appendix C

Total Aboveground Biomass (Figures 1 & 5)

Program:

```
title 'total aboveground';

proc mixed data=aboveground;
      class block speciescomp clip;
      model total_biomass= speciescomp clip speciescomp*clip;
      random block;
      lsmeans clip speciescomp clip*speciescomp / adjust=tukey;
      run;
```

Output:

```
                          total aboveground                              2
                                         15:20 Sunday, February 27, 2011

                         The Mixed Procedure

                           Fit Statistics

                 -2 Res Log Likelihood          408.3
                 AIC (smaller is better)        412.3
                 AICC (smaller is better)       412.7
                 BIC (smaller is better)        411.9


                    Type 3 Tests of Fixed Effects

                           Num     Den
           Effect           DF      DF    F Value    Pr > F

           Speciescomp       2      25       1.37    0.2735 (Figure 5)
           Clip              1      25       7.94    0.0093 (Figure 1)
           Speciescomp*Clip  2      25       2.17    0.1353
```

Grass Aboveground Biomass (Figure 2)

Program:

```
title 'grass aboveground';

proc mixed data=aboveground;
      class block speciescomp clip;
      model live_grass= speciescomp clip speciescomp*clip;
      random block;
      lsmeans clip speciescomp clip*speciescomp / adjust=tukey;
      run;
```

Output:

```
                         grass aboveground                         10
                                      15:20 Sunday, February 27, 2011

                        The Mixed Procedure

                   Type 3 Tests of Fixed Effects

                          Num     Den
          Effect           DF      DF    F Value    Pr > F

          Speciescomp       2      25      40.97    <.0001
          Clip              1      25       7.28    0.0123
          Speciescomp*Clip  2      25       3.41    0.0492


                  Differences of Least Squares Means

  Effect        Species  Clip    Species  Clip    Adjustment      Adj P

  Species*Clip  Both     Clip    Both     NoClip  Tukey          0.9740
  Species*Clip  Both     Clip    Grass    Clip    Tukey          0.0416
  Species*Clip  Both     Clip    Grass    NoClip  Tukey          <.0001
  Species*Clip  Both     Clip    Sedge    Clip    Tukey          0.7974
  Species*Clip  Both     Clip    Sedge    NoClip  Tukey          0.9090
  Species*Clip  Both     NoClip  Grass    Clip    Tukey          0.1875
  Species*Clip  Both     NoClip  Grass    NoClip  Tukey          <.0001
  Species*Clip  Both     NoClip  Sedge    Clip    Tukey          0.3614
  Species*Clip  Both     NoClip  Sedge    NoClip  Tukey          0.5082
  Species*Clip  Grass    Clip    Grass    NoClip  Tukey          0.0130
  Species*Clip  Grass    Clip    Sedge    Clip    Tukey          0.0020
  Species*Clip  Grass    Clip    Sedge    NoClip  Tukey          0.0038
  Species*Clip  Grass    NoClip  Sedge    Clip    Tukey          <.0001
  Species*Clip  Grass    NoClip  Sedge    NoClip  Tukey          <.0001
  Species*Clip  Sedge    Clip    Sedge    NoClip  Tukey          0.9998
```

Total Belowground Production (Figures 3a & 6a)

Program:

```
title 'total belowground';

proc mixed data=belowground;
       class block species clip replicate;
       model total_below= block species clip species*clip;
       lsmeans clip species clip*species / adjust=tukey;
       run;
```

Output:

```
                          total belowground                              2
                                         15:20 Sunday, February 27, 2011

                         The Mixed Procedure

                    Type 3 Tests of Fixed Effects

                         Num     Den
         Effect           DF      DF    F Value    Pr > F

         Block             5      59       0.46    0.8067
         Species           2      59       0.53    0.5929 (Figure 6a)
         Clip              1      59       0.37    0.5465 (Figure 3a)
         Species*Clip      2      59       0.23    0.7977
```

Fine Root Production (Figures 3b & 6b)

Program:

```
title 'total fine';

proc mixed data=belowground;
       class block species clip replicate;
       model total_fine= block species clip species*clip;
       lsmeans clip species clip*species / adjust=tukey;
       run;
```

Output:

```
                                total fine                                 6
                                            15:20 Sunday, February 27, 2011

                            The Mixed Procedure

                       Type 3 Tests of Fixed Effects

                          Num     Den
             Effect        DF      DF    F Value    Pr > F

             Block          5      59       0.77    0.5779
             Species        2      59       2.21    0.1188 (Figure 6b)
             Clip           1      59       0.65    0.4219 (Figure 3b)
             Species*Clip   2      59       0.92    0.4034
```

Stem Density (Figure 4)

Program:

```
title 'sedge density';

proc mixed data=aboveground;
      class block speciescomp clip;
      model sedge_stems= speciescomp clip speciescomp*clip;
      random block;
      lsmeans clip speciescomp clip*speciescomp / adjust=tukey;
      run;

title 'grass density';

proc mixed data=aboveground;
      class block speciescomp clip;
      model grass_stems= speciescomp clip speciescomp*clip;
      random block;
      lsmeans clip speciescomp clip*speciescomp / adjust=tukey;
      run;
```

Output:

```
                          sedge density                              14
                                     15:20 Sunday, February 27, 2011

                       The Mixed Procedure

                  Type 3 Tests of Fixed Effects

                  Num     Den
Effect             DF      DF    F Value    Pr > F

Speciescomp         2      25      35.24    <.0001
Clip                1      25       0.00    0.9756
Speciescomp*Clip    2      25       0.87    0.4326


                          grass density                              22
                                     15:20 Sunday, February 27, 2011

                       The Mixed Procedure

                  Type 3 Tests of Fixed Effects

                  Num     Den
Effect             DF      DF    F Value    Pr > F

Speciescomp         2      25      25.71    <.0001
Clip                1      25       1.43    0.2425
Speciescomp*Clip    2      25       0.47    0.6317
```

Appendix D: Statistical Models and Analysis for Chapter 3

This appendix provides statistical models and outputs from SAS for all data presented in tables and figures within chapter III. Each Program code is preceded by a title indicating the data it will analyze and the table or figure it corresponds with. To save space, parts of the out puts have been omitted. Generally, only the main effects are included unless further analyses (e.g. Tukey test) were used. Paired T-tests were performed in MS Excel 2007.

Competition Aboveground with Canopy Removal (Figure 1a)

Paired T-test using MS Excel 2007

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	366.1742617	139.3725731
Variance	7481.293349	9886.292992
Observations	6	6
Pearson Correlation	0.111242814	
Hypothesized Mean Difference	0	
df	5	
t Stat	4.468882287	
P(T<=t) one-tail	0.003293034	
t Critical one-tail	2.015048372	
P(T<=t) two-tail	0.006586068	
t Critical two-tail	2.570581835	

Competition Aboveground without Canopy Removal (Figure 2b)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	382.5613262	214.7294914
Variance	11496.95257	26922.71801
Observations	6	6
Pearson Correlation	-0.400287045	
Hypothesized Mean Difference	0	
df	5	
t Stat	1.794120474	
P(T<=t) one-tail	0.066379377	
t Critical one-tail	2.015048372	
P(T<=t) two-tail	0.132758754	
t Critical two-tail	2.570581835	

Competition Belowground with Canopy Removal (Figure 2a)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	112.8063652	55.61202206
Variance	8523.50636	4564.240154
Observations	12	12
Pearson Correlation	0.116807826	
Hypothesized Mean Difference	0	
df	11	
t Stat	1.837139543	
P(T<=t) one-tail	0.046665919	
t Critical one-tail	1.795884814	
P(T<=t) two-tail	0.093331839	
t Critical two-tail	2.200985159	

Competition Belowground without Canopy Removal (Figure 2b)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	75.95790121	52.75198211
Variance	7252.277551	2396.231189
Observations	10	10
Pearson Correlation	-0.068001043	
Hypothesized Mean Difference	0	
df	9	
t Stat	0.726055418	
P(T<=t) one-tail	0.243128169	
t Critical one-tail	1.833112923	
P(T<=t) two-tail	0.486256337	
t Critical two-tail	2.262157158	

Competition in Fine Roots with Canopy Removal (Figure 3a)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	80.72051822	28.01068883
Variance	3294.069522	1454.227186
Observations	12	12
Pearson Correlation	0.038565013	
Hypothesized Mean Difference	0	
df	11	
t Stat	2.698198995	
P(T<=t) one-tail	0.010361664	
t Critical one-tail	1.795884814	
P(T<=t) two-tail	0.020723328	
t Critical two-tail	2.200985159	

Competition in Fine Roots without Canopy Removal (Figure 3b)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	48.39287888	26.86645745
Variance	1008.33726	594.7332036
Observations	10	10
Pearson Correlation	-0.227350791	
Hypothesized Mean Difference	0	
df	9	
t Stat	1.539491601	
P(T<=t) one-tail	0.079034495	
t Critical one-tail	1.833112923	
P(T<=t) two-tail	0.158068991	
t Critical two-tail	2.262157158	

Relative Yield of S. americanus aboveground under canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	732.3485233	576.7303567
Variance	29925.1734	5718.486881
Observations	6	6
Pearson Correlation	0.728099008	
Hypothesized Mean Difference	0	
df	5	
t Stat	2.959074118	
P(T<=t) one-tail	0.015776314	
t Critical one-tail	2.015048372	
P(T<=t) two-tail	0.031552627	
t Critical two-tail	2.570581835	

Relative Yield of S. americanus aboveground under no canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	765.1226523	617.7333858
Variance	45987.81027	4093.802119
Observations	6	6
Pearson Correlation	-0.24547554	
Hypothesized Mean Difference	0	
df	5	
t Stat	1.51460279	
P(T<=t) one-tail	0.09514994	
t Critical one-tail	2.015048372	
P(T<=t) two-tail	0.19029988	
t Critical two-tail	2.570581835	

Relative Yield of D. spicata aboveground under canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	278.7451463	459.3093765
Variance	39545.17197	51785.15522
Observations	6	6
Pearson Correlation	0.092619893	
Hypothesized Mean Difference	0	
df	5	
t Stat	-1.535696337	
P(T<=t) one-tail	0.09260435	
t Critical one-tail	2.015048372	
P(T<=t) two-tail	0.1852087	
t Critical two-tail	2.570581835	

Relative Yield of D. spicata aboveground under no canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	429.4589827	830.2464972
Variance	107690.872	93532.70114
Observations	6	6
Pearson Correlation	-0.339596264	
Hypothesized Mean Difference	0	
df	5	
t Stat	-1.89147188	
P(T<=t) one-tail	0.058569242	
t Critical one-tail	2.015048372	
P(T<=t) two-tail	0.117138483	
t Critical two-tail	2.570581835	

Relative Yield of S. americanus stems under canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	148	83.83333333
Variance	1540.8	189.3666667
Observations	6	6
Pearson Correlation	0.587230057	
Hypothesized Mean Difference	0	
df	5	
t Stat	4.748167836	
P(T<=t) one-tail	0.002556417	
t Critical one-tail	2.015048372	
P(T<=t) two-tail	0.005112833	
t Critical two-tail	2.570581835	

Relative Yield of S. americanus stems under no canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	128	81.66666667
Variance	2224	59.86666667
Observations	6	6
Pearson Correlation	0.328867772	
Hypothesized Mean Difference	0	
df	5	
t Stat	2.510399792	
P(T<=t) one-tail	0.026900855	
t Critical one-tail	2.015048372	
P(T<=t) two-tail	0.05380171	
t Critical two-tail	2.570581835	

Relative Yield of D. spicata stems under canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	54.33333333	117
Variance	1072.666667	9060
Observations	6	6
Pearson Correlation	-0.331683637	
Hypothesized Mean Difference	0	
df	5	
t Stat	-1.38969802	
P(T<=t) one-tail	0.111660877	
t Critical one-tail	2.015048372	
P(T<=t) two-tail	0.223321755	
t Critical two-tail	2.570581835	

Relative Yield of D. spicata stems under no canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	88.66666667	154.1666667
Variance	2890.666667	3164.166667
Observations	6	6
Pearson Correlation	0.670121639	
Hypothesized Mean Difference	0	
df	5	
t Stat	-3.586238164	
P(T<=t) one-tail	0.007885287	
t Critical one-tail	2.015048372	
P(T<=t) two-tail	0.015770574	
t Critical two-tail	2.570581835	

Relative Yield of S. americanus belowground under canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	225.6127304	188.174741
Variance	34094.02544	20489.07797
Observations	12	12
Pearson Correlation	-0.368702412	
Hypothesized Mean Difference	0	
df	11	
t Stat	0.47651173	
P(T<=t) one-tail	0.321517402	
t Critical one-tail	1.795884814	
P(T<=t) two-tail	0.643034803	
t Critical two-tail	2.200985159	

Relative Yield of S. americanus belowground under no canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	151.9158024	173.110769
Variance	23734.72653	17121.28324
Observations	12	12
Pearson Correlation	0.393800736	
Hypothesized Mean Difference	0	
df	11	
t Stat	-0.464552952	
P(T<=t) one-tail	0.325655604	
t Critical one-tail	1.795884814	
P(T<=t) two-tail	0.651311208	
t Critical two-tail	2.200985159	

Relative Yield of D. spicata belowground under canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	111.2240441	148.3195947
Variance	18256.96062	21068.95501
Observations	12	12
Pearson Correlation	0.187081883	
Hypothesized Mean Difference	0	
df	11	
t Stat	-0.718491673	
P(T<=t) one-tail	0.243717689	
t Critical one-tail	1.795884814	
P(T<=t) two-tail	0.487435378	
t Critical two-tail	2.200985159	

Relative Yield of D. spicata belowground under no canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	105.5039642	153.345605
Variance	7842.211166	6106.843693
Observations	12	12
Pearson Correlation	-0.234205537	
Hypothesized Mean Difference	0	
df	11	
t Stat	-1.264011171	
P(T<=t) one-tail	0.116177354	
t Critical one-tail	1.795884814	
P(T<=t) two-tail	0.232354707	
t Critical two-tail	2.200985159	

Relative Yield of S. americanus fine roots under canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	161.4410364	105.6395061
Variance	13176.27809	2570.75579
Observations	12	12
Pearson Correlation	0.259765448	
Hypothesized Mean Difference	0	
df	11	
t Stat	1.713705566	
P(T<=t) one-tail	0.057292872	
t Critical one-tail	1.795884814	
P(T<=t) two-tail	0.114585744	
t Critical two-tail	2.200985159	

Relative Yield of S. americanus fine roots under no canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	96.78575777	109.430913
Variance	3300.01285	2523.280282
Observations	12	12
Pearson Correlation	0.557095702	
Hypothesized Mean Difference	0	
df	11	
t Stat	-0.857725928	
P(T<=t) one-tail	0.204671634	
t Critical one-tail	1.795884814	
P(T<=t) two-tail	0.409343267	
t Critical two-tail	2.200985159	

Relative Yield of D. spicata fine roots under canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	56.02137767	75.30301406
Variance	5816.908742	3243.356809
Observations	12	12
Pearson Correlation	0.349412787	
Hypothesized Mean Difference	0	
df	11	
t Stat	-0.860517908	
P(T<=t) one-tail	0.203934177	
t Critical one-tail	1.795884814	
P(T<=t) two-tail	0.407868353	
t Critical two-tail	2.200985159	

Relative Yield of D. spicata fine roots under no canopy removal (Table 2)

t-Test: Paired Two Sample for Means

	Variable 1	*Variable 2*
Mean	53.7329149	75.73267639
Variance	1946.399576	1624.601565
Observations	12	12
Pearson Correlation	0.034560653	
Hypothesized Mean Difference	0	
df	11	
t Stat	-1.297834991	
P(T<=t) one-tail	0.110449286	
t Critical one-tail	1.795884814	
P(T<=t) two-tail	0.220898573	
t Critical two-tail	2.200985159	

Light Availability (Figure 5)

Program:

```
title 'light averages';

proc mixed data=alight;
      class canopy species block date pot;
      model percent_of_av = canopy|species|date;
      repeated date/subject = pot type=arh(1);
      run;
```

Output:

```
light averages                             2
                                                 15:01 Sunday, May 1, 2011

                            The Mixed Procedure

                         Convergence criteria met.


                       Covariance Parameter Estimates


                              Fit Statistics

                    -2 Res Log Likelihood          1858.6
                    AIC (smaller is better)        1872.6
                    AICC (smaller is better)       1873.3
                    BIC (smaller is better)        1883.7


                      Null Model Likelihood Ratio Test

                        DF    Chi-Square      Pr > ChiSq

                         6         28.35          <.0001


                       Type 3 Tests of Fixed Effects

                                Num     Den
         Effect                  DF      DF    F Value    Pr > F

         canopy                   1      30       9.45    0.0045
         species                  2      30       4.62    0.0178
         canopy*species           2      30       0.57    0.5700
         Date                     5     150       2.54    0.0305
         canopy*Date              5     150       0.60    0.6970
         species*Date            10     150       1.68    0.0899
         canopy*species*Date        10          150              0.66        0.7588
```

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