Steve W. Roberts. PRIMARY PRODUCTION OF *DISTICHLIS SPICATA* AND *SPARTINA PATENS* AND EFFECTS OF INCREASED INUNDATION ON A SALT MARSH. (Under the direction of Dr. Robert R. Christian) Department of Biology, May 2000.

Distichlis spicata and *Spartina patens* are two salt marsh grasses that dominate high salt marshes along the mid-Atlantic coast. This study describes the growth of each species and used this information to develop a method for estimating Aboveground Net Primary Production (ANPP) specific to these species. A previous method of estimating production was by harvesting end of year biomass (EOYB) in September. EOYB accounted for 70-75% of ANPP of *S. patens* during 1998 and 1999, while accounting for only 54-71% of *D. spicata* during the same years. In this study, I recommend how future estimates of ANPP should be streamlined while maintaining accuracy. I suggest a modest effort in tagging culms to assess mortality during the growing season harvesting EOYB in August will improve future estimates of ANPP of *D. spicata* and *S. patens*.

Growth characteristics of *D. spicata* and *S. patens* differed in degrees of state change from high marsh to low marsh. Data were analyzed for three zones experiencing different degrees of high to low marsh transition; (1) Creek, (2) Non-hummock, and (3) Hummock. Species co-existed best in the creek zone of the high marsh, where each species appeared to benefit from its proximity to the creek. *S. patens* showed the ability to out-compete *D. spicata* in the Non-hummock zone, but showed signs of stress in the Hummock zone. *D. spicata* appeared to do better in Hummock zone than the Creek and Non-hummock zone due to a decreased competition with *S. patens* despite showing signs of stress by having higher turnover than in the Non-hummock zone. Thus, *D. spicata*

appears more limited by competition with *S. patens* than it is by stress experienced in the Hummock zone.

An increase in the frequency of inundation of high salt marshes is expected as a result of sea-level rise. This study examined the effect of experimentally increased inundation on growth characteristics of *D. spicata* and *S. patens* in context of Hummock and Non-hummock zones. Increased inundation in the Non-hummock zone did not have a positive effect *D. spicata* as hypothesized. Contrary to what was hypothesized, increased inundation in the Non-hummock zone had negative effects on density and ANPP of *S. patens*. Increased inundation in the Hummock zone had negative effects on *S. patens* growth characteristics as hypothesized. Contrary to what was hypothesized, *D. spicata* did not benefit from a reduction in competition with *S. patens* as a result of increased inundation in the Hummock zone. *D. spicata* showed signs of stress to increased inundation in the Hummock zone through a reduction in density, thus signifying adding stress to an already stressed system.

Interannual variation occurred for growth characteristics of *D. spicata* and *S. patens*. *D. spicata* showed significantly lower production per culm and significantly higher turnover in 1999 compared to 1998. *S. patens* produced significantly less in 1999 compared to 1998. The negative responses shown in growth characteristics were ascribed to lower precipitation during crucial stages of the growing season in 1999 compared to 1998.

PRIMARY PRODUCTION OF *DISTICHLIS SPICATA* AND *SPARTINA PATENS* AND EFFECTS OF INCREASED INUNDATION ON A SALT MARSH

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1. INTRODUCTION

1.1. Scope of research

Hydrology has been recognized as the most important factor controlling both structure and function in wetlands (Odum 1971, Odum 1980, Mitsch and Gosselink 1993). Tidal inundation of salt marshes is important for the input of nutrients, exchanges of organic matter, and addition of and flushing of salt (Hackney and De la Cruz 1978, Nuttle and Harvey 1995). Salt marshes along the mid-Atlantic coast of the U.S.A. typically experience semi-diurnal flooding and may be considered to have distinct communities of flowering halophytes as a result of tidal inundation and associated factors (Warren and Niering 1993). In order from the creek to upland, the zonations typically follow a pattern of mineral low marsh, transition marsh, and organic high marsh (Christian *et al*. 2000).

A high marsh is typically flooded only during extreme high tides and storm events (Stasavich 1998). Its elevation is largely determined by accumulated organic material in the soil (Delaune *et al*. 1994). Hayden and co-workers (1991) identified the area by the growth of *Distichlis spicata* (Loisel) Greene, *Spartina patens* (Aiton) Muhl., and dense stands of *Juncus romoerianus* (Scheele). A hummock and hollow area is pictured in Figure 1, and is dominated by two halophytic grasses, *D. spicata* and *S. patens* (Figure 2). These areas occur in high marshes, and are believed to be a key link in the state change from high to low marsh as sea level rises (Christian *et al*. 2000). A state change has been defined as transformations from one ecosystem to another (shrublands to grasslands) as a result of changes in environmental variables (Hayden et. al 1991, Brinson *et al*. 1995).

Figure 1. Hummock and hollow area of *Distichlis spicata* and *Spartina patens.*

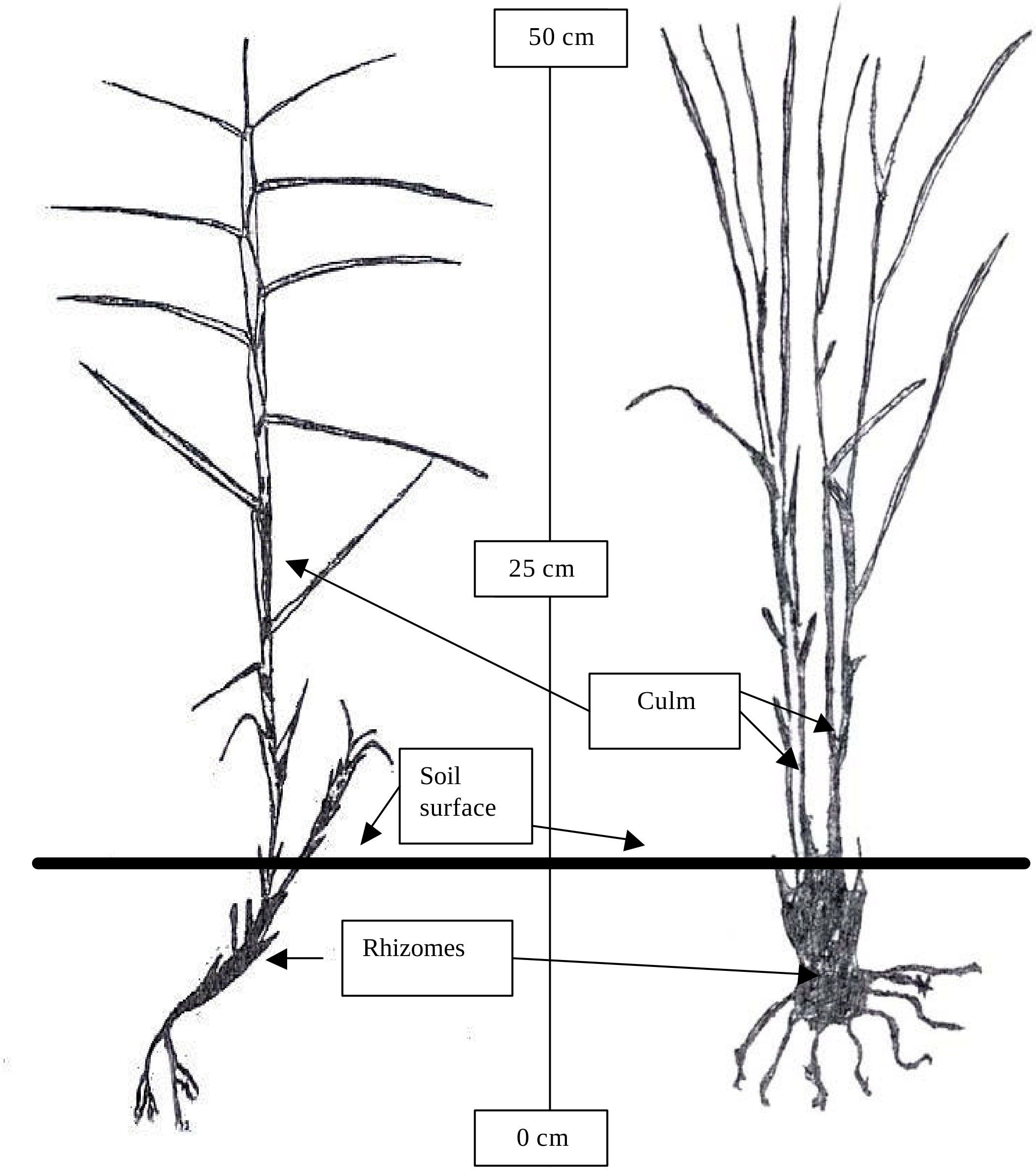


Figure 2. Adult culms of *Distichlis spicata* and *Spartina patens*.

1.2. Objectives

This study focused on *D. spicata* and *S. patens* co-dominated communities in an irregularly flooded high marsh in Virginia. The study had two main objectives. The first was to develop a method of estimating aboveground net primary production (ANPP) of *D. spicata* and *S. patens* that would improve upon the use of end of year biomass (EOYB) estimates from samples harvested annually in September. The second objective was to examine the species response to increased ponding with brackish water in the context of state change (i.e. hummock vs. non-hummock areas).

1.3. Responses to transition

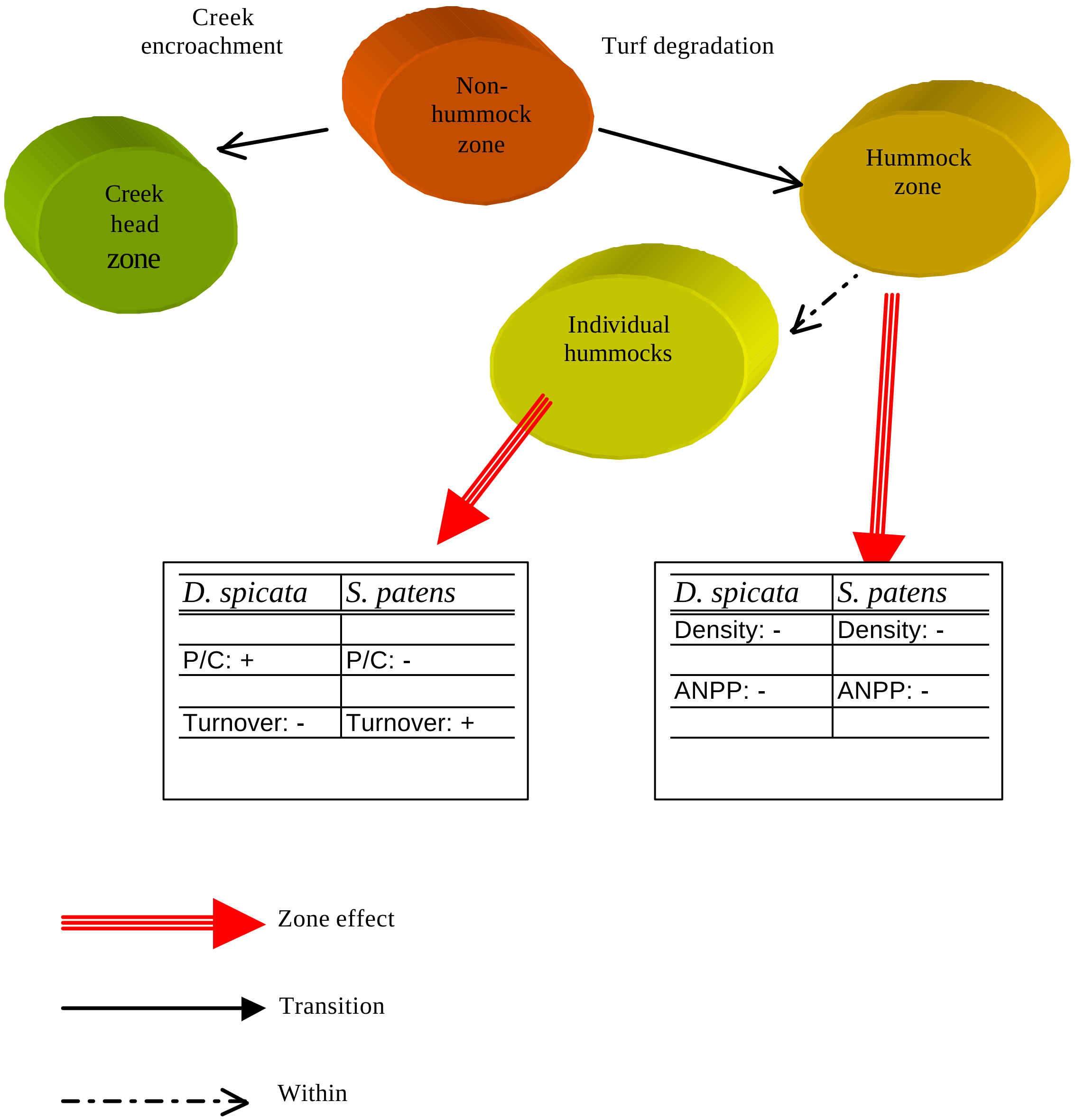
Hypotheses for ANPP tested by observation were postulated in the context of aboveground response of each species to 2 stages of high marsh transition to low marsh, that is hummock and hollow areas, and non-hummock areas. I treated a creek side zone separate from other zones because it possessed advantages, and possible disadvantages to plants that were unique to this zone. For the remainder of the thesis, I will refer to hummock and hollow areas as the Hummock zone, non-hummock areas as the Non-hummock zone, and the creek side area as the Creek zone. There are 4 factors affecting potential aboveground production of plants in these zones that were assessed in this study; (1) culm density, (2) production per culm, (3) early culm mortality, and (4) available turf (i.e. microtopography).

In hummock and hollow areas, there are two scales at which to assess effects of zone on measures of growth. Density and ANPP are measures of the entire hummock and hollow area. Specifically, one would expect these measures to be lower in a hummock and hollow area than a non-hummock area due to less surface area for culms to establish. Responses of production per culm and turnover are measures that represent the individual culms that exist on the hummocks.

I predicted *D. spicata* to have higher production per culm and out-produce *S. patens* in the Hummock zone, since *S. patens* lacks vital arenchyma (Burdick and Mendelssohn 1987, Naidoo *et al*. 1992) and is less adapted to stressful conditions than *D. spicata* (Bertness 1991b) (Figure 3). However, I also predicted *S. patens* would out-produce *D. spicata* in the Non-hummock (or less stressed) zone as found in a New England marsh by Bertness (1991b). I further predicted the Hummock zone would have reduced growth per unit area of each species based on prolonged ponding during the growing season and less surface area for culms to establish. There would be positive effects on *D. spicata* growing on the hummock scale (Figure 3) due to reduced competition with *S. patens*.

1.4. Possible responses to increased ponding

Hypotheses concerning experimentation were formed in the context of aboveground response by each species to a rise in sea level in Hummock and Non-hummock zones. Based on the literature, I considered production of species in the Non-hummock zone at upper Phillips Creek to be limited by water and nutrients during summer months (Parrando *et al*. 1978, Smart and Barko 1980, Kemp and Cunningham



D. spicata	*S. patens*
P/C: +	P/C: -
Turnover: -	Turnover: +

D. spicata	*S. patens*
Density: -	Density: -
ANPP: -	ANPP: -

Figure 3. Hypothesized response of *D. spicata* and *S. patens* to zone in the context of high to low marsh state change. P/C = production per culm, ANPP = Annual Net Primary Production. + and - signs indicate the hypothesized growth response in the Hummock zone relative to the Non-hummock zone.

1981, Shumway and Bertness 1994, Stasavich 1998). Thus I predicted that increasing high tide events through experimental flooding during each month of the growing season would have positive effects on growth characteristics of each species.

If hummock and hollow areas experience lower soil redox potential as a result of higher groundwater, or experience salt stress, *S. patens* growing on hummocks may be more stressed than *D. spicata* (Smart and Barko 1978, Broome *et al*. 1995, Baldwin and Mendehlssohn 1998). Given that *D. spicata* tolerates higher stress (Smart and Barko 1978), it may in turn be positively affected by ponding in hummock and hollow areas because competition with *S. patens* would be reduced (Bertness1991b) (Figure 4).

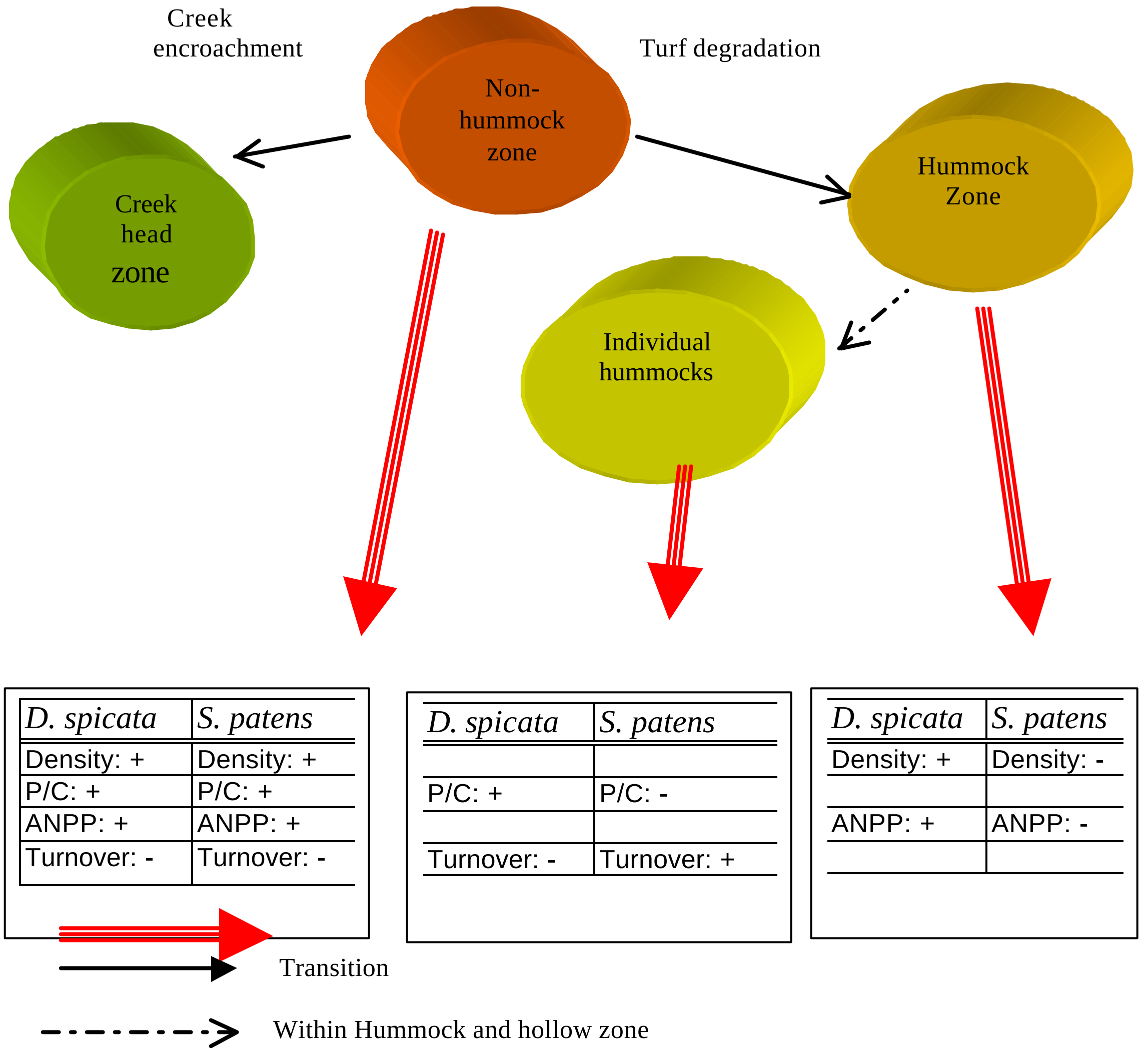
1.5. The testable hypotheses for both observational (by zone) and experimental aspects (by treatment) are as follows:

H_1 (species) : *D. spicata* will out-produce *S. patens* in the Hummock zone, and *S. patens* will out-produce *D. spicata* in Non-hummock areas.

H_2 (zones): The Hummock zone will have negative affects on growth per unit area of each species, and positive effects on growth of *D. spicata* on hummocks.

H_3 (treatment): Monthly tidal simulations (i.e. ponding) will have an overall positive effect on growth characteristics of each species in the Non-hummock zone.

H_4 (treatment)*:* *S. patens* in the Hummock zone will show signs of stress, and *D. spicata* in the Hummock zone will respond positively if competition with *S. patens* is reduced.



D. spicata	*S. patens*
Density: +	Density: +
P/C: +	P/C: +
ANPP: +	ANPP: +
Turnover: -	Turnover: -

D. spicata	*S. patens*
P/C: +	P/C: -
Turnover: -	Turnover: +

D. spicata	*S. patens*
Density: +	Density: -
ANPP: +	ANPP: -

Figure 4. Hypothesized response of *D. spicata* and *S. patens* to ponding in the context of high to low marsh state change. P/C = production per culm, ANPP = Annual Net Primary Production. + and - signs indicate the hypothesized growth response to experimentally increased inundation.

2. LITERATURE REVIEW

2.1. Marsh response to increased sea level:

Salt marshes communities are arranged according to inundation patterns; soil conditions, such as salinity and sulfide conditions; and interspecific competition (Chambers *et al.* 1998, Pennings and Callaway 1992). The transformation from one ecosystem class to the next has been identified as state change (Hayden *et al*. 1991, Brinson *et al*. 1995). Ecosystem state change typically results in changes of plant community composition and changes of ecosytem function (Brinson *et al*. 1995, Hayden *et al*. 1995, Brinson and Christian 1999, Nyman and Delaune 1999). This event is not to be confused with succession in which a climax community is reached, because state change is driven by altered external controls and potentially disturbance such as tidal creek encroachment and brackish water intrusion (Odum 1980, Brinson *et al*. 1995).

Salt marshes on the Delmarva (Delaware, Maryland, and Virginia) Peninsula are currently experiencing a relative sea-level rise from 2 -3mm per year (Oertel *et al*. 1992, Kestler and Wiberg 1996, Nerem *et al*. 1998). Salt marshes have the potential to migrate overland in response to this phenomenon if the slope of the upland border is gentle (Fletcher 1990, Oertel 1992, Brinson *et al*. 1995). Alternatively, marshes can progress in the opposite direction over previously subtidal areas by colonizing sediments deposited by storms (Osgood *et al*. 1995, Olff *et al*. 1997).

The ability and the direction a marsh responds to rises in sea level depends heavily on slope from creek to forest (whether steep or gentle) and tidal sediment supply (whether high or low). For example, if the slope and sediment supply were low, one could predict the marsh to erode at the creek head, and move inland to colonize the upland forest, which could not tolerate increased salinity and inundation. On the opposite end of the spectrum, if sediment supply were high and slope steep, the marsh may prograde towards the estuary and stall at the upland border (Brinson *et al*. 1995). If sediment supply were high and slope gentle, the marsh could be expected to prograde towards the estuary and expand into upland forest. The final response would be a loss of surface area due to low sediment supply and a steep slope at the upland border (Brinson *et al*. 1995).

For erosional mainland marshes of the southern Delmarva Peninsula, upland forest is predicted to convert to high marsh by increased salt water intrusion. High marsh conversion to low marshes would be facilitated by disturbances such as wrack deposition and processes such as root collapse, ponding of water, and loss of organic rich soils. Because of increasing water depth and erosive currents , low marshes are expected to convert to tidal flats. Lastly, tidal flats are expected to convert to subtidal areas (Brinson *et al*. 1995).

Hummock and hollow areas are believed to be a key link of the state change between high and low marsh (Brinson *et al.* 1995, Christian *et al*. 2000). Hummock degradation is the development of intact turf into pothole areas or "hollows" that are ponded for much of the year. Hummock areas are characterized by extensive patches of *D. spicata* and *S. patens* with sporadic hollows, to patchy islands of these species surrounded by large potholes (Figure 1). Hollow areas are typically flooded and colonized by *Ruppia maritima, S. alterniflora,* algae, and small nekton (Christian 1981, Kneib 1993, Christian *et al*. 2000).

Hummock and hollow areas are believed to form as a result of vegetative dieback and deflation of marsh sediment (Nyman *et al*. 1993, DeLaune *et al*. 1994). Dieback can occur from different stresses, such as toxic edaphic conditions or wrack deposition (Redinbaugh and Banta 1980, Burdick and Mendehlssohn 1987). One of the major links to subsidence in this case is an increase in the decomposition rate of root tissue, or a loss of root turgor (DeLaune *et al*. 1994). Nyman and co-workers (1994) suggest further that upon "pond" (i.e. hollow) initiation, marsh loss could proceed via erosion.

Hummock degradation was found to occur in a 6 year study of a Virginia marsh when intact turf communities of *D. spicata* and *S. patens* lost 25 – 50% of their original surface area (Brinson and Christian 1999, Christian *et al*. 2000). Creek encroachment is hypothesized to eventually connect this area to tidal flushing. This will likely facilitate *S. alterniflora* establishment and provide opportunities for low marsh development (Brinson *et al*. 1995, Christian *et al*. 2000). Information on how these species respond to increased inundation in the context of marsh transition could provide insight into understanding the development of salt marshes in response to sea-level rise.

2.2. Characteristics of *D. spicata* and *S. patens*

D. spicata and *S. patens* are clonal grasses found intermixed in transition and high marsh communities along the Atlantic coast from New England to northern Florida (Beal 1977, Mitsch and Gosselink 1993) . These species are known for their slow decomposition and turf building, and are believed to be important controls against erosion and storm damage (DeLaune 1994, White *et al*. 1978). Seeds, rhizomes, and young plants of *D. spicata* and *S. patens* can provide food sources for black ducks, geese, sparrows, muskrat, and deer (Gough and Grace 1998, Miller *et al*. 1998). Although they often grow together and share similar attributes, these species are quite distinct from a botanical perspective (Table 1). For example *D. spicata* is dioecious, which is rather rare in the grass family (Lynn 1996). *D. spicata* is generally shorter than *S. patens*, contains more leaves per culm, and its leaves are usually shorter.

Each species has adapted to saline environments as salt eliminators (Hansen *et al*. 1976, Naidoo *et al*. 1992), as opposed to salt excluders such as mangroves, and salt compartmentalizers such as *Salicornia* sp. (Mitsch and Gosselink 1993, Pennings and Bertness 1999a). That is, they are known to eliminate salt and toxic ions via their roots and stomates (Smart and Barko 1978, Kemp and Cunningham 1981). *D. spicata* has been shown to tolerate higher salinities of the two species (Smart and Barko 1978). Despite the resilience of *D. spicata* and *S. patens* to saline soils, biomass accrual of all salt marsh halophytes is proven to be greatest at low salinities (Smart and Barko 1980).

Another adaptive advantage in marshes is their clonal morphology. Clonal plants can share resources and redistribute photosynthate among ramets (Kemball and Marshall 1995). These advantages allow the clone to support individual ramets under stresses such as competition and herbivory (Harnett and Bazzaz 1983, Evans 1991). Clonal growth aids further in foraging for resources and selecting new habitat such as disturbed areas (Shumway 1995, Brewer and Bertness 1996).

Table 1. Natural history of *Distichlis spicata* and *Spartina patens* (Lynn 1996).

	S. patens	*D. spicata*
Family	Graminaea	Graminaea
Tribe	Cynodonteae	Eragostideae
Sex	monoecious	dioecious
Inflorescence	1-4 spikes	1-5 spikes
	1 spikelet	several spikelets
	1 floret	1 - many florets
Stem height	40.5 - 64.5 cm	32.5 - 55 cm
Stem width	approximately 1.5 mm	approximately 2 mm
Leaf length	10.5 - 19 cm	6.7 - 7.7 cm
Leaf number	4 - 7 leaves	14 - 18 leaves
Leaf production	via length	via increase in #
Leaf blade	rounded	flat
Ligule	not hairy	not hairy
Rhizomes	slender, wiry	thick, extensive
Meristem location	tips of roots, buds of culm	tips of roots, buds of culm

Much research has been conducted on *D. spicata* and *S. patens* in New England salt marshes (Bertness and Ellison 1987, Bertness 1991a, Bertness 1991b, Bertness *et al*. 1992, Levine *et al*. 1998). Conclusions of this research should be interpreted in the context of latitude because of possible differences in climate between this region and others. Mechanisms of plant zonation are currently understood to differ between high and low latitude marshes (Pennings and Bertness 1999a, Pennings and Bertness 1999b). Due to shorter and cooler growing seasons, high marshes in the higher latitudes generally have lower salinities than those of lower latitudes (Pennings and Bertness 1999b). Another consideration is the possible differences in the definition of high marshes among scientists.

D. spicata is a rapid colonizer of disturbed habitats (Hansen *et al*. 1976), and is considered to be the most tolerant of marsh species to environmental stresses (Bertness 1991b). *D. spicata* has a better developed arynchema system and is thus better adapted to saturated soils than *S. patens* (Bandyopadhyay *et al*. 1993, Bertness 1991a, Burdick and Mendelson 1989, Hansen *et al*. 1976). *D. spicata* growth was less affected by a higher soil salinity than *Spartina alterniflora and Spartina cynusoides* under the same conditions (Parrondo *et al*. 1978). Kemp and Cunningham (1981) suggest higher light intensity levels with a prolonged photoperiod during summer months helps *D. spicata* overcome much of the growth inhibition caused by high salt concentrations.

Although *D. spicata* is usually the first to colonize disturbed areas, it can be out competed by other species. In a New England salt marsh, Bertness and Ellison (1987), and Bertness (1991b) found that *D. spicata* played the role of facilitator in marsh communities by colonizing salt flats. It then changes its local environment with shade and decreases evaporation and in turn, local salinity. This allows opportunity for others to invade. In fact, *D. spicata* is only sparsely present except in similarly disturbed areas in New England marshes. Specifically, it is out-competed by *S. paten*s and *Juncus gerardi* (Bertness 1991b).

Arenchyma affects the ability of a plant to cope with low redox potential. It may indirectly affect the ability of a plant to cope with high salinties because respiration increases to meet the metabolic demands of salt excretion (Warren and Brockelman 1989). *S. patens* lacks important arenchyma tissue that promotes root oxygenation and is therefore less adapted to stresses such as high salinity and low redox potential (Anderson 1973). This is the primary reason it is excluded from low marsh areas in New England (Bertness 1991a). Bertness (1991a) further found that competition from *S. patens* for available resources is what limits *S. alterniflora* to low marsh areas. However, *S. patens* was also found to be out-competed by *Juncus gerardi* in less stressed areas of New England marshes (Bertness 1991a).

In upper Phillips creek salt marsh, Tolley and Christian (1999) examined impacts of increased flooding and wrack deposition on a *D. spicata*, *S. patens*, and *J. roemerianus* high marsh community. They found increases in both stresses could lead to a change in community composition, but flooding alone produced little response in plant biomass. They found that *D. spicata* and *S. patens* recovered faster from wrack deposition *than J. roemerianus,* and found colonization of bare areas caused by wrack was initially dominated by *D. spicata.* They concluded inundation may have a greater effect in reestablishment on a plant community after wrack deposition than without wrack deposition.

2.3. Terminology in production studies

Aboveground primary production has long been considered an important factor in the analysis of nutrient and energy flows in marsh ecosystems (Howes *et al*. 1986, Hsieh 1996, Teal 1962). Although studies of production have continued for decades (e.g. Milner and Hughes 1964 , Wiegert and Evans 1968), terminology on the subject remains variable. Perhaps the first problem encountered in discussing production and phenology of grasses is the definition of a plant. For example, *D. spicata* and *S. patens* are rhizomatous and clonal. Therefore, a "plant" is rarely one culm. A culm is considered any specialized stem of a grass. A culm of *D. spicata* or *S. patens* may also be referred to as a ramet, which is any individual of a clone. For the purpose of this study I will refer to what may be commonly thought of as "plant" in the botanical manner as "culm".

The maximum amount of biomass contained by a group of living plants at the end of the growing season is known as peak standing stock. End of year biomass (EOYB) harvest methods have often been used to assess production and have been extensively reviewed by Kirby and Gosselink (1976), Shew and co-workers (1981), and Dickerman and co-workers (1986). End of year biomass samples harvested at the end of the growing season to assess primary production target the approximate time of peak standing stock for harvesting. This can underestimate ANPP because it does not account for losses during the growing season due to herbivory and mortality (Milner and Hughes 1968, Hsieh 1996).

Another potentially unclear concept in production includes the terms "gross" and "net". Gross primary production is the total amount of energy or matter an organisms invests in living. Gross production includes incorporation into both biomass and respiration. Net production, however, is the assimilation into biomass after respiratory loss. Of the two, net primary production is quantified more in the literature because it is an easier and more direct measure.

Aboveground production is easier to measure and is more commonly measured than belowground production. Belowground production is an estimation of root and rhizome growth below the soil, and involves extracting roots and surrounding soil with cores. Due to difficulties of extracting soil cores, separating live and dead roots, and identifying below ground portions by species, few completely successful techniques have been evolved for use in ecological studies (Milner and Hughes 1968, Gallagher 1974, Blum 1993).

Turnover rate of biomass is a measure in production literature of *S. alterniflora*, that can aid in this study, and is defined as the ratio of ANPP to peak standing stock (Table 2, Kaswadji *et al*. 1990, Morris and Haskin 1990). As shown by Kaswadji and co-workers (1990), turnover of *S. alterniflora* can range from 1 to 2.2 yr^{-1} depending upon the method of production used (Table 2). When EOYB equals ANPP, that estimate would have a turnover of 1.0 per year.

Table 2. Summary of Aboveground Net Primary Production (g m^{-2} yr^{-1}) and turnover rates (yr^{-1}) for *S. alterniflora.*

Methods	Kaswadj *et al.* 1990	Kirby and Gosselink 1976	Hopkinson *et al.* 1980	Shew *et al.* 1981	Annual turnover (productions/peak standing crop)
Peak standing crop	831	903	754	242	1.0
Milner-Hughes	831	811	X	241	1.0
Smalley	1231	1200	X	225	1.5
Weigert-Evans	1873	1988	2658	1029	2.2
Lomnicki *et al*.	1437	X	X	1028	1.7

Source: Kaswadj *et al*. 1990

Turnover is significant because the peak standing crop and net primary production would only be identical if the vegetation stopped growing at a single instant in time, mortality occurred only during the post-growth period, and the vegetation was not grazed upon during the growing season (Wiegert and Evans 1964, Milner and Hughes 1968). Turnover is one way to assess the stress on a particular species or community during the growing season. For example, a species with a turnover rate closer to 2 yr^{-1} may be expected to lose significant amounts of leaf blade biomass during the growing season, or experience considerable mortality. Turnover is a measure of stress a species experiences, and can be considered a measure of the longevity of a species. Turnover rates can additionally be helpful in comparisons among and within species to assess response to environmental factors.

2.4. Previous studies of primary production in salt marsh plants

Large amounts of literature have contributed to the better understanding of the primary production of *S. alterniflora* and its contributions to estuarine trophic structure and energetics (e.g. Table 2, Turner 1976, Marinucci 1982, Morris and Haskin 1990, and Newell *et al*. 1998). Studies of high marsh species such as *J. roemerianus* and *S. patens* have been reported to a much lesser extent (e.g. Turner 1979, Christian *et al*. 1990, Brinson and Christian 1999), and *D. spicata* has rarely received direct focus in salt marsh production studies (e.g. Table 3, Waits 1967, de la Cruz 1974, Hopkinson *et al*. 1978, White *et al*. 1978, Bellis and Gaither 1985).

Table 3. Comparisons of annual net primary production estimates (g m^{-2} yr^{-1}) of marsh species at different locations in the U.S.A.

Species	Production	Source
Louisiana		
D. spicata	1169-1291	White *et al*. (1978)
D. spicata	1967	Hopkinson *et al*. (1980)
S. patens	4159	
Missippi		
D. spicata	1072	de la Cruz (1974)
North Carolina		
S. patens	1296	Waits (1967)
	Peak Standing Stock (g m^{-2})	
D. spicata	760	Bellis and Gaither (1985)
Virginia		
D. spicata	31-211	Tolley (1996)
S. patens	119-439	
D. spicata	108-440	Buck (personal communication)
S. patens	111-530	

Primary production can vary within a marsh and between marshes (Bellis and Gaither 1985, Hackney and Hackney 1978). This is primarily a result of the physiological costs of coping with physical and chemical factors present in each community (Bertness 1991a). Production within a marsh can be attributed to different salt concentrations and to the toxic environments of anaerobic soils (Bertness 1991b). For example, creek banks of low marsh zones are believed to exhibit the highest aboveground production in a marsh as a result of frequent exposure to tidal water (Odum 1980).

Plant biomass production in any marsh can also be expected to vary annually due to environmental fluctuations and relative abundance of constituent species (Turner 1979, Bellis and Gaither 1985, Morris and Haskin 1990). For example, Morris and Haskin (1990) estimated *S. alterniflora* annual aboveground production at 402 g m^{-2} yr^{-1} at Goat Island, South Carolina in 1984. The following year, they estimated production at 1042 g m^{-2} yr^{-1} at the same site. In this case, production was positively correlated with cumulative rainfall during summer months.

2.5. Variability among production methods

Methods for estimating production are often based on different assumptions and focus on different aspects of growth (Dickerman *et al*. 1986). Primary production values from many studies have been derived by using methods originally created for other plants. As a result, it is generally accepted that the wide divergence in measurements of primary production among sites may be as much a result of the methods used as it is a result of the difference in production (Dai and Wiegert 1996a, Hsieh 1996).

Techniques used for estimating tidal salt marsh production range from conceptually simple techniques such as the standard peak standing crop technique to methods more complicated and costly that measure disappearance of above and below ground material, respiration, or increases in living material (Wiegert and Evans 1964, Hackney and Hackney 1978, Hopkinson *et al.* 1978, Turner 1976, White 1978). The popular Wiegert and Evans method was originally developed for an old field successional community, and overestimates primary production due to export of material by tides (Hsieh 1996). Many other harvest methods are believed to underestimate production by focusing on the difference in standing crops between consecutive samples, which does not accurately assess herbivory, or disappearance of vegetation between intervals (Lomnicki *et al.* 1968, Coupland 1979, Hsieh 1996).

Non-destructive techniques that sufficiently account for turnover have been incorporated in other methods to better estimate production (Dickerman *et al*. 1986, Morris and Haskin 1990). For example, non-destructive production measures of the freshwater cattail, *Typha latifolia*, were refined by Dickerman and co-workers (1986). This study incorporated growth characteristic measurements with nearby biomass harvests throughout the growing season.

D. spicata and *S. patens* have received relatively little focus in production literature. The highest estimates of aboveground production of *D. spicata* and *S. patens* occurred in a Louisiana marsh, where *D. spicata* was estimated to be as high as 1967 g

m^2 yr^{-1} and *S. patens* was estimated to produce up to 4159 g m^{-2} yr^{-1} (Table 3, Hopkinson *et al*. 1978). In upper Phillips Creek marsh, the site of the present study, on the Eastern Shore of Virginia, EOYB of live *D. spicata* has been measured as high as 410 g m^{-2}, and the EOYB of live *S. patens* has been measured up to 530 g m^{-2} (Table 3). One likely factor in production differences between sites is the assumption that on a geographical scale, production is found to increase with greater exposure to solar energy, temperature, and longer growing seasons (Turner 1976).

2.6. Lessons learned from *S. alterniflora* studies

Results from past primary production studies have answered many questions, but uncertainties remain. For example, Gallagher and co-workers (1980) suggest production of tall *S. alterniflora* is roughly twice that of the short form. Dai and Wiegert (1996b) state the leaf area index (LAI) is about twice as high in the tall form of *S. alterniflora* as the short, thus the net leaf photosynthesis of each form is comparable. However, Gurgevich and Dunn (1979) report that net leaf photosynthetic rate in short form *S. alterniflora* to be half of the tall form. These kinds of discrepancies are not uncommon in *S. alterniflora* production literature, and it is apparent that knowledge of even our most studied salt marsh species is not yet complete.

Morris and Haskin (1990) performed a detailed analysis of aboveground primary production of *S. alterniflora* using a nondestructive census method. They presented a numerical simulation of the sensitivity of destructive harvest methods to sampling errors propagated by spatial variability. Net aboveground production was estimated by censusing the heights of shoots on a monthly basis from permanent quadrats. Mass of individually tagged shoots were estimated from allometric equations derived from previous biomass harvests. By measuring stem and leaf turnover, they found aboveground production was 2.3 times larger than the end of year standing stock.

It is primarily the methodologies performed by Morris and Haskin (1990) on *S. alterniflora* that I chose to modify to an aboveground production study of *D. spicata* and *S. patens*. Modifying this approach has considerable advantages over the EOYB method presently used at the Virginia Coast Reserve-Long Term Ecological Research site in Virginia. The modified method will account for significant amounts of previously unaccounted biomass that has senesced, fallen, and otherwise disappeared from the canopy during the summer. This method will provide information on the natural history of these understudied plants (Hadley and Kieckhefer 1963, Kucera *et al*. 1967, Sims and Coupland 1979).

3. MATERIALS AND METHODS

3.1. Site description:

The Virginia Coast Reserve is the site for the current research and is one of 24 Long Term Ecological Research sites in the United States. It consists of roughly 14,000 ha that are owned partially by The Nature Conservancy and covers 110 km along the southern Delmarva Peninsula (Figure 5, www.vcrlter.virginia.edu). Three types of marshes typical of the VCR are mainland fringe marshes, Hog Island Bay lagoonal marshes, and barrier island fringe marshes (Oertel *et al*. 1992, Brinson *et al*. 1995). The tidal range of the area is 1.5 – 2 m. Sixteen percent of marsh land in this area is estimated to have been lost to rising sea level in the past 145 years (Hayden *et al*. 1991).

Current research of the VCR-LTER program includes monitoring changes of aquatic, wetland, and terrestrial ecosystems as a result of sea-level rise (Brinson *et al*., 1995, Hayden *et al*. 1995). This study examines the aboveground responses of *D. spicata* and *S. patens* through ANPP in different stages of high marsh transition to low marsh that are hypothesized to develop as a result of increased sea level.

My research was located in North Hampton County, Virginia, and examined high marsh primary production at Brownsville in upper Phillips Creek marsh (37^{o}26’38. 5”N, 75^{o}50’4.99”W). Mean annual temperature is 15 ^{o}C, with a mean annual low of –11 ^{o}C and a mean annual high of 36 ^{o}C (Stasavich 1998). This marsh is part of the Machipango drainage system and is flooded with estuarine waters of Phillips Creek that have a salinity between 8 and 36 ppt. Tidal amplitudes have been estimated from 10 – 210 cm (Christiansen 1999). The high marsh soil is predominantly poorly drained and classified

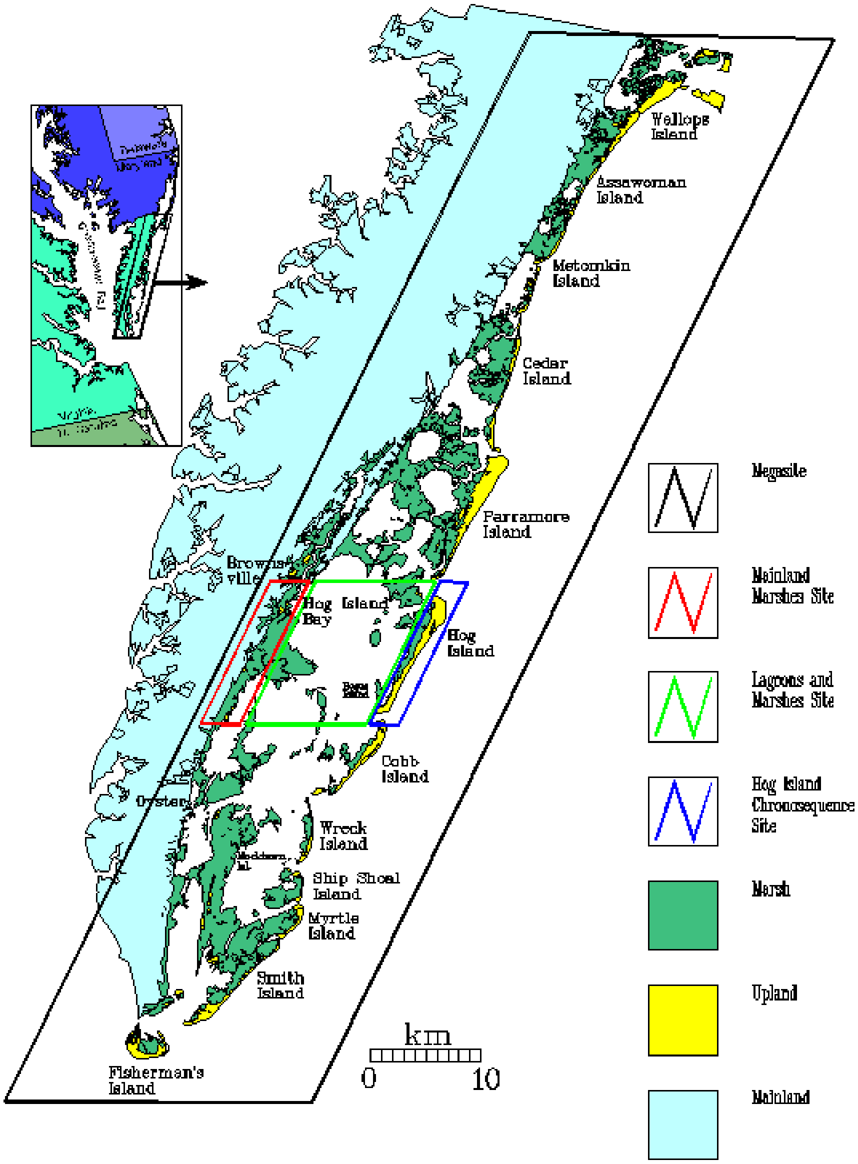


Figure 5. Virginia Coast Reserve mega-site. Source is www.vcrlter.virginia.edu.

as Chincoteague-Magotha series. Slope from the creek to the high marsh is estimated to be 0.81×10^{-3}m (Hmieleski 1993). The high marsh community consists of dense stands of *J. roemerianus*, co-dominant stands of *S. patens* and *D. spicata*, and *S. alterniflora* near the tidal creeks (Brinson *et al*. 1995).

The study area located in the organic high marsh at Upper Phillips Creek marsh encompasses approximately a 1.4 hectare region. Five study sites within the marsh were chosen based on differences in micro-topography and distance to the tidal creek (Figure 6). Sites were numbered 1-5 based on their proximity to the creek. All sites possessed similar species composition of *D. spicata* and *S. patens* and similar elevation from mean sea level at approximately 1.01-1.09 m above mean sea level (Appendix 1, www.vcrlter.virginia.edu/~crc7m/brnv/traci27.txt).

Site 1, the Creek zone, was located at the head of a tributary of Phillips Creek. The tributary is steadily encroaching, and eroding the organic rich substrate in this area of the high marsh. The site is well drained and has some micro-topographic relief, mostly due to muskrat burrowing. Site 2 was located at 40-45 m west-northwest of the creek head. It differed from site 1 in that the organic substrate was both intact and solid. Site 3 was located approximately 75 m northeast from the creek head, and differed from the first 2 sites in that its micro-topographic relief was well developed with hummocks and hollows. Site 4 was 120 m east-northeast of the creek head and was similar to site 2 in that it had little or no headward creek erosion. Site 5 was located approximately 200 m

Figure 6. Study sites at upper Phillips Creek.

North of the creek and its micro-topographic relief was well developed with hummocks and hollows. The intact turf sites of 2 and 4 comprised the Non-hummock zone. Lastly, the Hummock zone consisted of the hummock and hollow sites of 3 and 5.

3.2. Background

This study examined *D. spicata* and *S. patens* aboveground production and growth characteristics over a period of 2 growing seasons at Upper Phillips Creek marsh. Field research spanned from May of 1998 to September of 1999. The primary goal for 1998 was to develop and refine field and laboratory techniques for estimating ANPP. During 1999, I focused on the effects of increased hydroperiod on ANPP. Each year, growth characteristics for each species were non-destructively measured in conjunction with nearby biomass harvests as similarly performed on *S. alterniflora* by Morris and Haskin (1990).

3.3. Experimental design

I was interested in examining aboveground plant response to increased inundation and ponding of brackish water. Increased spring tide flooding was simulated during the growing season on a monthly basis by pumping brackish creek water on specific plots designed to pond water.

Site 2, 4, and 5 were used to experimentally modify hydroperiod. Each experimental site contained 3 pairs of plots; 2 “Ponded” plots, 2 “Control” plots, and 2 plots were designated “Subsurface control” (Figure 7). Sites 1 and 3 contained 4 and 6 plots respectively, and were used for control purposes.

Ponded plots consisted of water proofed, plywood borders with dimensions of 2cm x 20 cm x 2.46 m. The borders were arranged in a 2.46 x 4.92 m rectangle and were caulked at each junction. The borders were buried into the substrate to form a border of 10 cm below ground and 10 cm above ground. The maximum amount of water each plot could contain from the surface to the top of the border was estimated to be 1210 L (or 320 gal). In 1999, a 2.6 cm diameter hole was drilled on each side of each ponded plot at 5cm above the marsh surface to allow regular tides to flood the plots. Holes were plugged with rubber stoppers during pumping.

Control plots received no treatment, received a normal hydroperiod and were marked with 1.2 x 50 cm PVC at the corners of each 2.46 x 4.92 m plot. There were a total of 16 Control plots. However, only 10 were used in the current study. That is, 2 Control plots were used per site.

Subsurface control plots were also 2.46 x 4.92 m with waterproofed plywood borders with a dimension of 2 cm x 10 cm. The border was inserted 10cm into the substrate and flush with the ground surface. The purpose of the Subsurface control plots was to account for any restriction of belowground water flow and disturbance of inserting borders caused by the borders used in the Ponding plots. Due to prolonged aboveground flooding at site 5, Subsurface controls were not installed until September 26, 1998.

3.4. Field Methods constant in 1998 and 1999

Brackish water (8-36 ppt) from a first order tributary of Phillips Creek was

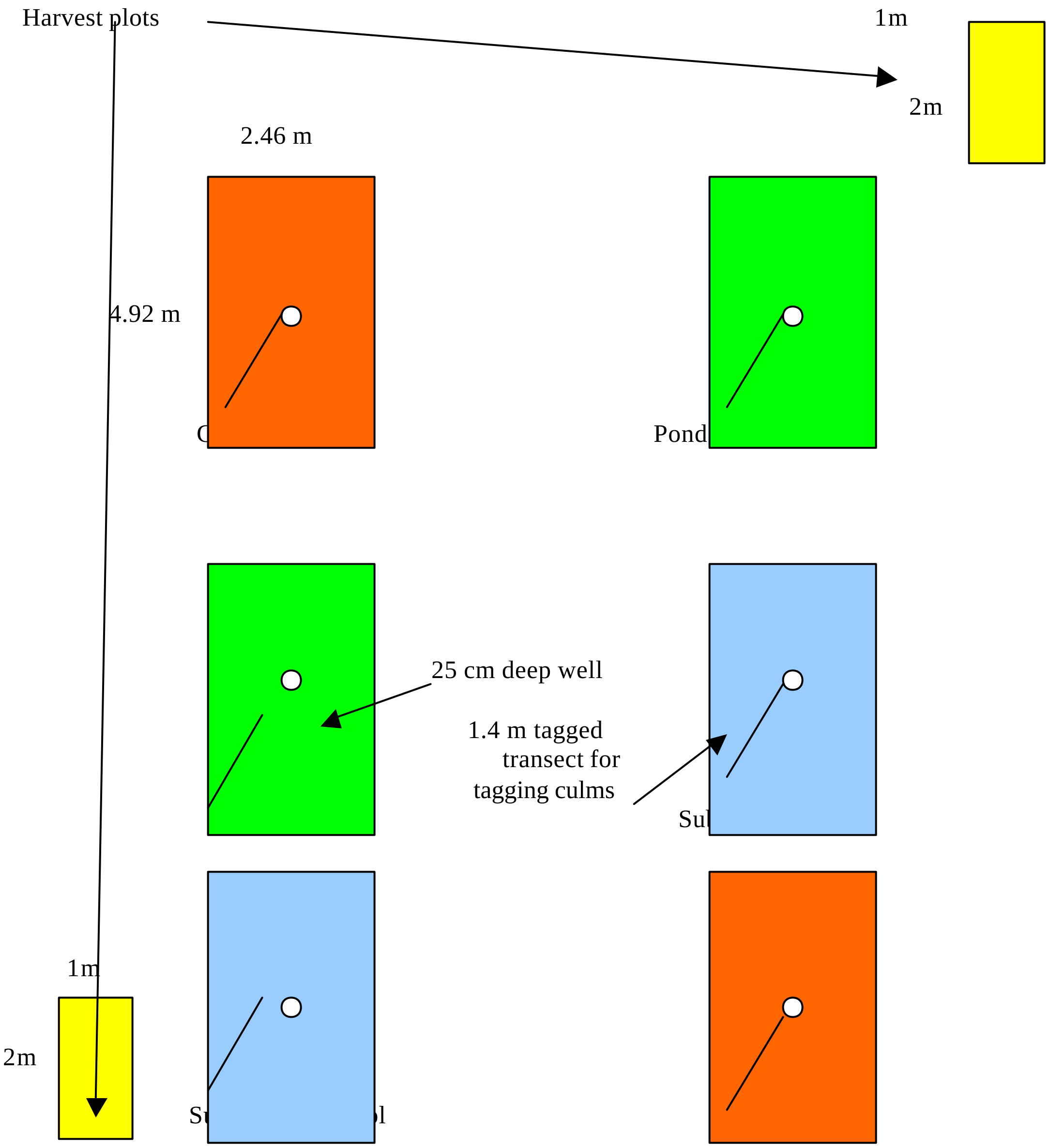


Figure 7. Design of experimental sites 2, 4, and 5. Wells were used in ground water analysis, transects were used to monitor growth characteristics, and monthly tracking of density and biomass was done in harvest plots.

pumped to Ponded plots to simulate flooding by extreme high tides and storm events (Appendix 2). A gasoline powered Briggs and Stratton 5hp Homelite centrifugal pump and a flexible 7.2 cm PVC hose were used. Water flow was baffled at the end of the hose to minimize plant damage (Figure 8). The baffle was constructed of PVC well tubing 1.25 m long with a diameter of 0.2 m. Slits of 0.2 m length were cut into the PVC every 0.1 m on each side. The baffle was suspended roughly 0.6 m above ground on a temporary plank crossing the center of each plot during pumping. The pump was rated at a maximum rate of 370 L/min without an attached hose. Output decreased with increased hose length, and usually fluctuated around 190-230 L/min. Creek salinity, and salinity within each Ponded plot was measured directly after each pumping with a refractometer.

To track monthly growth of plants within plots, ten culms per species were tagged and measured to the closest 0.5 cm along a 1.4 m transect. Culms were tagged with 1cm tygon tubing cut to approximately 1cm heights. Each tag was tied with flagging tape approximately 6 cm long to better locate each specimen in the dense foliage. In 1998, transects were used in Control plots at all five sites. In 1999 transects were used in all three treatments at the 3 experimental sites in addition to 2 control plots at sites 1 and 3.

Any lost tags were noted each month, and the culm was replaced with one of similar height between adjacently tagged culms. If a culm died, another culm of similar stature was tagged and served as a replacement. This continued until the last measuring date when the mortality rate was the greatest and field measures were no longer taken (Table 4).

Two permanent harvest plots of 1 x 2 m were delineated in close proximity to

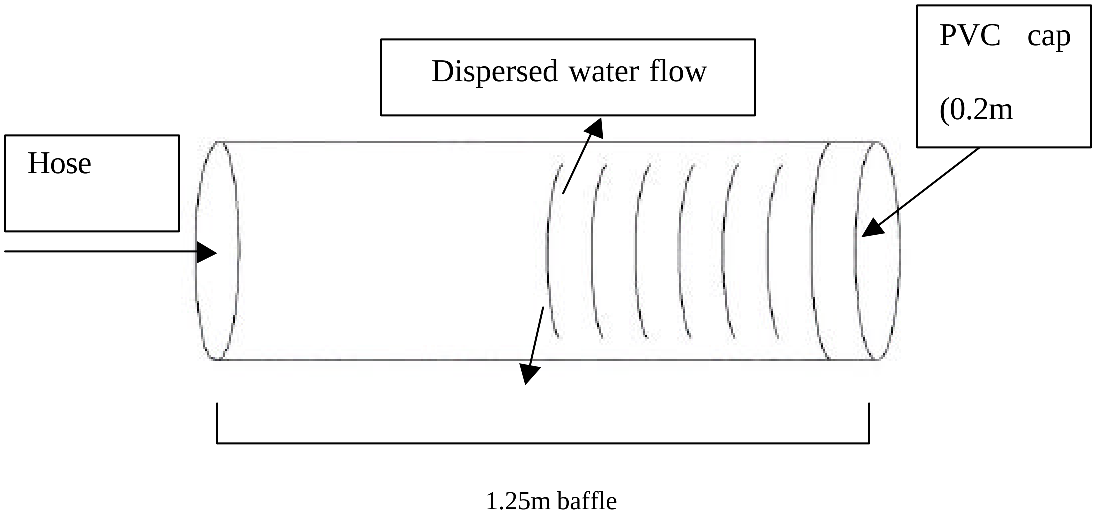


Figure 8. Design of PVC Baffle used for pumping.

each site so as to contain similar characteristics (Figure 7). Aboveground biomass from two 0.0625 m^{-2} quadrats were harvested monthly from each harvest plot, except in the month of September when EOYB harvests occurred. Each monthly harvest was haphazardly selected by tossing a quadrat into the plots from approximately 4 m and repeated if the quadrat landed on a previously harvested area. Removal of biomass involved clipping all standing vegetation to the soil surface within the quadrat, and removing all mass above the soil surface (Milner and Hughes 1964).

EOYB harvests were performed in triplicate in September of both years. EOYB occurred within each Control plot in 1998, and each Control, Subsurface control, and Ponded plot in 1999. Each plot was divided into 4 quarters, and 1 quarter was selected with a table of random numbers for quadrat placement. The placement of the quadrat within the quarter was haphazard unless it landed on the tagged transect. Harvested biomass did not include tagged culms, so that the monitoring of each species could have continued beyond the time of the estimated standing stock.

Daily precipitation was recorded at the on-site meteorological station in Brownsville. Groundwater salinity and depth were recorded in the center of the plots from 2-cm diameter wells with screened holes from 10 to 25 cm depth. Ground water was extracted from the wells with a Nalgene hand pump, and salinity was measured using a refractometer. Ground water was monitored every 2-4 weeks during each growing season. Ground water depth was measured with a battery operated meter stick designed to beep when it touched water.

Herbivory on *D. spicata* and *S. patens* was assumed to be negligible and was not

Table 4. Monthly mortality and lost control tags

Year	Date	Species	# tags lost	# dead plants	# of new tags
1998	21-Jun	*D. spicata*	0	1	1
1998	22-Jul	*D. spicata*	3	2	5
1998	22-Aug	*D. spicata*	0	6	6
1998	19-Sep	*D. spicata*	0	20	20
1998	1-Nov	*D. spicata*	4	68	0
1998	21-Jun	*S. patens*	0	0	0
1998	22-Jul	*S. patens*	1	6	7
1998	22-Aug	*S. patens*	1	4	5
1998	19-Sep	*S. patens*	0	21	21
1998	1-Nov	*S. patens*	6	75	0
1999	11-May	*D. spicata*	21	0	21
1999	8-Jun	*D. spicata*		1	1
1999	7-Jul	*D. spicata*	3	2	4
1999	5-Aug	*D. spicata*	4	5	9
1999	10-Sep	*D. spicata*	3	36	0
1999	11-May	*S. patens*	7	0	7
1999	8-Jun	*S. patens*	0	1	1
1999	7-Jul	*S. patens*	1	1	2
1999	5-Aug	*S. patens*	3	3	6
1999	10-Sep	*S. patens*	2	15	0

addressed during the study. Personal observation that occurred both prior to and during the study was justification for this. However, Wiegert and Evans 1967 suggested herbivory can account for 8 percent of *S. alterniflora* ANPP. Nutria and wild pigs can reduce aboveground biomass in marshes, but these conclusions were formed when the animals were not in a natural setting (Gough and Grace 1998). In all likelihood, a relatively small amount of herbivory may occur from insects, fowl, and occasional mammals, and should be noted when interpreting results. However, at no point in the study did I notice any signs of herbivory.

This study did not assess dissolved organic carbon (DOC) from either *D. spicata or S. patens.* Loss of DOC oocurrs when plants are wetted or immersed in water (Tukey 1970, Gallagher *et al*. 1975). No published work has examined DOC of *D. spicata or S. patens*, however, Galleghe r and co-workers determined 0.61g m^{-2} yr^{-1} of soluble carbon compounds was released by *S. alterniflora* leaves in a Georgia salt marsh.

3.5. Laboratory Methods during 1998 and 1999

Each month harvests were taken to the lab and stored in a cold room (40^{o}C) to await analysis. Biomass harvests were sorted in lab into living and dead material and by species. Living material was identified as any plant mass containing green color. Densities and biomass of living and dead material were recorded in both species. For the purposes of density measures, a culm was counted as long as it contained its apical meristem (Figure 2). If a specimen was fragmented, it was not counted, but was included in each respective weight measure. Growth characteristics similar to field measures were recorded for 12 living and dead culms of each species that were haphazardly chosen from respective piles. Afterwards, biomass for each of the categories was dried at 85 ^{o}C degrees for 48 hours, then weighed on a Delta Range PB3002 balance with an accuracy of 0.01 g.

3.6. Specific field methods in 1998

Field research in 1998 began on May 26 and concluded November 4. In 1998, 2 control plots at each of the 5 sites were used to monitor monthly growth of each species. In each control plot, 10 culms of each species were tagged along a 1.4 m transect without particular order of species. This accounted for a total of 100 culms tagged per species. Measured variables included culm height, height to lowest leaf, height to uppermost leaf, and inflorescence length (Table 5). Culm heights were measured by placing a meter stick adjacent to the culm base and extending the tallest leaf to its maximum. Leaf length was recorded in order of lower leaves to uppermost leaves, by measuring the distance from where the leaf blade attached to the stem to leaf tip after each leaf was straightened to its maximum. Lastly, leaf color was recorded as brown, partly brown, and green to aid in tracking monthly senescense and leaf fall.

Pumping occurred as one event on June 29 and July 25 of 1998. On July 27, a decision was made to pump on consecutive days each month. Pumping continued again on August 22 and 23, and on September 26, and 27, 1998. On August 23, a decision was made to re-pump any plot whose water level dropped more than 2 cm in 10 minutes.

Table 5. Example of data recorded on field sheets used in 1998.

Date: June 1, 1998
Site:1c1

Species: *S. patens*	Species: *D. spicata*	Species: *S. patens*
Shoot height: 45.5cm	Shoot height: 41	Shoot height: 42.5cm
Height to1st leaf: 7.5cm	Height to1st leaf: 8.5	Height to1st leaf: 9cm
Height to upper leaf: 37.5cm	Height to upper leaf: 38	Height to upper leaf: 37cm
Leaf1: 5cm/green	Leaf1: 4cm/green	Leaf1: 5cm/green
Leaf2: 16.5cm/green	Leaf2: 6cm/green	Leaf2: 16.5cm/green
Leaf3: 10cm/brown	Leaf3: 14.5cm/brown	Leaf3: 10cm/brown
Leaf4: 5.5cm/green	Leaf4: 15cm/green	Leaf4: 5cm/green
Leaf5:	Leaf5: 5cm/brown	Leaf5: 5.5cm/brown
Leaf6:	Leaf6: 8cm/green	Leaf6:
Leaf7:	Leaf7: 12cm/green	Leaf7:
Leaf8:	Leaf8:	Leaf8:
Leaf9: 1inflorescence/3cm	Leaf9:	Leaf9:

Each pumping event continued until the water level reached the top of the border at 10 cm. Site 5 was pumped only in September, as it had standing water during all other times.

3.7. Specific laboratory methods during 1998

For each harvested sample, culms were separated into piles based on species and live or dead. Twelve culms were haphazardly selected from each pile for growth characteristic measures. The measures for living specimens were culm height, height to leaf 1, height to uppermost leaf, and inflorescence length. Leaf lengths, and leaf color (brown or green) were also recorded from culm base upwards (Table 6). The purpose of this was to track monthly senescensce and leaf loss. Measures for dead culms were stem height, height to leaf 1, height to last leaf, and number of leaves. Leaves of dead culms were often detached, so estimates of leaf number were made based on leaf scars or "nodes". To assess the mass lost in leaves during the growing season, over 100 leaves were removed from harvested culms in July to record leaf mass and leaf length.

3.8. Specific field methods during 1999

Field research in 1999 began on April 7 and ended September 9, 1999. On April 7, 10 culms of each species were tagged in all plots at sites 2 and 4, and within 4 control plots in sites 1 and 3. (Due to standing water, and the low stature of culm height, the six transects at site 5 were not tagged until May 10, 1999. A total of 220 culms of each species were tagged in 1999. Plants were tagged in an alternating species pattern to minimize possible errors made in the field. Plastic flags 0.5 m tall were placed at the

Table 6. Example of data recorded on lab sheets used in harvest data 1998.

Date: April 1, 1998	Site:3-1a	
Species: Live *S. patens*		
Density/Biomass= 220 / 29.56g		
Shoot height: 35.5 cm	Shoot height: 32 cm	Shoot height: 39.5 cm
Height to1st leaf: 3 cm	Height to1st leaf: 3 cm	Height to1st leaf: 5 cm
Height to upper leaf: 31 cm	Height to upper leaf: 28 cm	Height to upper leaf: 32 cm
Leaf1: 4.5 cm/green	Leaf1: 6 cm/brown	Leaf1: 10 cm/brown
Leaf2: 6 cm/green	Leaf2: 9 cm/brown	Leaf2: 16 cm/green
Leaf3: 14 cm/brown	Leaf3: 16.5 cm/green	Leaf3: 19.5 cm/green
Leaf4: 15.5 cm/green	Leaf4: 4 cm/green	Leaf4: 6 cm/green
Leaf5: 4 cm/green	Leaf5:	Leaf5:
Leaf6:	Leaf6:	Leaf6:
Leaf7:	Leaf7:	Leaf7:
Leaf8:	Leaf8:	Leaf8:
Leaf9: 1inflorescence/3 cm	Leaf9: 1inflorescence/2.5 cm	Leaf9:

beginning and end of each 1.4 m transect to aid in its location in dense foliage. Pumping occurred on May 11 and 12, June 8 and 9, July 7 and 8, August 5 and 6, and September 9 and 10 (Appendix 2).

In 1999, growth characteristic measures were made on 10 culms of each species in each transect. I continued to measure culm height, height to lower leaf, height to uppermost leaf, and inflorescence length. Instead of measuring individual leaf length and color, I measured the number of green and brown leaves per culm (Table 7). This approach made individual leaf loss measures impossible, however, leaf loss estimates were attainable. Leaf loss could later be estimated by multiplying the number of brown leaves present in 1999 by (fallen leaves in 98:number of brown leaves present in 1998).

A question concerning the effect of monitoring culms on culm mortality was raised prior to the 1999 growing season. To examine possible effects on mortality, subsets of 10 culms per species were tagged within an area of 0.0625 m^{-2} at all control plots on April 7, 1999. These plants were left alone until September 9, then monitored to see if the percent mortality of unmonitored culms was significantly different than culms monitored on a monthly basis. On July 7, I began to track the growth of a second cohort of culms over the latter part of the growing season. A total of 32 culms per species were tagged in a 0.0625 m^{-2} area over control plots. These newly tagged culms were all less than 15 cm tall and represented a new cohort of culms. The sample size was small due to a lack of short culms in the given area at this point in the growing season.

Table 7. Example of data recorded on field sheets used in 1999.

Date: May 12, 1999
Site:1c1

Species	Culm Height	Height to 1st leaf	Height to upper leaf	# green leaves	# brown leaves	# Inflorescence /length
S. patens	45.5	5	41.5	3	1	1/ (3cm)
D. spicata	38	6.5	33	8	3	
S. patens	52.5	8	45	4	1	
D. spicata	33	9.5	27	6	2	
S. patens	41	5	37	5	2	
D. spicata	36.5	6.5	41	10	4	
S. patens	45.5	8	33.5	3	1	
D. spicata	38	9.5	45	8	3	
S. patens	52	5	27	4	1	1/ (2cm)
D. spicata	33	6.5	37	6	2	
S. patens	41.5	8	41	5	2	
D. spicata	36	9.5	33	10	4	

3.9. Laboratory methods specific to 1999

For each harvested sample, living and dead culms were separated into piles based on species and color. Twelve culms were haphazardly selected from the pile for growth characteristic measures. These measures for living culms were stem height, height to lower leaf, and height to uppermost leaf, number of green leaves, number of brown leaves, and number and length of inflorescence (Table 8). Measures of culm height were recorded on selected dead culms.

3.10. Estimating Aboveground Net Primary Production

Estimates of ANPP for 1998 and 1999 encompassed data from EOYB harvests and growth characteristic measures. The process began with EOYB biomass and density data harvested in September of each year. Non-destructive measures of growth characteristics such as leaf fall and percent mortality were used to correct EOYB data that did not account for biomass lost during the growing season. The mass estimated to have been lost during each growing season was added to the EOYB harvested within each study plot for the estimate of ANPP. Data were extrapolated to a square meter from the area of the quadrat by multiplying 0.0625 m^{-2} by 16.

ANPP (g m^{-2} yr^{-1}) = EOYB (g m^{-2}) + culm mortality (g m^{-2}) + leaf loss (g m^{-2})

Where: - culm mortality (g m^{-2})= (# that died x mass:density ratio)*16

- # that died= [(density harvested/ %survival of tagged culms)- harvested density]

Table 8. Example of data recorded on lab sheets used in harvest data 1999.

Date: April 1, 1999 Site: 3-1b
Species: Live *S. patens*
Density/Biomass= 212 / 12.56g

Species	Culm Height	Height to 1st leaf	Height to upper leaf	# green leaves	# brown leaves	# Inflorescence/ (length)
S. patens	45	5	45	3	1	
S. patens	38	6.5	27	8	3	
S .patens	52	8	37	4	1	
S. patens	33	9.5	41.5	6	2	
S. patens	45.5	5	41.5	3	1	1/(2.5cm)
S. patens	38	6.5	33	8	3	
S. patens	52.5	8	45	4	1	
S. patens	33	9.5	27	6	2	
S. patens	41	5	37	5	2	
S. patens	36.5	6.5	41	10	4	
S. patens	45.5	8	33.5	3	1	

- mass:density = EOYB (g)/EOYB density
- Leaf loss (g)= [(# of leaves lost per tagged culm*EOYB density) *average mass of fallen leaves (g)]*16

In 1998, 5 ANPP estimates of each species were derived from combining data from control plots at each of the 5 sites. Leaf loss estimates were derived from the monthly tracking of individual leaves of tagged culms. In 1999, 11 ANPP estimates per species were derived from combining data from Control plots at each site (5), Subsurface control plots at each experimental site (3), and Ponded plots at each experimental site (3). Leaf loss estimates in 1999 were derived from [(fallen leaves in 1998:brown leaves in 1998)* number of brown leaves in 1999].

3.11. Estimating biomass turnover

Biomass turnover was calculated for each Control plot by using the following equation: Turnover (yr^{-1}) = ANPP ($g\ m^{-2}\ yr^{-1}$)/ EOYB harvest in September ($g\ m^{-2}$).

3.12. Statistical analyses

All reported statistical analyses were performed with SPSS 9.0. To explain trends in production data, it was necessary to assess site and treatment effects on groundwater depth and salinity. Two Repeated Measures analysis of variance tests (ANOVA) were performed to analyze differences in ground water between sites and treatments, and salinity differences between sites and treatments. Each test was performed on data collected from each plot at monthly intervals during the growing season. If data were recorded more than once each month, (e.g. consecutive days), the averages of the data were used to represent the monthly record. Each test had 1 within subject factor with 7 levels representing each month from March to September.

To analyze differences of groundwater depth and salinity by site, only control data were used. Repeated measures analysis for site was performed on 2 sets of data; (1) the combined depth to ground water recorded in 1998 and 1999, and (2) salinity data in 1998 and 1999 from all control sites. To analyze treatment effects on groundwater depth and salinity, two data sets were used after control sites 1 and 3 were excluded. Repeated measures analysis was performed on (1) combined data from 1998 and 1999 depth to groundwater, and (2) combined salinity data from 1998 and 1999.

The 5 sites were classified apriori into 3 zones (Creek, Non-hummock, and Hummock) to assess different stages of high marsh transition. These groupings were based on similarities in micro-topography, community structure, and position relative to the headward eroding creek. To determine if this decision was justifiable, I combined 1998 and 1999 depth to ground water data from each plot and performed a K-means cluster analysis requesting the 5 sites be classified into 3 similar groups. Other variables such as salinity, culm height, and mortality were initially included in the analysis but clear clusters were not found.

Ten 1-way ANOVAs were performed on growth characteristics using density, production per culm, ANPP, and turnover as dependent variables. The first 4 ANOVAs were performed separately on 1998 and 1999 control data for each species. These analyses used zone as the fixed factor and density, production per culm, ANPP, and turnover as dependent variables. Four ANOVAs were performed on 1999 data for each species at separate zones (Hummock and Non-hummock) and used treatment as the fixed factor and density, production per culm, ANPP, and turnover as dependent variables. The final 2 ANOVAs were performed on each species using combined data from 1998 and 1999 to examine interannual variation in growth characteristics. These analyses used year as the fixed factor, and density, production per culm, ANPP, and turnover as dependent variables. The LSD post hoc method was used to test for differences among factor levels and the experimental error rate for comparisons was set at 0.05.

A Chi square analysis (cross tabulations) was used to test for significance in mortality between retrieved unmonitored culms and monitored culms in control plots. Rows were designated monitored (yes/no) and columns were designated number of culms (live/dead).

A linear regression was performed on mass lost in leaves and mass lost in culm mortality in 1998. These results were used to test the assumption that the two were positively related, and could therefore be used to assess leaf loss based on culm mortality in 1999.

4. RESULTS

4.1. Groundwater depth, groundwater salinity, monthly precipitation, and creek salinity at times of pumping during 1998 and 1999.

Groundwater depth, groundwater salinity, monthly precipitation, and creek salinities at times of pumping during 1998 and 1999 are presented to give insight to differences in abiotic factors between sites that may affect ANPP (Figures 9-13, Appendices 3 and 4). Groundwater depth and salinity, and precipitation appear to vary with year. Sites in 1999 experienced the lowest levels of ground water, highest ground water salinities, and less precipitation at an earlier time in the growing season (June) than in 1998 (August) (Figures 9 - 10). Box and whisker plots are used to express many of the results and trends in this study. The line inside the box represents the median number of the data while the box itself represents the interquartiles where 50% of the data fall. The whiskers that extend from the box represent extreme data points barring outliers.

The depth to ground water was significantly different (p=0.001) among sites (Table 9). LSD’s post hoc test revealed a trend where sites 5 and 3 contained the highest groundwater, while site 1 contained the lowest groundwater during the study. Salinity was also found to be significantly different (p=0.006) between sites (Table 10). LSD's post hoc test revealed a trend where sites 4 and 5 contained the highest groundwater salinities, while site 1 had the lowest salinity during the study.

Descriptive statistics of ground water depth and salinity by experimental treatment are listed in Appendix 4 and depicted in Figures 11-12. Data were

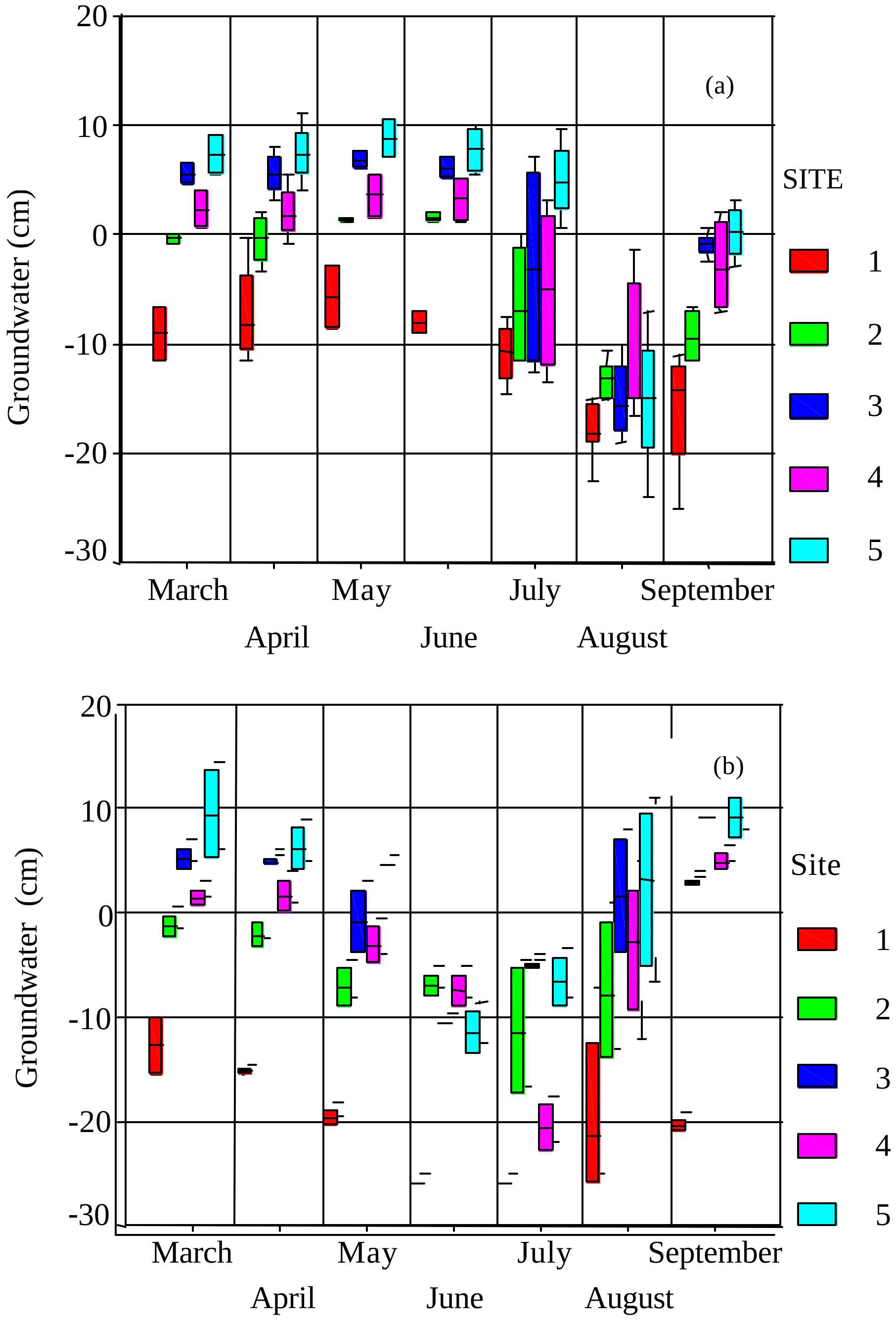


Figure 9. Groundwater depth at each site during growing season (a) in 1998 and (b) in 1999. The line inside the box represents the median number of the data while the box itself represents the interquartiles where 50% of the data fall. The whiskers that extend from the box represent extreme data points barring outliers.

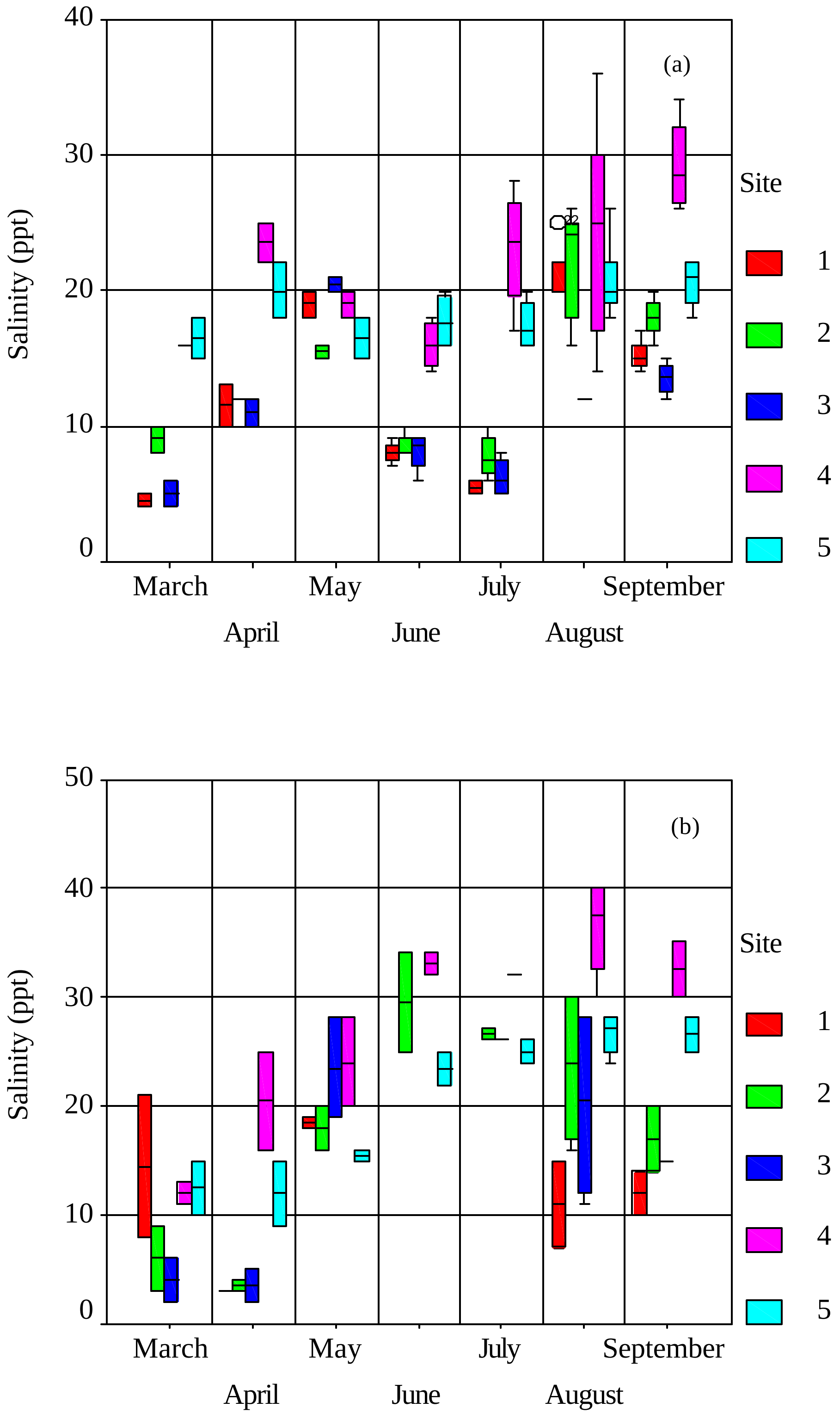


Figure 10. Groundwater salinity by site in during growing season (a) 1998 and (b) 1999.

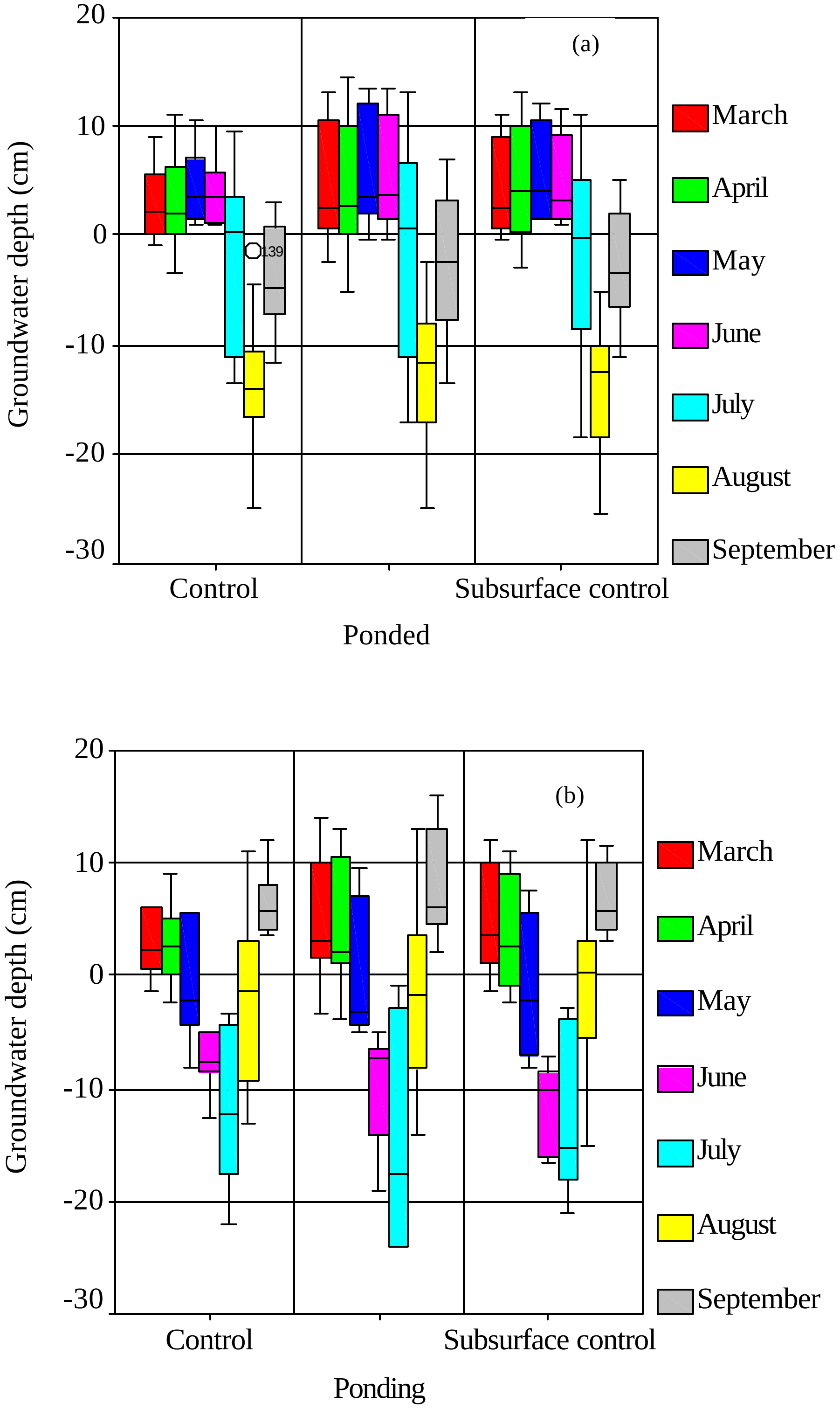


Figure 11. Groundwater depth of treatment in during growing season (a) 1998 and (b) 1999.

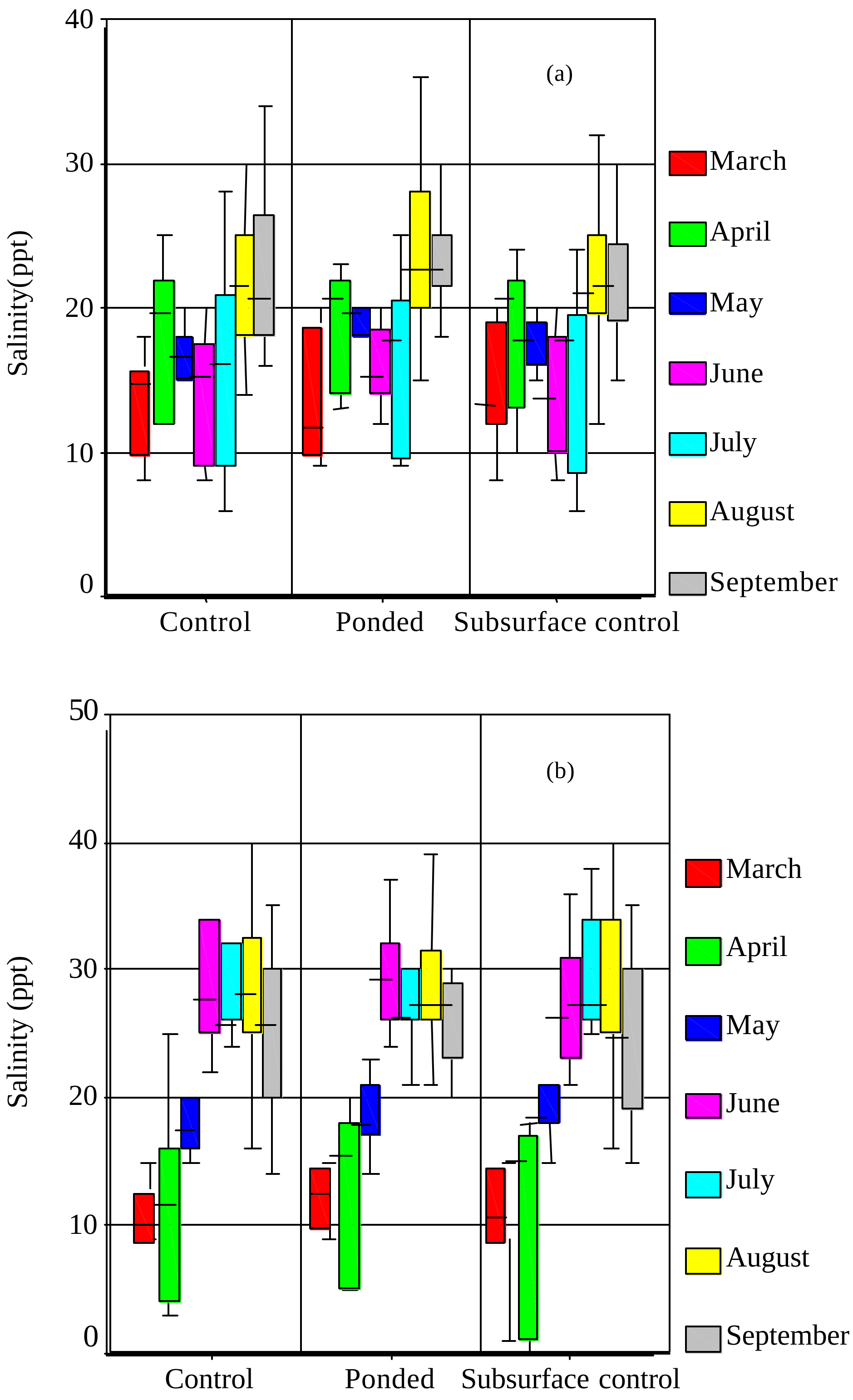


Figure 12. Groundwater salinity by treatment in (a) 1998 and (b) 1999.

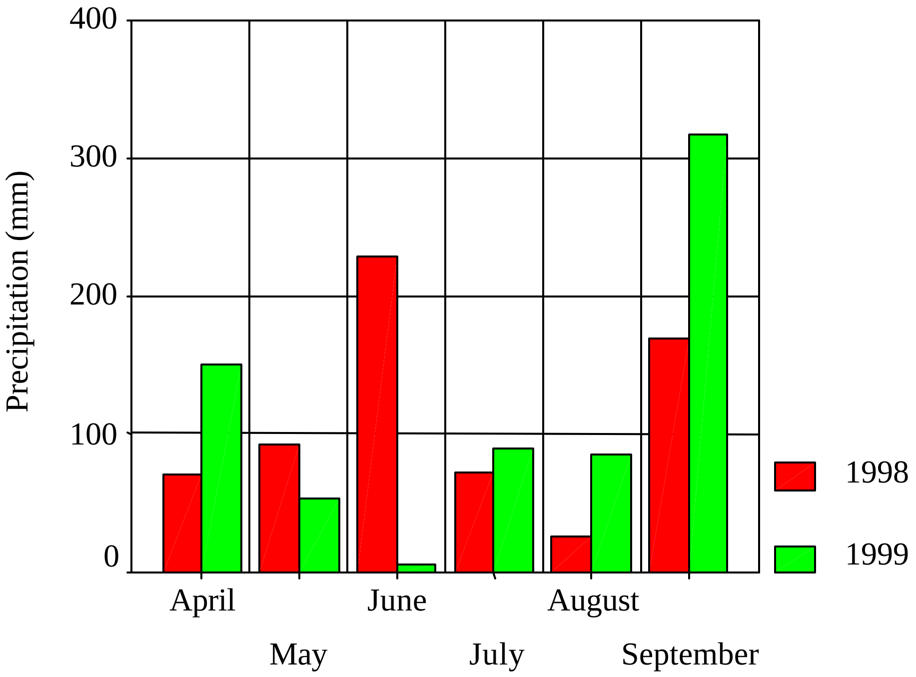


Figure 13. Precipitation during the growing season (1998-1999).

Table 9. Repeated measures analysis of groundwater 1998-1999.

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	1619.53	1	1619.53	45.40	0.001
SITE	5385.44	4	1346.36	37.74	0.001
Error	178.34	5	35.66		

Multiple Comparisons
LSD

(I) SITE	(J) SITE	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
1	2	-10.73	1.59	0.001	-14.84	-6.63
	3	-15.90	1.59	0.000	-20.00	-11.79
	4	-12.72	1.59	0.001	-16.83	-8.62
	5	-17.71	1.59	0.000	-21.82	-13.61
2	1	10.73	1.59	0.001	6.63	14.84
	3	-5.16	1.59	0.023	-9.26	-1.06
	4	-1.99	1.59	0.267	-6.09	2.11
	5	-6.97	1.59	0.007	-11.08	-2.87
3	1	15.90	1.59	0.000	11.79	20.00
	2	5.16	1.59	0.023	1.06	9.26
	4	3.17	1.59	0.104	-0.93	7.27
	5	-1.81	1.59	0.307	-5.91	2.28
4	1	12.72	1.59	0.001	8.62	16.83
	2	1.99	1.59	0.267	-2.11	6.09
	3	-3.17	1.59	0.104	-7.27	0.93
	5	-4.98	1.59	0.026	-9.09	-0.88
5	1	17.71	1.59	0.000	13.61	21.82
	2	6.97	1.59	0.007	2.87	11.08
	3	1.81	1.59	0.307	-2.28	5.91
	4	4.98	1.59	0.026	.88	9.09

* The mean difference is significant at the .05 level.

Table 10. Repeated measures analysis of salinity over sites (1998-99).

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	42357.40	1	42357.40	1130.27	0.000
SITE	2179.05	4	544.76	14.53	0.006
Error	187.37	5	37.47		

Multiple Comparisons
LSD

		Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
(I) SITE	(J) SITE				Lower Bound	Upper Bound
1	2	-1.75	1.63	0.332	-5.96	2.44
	3	-.42	1.63	0.806	-4.62	3.78
	4	-10.47	1.63	0.001	-14.68	-6.27
	5	-5.62	1.63	0.018	-9.83	-1.41
2	1	1.75	1.63	0.332	-2.44	5.96
	3	1.33	1.63	0.452	-2.87	5.53
	4	-8.72	1.63	0.003	-12.92	-4.51
	5	-3.86	1.63	0.064	-8.07	0.33
3	1	.42	1.63	0.806	-3.78	4.62
	2	-1.33	1.63	0.452	-5.53	2.87
	4	-10.05	1.63	0.002	-14.25	-5.84
	5	-5.20	1.63	0.025	-9.40	-0.99
4	1	10.47	1.63	0.001	6.27	14.68
	2	8.72	1.63	0.003	4.51	12.92
	3	10.05	1.63	0.002	5.84	14.25
	5	4.85	1.63	0.031	0.64	9.05
5	1	5.62	1.63	0.018	1.41	9.83
	2	3.86	1.63	0.064	-0.33	8.07
	3	5.20	1.63	0.025	099	9.40
	4	-4.85	1.63	0.031	-9.05	-0.64

* The mean difference is significant at the .05 level.

recorded just prior to pumping because I expected the groundwater depth, and perhaps groundwater salinity to be affected by pumping on the days immediately following pumping events. This way, if significance were found, I could argue that every opportunity was allowed for these measures to return to normal before sampling. Although the salinity of Phillips Creek during each pumping event was higher in 1999 than in 1998 (Figure 14), no trends in the effect of treatment on groundwater depth or salinity were discernible either year. The depth to groundwater was not significantly different (p=0.969) between treatments during the study (Table 11). Salinity was not significantly different (p=0.842) among treatments during the study (Table 12).

Cluster analysis of individual plots was performed to support having previously grouped the 5 sites into 3 zones. Plots from each site separated perfectly into the 3 predicted zones (Table 13, Figure 15). Site 1, (Creek zone) stood as its own cluster, and its cluster center was the farthest distance from sites 2 and 4 (Non-hummock zone) (Table 13). Sites 3 and 5 were grouped into the final cluster (Hummock zone).

4.2. Aboveground growth of *D. spicata* and *S. patens*

A key focus of the present study was to assess growth of *D. spicata* and *S. patens* during the growing season. Results here do not necessarily reflect statistical rigor, but rather give a brief overview and highlight any apparent trends for a representative culm of each species. Due to a majority of similarities in trends found in 1998 and 1999, the data set recorded in 1999 was chosen for the present description. Measures of growth characteristics were recorded monthly and included (1) culm height, (2) height from base

Table 11. Repeated measures analysis of groundwater at treatments (1999-98).

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	131.92	1	131.92	0.39	0.539
Treatment	21.36	2	10.68	0.03	0.969
Error	5013.41	15	334.22		

Multiple Comparisons
LSD

(I) Treatment	(J) Treatment	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	Upper Bound
Control	Ponding	-0.71	2.82	0.804	-6.72	5.30
	Subsurface control	-0.38	2.82	0.892	-6.40	5.62
Ponding	Control	0.71	2.82	0.804	-5.30	6.72
	Subsurface control	0.32	2.82	0.910	-5.68	6.33
Subsurface control	Control	0.38	2.82	0.892	-5.62	6.40
	Ponding	-0.32	2.82	0.910	-6.33	5.68

Table 12. Repeated measures analysis of salinity at treatments (1998-99).

Tests of Between-Subjects Effects

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	99782.58	1	99782.58	577.14	0.000
Treatment	60.13	2	30.06	0.17	0.842
Error	2593.34	15	172.89		

Multiple Comparisons
LSD

(I) Treatment	(J) Treatment	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
Control	Ponding	-0.88	2.02	0.670	-5.20	3.44
	Subsurface control	0.25	2.02	0.901	-4.06	4.58
Ponding	Control	0.88	2.02	0.670	-3.44	5.20
	Subsurface control	1.14	2.02	0.582	-3.18	5.46
Subsurface control	Control	-0.25	2.02	0.901	-4.58	4.06
	Ponding	-1.14	2.02	0.582	-5.46	3.18

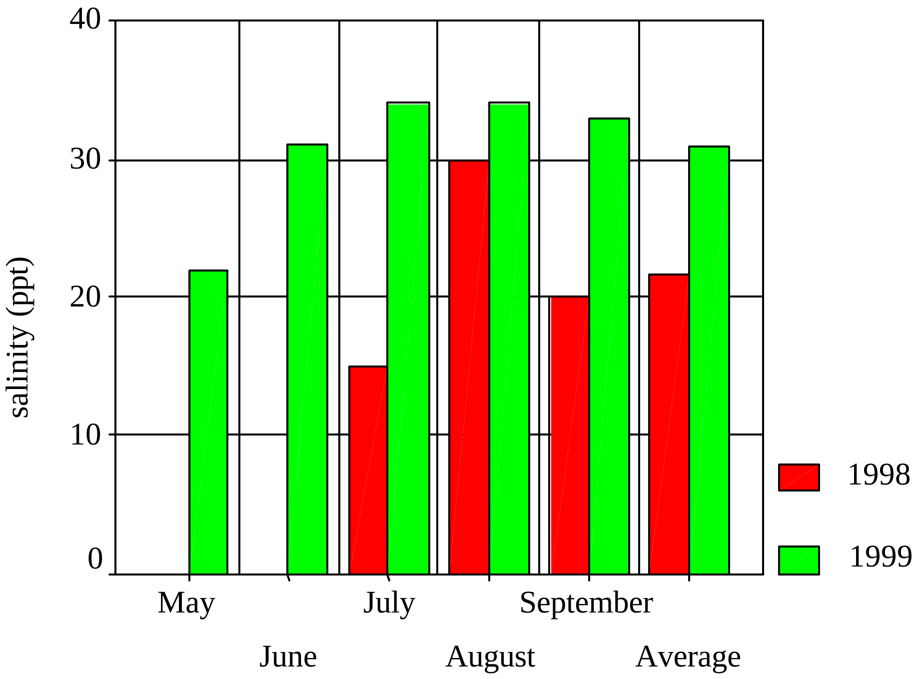


Figure 14. Salinity of creek water at times of pumping (1998-1999).

Table 13. Cluster memberships of site based on groundwater depth.

Cluster Membership

Case Number	Site	Cluster	Distance
1	1	1	7.16
2	1	1	7.16
3	2	2	5.61
4	2	2	13.74
5	3	3	3.38
6	3	3	9.18
7	4	2	15.34
8	4	2	4.02
9	5	3	11.88
10	5	3	6.93

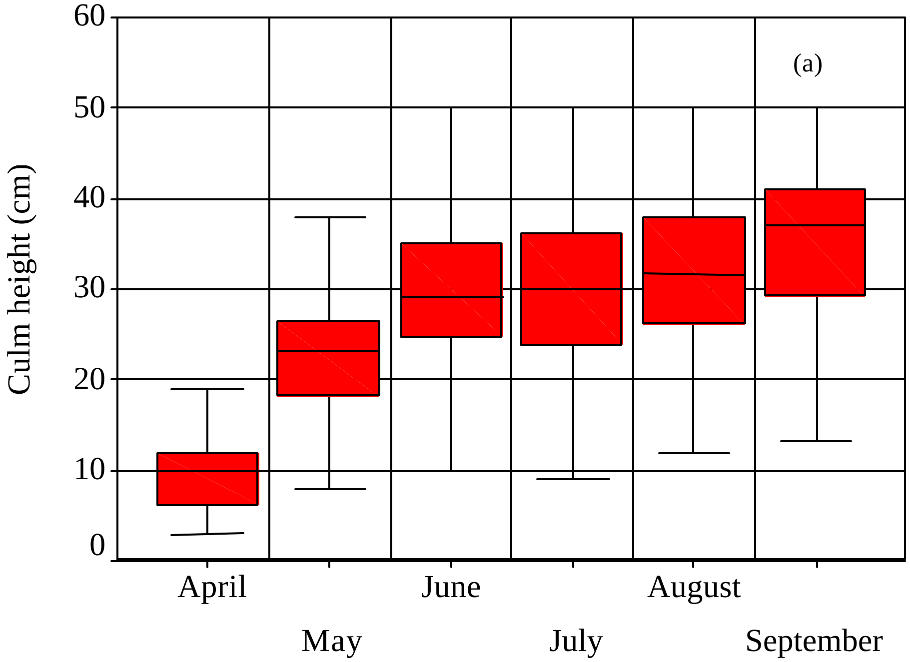
Figure 15. Cluster memberships of each site based on 1998 and 1999 groundwater depth.

of culm to first leaf, (3) height from base of culm to uppermost leaf, (4) number of green leaves, and (5) number of leaves lost per month. Data were analyzed after control plots were combined by site and species (Appendix 5). Density and biomass were also recorded from monthly harvest data at each site (Appendix 6). During this study, some leaf measures were not recorded until May and June due to the scale-like nature of the short leaves and a lack of brown leaves present on young culms.

4.2.1. *D. spicata* growth

D. spicata shows a trend of rapid increases in height, mass, and density from the beginning of the growing season until June (Figure 16a-c). These attributes plateau throughout the remainder of the growing season. The height from culm base to uppermost leaf was measured from June and shows a more steady increase from June to September (Figure 16d). The number of brown leaves per culm and the estimated number of leaves lost per culm also gradually increased from June through August, and then increased considerably from August to September (Figures 16f-g). Mass appears to peak by June and decline slightly throughout the remainder of the growing seasons. However, density peaks by June but shows no obvious decline until September (Figure 17 b-c, Appendix 6).

By August the average culm of *D. spicata* was 32.0 cm tall ± a standard deviation of 8.4 cm, had 7.2 ± 2.6 green leaves, and had 3.4 ± 1.9 brown leaves. In September, the average culm was 35.4 ± 9.4 cm tall, had 5.7 ± 3.1 green leaves, and 6.6 ± 3.3 brown leaves (Appendix 5).



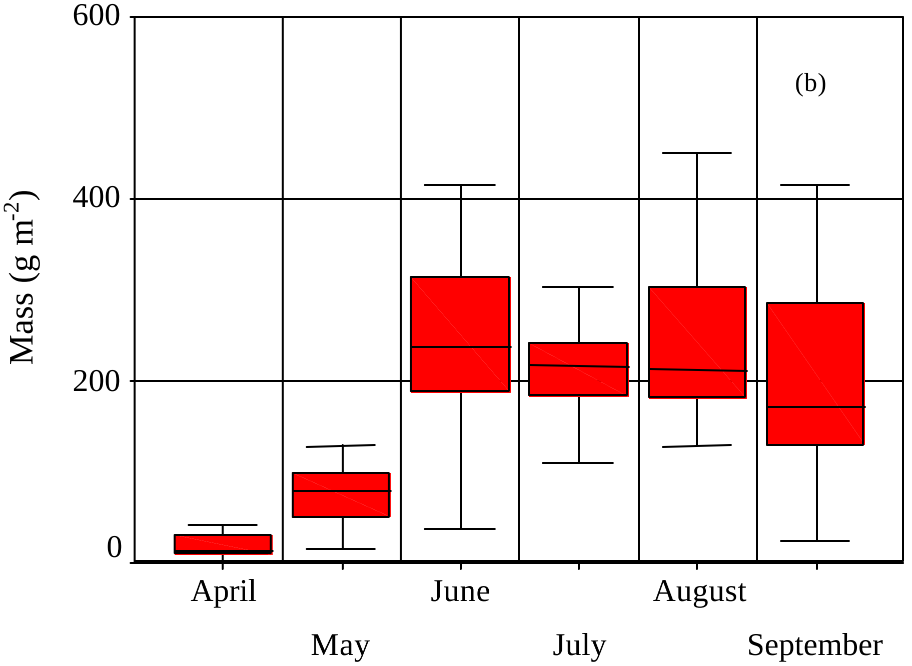
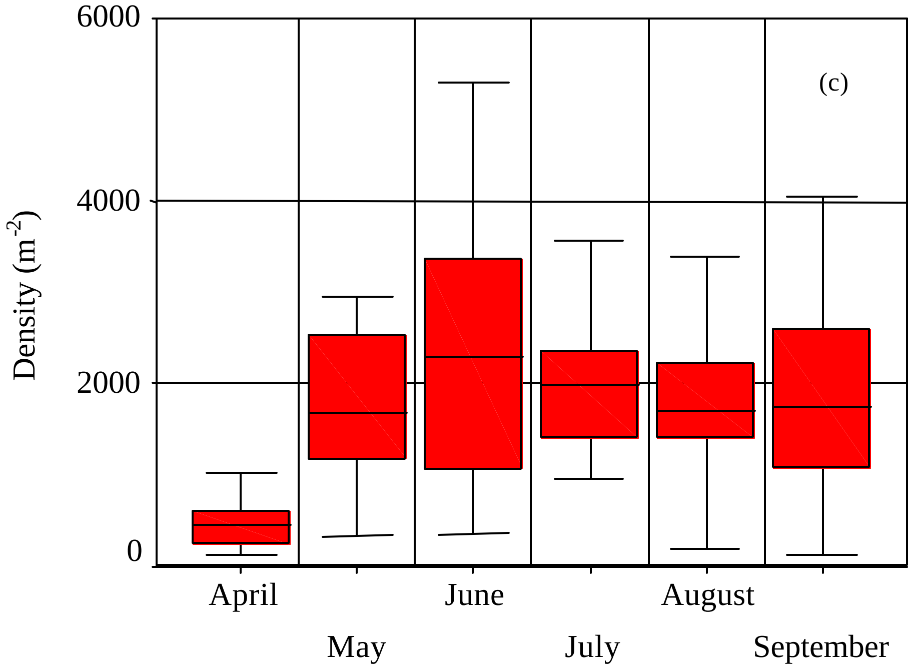
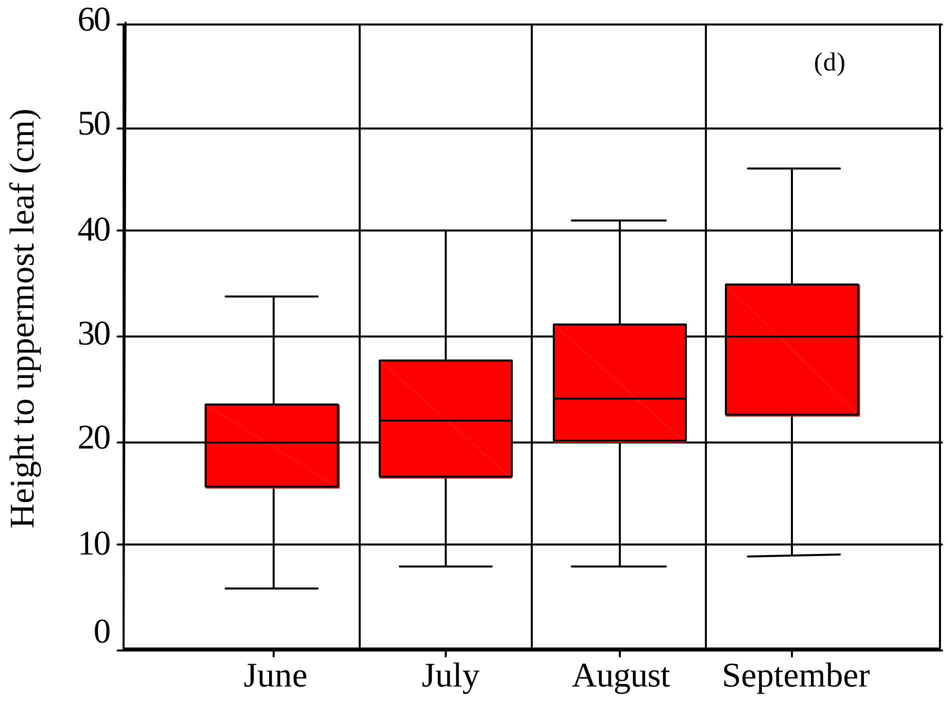


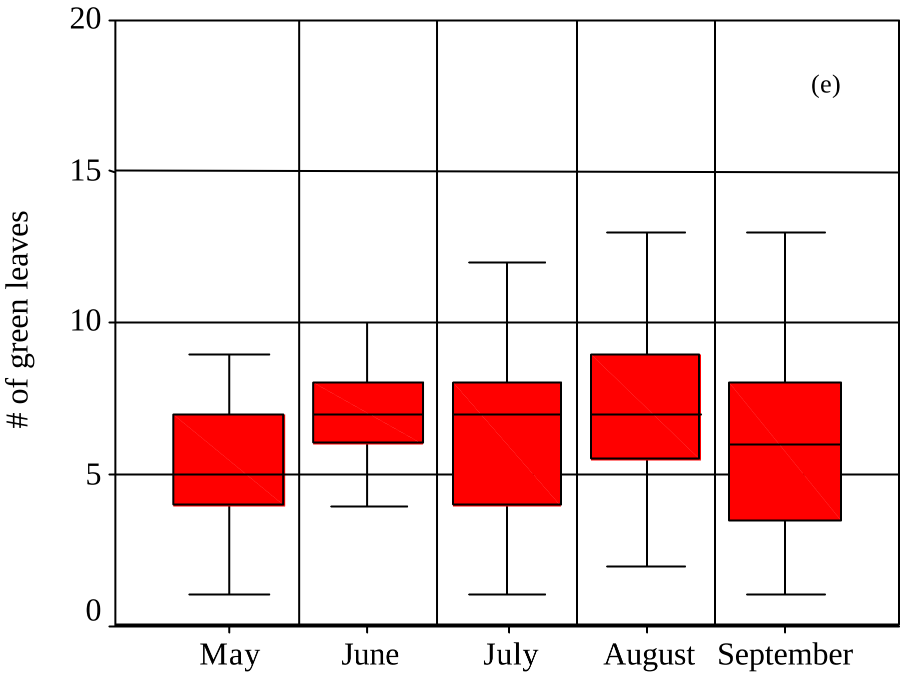
Figure 16. Characteristics of *D. spicata* in 1999 (a) Culm height, (b) harvested living mass, (c) harvested density, (d) height to uppermost leaf, (e) number of green leaves, (f) number of brown leaves and (g) leaf loss per culm.



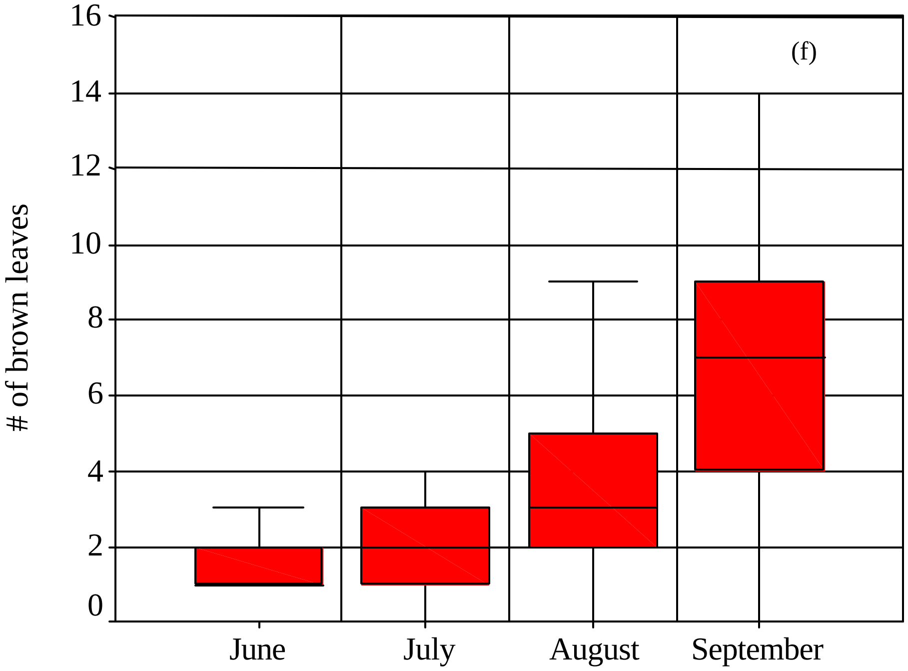
6000
4000
2000
0
Density (m^{-2})
(c)
April
May
June
July
August
September



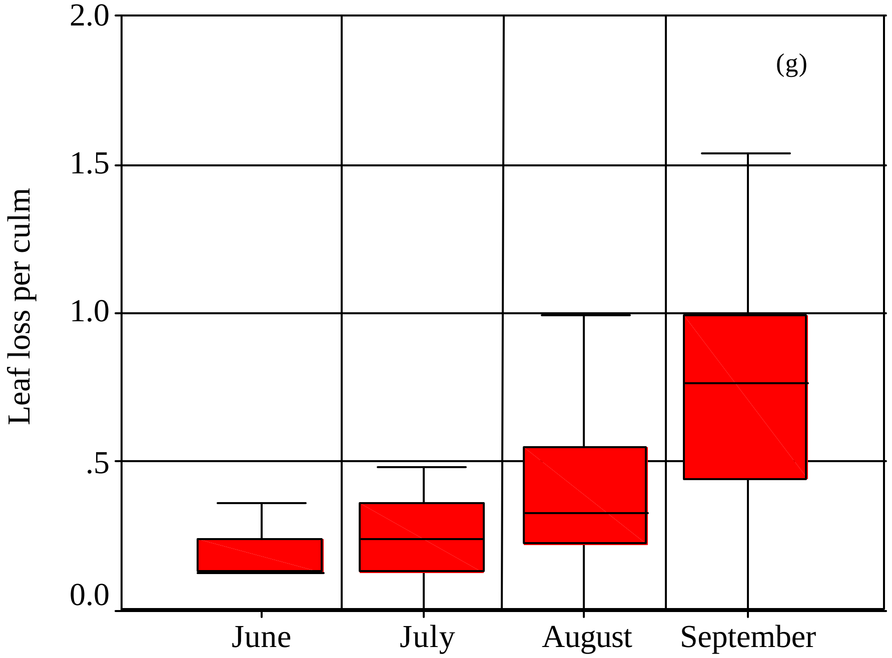
60
50
40
30
20
10
0
Height to uppermost leaf (cm)
(d)
June
July
August
September



(e)
# of green leaves
20
15
10
5
0
May
June
July
August
September



(f)
# of brown leaves
16
14
12
10
8
6
4
2
0
June
July
August
September



(g)
Leaf loss per culm
2.0
1.5
1.0
.5
0.0
June
July
August
September

4.2.2. *S. patens* growth

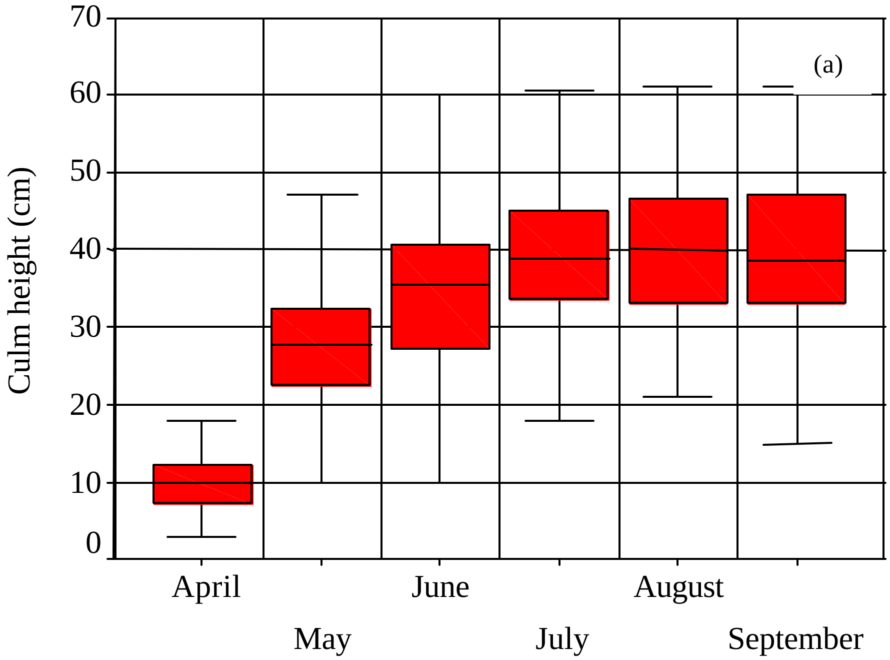
S. patens showed a trend of rapid increase in culm height from April through June, but growth slowed from June to July. Maximum culm height appeared to be reached by July and remained the same through September (Figure 17a). The number of green leaves per culm remained the same from May to July and showed a decrease towards the end of the season (Figure 17b) as the number of brown leaves per culm and estimated leaves lost per culm increased (Figures 17c-d). Mass and density of *S. patens* appeared to peak between July and August (Figures 17 e-f, Appendix 6).

By August the average culm of *S. patens* was 40.7 ± 9.3 (SD) cm tall, had 3.4 ± 4.3 green leaves, and had 2.0 ± 1.0 brown leaves. In September, the average culm was 38.9 ± 11.6 cm tall, had 2.7 ± 1.2 green leaves, and 2.9 ± 1.3 brown leaves (Appendix 5).

4.2.3. Mortality trends of the growing season

The monthly percent mortality of tagged culms in control plots shows a trend where mortality increased slightly by August and increased greatly by September in both species (Figure 18 a-b). It should be noted that although the trends were similar, the degree of mortality for each species differed. *D. spicata* had 20% and 35% culms die between August and September of 1998 and 1999, respectively; whereas *S. patens* had only 21% and 15% culms experience mortality in 1998 and 1999 (Figures 18 a-b).

Chi square analysis revealed a trend toward a negative effect (p=0.072) on mortality of monitored culms of *D. spicata* (Table 14). There was also no significant positive effect (p=0.194) on mortality by monitoring culms of *S. patens* (Table 15).



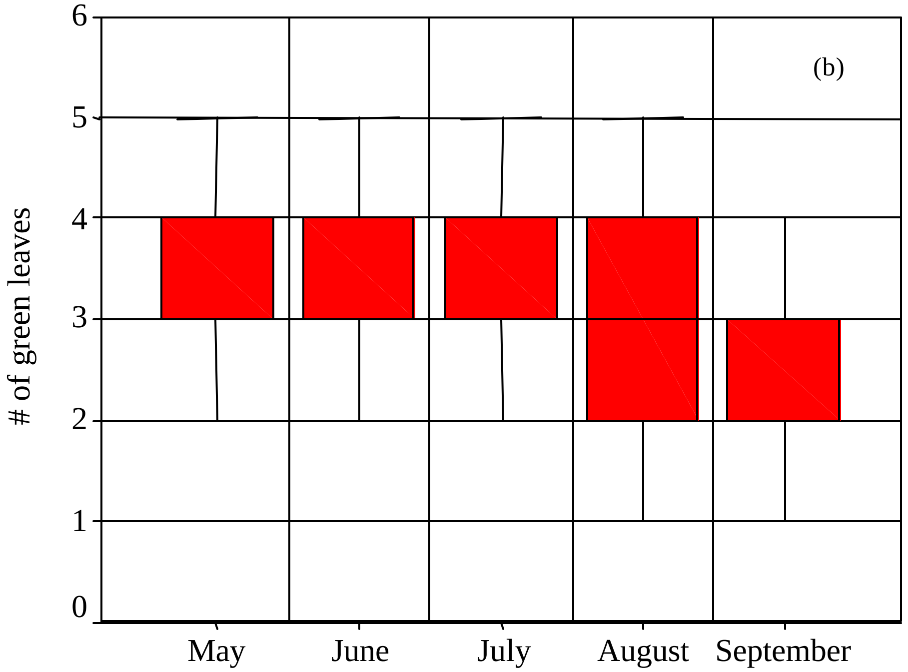
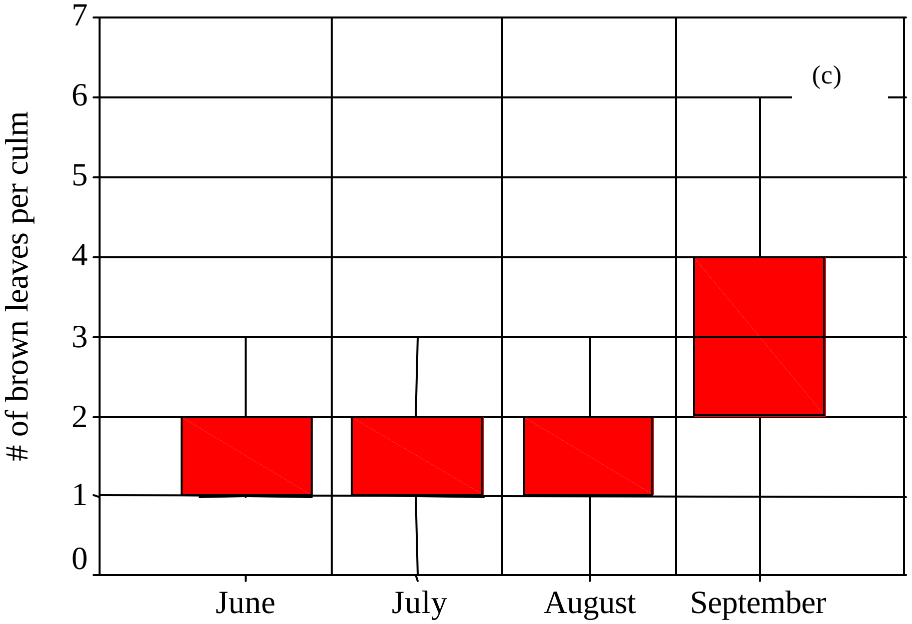
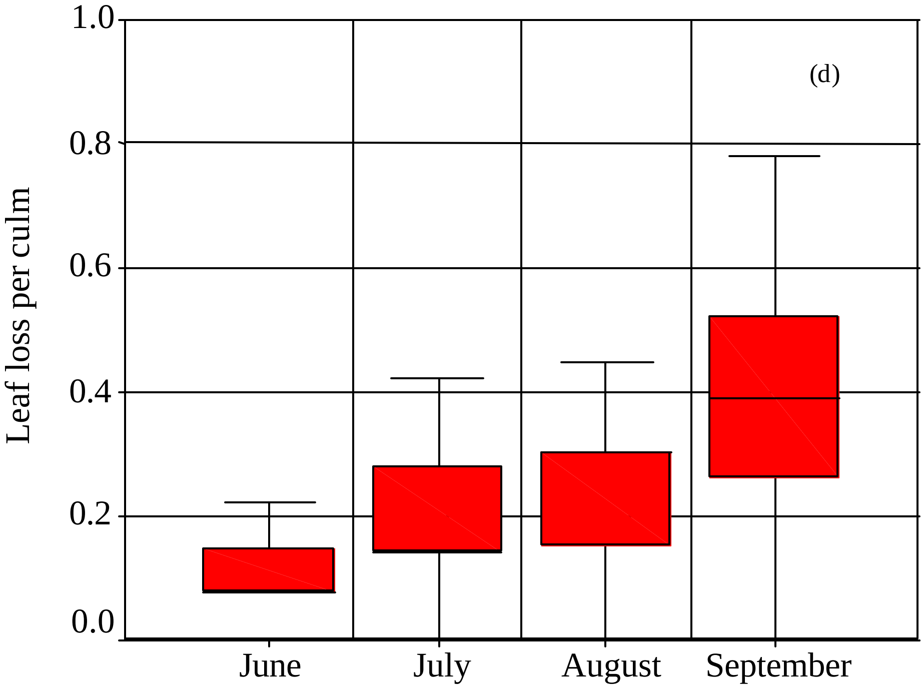
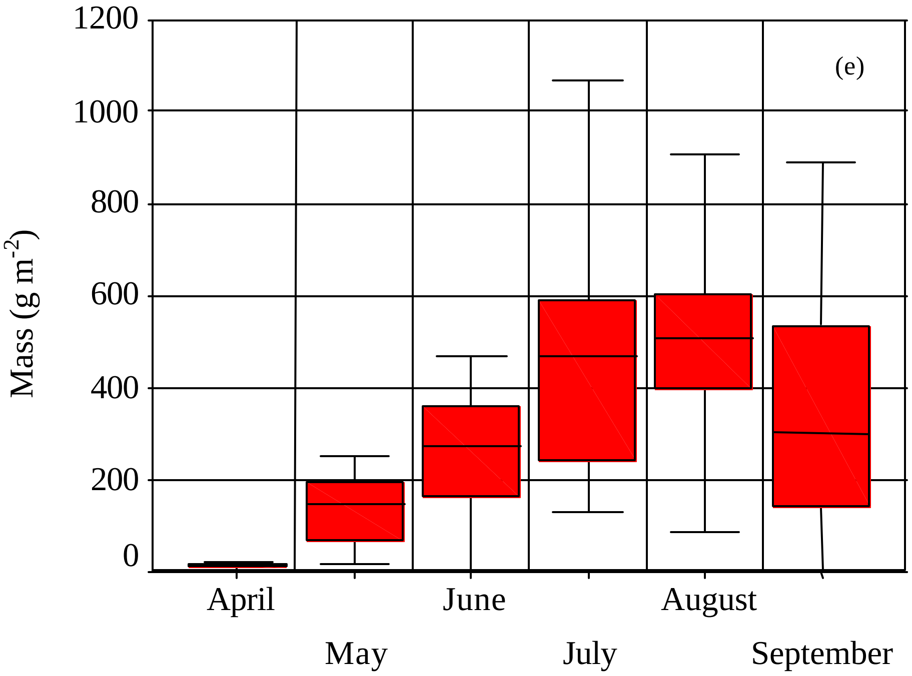


Figure 17. Characteristics of *S. patens* in 1999 (a) culm height, (b) number of green leaves, (c) number of brown leaves, (d) leaf loss per culm, (e) harvested mass, and (f) harvested density of living culms


(c)
# of brown leaves per culm
0
1
2
3
4
5
6
7
June
July
August
September


(d)
Leaf loss per culm
0.0
0.2
0.4
0.6
0.8
1.0
June
July
August
September



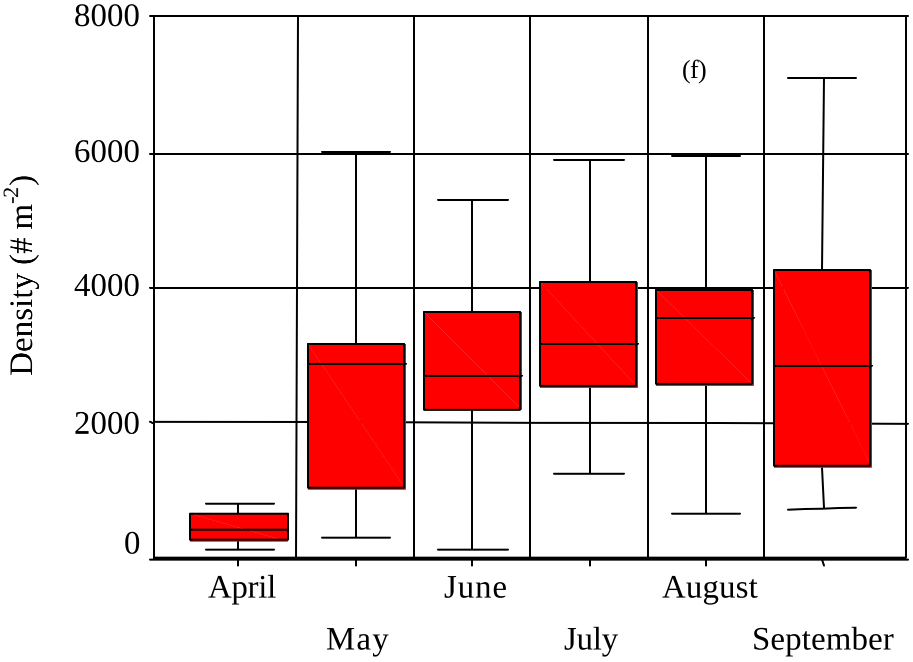
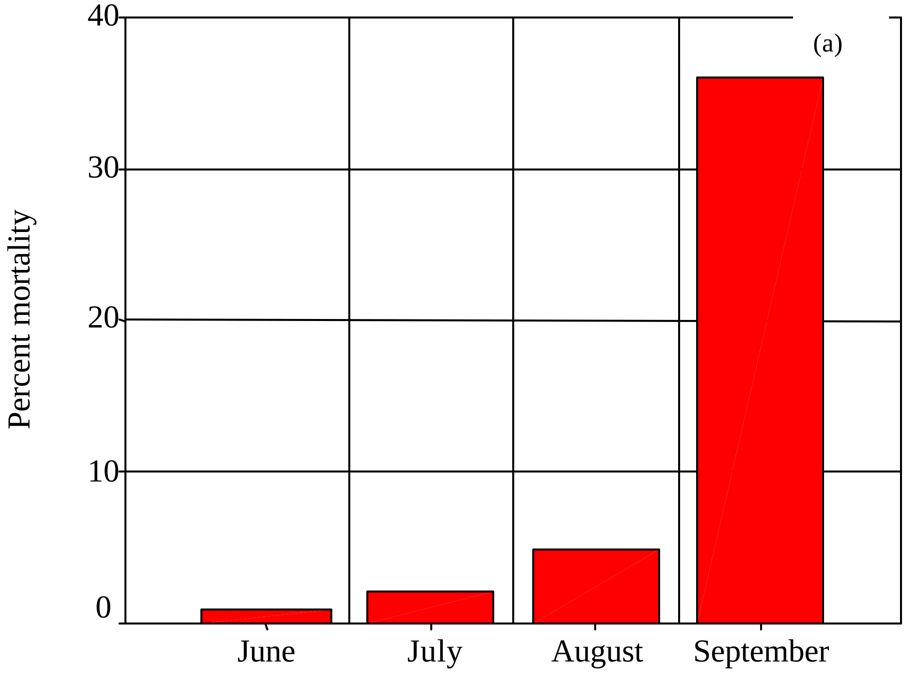


Figure 17. (e) Harvested mass and (f) density of living *S. patens.*



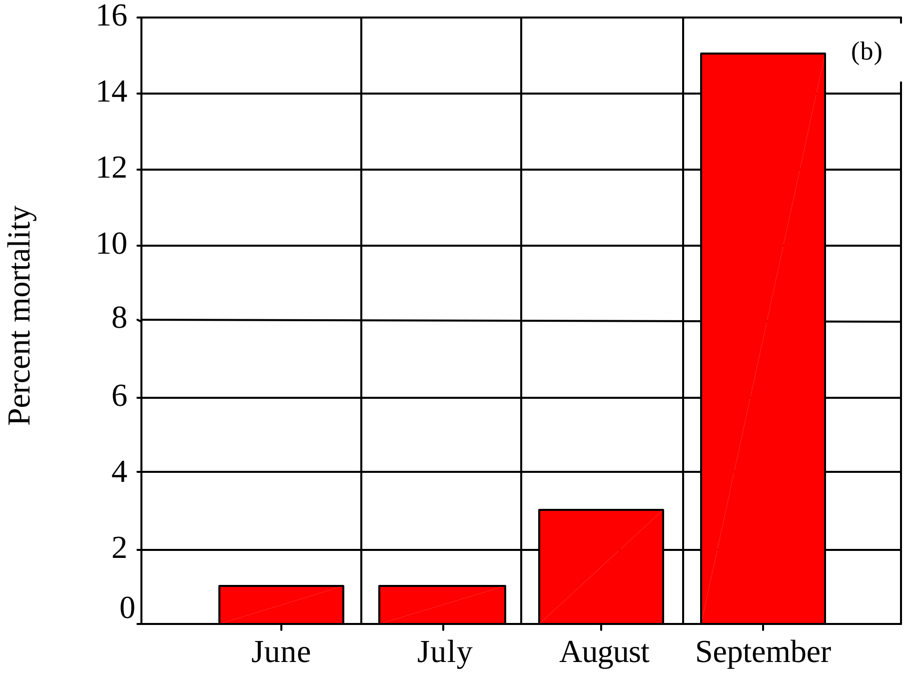


Figure 18. Percent mortality of tagged culms of (a) *D. spicata* and (b) *S. patens.*

4.3. Method of ANPP in 1998 and 1999

Another goal of the study was to describe the method of estimating ANPP, its components, and variations associated with its components. Components of the estimate of ANPP included EOYB harvests, mass of leaf loss, and mass lost to culm mortality (Appendix 7). Components of dead material at EOYB harvesting were also examined and included the amount of material left over from previous years, the amount of new dead material from culm mortality, and amount of new material from loss of leaves (Appendix 8).

The ability of EOYB to represent ANPP varied between sites and years for each species. Variability was a result of changes in culm mortality and leaf loss, of which leaf loss was found to be a minor contributor. EOYB best represented ANPP of *D. spicata* at site 2 (80%), but least represented it at site 3 (69%) in 1998 (Figure 19a). EOYB best represented *S. patens* ANPP at site 2 (80 ± 0%) but was least accurate at site 5 (64 ± 1%) in 1998 (Figure 19b). EOYB best represented ANPP of *D. spicata* at site 2 (61 ± 2%), and was least accurate at site 5 (45 ± 1%) in 1999 (Figure 20a). EOYB best represented *S. patens* ANPP at site 2 (83 ± 2%), and was least accurate at site 5 (58 ± 2%) in 1999 (Figure 20b, Table 16).

The average EOYB of *D. spicata* accounted for 74 ± 5% of estimated ANPP in 1998, but in 1999 the average EOYB accounted for only 54 ± 6%. Due to a higher percentage of *D. spicata* mortality in 1999, the average contribution to ANPP by mass lost to culm mortality increased by 20% to 46% from 1998 to 1999 (Table 17). The average EOYB of *S. patens* accounted for 72 + 6% of the estimated ANPP in 1998, and

Table 14. Chi square mortality testing for significance of monitoring on mortality of ***D. spicata.***

MONITORED * DEAD Crosstabulation
Count

		Live	Dead	Total
	Unonitored	70	17	87
	Monitored	108	44	152
Total		178	61	239

D. spicata

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	2.57	1	0.109		
Continuity Correction	2.10	1	0.147		
Likelihood Ratio	2.64	1	0.104		
Fisher's Exact Test				0.124	0.072
N of Valid Cases	239				

Table 15. Chi square mortality testing for significance of monitoring on mortality of *S. patens*.

MONITORED * DEAD Crosstabulation
Count

		Live	Dead	Total
	Unmonitored	69	15	84
	Monitored	105	15	120
Total		174	30	204

a *S. patens*

Chi-Square Tests

	Value	df	Asymp. Sig. (2-sided)	Exact Sig. (2-sided)	Exact Sig. (1-sided)
Pearson Chi-Square	1.13	1	0.288		
Continuity Correction	0.74	1	0.388		
Likelihood Ratio	1.11	1	0.291		
Fisher's Exact Test				0.319	0.194
N of Valid Cases	204				

S. patens

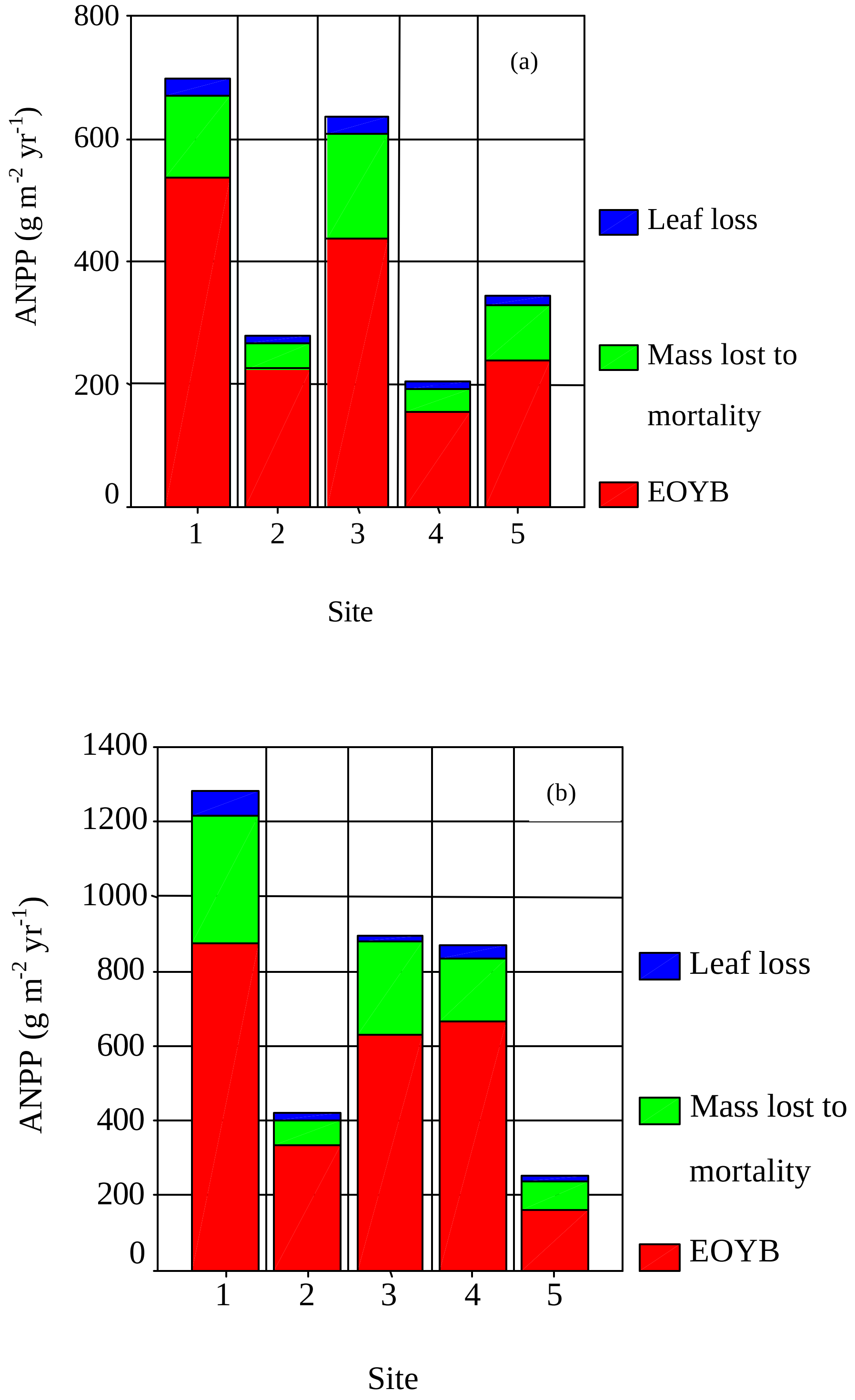


Figure 19. 1998 components of aboveground net primary production (ANPP) of (a) *D. spicata* and (b) *S. patens*. EOYB=end of year biomass harvest.

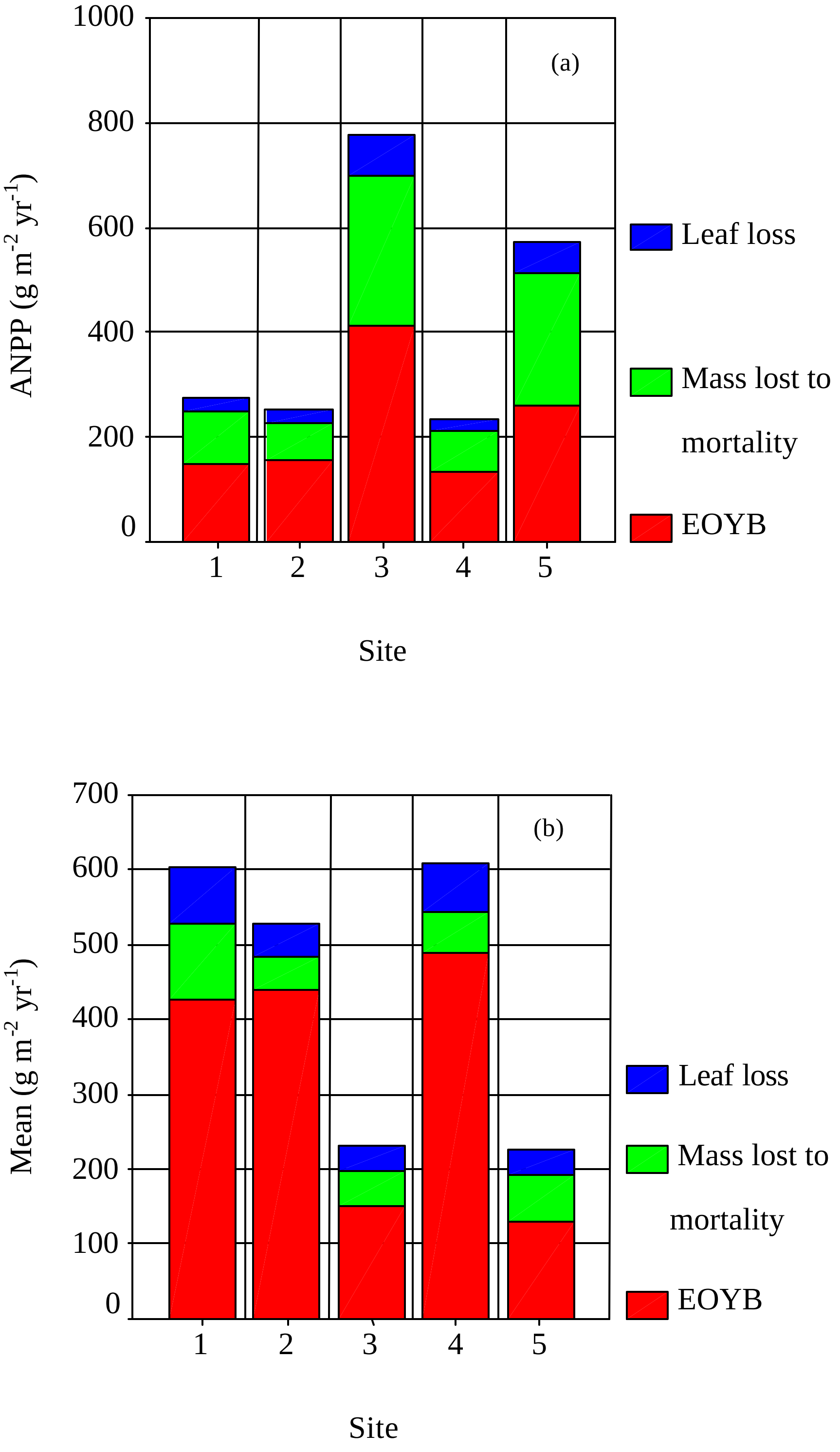


Figure 20. 1999 Components of (a) *D. spicata* ANPP and (b) *S. patens* ANPP.

Table 16. Percentages of components of ANPP by site in 1998 and 1999.

				YEAR			
				1998		1999	
				Mean	Std Deviation	Mean	Std Deviation
D. spicata	SITE	1	EOYB	77	0	53	3
			Mass lost to mortality	19	0	36	2
			Leaf loss	4	0	11	5
		2	EOYB	80	1	61	2
			Mass lost to mortality	15	0	30	1
			Leaf loss	5	1	8	2
		3	EOYB	69	0	53	1
			Mass lost to mortality	27	0	37	1
			Leaf loss	4	1	10	2
		4	EOYB	76	1	56	1
			Mass lost to mortality	19	0	34	1
			Leaf loss	5	1	10	2
		5	EOYB	69	0	45	1
			Mass lost to mortality	27	0	45	1
			Leaf loss	4	0	10	1
S. patens	SITE	1	EOYB	68	1	70	2
			Mass lost to mortality	27	0	17	1
			Leaf loss	5	1	13	3
		2	EOYB	80	0	83	2
			Mass lost to mortality	15	0	9	0
			Leaf loss	4	1	9	2
		3	EOYB	70	1	64	4

Table 16, continued

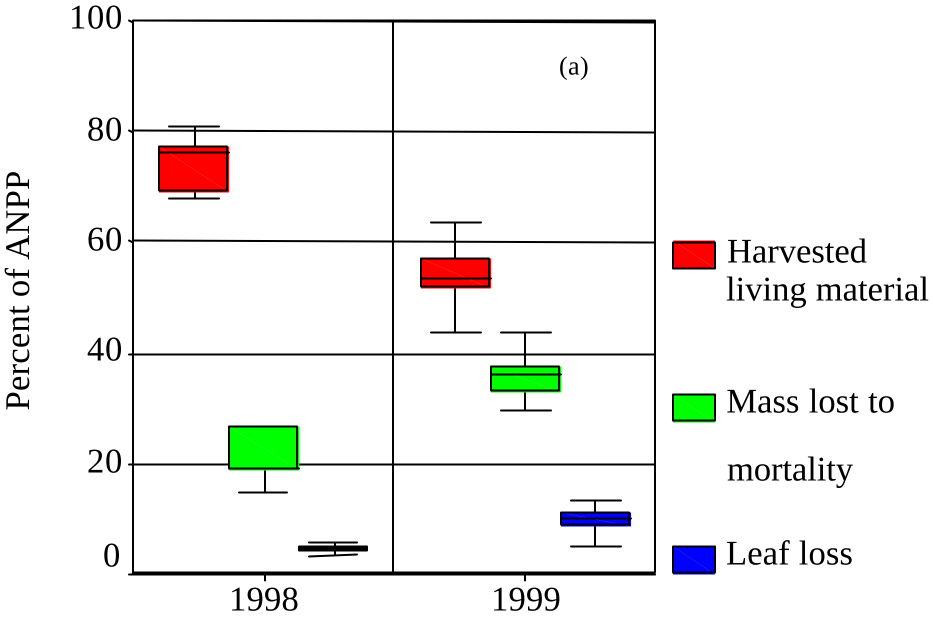
			1998		1999	
			Mean	Std Deviation	Mean	Std Deviation
S. patens		Mass lost to mortality	27	0	20	1
		Leaf loss	3	1	15	5
	4	EOYB	76	1	80	2
		Mass lost to mortality	19	0	9	0
		Leaf loss	5	1	11	2
	5	EOYB	64	1	58	2
		Mass lost to mortality	30	0	27	1
		Leaf loss	6	1	16	2

accounted for 70 ± 13 % if the estimated ANPP in 1999 (Table 17).

Regression analysis showed that the mass lost in leaves in 1998 was significantly correlated with the mass lost to culm mortality in *D. spicata* (R^2 0.90, p=0.000) where mass of lost leaves in grams (y) is 3.16 +.163*mass of culm mortality (g), and *S. patens* (R^2 = 0.93, p=0.000) where mass of lost leaves in grams (y) is 3.384 + .171*mass of culm mortality (g) (Figures 21 c-d).

There is a difference between total and green biomass harvested. Components of dead material were analyzed to assess the amount of material that can be left over from a previous growing season. Dead biomass of *D. spicata* left over from the previous years also varied between sites and years for each species due to differences in mortality and leaf loss (Appendix 9). Percentage of dead biomass of *D. spicata* from previous years was highest at site 4 at (84 ± 4%) but was lowest at site 3 (57 ± 13%) in 1998 (Figure 22a, Table 18). Percentage of material of *S. patens* leftover was highest at site 2 (85 ± 9%) lowest at site 3 (42 ± 26%) in 1998 (Figure 22b, Table 18). Dead material of *D. spicata* that was leftover was highest at site 1 (73 ± 12%) and was lowest at site 5 (29 ± 13%) in 1999 (Figure 23a). Leftover material from *S. patens* was highest at site 2 (82 ± 20%) and was lowest at site 5 (42 ± 22%) in 1999 (Figure 23b, Table 18).

A greater percentage (51% vs. 29%) of *D. spicata* material produced during the growing season that contributed to the harvested dead material was higher in 1999 than 1998 (Figure 24a, Table 19). Percent contribution of material produced during the growing season to harvested dead mass remained steady over each year for *S. patens* at 38% and 39%, respectively (Figure 24b, Table 19).



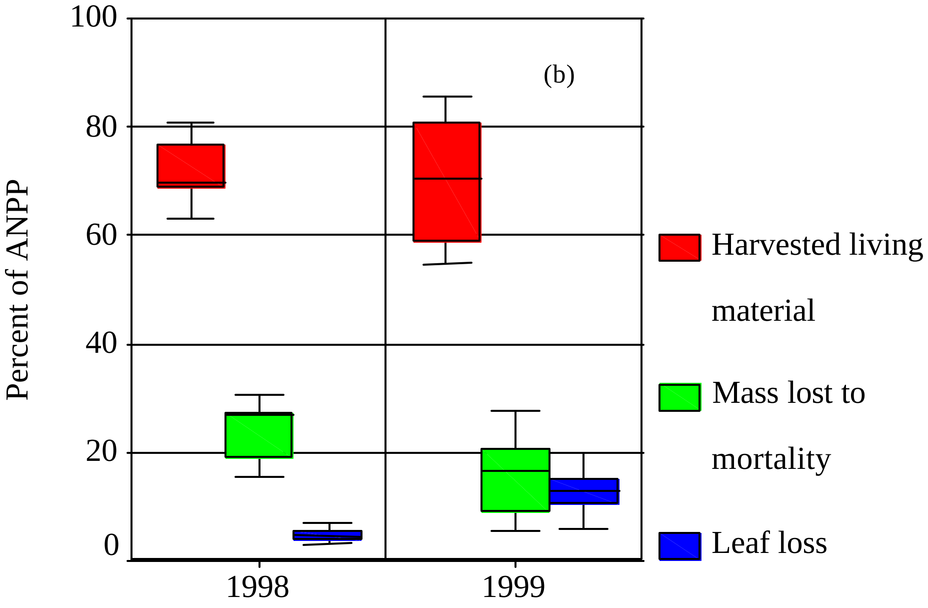
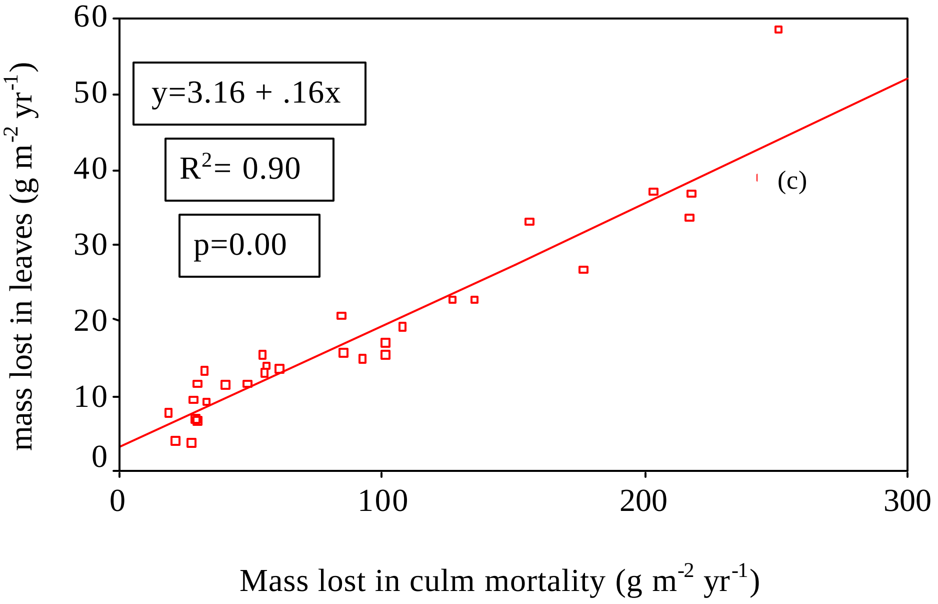


Figure 21. Percentage of ANPP components of (a) *D. spicata* and (b) *S. patens* and mass of lost leaves vs. mass lost in culm mortality of (c) *D. spicata* and (d) *S. patens.*


y=3.16 + .16x
R^2= 0.90
p=0.00
(c)
mass lost in leaves (g m^{-2} yr^{-1})
Mass lost in culm mortality (g m^{-2} yr^{-1})
0
10
20
30
40
50
60
0
100
200
300

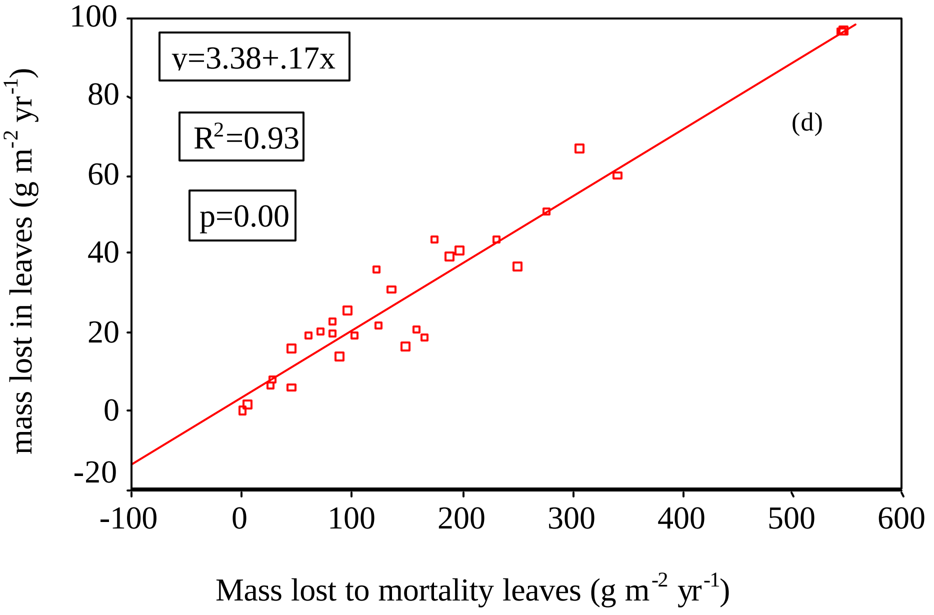

y=3.38+.17x
R^2=0.93
p=0.00
(d)
mass lost in leaves (g m^{-2} yr^{-1})
Mass lost to mortality leaves (g m^{-2} yr^{-1})
-20
0
20
40
60
80
100
-100
0
100
200
300
400
500
600

Table 17. Average percentage of components of ANPP in 1998 and 1999.

		YEAR			
		1998		1999	
		Mean	Std Deviation	Mean	Std Deviation
D. spicata	EOYB	74	5	54	6
	Mass of culm mortality	21	5	36	5
	Mass of leaf loss	5	1	10	3
S. patens	EOYB	72	6	70	13
	Mass of culm mortality	23	6	16	7
	Mass of leaf loss	5	1	15	11

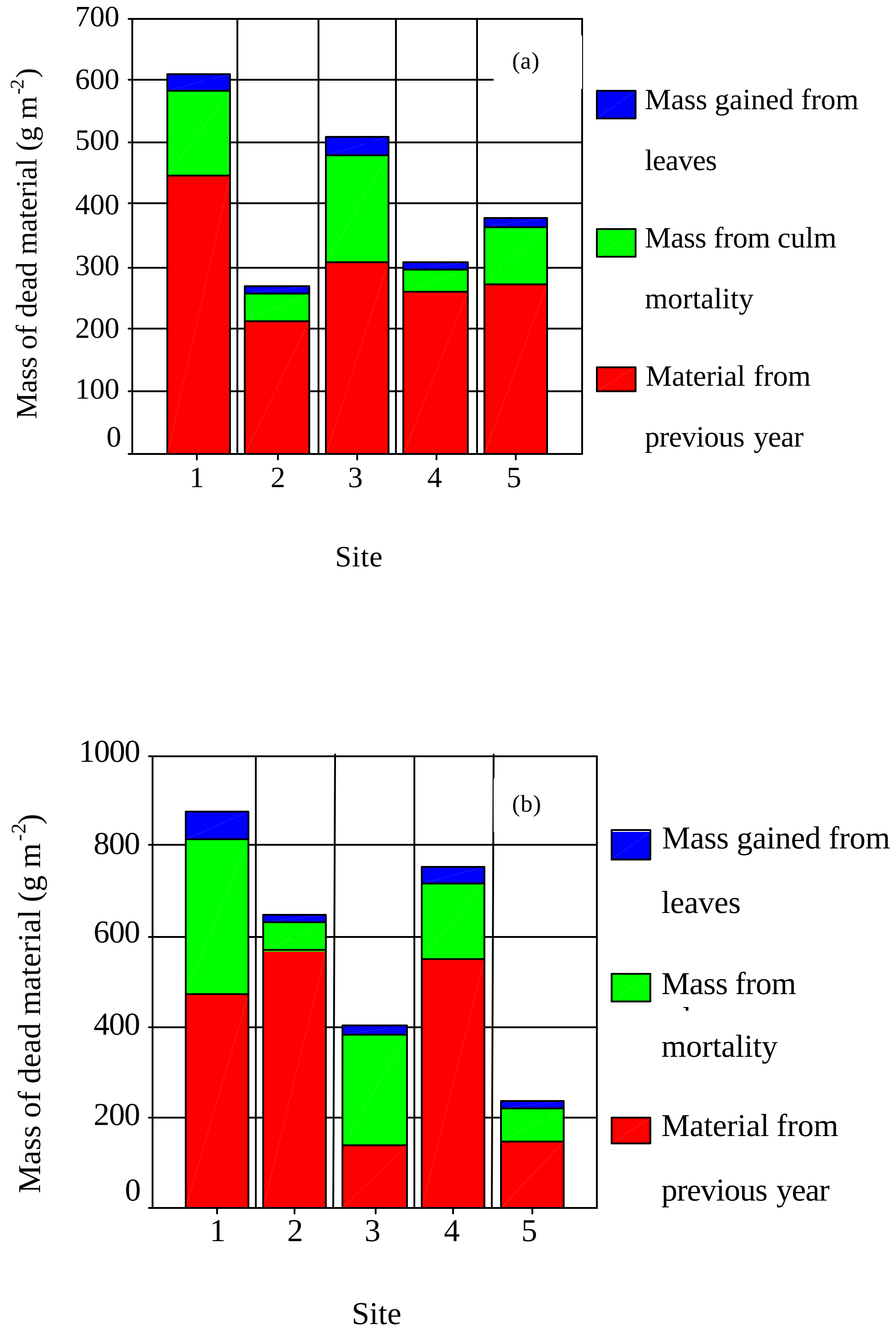


Figure 22. 1998 components of harvested dead material by site of (a) *D. spicata* and (b) *S. patens.*

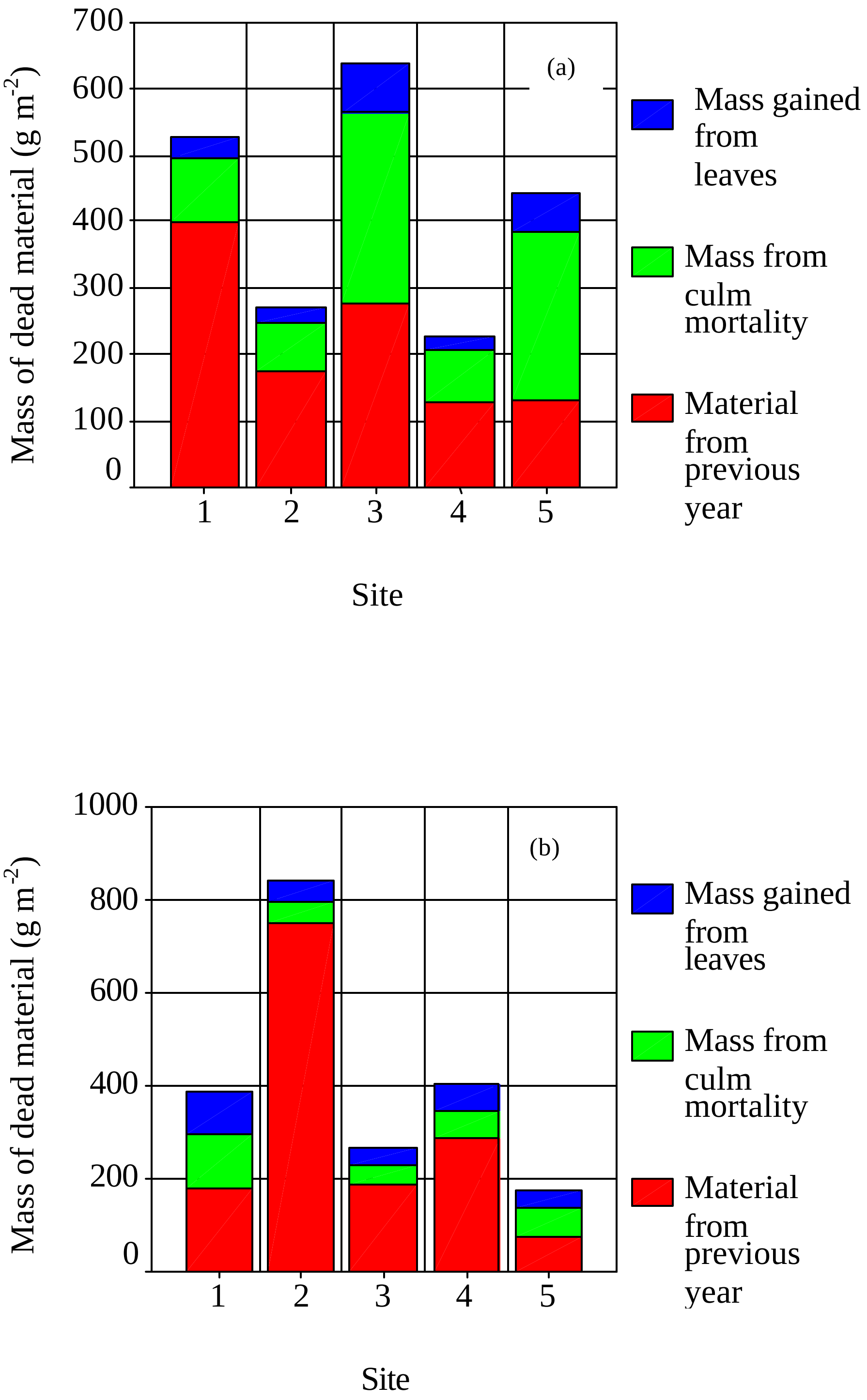


Figure 23. 1999 Components of harvested dead material by site of (a) *D. spicata* and (b) *S. patens*.

Table 18. Percentageof components of harvested dead material.

				YEAR			
				1998		1999	
				Mean	Std Deviation	Mean	Std Deviation
D. spicata	SITE	1	%old material in EOYB	63	22	73	12
			%mortality of EOYB	31	19	21	9
			%leaffall of EOYB	06	4	6	3
		2	%old material in EOYB	78	7	53	32
			%mortality of EOYB	17	5	37	.25
			%leaffall of EOYB	05	2	10	7
		3	%old material in EOYB	57	13	42	31
			%mortality of EOYB	37	12	45	25
			%leaffall of EOYB	6	2	12	7
		4	%old material in EOYB	84	4	46	23
			%mortality of EOYB	13	2	42	18
			%leaffall of EOYB	4	2	12	6
		5	%old material in EOYB	73	5	29	13
			%mortality of EOYB	23	5	58	12
			%leaffall of EOYB	4	1	13	2

Table 18, continued

				1998		1999	
				Mean	Std Deviation	Mean	Std Deviation
S. patens	SITE	1	%old material in EOYB	53	0.01	.46	18
			%mortality of EOYB	39	0.00	.30	11
			%leaffall of EOYB	8	0.01	.24	.08
		2	%old material in EOYB	85	0.09	.82	.20
			%mortality of EOYB	12	8	10	13
			%leaffall of EOYB	3	2	8	8
		3	%old material in EOYB	42	26	67	17
			%mortality of EOYB	52	25	19	11
			%leaffallof EOYB	5	3	14	7
		4	%old material in EOYB	72	10	62	25
			%mortality of EOYB	23	8	17	12
			%leaffall of EOYB	5	2	21	14
		5	%old material in EOYB	59	11	42	22
			%mortality of EOYB	34	9	37	14
			%leaffall of EOYB	7	2	21	8

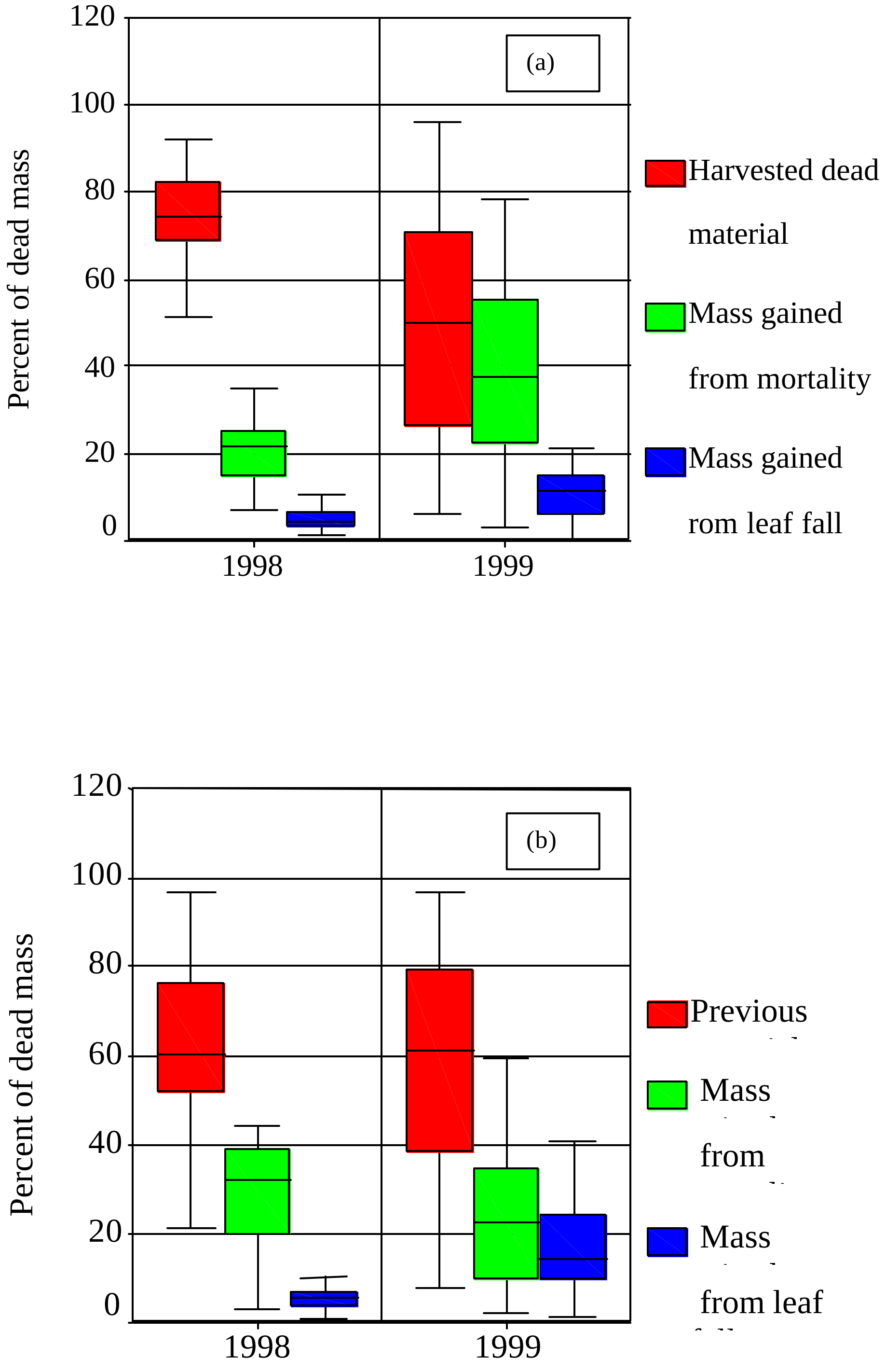


Figure 24. Percentage of components of harvested dead material of (a) *D. spicata* and (b) *S. patens.*

Table 19. Percentage components of dead material of the average biomass harvest.

		YEAR 1998		1999	
		Mean	Std Deviation	Mean	Std Deviation
D . spicata	Material from previous year	71	15	49	27
	Mass of culm mortality	24	13	41	22
	Mass gained from leaf loss	5	2	10	6
S. patens	Material from previous year	62	20	60	24
	Mass of culm mortality	32	19	22	15
	Mass gained from leaf loss	6	2	17	10

The annual turnover rate also varied by site and year. However, a trend appeared in each species where site 2 typically had the lowest turnover and site 5 the highest. *D. spicata* had the highest turnover at sites 3 and 5 at 1.45 ± 0.01 per year, and the lowest at site 2 (1.25 ± 0.01 per year). *S. patens* had the highest turnover at site 5 in 1998 (1.56 ± 0.02) and the lowest turnover at site 2 (1.25 ± 1.21 per year) in 1998. *D. spicata* had the lowest turnover at site 2 again (1.63 ± .04 per year) and the highest turnover at site 5 again (2.23 ± 0.04 per year) (Table 20).

Turnover of *D. spicata* in control plots averaged 1.36 ± 0.09 per year in 1998 and 1.89 ± 0.21 per year in 1999 (Table 21). Turnover of *D. spicata* was significantly higher (p=0.000) in 1999 than in 1998 (Figure 25, Table 22). Turnover for *S. patens* in control plots averaged 1.40 ± 0.11 per year in 1998, and 1.44 ± 0.21 per year in 1999 (Table 22). There was no significant difference (p=0.200) in *S. patens* turnover between the 1998 and 1999 (Figure 25, Table 23).

4.4. Response of growth to zone and experimental treatment

I was interested in examining how growth characteristics might vary between zones and how treatment may have affected these characteristics in Hummock and Non-hummock zones. Zone had a significant effect on EOYB density (1998 p=0.005, 1999 p=0.002), ANPP (1998 p=0.004, 1999 p=0.000), and turnover (1998 p=0.000, 1999 p=0.000) of *D. spicata* in both years. However, zone showed no effect on production per culm in either year (Figures 26 a-d ,Tables 24 and 25). Each year, the Non-hummock zone was found to have the lowest harvest density (1998 = 82.92 ± 37.16 culms

Table 20. Turnover rate (yr^{-1}) by species, site, and year.

			YEAR			
			1998		1999	
			Mean	Std Deviation	Mean	Std Deviation
D. spicata	SITE	1	1.30	0.01	1.91	0.11
		2	1.25	0.01	1.63	0.04
		3	1.45	0.01	1.89	0.04
		4	1.32	0.02	1.79	0.05
		5	1.45	0.01	2.23	0.04
S. patens	SITE	1	1.47	0.01	1.42	0.05
		2	1.25	0.01	1.21	0.03
		3	1.43	0.01	1.56	0.11
		4	1.31	0.01	1.25	0.03
		5	1.56	0.02	1.74	0.05

Table 21. Average annual turnover rate (yr^{-1}) of species by year.

	YEAR			
	1998		1999	
	Mean	Std Deviation	Mean	Std Deviation
D. spicata	1.36	0.09	1.89	0.21
S. patens	1.40	0.11	1.44	0.21

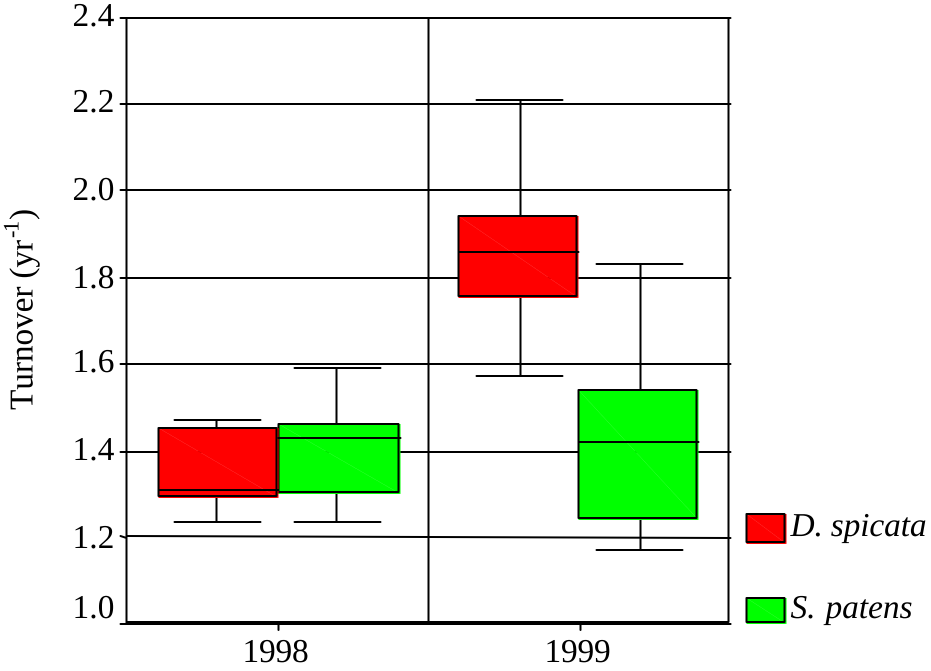


Figure 25. Turnover rates of *D. spicata* and *S. patens* (1998-1999).

Table 22. ANOVA of *D. spicata* turnover rates (yr^{-1}) for differences between 1998 and 1999 in Control plots.

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	4.258	1	4.258	169.202	0.000
Within Groups	1.460	58	2.517E-02		
Total	5.718	59			

Table 23. ANOVA of *S. patens* turnover rates (yr^{-1}) for differences between 1998 and 1999 in Control plots.

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	2.016E-02	1	2.016E-02	0.698	0.407
Within Groups	1.618	56	2.889E-02		
Total	1.638	57			

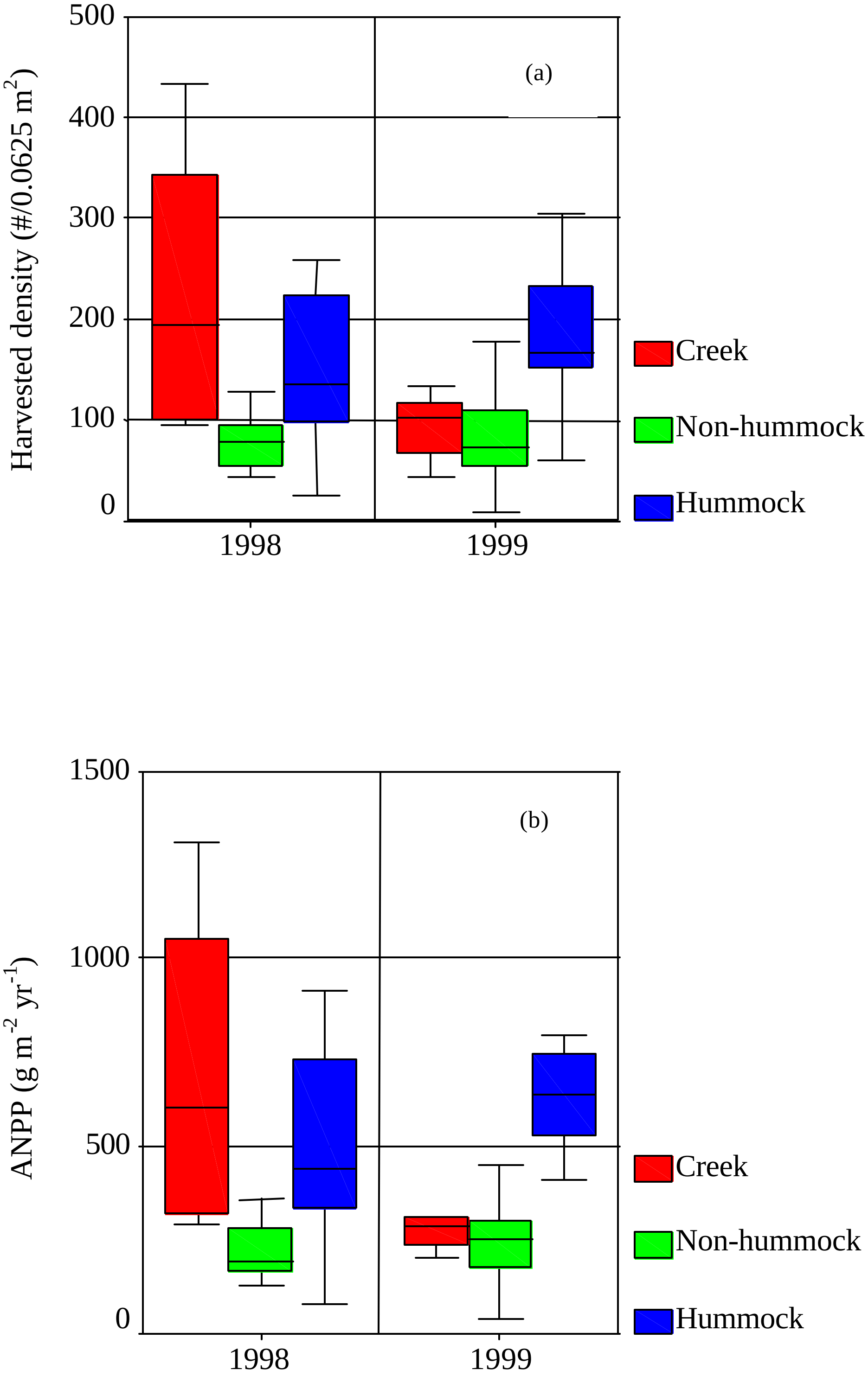
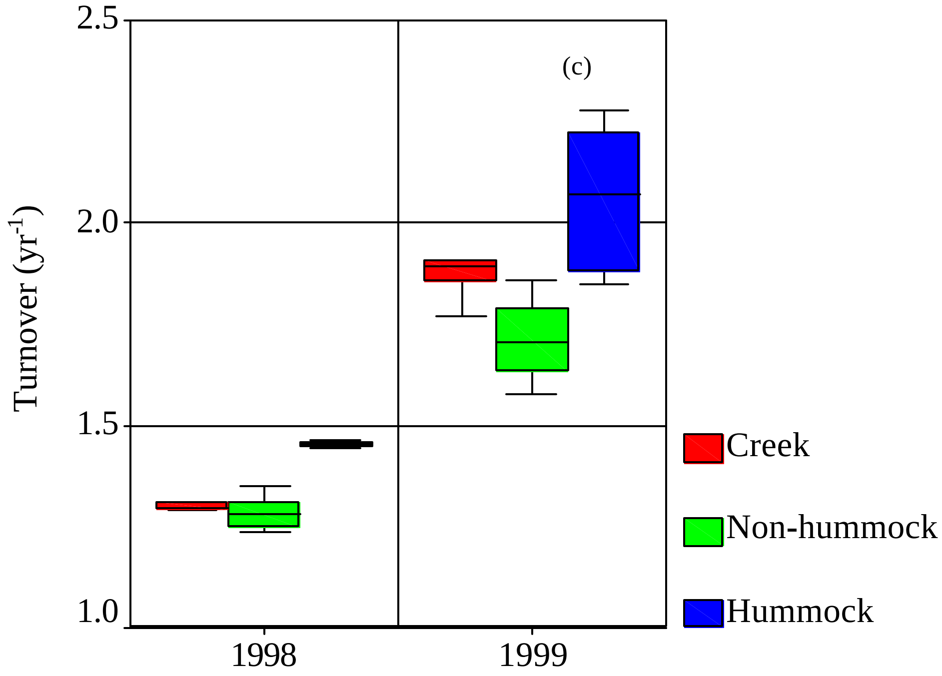


Figure 26. *D. spicata* (a) harvested EOYB density of living culms, (b) ANPP by zone, (c) turnover rates, and (d) production per culm by zone.


(c)
Turnover (yr^{-1})
2.5
2.0
1.5
1.0
1998
1999
🟥 Creek
🟩 Non-hummock
🟦 Hummock

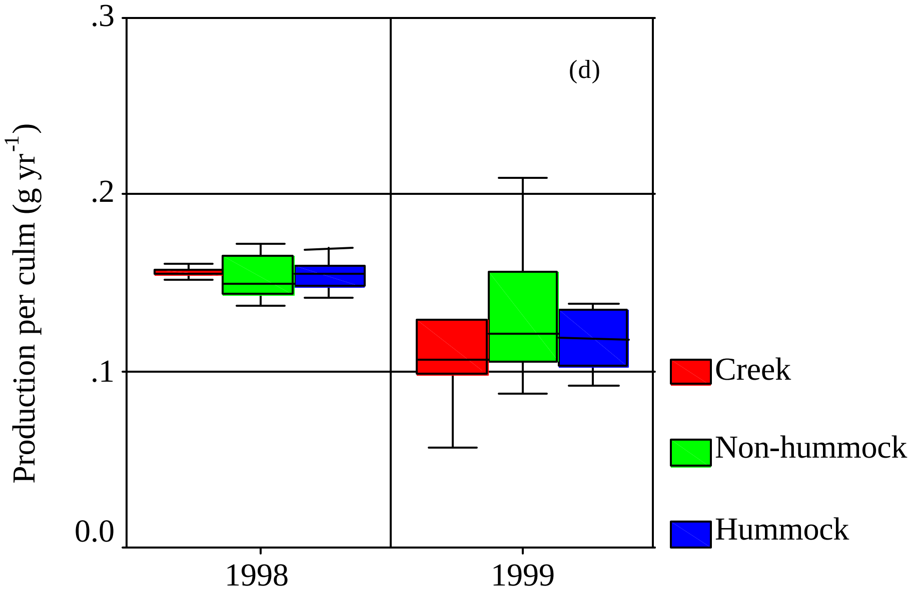

(d)
Production per culm ($g\ yr^{-1}$)
.3
.2
.1
0.0
1998
1999
🟥 Creek
🟩 Non-hummock
🟦 Hummock

Table 24. ANOVAs of zone effect on density (# 0.0625 m^{-2}), production/culm (g culm^{-1}), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1}) of *D. spicata* in 1998.

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
Density	Between Groups	83112.30	2	41556.15	6.39	0.005
	Within Groups	175363.16	27	6494.93		
	Total	258475.46	29			
Production/ culm	Between Groups	1.16E-04	2	5.81E-05	0.25	0.778
	Within Groups	6.18E-03	27	2.29E-04		
	Total	6.30E-03	29			
ANPP	Between Groups	896783.26	2	448391.63	6.71	0.004
	Within Groups	1802197.13	27	66748.04		
	Total	2698980.40	29			
Turnover	Between Groups	0.19	2	9.73E-02	161.28	0.000
	Within Groups	1.62E-02	27	6.03E-04		
	Total	0.21	29			

Multiple Comparisons LSD

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
Dependent Variable	(I) ZONE	(J) ZONE				Lower Bound	Upper Bound
Density	Creek	Non-hummock	142.75	40.29	0.001	60.07	225.42
		Hummock	80.25	40.29	0.057	-2.42	162.92
	Non-hummock	Creek	-142.75	40.29	0.001	-225.42	-60.07
		Hummock	-62.50	32.90	0.068	-130.00	5.00
	Hummock	Creek	-80.25	40.29	0.057	-162.92	2.42
		Non-hummock	62.50	32.90	0.068	-5.00	130.01

Table 24, continued

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
Production /culm	Creek	Non-hummock	5.37E-03	7.56E-03	0.483	-1.01E-02	2.09E-02
		Hummock	3.30E-03	7.56E-03	0.666	-1.22E-02	1.88E-02
	Non-hummock	Creek	-5.37E-03	7.56E-03	0.483	-2.09E-02	1.01E-02
		Hummock	-2.07E-03	6.17E-03	0.740	-1.47E-02	1.06E-02
	Hummock	Creek	-3.30E-03	7.56E-03	0.666	-1.88E-02	1.22E-02
		Non-hummock	2.07E-03	6.17E-03	0.740	-1.06E-02	1.47E-02
ANPP	Creek	Non-hummock	455.38	129.17	0.002	190.33	720.43
		Hummock	206.92	129.17	0.121	-58.12	471.97
	Non-hummock	Creek	-455.38	129.17	0.002	-720.43	-190.33
		Hummock	-248.45	105.47	0.026	-464.87	-32.04
	Hummock	Creek	-206.92	129.17	0.121	-471.97	58.12
		Non-hummock	248.45	105.47	0.026	32.04	464.87
Turnover	Creek	Non-hummock	1.65E-02	1.22E-02	0.190	-8.68E-03	4.17E-02
		Hummock	-0.15	1.22E-02	0.000	-0.17	-0.12
	Non-hummock	Creek	-1.65E-02	1.22E-02	0.190	-4.17E-02	8.684E-03
		Hummock	-0.16	1.00E-02	0.000	-0.19	-0.14
	Hummock	Creek	0.15	1.22E-02	0.000	0.12	0.17
		Non-hummock	0.16	1.00E-02	0.000	0.14	0.19

Table 25. ANOVAs of zone effect on density (# 0.0625 m^{-2}), production/culm (g $culm^{-1}$), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1}) of *D. spicata* in 1999.

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
Density	Between Groups	84012.70	2	42006.35	8.34	0.002
	Within Groups	135989.16	27	5036.63		
	Total	220001.86	29			
Production /culm	Between Groups	1.08E-03	2	5.41E-04	.35	0.702
	Within Groups	4.07E-02	27	1.50E-03		
	Total	4.18E-02	29			
ANPP	Between Groups	1277797.45	2	638898.72	12.06	0.000
	Within Groups	1430184.40	27	52969.79		
	Total	2707981.86	29			
Turnover	Between Groups	0.72	2	0.36	18.70	0.000
	Within Groups	0.52	27	1.93E-02		
	Total	1.24	29			

Multiple Comparisons
LSD

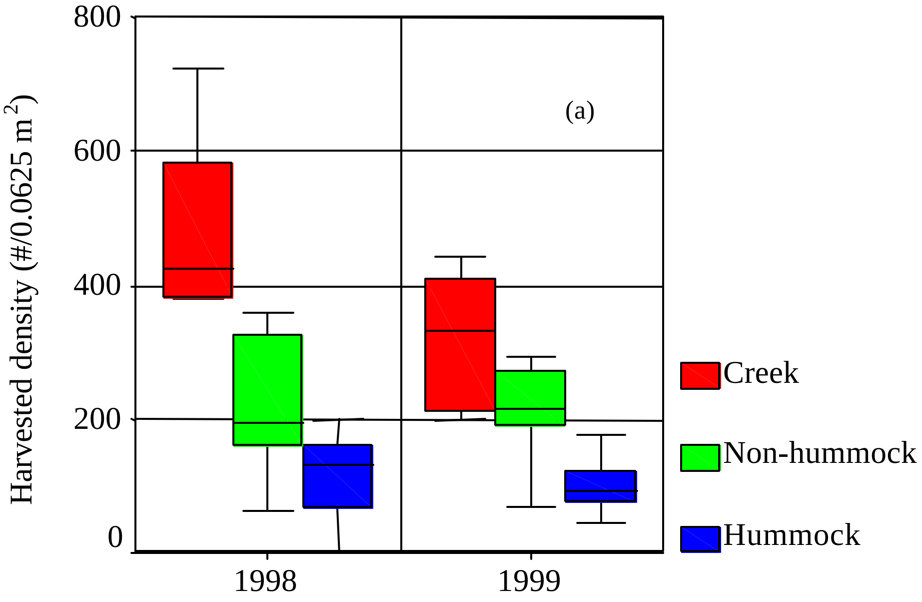
			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
Dependent Variable	(I) ZONE	(J) ZONE				Lower Bound	Upper Bound
Density	Creek	Non-hummock	10.25	35.48	0.775	-62.55	83.05
		Hummock	-100.91	35.48	0.008	-173.72	-28.10
	Non-hummock	Creek	-10.25	35.48	0.775	-83.05	62.55
		Hummock	-111.16	28.97	0.001	-170.61	-51.71
	Hummock	Creek	100.91	35.48	.008	28.10	173.72

Table 25, continued

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
		Non-hummock	111.16	28.97	0.001	51.71	170.61
Production /culm	Creek	Non-hummock	-5.18E-03	1.94E-02	0.792	-4.50E-02	3.46E-02
		Hummock	8.18E-03	1.94E-02	0.677	-3.16E-02	4.80E-02
	Non-hummock	Creek	5.18E-03	1.94E-02	0.792	-3.46E-02	4.50E-02
		Hummock	1.33E-02	1.58E-02	0.407	-1.91E-02	4.59E-02
	Hummock	Creek	-8.18E-03	1.94E-02	0.677	-4.80E-02	3.16E-02
		Non-hummock	-1.33E-02	1.58E-02	0.407	-4.59E-02	1.91E-02
ANPP	Creek	Non-hummock	31.96	115.07	0.783	-204.15	268.07
		Hummock	-399.29	115.07	0.002	-635.40	-163.17
	Non-hummock	Creek	-31.96	115.07	0.783	-268.07	204.15
		Hummock	-431.25	93.95	0.000	-624.04	-238.46
	Hummock	Creek	399.29	115.07	0.002	163.17	635.40
		Non-hummock	431.25	93.95	0.000	238.46	624.04
Turnover	Creek	Non-hummock	0.194	6.96E-02	0.009	5.18E-02	0.33
		Hummock	-0.152	6.96E-02	0.037	-0.29	-9.70E-03
	Non-hummock	Creek	-0.195	6.96E-02	0.009	-.3375	-5.18E-02
		Hummock	-0.347	5.68E-02	0.000	-0.46	-0.23
	Hummock	Creek	0.152	6.96E-02	0.037	9.7E-03	0.29
		Non-hummock	0.347	5.68E-02	0.000	0.23	0.46

0.0625 m^{-2}, or 1326.72 ± 594.56 culms m^{-2},1999 = 83.75 ± 48.57 culms 0.0625m^{-2}, or 1340 ± 777.12 culms m^{-2}) and ANPP (1998 = 242.49 ± 118.22 g m^{-2} yr^{-1}, 1999 = 242.49 ± 110.50 g m^{-2} yr^{-1}) of *D. spicata.* In 1998, *D. spicata* was most abundant (225.67 ± 135.6 culms 0.0625 m^{-2}, or 3609.6 ± 2169.6 culms m^{-2}) at harvest and productive (697.86 ± 408.1 g m^{-2} yr^{-1}) in the creek zone, but was most abundant at time of harvest (194.92 ± 97.57 culms 0.0625m^{-2}, or 3118.72 ± 1561.12 culms m^{-2}) and productive (673.74 ± 341.72 g m^{-2} yr^{-1}) in the Hummock zone in 1999 (Appendix 9, Figures 27 a-b). Turnover was significantly higher in the Hummock zone in 1998 and 1999 (Figure 27c, Tables 25-26).

Zone had a significant effect on *S. patens* EOYB density (1998 p=0.000, 1999 p=0.000), ANPP (1998 p=0.001, 1999 p=0.000), and turnover (1998 p=0.000, 1999 p=0.000), and production per culm in 1999 (p=0.001) (Figure 27 a-d, Tables 26 and 27). Each year a trend appeared where *S. patens* was most abundant at harvest (1998 = 429 ± 230.33 culms 0.0625 m^{-2}, or 6864 ± 3685.28 culms m^{-2}, 1999 = 319.60 ± 111.65 culms 0.0625m^{-2}, or 5113.6 ± 1786.4 culms m^{-2}) and productive (1998 = 1280.17 ± 727.19 g m^{-2} yr^{-1}, 1999 = 719.73 ± 328.84 g m^{-2} yr^{-1}) in the creek zone, and least abundant at harvest (1998 = 128.83 ± 96.85 culms 0.0625m^{-2}, or 2061.28 ± 154.96 culms m^{-2}, 1999 = 100.67 ± 36.19 culms 0.0625m^{-2}, 1610.72 ± 590.4 culms m^{-2}) and productive (1998 = 575.83 ± 675.69 g m^{-2} yr^{-1}, 1999 = 228.32 ± 84.96 g m^{-2} yr^{-1}) in the Hummock zone, where turnover was highest (Appendix 10, Figure 27 a-b). *S. patens* growing in the Non-hummock zone had significantly higher production per culm (0.15 ± 0.04g culm^{-1}) than the Creek (0.11 ± 0.02 g culm^{-1}) and Hummock (0.10 ± 0.02 g culm^{-1}) zones in 1999, but



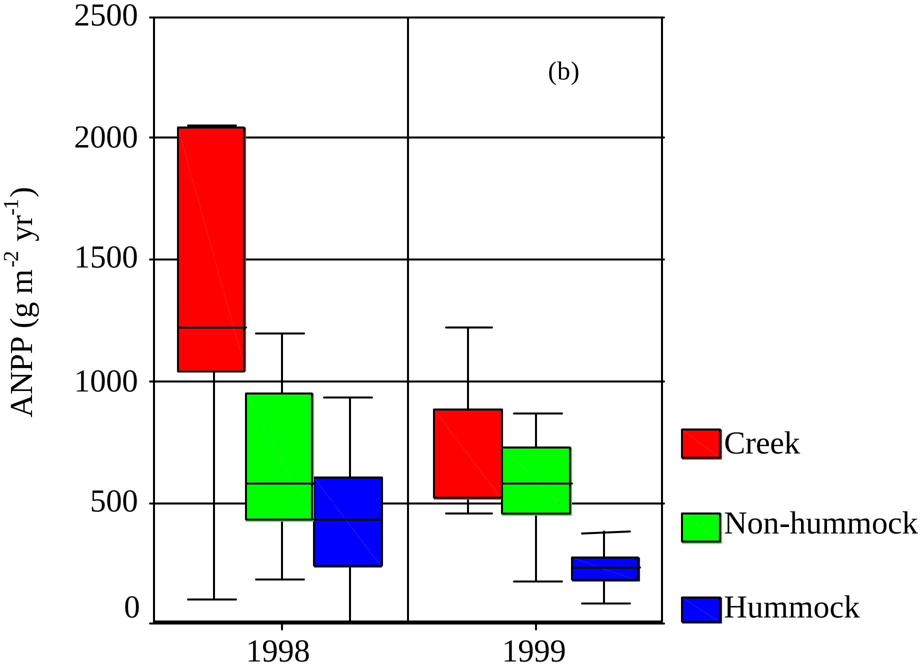
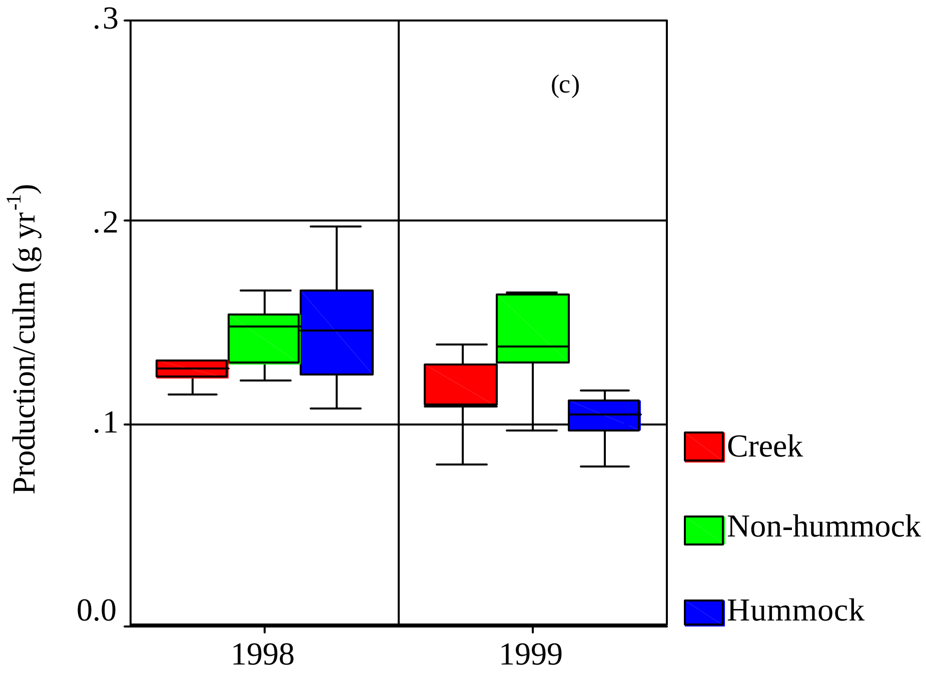


Figure 27. *S. patens* (a) harvested EOYB density of living culms, (b) ANPP by zone, (c) production per culm, and (d) turnover by zone.


(c)
Production/culm (g yr^{-1})
.3
.2
.1
0.0
1998
1999
Creek
Non-hummock
Hummock

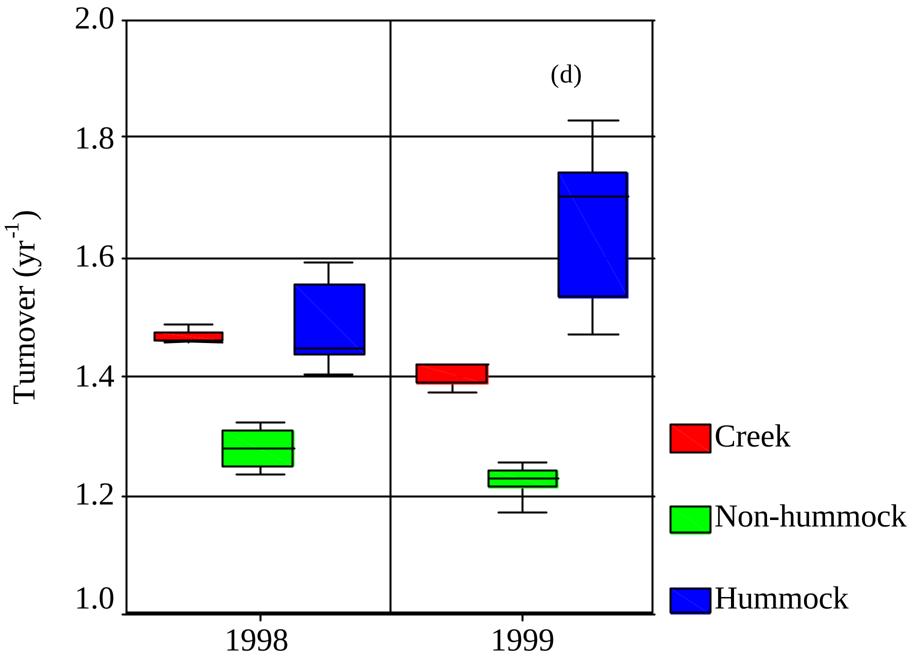

(d)
Turnover (yr^{-1})
2.0
1.8
1.6
1.4
1.2
1.0
1998
1999
Creek
Non-hummock
Hummock

Table 26. ANOVAs of zone effect on density (# 0.0625 m^{-2}), production/culm (g culm^{-1}), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1} of *S. patens* in 1998.

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
Density	Between Groups	360572.20	2	180286.10	10.29	0.000
	Within Groups	473025.66	27	17519.46		
	Total	833597.86	29			
Production /culm	Between Groups	1.35E-02	2	6.77E-03	0.97	0.392
	Within Groups	0.18	26	6.96E-03		
	Total	0.19	28			
ANPP	Between Groups	2182461.55	2	1091230.77	3.35	0.050
	Within Groups	8792450.97	27	325646.33		
	Total	10974912.53	29			
Turnover	Between Groups	0.30	2	0.15	60.51	0.000
	Within Groups	6.44E-02	26	2.48E-03		
	Total	0.36	28			

Multiple Comparisons
LSD

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
Dependent Variable	(I) ZONE	(J) ZONE				Lower Bound	Upper Bound
Density	Creek	Non-hummock	205.00	66.18	0.005	69.20	340.79
		Hummock	300.16	66.18	0.000	164.37	435.95
	Non-hummock	Creek	-205.00	66.18	0.005	-340.79	-69.20
		Hummock	95.16	54.03	0.090	-15.70	206.03
	Hummock	Creek	-300.16	66.18	0.000	-435.95	-164.37

Table 26, continued

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
		Non-hummock	-95.16	54.03	0.090	-206.03	15.70
Production /culm	Creek	Non-hummock	-1.43E-02	4.174E-02	0.734	-0.10	7.14E-02
		Hummock	-5.27E-02	4.23E-02	0.224	-0.13	3.43E-02
	Non-hummock	Creek	1.432E-02	4.17E-02	0.734	-7.14E-02	0.10
		Hummock	-3.84E-02	3.48E-02	0.281	-.11	3.32E-02
	Hummock	Creek	5.27E-02	4.23E-02	0.224	-3.43E-02	0.13
		Non-hummock	3.84E-02	3.48E-02	0.281	-3.32E-02	0.11
ANPP	Creek	Non-hummock	635.42	285.32	0.034	49.97	1220.86
		Hummock	704.34	285.32	0.020	118.90	1289.78
	Non-hummock	Creek	-635.42	285.32	0.034	-1220.86	-49.97
		Hummock	68.92	232.96	0.770	-409.08	546.93
	Hummock	Creek	-704.34	285.32	0.020	-1289.78	-118.90
		Non-hummock	-68.92	232.96	0.770	-546.93	409.08
Turnover	Creek	Non-hummock	0.18	2.49E-02	0.000	0.13	0.23
		Hummock	-2.71E-02	2.52E-02	0.293	-7.90E-02	2.48E-02
	Non-hummock	Creek	-0.18	2.490E-02	0.000	-0.23	-0.13
		Hummock	-0.21	2.079E-02	0.000	-0.25	-0.17
	Hummock	Creek	2.7E-02	2.528E-02	0.293	-2.48E-02	7.90E-02
		Non-hummock	0.21	2.079E-02	0.000	0.17	0.25

Table 27. ANOVAs of zone effect on density (# 0.0625 m^{-2}), production/culm (g $culm^{-1}$), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1}) of *S. patens* in 1999.

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
Density	Between Groups	185621.07	2	92810.53	19.34	0.000
	Within Groups	124764.78	26	4798.64		
	Total	310385.86	28			
Production /culm	Between Groups	1.70E-02	2	8.52E-03	8.82	0.001
	Within Groups	2.51E-02	26	9.65E-04		
	Total	4.21E-02	28			
ANPP	Between Groups	1117442.70	2	558721.35	14.93	0.000
	Within Groups	972506.85	26	37404.11		
	Total	2089949.55	28			
Turnover	Between Groups	1.06	2	0.53	72.25	0.000
	Within Groups	0.19	26	7.34E-03		
	Total	1.25	28			

S. patens 1999

Multiple Comparisons
LSD

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
Dependent Variable	(I) ZONE	(J) ZONE				Lower Bound	Upper Bound
Density	Creek	Non-hummock	106.18	36.87	0.008	30.38	181.97
		Hummock	218.93	36.87	0.000	143.13	294.72
	Non-hummock	Creek	-106.18	36.87	0.008	-181.97	-30.38
		Hummock	112.75	28.28	0.000	54.61	170.88
	Hummock	Creek	-218.93	36.87	0.000	-294.72	-143.13

Table 27, continued

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
		Non-hummock	-112.75	28.28	0.000	-170.88	-54.61
Production /culm	Creek	Non-hummock	-4.10E-02	1.65E-02	0.020	-7.50E-02	-7.06E-03
		Hummock	1.07E-02	1.65E-02	0.522	-2.32E-02	4.47E-02
	Non-hummock	Creek	4.10E-02	1.65E-02	0.020	7.07E-03	7.50E-02
		Hummock	5.17E-02	1.26E-02	0.000	2.57E-02	7.78E-02
	Hummock	Creek	-1.07E-02	1.65E-02	0.522	-4.47E-02	2.32E-02
		Non-hummock	-5.17E-02	1.26E-02	0.000	-7.78E-02	-2.57E-02
ANPP	Creek	Non-hummock	152.72	102.94	0.150	-58.88	364.33
		Hummock	491.40	102.94	0.000	279.79	703.01
	Non-hummock	Creek	-152.72	102.94	0.150	-364.33	58.88
		Hummock	338.67	78.95	0.000	176.38	500.97
	Hummock	Creek	-491.40	102.94	0.000	-703.01	-279.79
		Non-hummock	-338.67	78.95	0.000	-500.97	-176.38
Turnover	Creek	Non-hummock	0.19	4.56E-02	0.000	9.94E-02	.28
		Hummock	-0.22	4.56E-02	0.000	-0.32	-.13
	Non-hummock	Creek	-0.19	4.56E-02	0.000	-0.28	-9.94E-02
		Hummock	-0.42	3.50E-02	0.000	-0.49	-.34
	Hummock	Creek	0.22	4.56E-02	0.000	0.13	.32
		Non-hummock	0.42	3.50E-02	0.000	0.34	.49

* The mean difference is significant at the .05 level.

S. patens, 1999

not 1998 (Appendix 9, Figure 27c).

Descriptive statistics of treatment effects on growth of each species by zone are listed in Table 28. Ponding plots consisted of a plywood border extending 10 cm above and below ground, Subsurface control plots consisted of a plywood border 10 cm belowground, and Control plots had no plywood border.

I will first discuss the Non-hummock zone in which there was a significant treatment effect on harvested density (p=0.000) and ANPP (p=0.000) for *D. spicata* (Figures 28 a-b, Table 29). A significant treatment effect was also found for density (p=0.032) and ANPP (p=0.004) for *S. patens* (Figures 29a-b, Table 30). Post hoc tests showed there was a significant negative effect of ponding on harvested density (*D. spicata* = 83.33±43.29 culms/0.0625 m^{-2} or 1333.28 ± 692.64 culms m^{-2}, p=0.019, *S. patens* 218.71±84.89 culms 0.0625 m^{-2}, or 3499.36 ± 1358.24 culms m^{-2}, p=0.041) and ANPP of *D. spicata* (242.48±111.91 g m^{-2} yr^{-1}, p=0.004), and a negative trend on *S. patens* ANPP (605.87±265.65 g m^{-2} yr^{-1}, p=0.079) (Tables 29, 30). However, negative results were also found for *D. spicata* in Subsurface controls in harvested density (p=0.019) and ANPP (p=0.006). Thus the negative effect of treatment on culm growth of *D. spicata* in the non-hummock zone can not be attributed to ponding.

Results found in the Hummock zone revealed that treatment may have different effects in different zones. An overall significant treatment effect on *D. spicata* was found for ANPP (p=0.005 and turnover (p=0.000) in the Hummock zone (Figure 30, Table 31). Post hoc analysis of treatments revealed *D. spicata* showed negative ponding effects in harvested density (170.17±90.33 culms 0.0625 m^{-2}, or 2722.72 ± 1445.28 culms m^{-2},

Table 28. Descriptive statistics of effect of treatment on on density (# 0.0625 m^{-2}), production/culm (g $culm^{-1}$), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1}) by zone.

			Treatment					
			Control		Ponding		Subsurface control	
			Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
D. spicata	Non-hummock	Density	83.33	42.29	40.17	9.62	52.83	24.07
		ANPP	242.48	111.91	118.81	20.29	146.92	50.28
		Production /culm	0.14	0.03	0.11	0.01	0.12	0.02
		Turnover	1.50	0.23	1.85	0.02	1.69	0.51
	Hummock	Density	170.17	90.33	95.50	66.26	94.32	60.20
		ANPP	582.34	316.31	256.92	162.94	319.55	51.16
		Production /culm	0.14	0.02	0.16	0.14	5.21	11.34
		Turnover	1.76	0.33	1.63	0.34	1.31	0.05
S. patens	Non-hummock	Density	218.71	84.89	164.25	51.89	211.83	38.27
		ANPP	605.87	265.65	411.34	131.08	717.16	270.75
		Production /culm	0.15	0.03	0.14	0.02	0.14	0.04
		Turnover	1.25	0.04	1.27	0.11	1.68	0.29
	Hummock	Density	114.75	72.94	49.00	41.21	29.80	29.68
		ANPP	402.07	503.30	76.38	42.58	102.81	104.08
		Production /culm	0.14	0.10	0.10	0.04	0.08	0.07
		Turnover	1.57	0.13	1.47	0.21	74.49	99.36

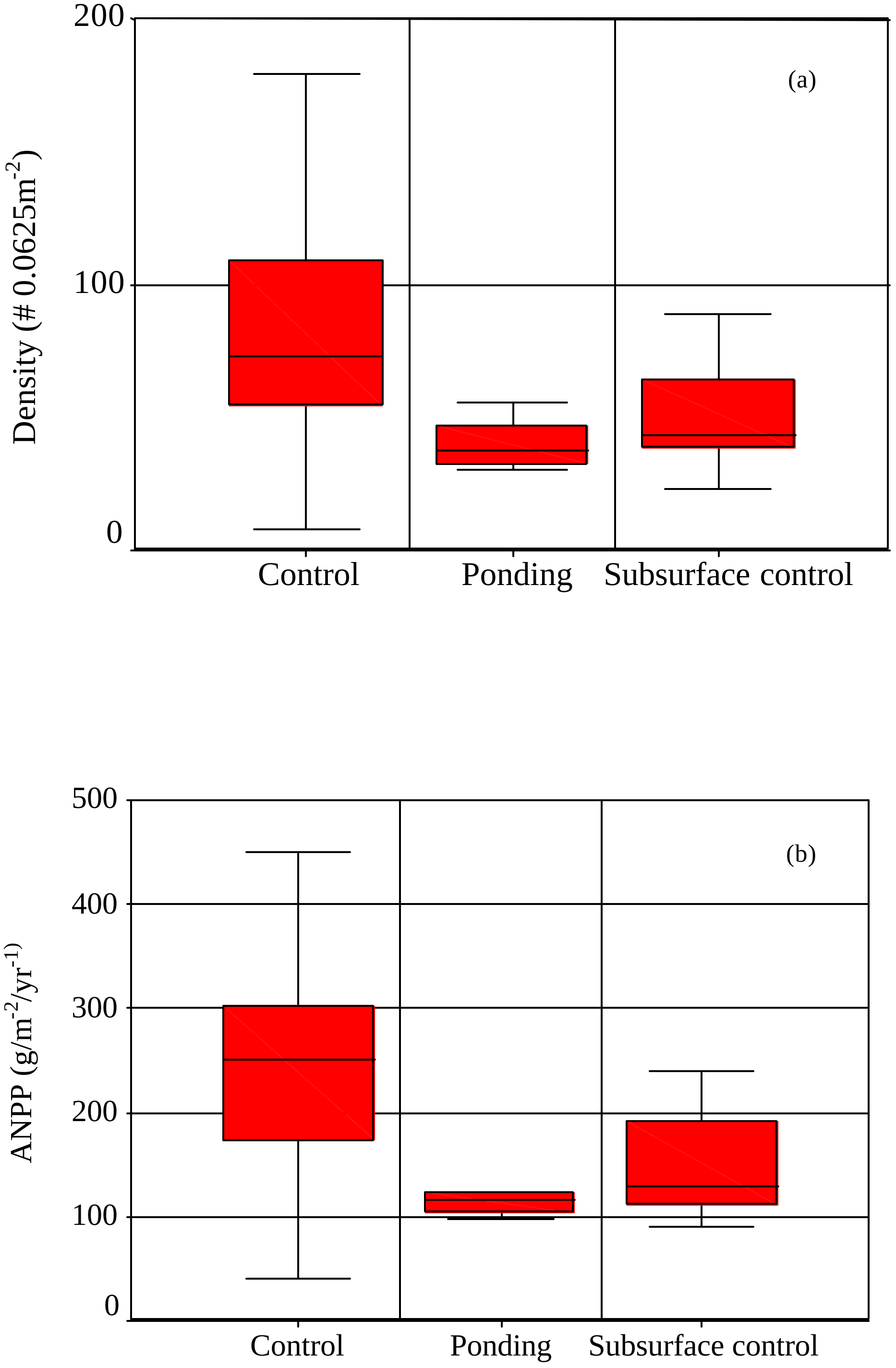


Figure 28. *D. spicata* (a) harvested living density and (b) ANPP by treatment in Non-hummock zone.

Table 29. Treatment effects on *D. spicata* on density (# 0.0625 m^{-2}), production/culm (g culm^{-1}), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1}) in the Non-hummock zone.

ANOVA

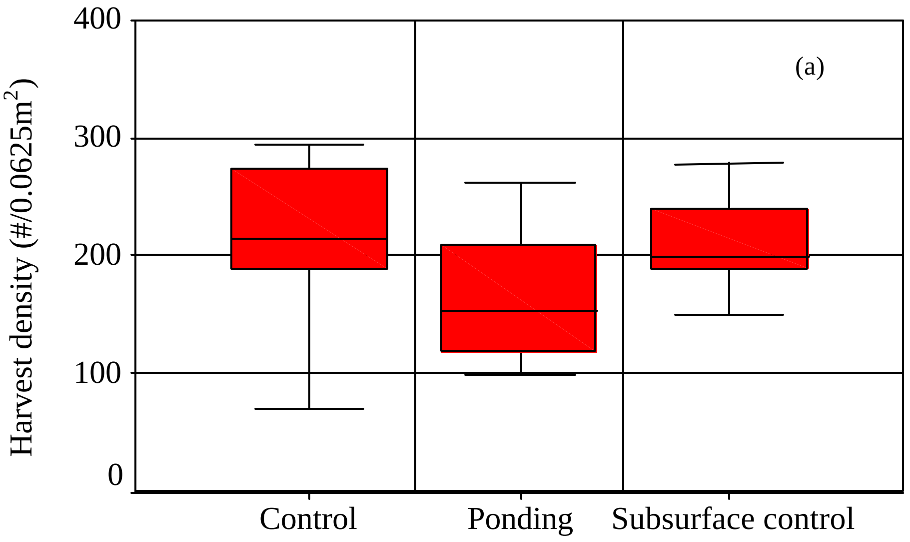
	Sum of Squares	df	Mean Square	F	Sig.
Density	9531.91	2	4765.95	3.92	0.032
Production /culm	1.58E-03	2	7.90E-04	1.06	0.359
ANPP	82451.37	2	41225.68	6.77	0.004
Turnover	.11	2	5.91E-02	0.53	0.593

Multiple Comparisons LSD

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
Dependent Variable	(I) Treatment	(J) Treatment				Lower Bound	Upper Bound
Density	Control	Ponding	43.58	17.42	0.019	7.83	79.33
		Subsurface control	30.91	14.22	0.039	1.72	60.10
	Subsurface control	Control	-43.58	17.42	0.019	-79.33	-7.83
		Subsurface control	-12.66	17.42	0.473	-48.41	23.08
	Subsurface control	Control	-30.91	14.22	0.039	-60.10	-1.72
		Ponding	12.66	17.42	0.473	-23.08	48.41
Production /culm	Control	Ponding	1.97E-02	1.36E-02	0.159	-8.23E-03	4.77E-02
		Subsurface control	8.37E-03	1.11E-02	0.459	-1.44E-02	3.12E-02
	Ponding	Control	-1.97E-02	1.36E-02	0.159	-4.77E-02	8.23E-03
		Subsurface control	-1.13E-02	1.36E-02	0.412	-3.93E-02	1.66E-02
	Subsurface control	Control	-8.37E-03	1.113E-02	0.459	-3.1212E-02	1.44E-02
		Ponding	1.13E-02	1.36E-02	0.412	-1.66E-02	3.93E-02
ANPP	Control	Ponding	123.68	38.99	0.004	43.67	203.68
		Subsurface control	95.57	31.83	0.006	30.24	160.89
	Ponding	Control	-123.68	38.99	0.004	-203.68	-43.67

Table 29, continued

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
		Subsurface control	-28.10	38.99	0.477	-108.11	51.89
	Subsurface control	Control	-95.57	31.83	0.006	-160.89	-30.24
		Ponding	28.10	38.99	0.477	-51.89	108.11
Turnover	Control	Ponding	-0.14	0.16	0.393	-0.48	0.19
		Subsurface control	2.11E-02	0.13	0.878	-0.25	0.30
	Ponding	Control	0.14	0.16	0.393	-0.19	0.48
		Subsurface control	0.16	0.16	0.329	-0.17	0.50
	Subsurface control	Control	-2.11E-02	0.13	0.878	-0.30	0.25
		Ponding	-0.16	0.16	0.329	-0.50	0.17



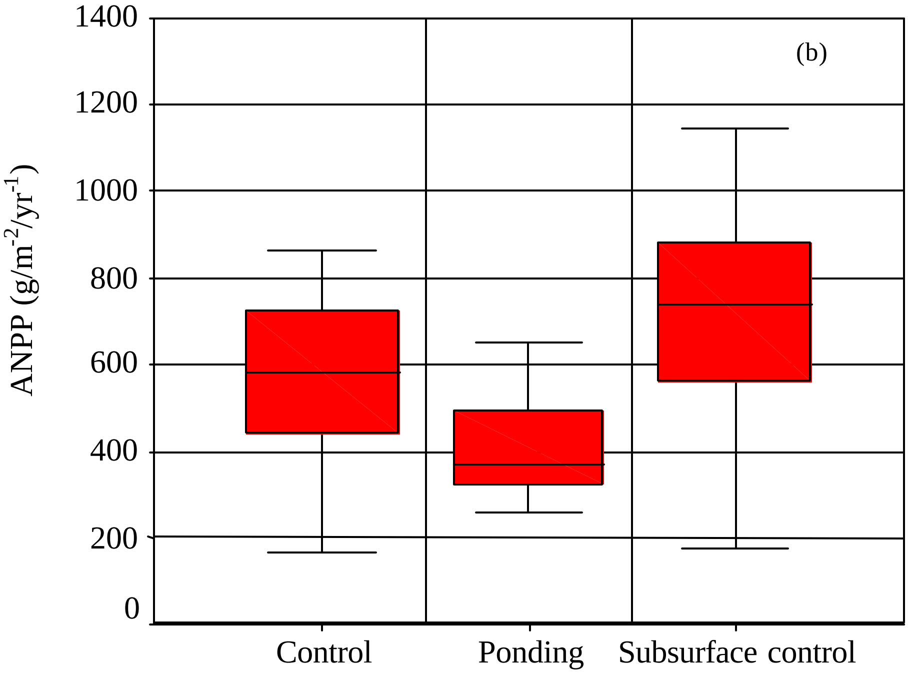


Figure 29. *S. patens* (a) harvested living density and (b) ANPP by treatment in the Non-hummock zone.

Table 30. Treatment effects on *S. patens* density (# 0.0625 m^{-2}), production/culm (g culm^{-1}), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1}) in the Non-hummock zone.

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
Density	Between Groups	18736.16	2	9368.08	2.91	0.069
Production /culm	Between Groups	1.64E-03	2	8.23E-04	0.70	0.501
ANPP	Between Groups	561234.97	2	280617.48	6.36	0.005
Turnover	Between Groups	1.47	2	0.73	22.24	0.000

Multiple Comparisons LSD

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
Dependent Variable	(I) Treatment	(J) Treatment				Lower Bound	Upper Bound
Density	Control	Ponding	49.16	23.16	0.041	2.04	96.29
		Subsurface control	1.58	23.16	0.946	-45.54	48.70
	Ponding	Control	-49.16	23.16	0.041	-96.29	-2.04
		Subsurface control	-47.58	23.16	0.048	-94.70	-.45
	Subsurface control	Control	-1.58	23.16	0.946	-48.70	45.54
		Ponding	47.58	23.16	0.048	.45	94.70
Production /culm	Control	Ponding	1.48E-02	1.39E-02	0.296	-1.35E-02	4.31E-02
		Subsurface control	1.38E-02	1.39E-02	0.328	-1.45E-02	4.22E-02
	Ponding	Control	-1.48E-02	1.39E-02	0.296	-4.31E-02	1.35E-02
		Subsurface control	-9.56E-04	1.39E-02	0.946	-2.93E-02	2.742E-02
	Subsurface control	Control	-1.38E-02	1.39E-02	0.328	-4.22E-02	1.453E-02
		Ponding	9.56E-04	1.39E-02	0.946	-2.74E-02	2.9E-02
ANPP	Control	Ponding	155.66	85.75	0.079	-18.79	330.12
		Subsurface control	-150.16	85.75	0.089	-324.62	24.29
	Ponding	Control	-155.66	85.75	0.079	-330.12	18.79

Table 30, continued

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
		Subsurface control	-305.82	85.75	0.001	-480.28	-131.36
	Subsurface control	Control	150.16	85.75	0.089	-24.29	324.62
		Ponding	305.82	85.75	0.001	131.36	480.28
Turnover	Control	Ponding	-4.21E-02	7.44E-02	0.575	-0.19	0.10
		Subsurface control	-0.44	7.44E-02	0.000	-0.60	-0.29
	Ponding	Control	4.2E-02	7.44E-02	0.575	-0.10	0.19
		Subsurface control	-0.40	7.44E-02	0.000	-0.55	-0.25
	Subsurface control	Control	0.44	7.44E-02	0.000	0.29	0.60
		Ponding	0.40	7.44E-02	0.000	0.25	0.55

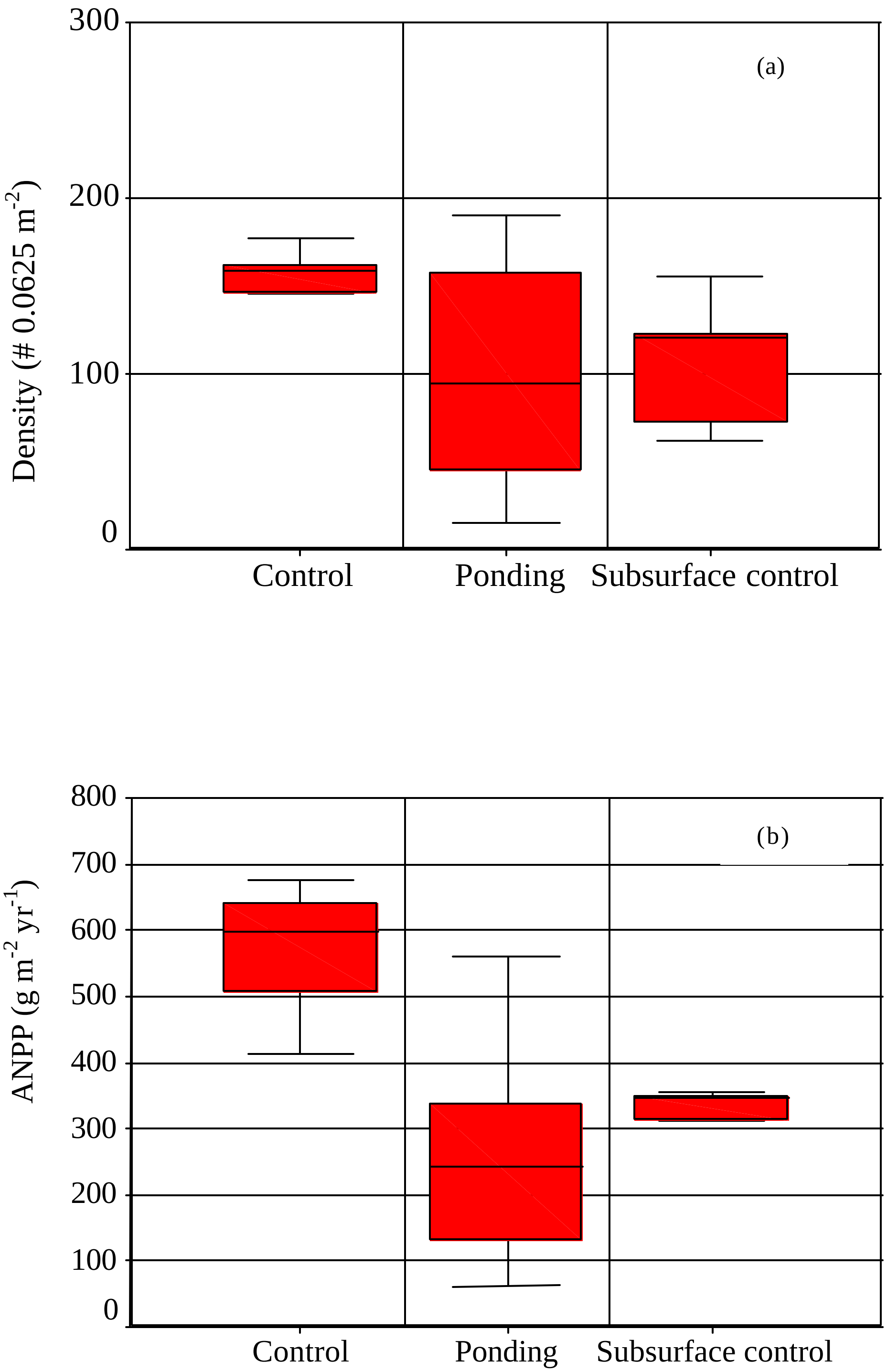


Figure 30. *D. spicata* (a) living density harvested at EOYB and (b) ANPP by treatment in Hummock zone, and (c) turnover of *D. spicata* by treatment in Hummock zone.

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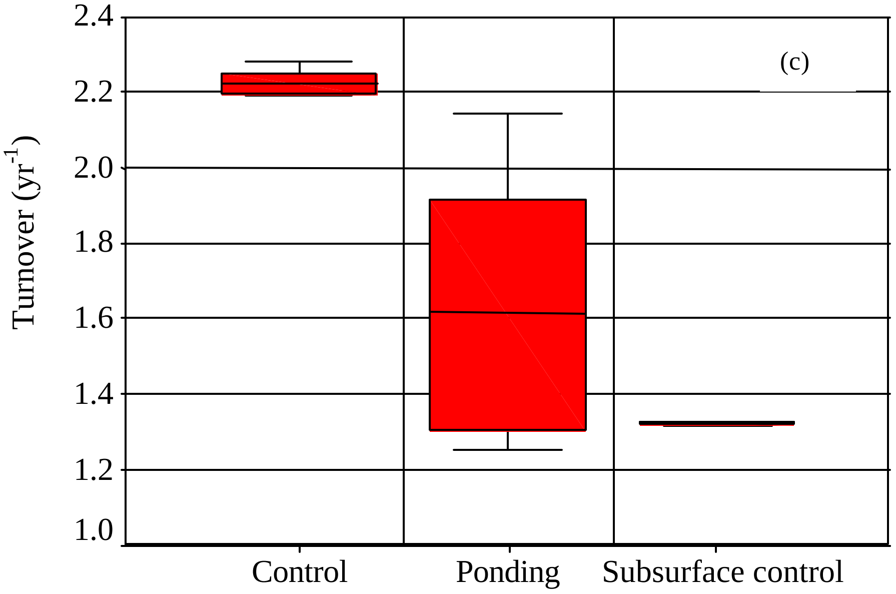

2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
Turnover (yr^{-1})
(c)
Control
Ponding
Subsurface control

Table 31. Treatment effects on *D. spicata* density (# 0.0625 m^{-2}), production/culm (g $culm^{-1}$), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1}) in Hummock zone.

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
Density	Between Groups	11100.75	2	5550.37	2.12	0.145
Production/culm	Between Groups	7.39E-03	2	3.69E-03	2.12	0.146
ANPP	Between Groups	402324.7	2	201162.39	11.41	0.000
Turnover	Between Groups	2.47	2	1.23	18.77	0.000

Multiple Comparisons
LSD

			Mean Difference (I-J)	Std. Error	Sig	95% Confidence Interval	
Dependent Variable	(I) Treatment	(J) Treatment				Lower Bound	Upper Bound
Density	Control	Ponding	51.83	25.54	0.056	-1.45	105.11
		Subsurface control	44.06	30.93	0.170	-20.46	108.59
	Ponding	Control	-51.83	25.54	0.056	-105.11	1.45
		Subsurface control	-7.76	27.19	0.778	-64.49	48.95
	Subsurface control	Control	-44.06	30.93	0.170	-108.59	20.46
		Ponding	7.76	27.19	0.778	-48.95	64.49
Production /culm	Control	Ponding	-3.27E-03	2.08E-02	0.877	-4.67E-02	4.02E-02
		Subsurface control	-4.55E-02	2.52E-02	0.087	-9.82E-02	7.19E-03
	Ponding	Control	3.272E-03	2.08E-02	0.877	-4.02E-02	4.68E-02
		Subsurface control	-4.22E-02	2.22E-02	0.072	-8.85E-02	4.09E-03
	Subsurface control	Control	4.55E-02	2.52E-02	0.087	-7.19E-03	9.82E-02
		Ponding	4.22E-02	2.22E-02	0.072	-4.09E-03	8.85E-02
ANPP	Control	Ponding	314.39	66.38	0.000	175.91	452.87

Table 31, continued

			Mean Difference (I-J)	Std. Error	Sig	95% Confidence Interval	
		Subsurface control	251.76	80.39	0.005	84.05	419.46
	Ponding	Control	-314.39	66.38	0.000	-452.87	-175.91
		Subsurface control	-62.63	70.67	0.386	-210.05	84.79
	Subsurface control	Control	-251.76	80.39	0.005	-419.46	-84.05
		Ponding	62.63	70.67	0.386	-84.79	210.0
Turnover	Control	Ponding	0.60	0.12	0.000	0.33	0.86
		Subsurface control	0.91	0.15	0.000	0.59	1.23
	Ponding	Control	-0.60	0.12	0.000	-0.86	-0.33
		Subsurface control	0.31	0.13	0.032	2.90E-02	0.59
	Subsurface control	Control	-0.91	0.15	0.000	-1.23	-0.59
		Ponding	-0.31	0.13	0.032	-0.59	-2.90E-02

p=0.059), ANPP, (582.34±316.61 g m^{-2} yr^{-1}, p=0.000) and turnover (1.76±0.33 yr^{-1}, p=0.000) in the Hummock zone (Figures 30 a-c, Tables 28, 31). However, ANPP (p=0.005) and turnover (p=0.000) subsurface control plots were also less than controls. An overall significant treatment effect on *S. patens* was also found for density at EOYB harvest (p=0.030), ANPP (p=0.015), and turnover (p=0.007) in the Hummock zone (Figure 31, Table 32). A negative effect on *S. patens* harvest density (49±41.21 culms 0.0625 m^{-2}, or 784 + 659.36 culms m^{-2}, p=0.052), and trend on ANPP (42.58±102.81 g m^{-2} yr^{-1}, p=0.079) was found by ponding, but ANPP was also negatively affected by subsurface controls (ANPP=102.81±104.08 g m^{-2} yr^{-1}, p=0.089) (Figures 31 a-b, Table 28, 32).

4.5. Interannual variation

Results of ANPP and other characteristics in control plots of each zone showed enough variability between 1998 and 1999 to warrant analysis. Production per culm of *D. spicata* was significantly higher (0.15 ± 0.02 g culm^{-1} vs. 0.13 ± 0.04 g culm^{-1}, p=0.000) while turnover was significantly lower (1.36 ± 0.09 yr^{-1} vs. 1.89 ± 0.21 yr^{-1}, p=0.000) in 1998 (Figures 32 a-b, Table 33). *S. patens* showed a trend toward higher production per culm (0.16 ± 0.08 g culm^{-1} vs. 0.13 ± 0.04 g culm^{-1}, p=0.080) and had significantly higher ANPP (744.26 ± 615.18 g m^{-2} yr^{-1} vs. 453.19 ± 273.21 g m^{-2} yr^{-1}, p=0.023) in 1998 (Figure 32c, Table 34).

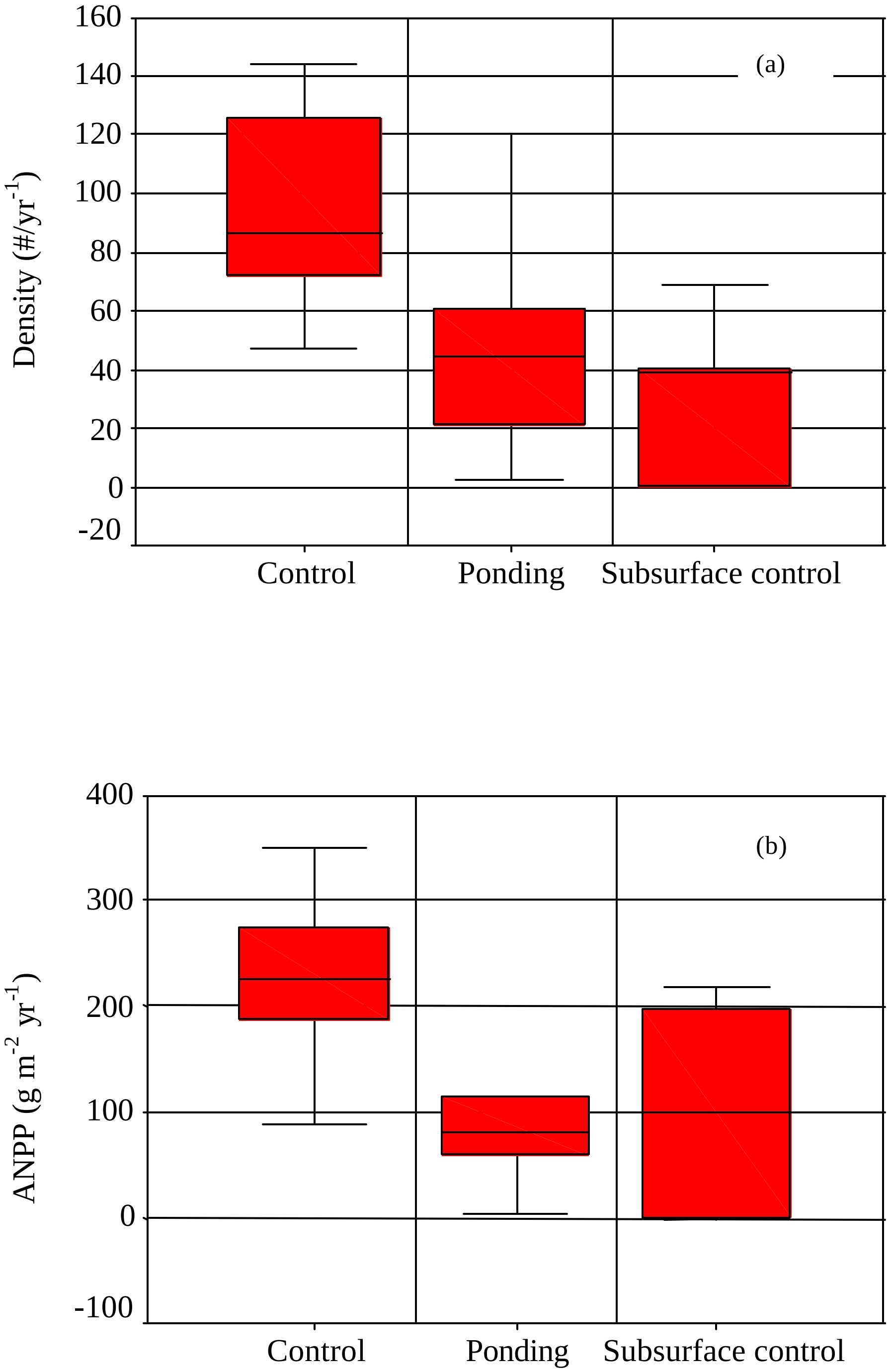


Figure 31. *S. patens* (a) harvested living density, (b) ANPP by treatment in Hummock zone, and (c) turnover by treatment in Hummock zone.

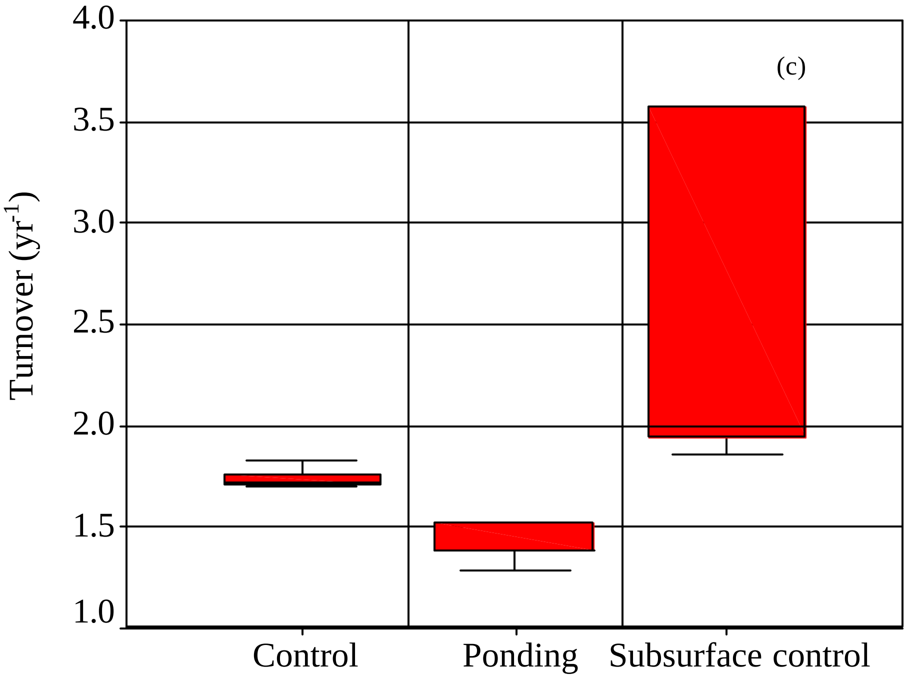

(c)
Turnover (yr^{-1})
4.0
3.5
3.0
2.5
2.0
1.5
1.0
Control
Ponding
Subsurface control

Table 32. Treatment effect on density (# 0.0625 m^{-2}), production/culm (g culm^{-1}), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1}) of *S. patens* in the Hummock zone.

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
Density	Between Groups	12004.64	2	6002.32	4.56	0.030
Production /culm	Between Groups	1.02E-03	2	5.14E-04	0.25	0.781
ANPP	Between Groups	74928.03	2	37464.01	5.73	0.015
Turnover	Between Groups	3.60	2	1.80	7.25	0.007

Multiple Comparisons
LSD

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
Dependent Variable	(I) Treatment	(J) Treatment				Lower Bound	Upper Bound
Density	Control	Ponding	44.50	20.93	0.052	-0.39	89.39
		Subsurface control	63.70	21.95	0.012	16.60	110.79
	Ponding	Control	-44.50	20.93	0.052	-89.39	0.39
		Subsurface control	19.20	21.95	0.397	-27.89	66.29
	Subsurface control	Control	-63.70	21.95	0.012	-110.79	-16.60
		Ponding	-19.20	21.95	0.397	-66.29	27.89
Production /culm	Control	Ponding	2.24E-03	2.60E-02	0.933	-5.37E-02	5.81E-02
		Subsurface control	1.80E-02	2.73E-02	0.520	-4.06E-02	7.67E-02
	Ponding	Control	-2.2398E-03	2.60E-02	0.933	-5.81E-02	5.37E-02
		Subsurface control	1.58E-02	2.73E-02	0.572	-4.28E-02	7.45E-02
	Subsurface control	Control	-1.80E-02	2.73E-02	0.520	-7.67E-02	4.06E-02
		Ponding	-1.58E-02	2.73E-02	0.572	-7.45E-02	4.28E-02
ANPP	Control	Ponding	149.16	46.66	0.006	49.08	249.24

Table 32, continued

			Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
		Subsurface control	122.71	48.93	0.025	17.75	227.68
	Ponding	Control	-149.16	46.66	0.006	-249.24	-49.08
		Subsurface control	-26.44	48.93	0.597	-131.40	78.51
	Subsurface control	Control	-122.71	48.93	0.025	-227.68	-17.75
		Ponding	26.44	48.93	0.597	-78.51	131.40
Turnover	Control	Ponding	0.26	0.28	0.372	-.35	0.88
		Subsurface control	-0.84	0.30	0.014	-1.49	-0.20
	Ponding	Control	-0.26	0.28	0.372	-0.88	0.35
		Subsurface control	-1.11	0.30	0.002	-1.76	-0.46
	Subsurface control	Control	0.84	0.30	0.014	0.20	1.49
		Ponding	1.11	0.30	0.002	0.46	1.76

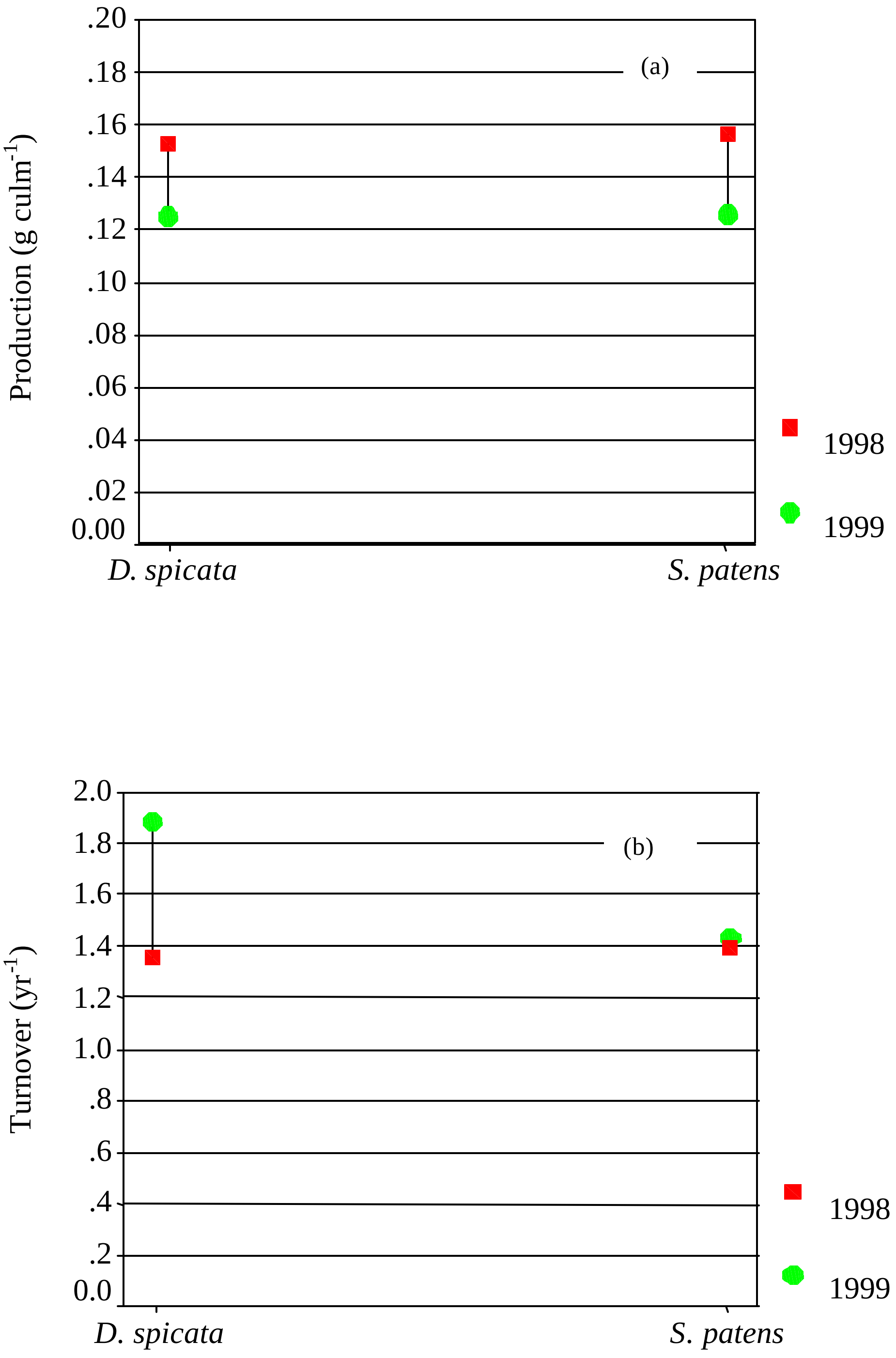


Figure 32. Interannual variation in (a) production per culm, (b) turnover and (c) ANPP of *D. spicata* and *S. patens*.

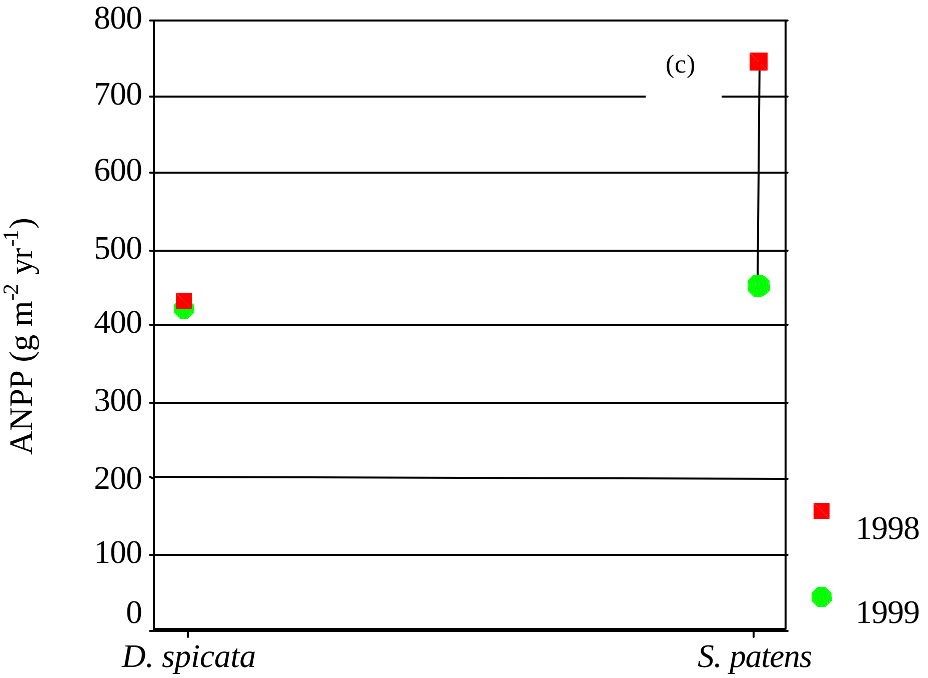

(c)
ANPP (g m-2 yr-1)
800
700
600
500
400
300
200
100
0
D. spicata
S. patens
1998
1999

Table 33. Interannual comparison of *D. spicata* density (# 0.0625 m^{-2}), production/culm (g $culm^{-1}$), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1}).

		N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Min.	Max.
						Lower Bound	Upper Bound		
Density	1998	30	136.47	94.40	17.23	101.21	171.71	25.00	432.00
	1999	30	130.27	87.09	15.90	97.74	162.79	8.00	429.00
	Total	60	133.367	90.10	11.63	110.08	156.64	8.00	432.00
Production /culm	1998	30	0.15	1.47E-02	2.69E-03	0.14	0.15	0.10	0.17
	1999	30	0.12	3.79E-02	6.93E-03	0.11	0.13	0.06	0.26
	Total	60	0.13	3.18E-02	4.10E-03	0.13	0.14	0.06	0.26
ANPP	1998	30	432.92	305.07	55.69	319.01	546.84	80.44	1311.32
	1999	30	421.38	305.57	55.79	307.27	535.48	40.03	1602.15
	Total	60	427.15	302.78	39.08	348.93	505.37	40.03	1602.15
Turnover	1998	30	1.35	8.52E-02	1.55E-02	1.32	1.38	1.24	1.47
	1999	30	1.88	0.20	3.78E-02	1.81	1.96	1.57	2.28
	Total	60	1.62	0.31	4.01E-02	1.54	1.70	1.24	2.28

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
Density	Between Groups	576.60	1	576.60	0.07	0.792
	Within Groups	478477.33	58	8249.60		
	Total	479053.93	59			
Production /culm	Between Groups	1.15E-02	1	1.15E-02	13.92	0.000
	Within Groups	4.81E-02	58	8.29E-04		
	Total	5.96E-02	59			
ANPP	Between Groups	2000.08	1	2000.08	0.02	0.884
	Within Groups	5406962.26	58	93223.48		
	Total	5408962.34	59			
Turnover	Between Groups	4.25	1	4.25	169.20	0.000
	Within Groups	1.46	58	2.51E-02		
	Total	5.71	59			

Table 34. Interannual comparison of *S. patens* density (# 0.0625 m^{-2}), production/culm (g culm^{-1}), ANPP (g m^{-2} yr^{-1}), and turnover (yr^{-1}).

		N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Min.	Max.
						Lower Bound	Upper Bound		
Density	1998	30	226.93	169.54	30.95	163.62	290.24	0.00	723.00
	1999	29	185.06	105.28	19.55	145.02	225.11	47.00	443.00
	Total	59	206.35	142.01	18.48	169.34	243.36	0.00	723.00
Production /culm	1998	29	0.15	8.34E-02	1.54E-02	0.12	0.18	0.11	0.58
	1999	29	0.12	3.88E-02	7.20E-03	0.11	0.14	0.06	0.24
	Total	58	0.14	6.62E-02	8.70E-03	0.12	0.15	0.06	0.58
ANPP	1998	30	744.26	615.17	112.31	514.55	973.97	0.00	2552.09
	1999	29	453.19	273.20	50.73	349.26	557.11	86.88	1223.56
	Total	59	601.19	496.78	64.67	471.73	730.65	0.00	2552.09
Turnover	1998	29	1.39	0.11	2.11E-02	1.35	1.44	1.24	1.59
	1999	29	1.43	0.21	3.92E-02	1.35	1.51	1.17	1.83
	Total	58	1.41	0.16	2.22E-02	1.37	1.46	1.17	1.83

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
Density	Between Groups	25843.79	1	25843.79	1.29	0.261
	Within Groups	1143983.72	57	20069.89		
	Total	1169827.52	58			
Production /culm	Between Groups	1.34E-02	1	1.34E-02	3.10	0.080
	Within Groups	.23	56	4.23E-03		
	Total	.25	57			
ANPP	Between Groups	1249310.95	1	1249310.95	5.45	0.023
	Within Groups	13064862.08	57	229208.10		
	Total	14314173.04	58			
Turnover	Between Groups	2.01E-02	1	2.01E-02	0.70	0.407
	Within Groups	1.61	56	2.88E-02		
	Total	1.63	57			

5. DISCUSSION

I will discuss the three major issues addressed in this study. I will first describe the biology and phenology of *D. spicata* and *S. patens* on a scale of individual culms and a square meter basis. Next I will address the method for estimating ANPP, cover the variation found between years, and give insight into how future estimates may be made. Finally, I will cover four different aspects of growth of these species; (1) density, (2), ANPP, (3), production per culm, and (4) turnover, and place these in the context of sea level rise and the transition of high marsh into a hollow and hummock microtopography.

One goal of the present study was to assess how *D. spicata* and *S. patens* grow from a naturalist perspective. Species-specific patterns indicate these species grow differently, but there are also some similarities. *D. spicata* typically experienced rapid growth through June, when growth slowed considerably. *S. patens* showed more of a consistent rate of growth through August, when growth stalled and culm mortality increased.

5.1. *D. spicata* growth

The most important variable in aboveground production per culm of *D. spicata* is culm height, given the stem of the culm weighs more than the leaves. In fact, leaf number and leaf length can be considered to be dependent on culm height. Rapid growth of *D. spicata* continued through June when a culm averaged 29 cm. Then growth slowed until August where a culm averaged 31 cm (Appendix 6). Rapid growth can also be seen on meter square scales as increases in biomass and density ceased in June (Appendix 6). Rapid growth is likely a result of cooler temperatures and ample groundwater in late spring and early summer as found for *D. spicata* in southern Utah by Hansen and co-workers (1976) (Figure 9). The ability for *D. spicata* to grow rapidly as shown here may benefit its ability to colonize disturbed areas as found by Bertness (1991b).

Although vertical growth of *D. spicata* stalled by June, growth continued in other ways. For example, although the number of brown leaves per culm increased from May (2 brown leaves) to September (7 brown leaves), the number of green leaves per culm remained steady from June to August at approximately 7 leaves (Figures 16e-f). Thus an increase in leaf number occurred during these months. This is supported by the fact the height to the uppermost leaf increases considerably from June to September (Figure 16d). Although new leaves that sprouted towards the end of the growing season do occured higher on the culm, they typically were shorter than leaves present lower on the culm. A pattern of slight decrease in live culms per square meter was seen from June to August (Figures 16b-c), but biomass (g dry mass m^{-2}) showed no such pattern. This too indicates culm production of leaves continued after maximum culm height is reached.

Culm height data indicate that June may be the time when growth of *D. spicata* stalls, but leaf number per culm increases after June. Collectively these data indicate harvesting EOYB of *D. spicata* in upper Phillips Creek in June to assess ANPP would be premature, and would be best assessed in August to allow for leaf proliferation and growth. Bellis and Gaither (1985) in North Carolina, and White and co-workers (1978) in Louisiana have also suggested that August is the best month to capture peak standing stock.

5.2. *S. patens* growth

As in *D. spicata*, the most important variable in production per culm of *S. patens* is culm height. However, peak culm height of *S. patens* was not reached in June as in *D. spicata.* Rapid growth of culm height of *S. patens* slowed by July, and average culm height generally peaked in August at 40 cm (Appendix 6). This is similar to a study by Broome and co-workers (1995) that found *S. patens* to peak at 35-44 cm in a Louisiana marsh. Data of biomass and density also indicate *S. patens* takes longer to grow than does *D. spicata* (Figures 17 e-f).

The average number of green leaves and brown leaves per *S. patens* culm remained stable from June through August at approximately 3.5 and 1.5, respectively (Appendix 6), indicating *S. patens* produced the majority of its leaves by May. Culms of *S. patens* produced less new leaves than *D. spicata*, but production is more by elongation of leaves established early in the growing season. I found no data in the literature that discusses such findings. The average biomass and density of living *S. patens* increased through August, and declined in September as a result of culm mortality (Figures 17e-f).

In summary, at upper Phillips Creek marsh *S. patens* grew approximately 10cm taller than *D. spicata*, and took an additional 2 months to do so. The vertical growth of *S. patens* through August was more consistent across years than growth of *D. spicata. S. patens* also had fewer and longer leaves on each culm than *D. spicata.* Biomass, density, and culm height data collectively indicated the best time to harvest EOYB in upper Phillips Creek marsh to assess *S. patens* ANPP was in August. However, White *et al.* (1978) did conclude June was the best month to capture peak standing stock of *S. patens* in a Louisiana marsh.

5.3. Method of estimating ANPP, current and future

In this study, the method of measuring primary production encompassed harvesting EOYB during September, and adding estimated values of mass of leaf fall and mass of culm mortality that occurred prior to EOYB. This method had both its advantages and disadvantages. I will now discuss the method and its results, and justify streamlining the method while maintaining its integrity for future estimates.

Turnover per year was calculated by dividing ANPP by EOYB in September. The difference between ANPP and peak standing stock is the amount of material produced in the growing season that is not counted in the live biomass harvest. This study focused on leaf loss and culm mortality during the growing season to better assess ANPP. The three components of the turnover estimate were EOYB harvested in September, estimated leaf loss, and culm mortality. The contribution of leaf mass loss to the estimate of turnover increased from 1998 to 1999 in both species. However, culm mortality comprised the majority of mass lost during each growing season (Figures 21a-b). Therefore, the ability to assess the mortality of culms of each species during a growing season is more vital than capturing lesser amounts of leaf fall to estimate ANPP.

The mortality of tagged culms prior to September of 1998 were similar for *D. spicata* (29 of 112 culms) and *S. patens* (31 of 112 culms) (Table 4). The difference of culm mortality between species increased in 1999, as mortality of tagged culms prior to September increased to 44 of 108 culms of *D. spicata*, and decreased to 20 of 105 culms of *S. patens*.

Variability in culm mortality was the driving force in the differences in turnover calculations between years. The highest variability among zones in turnover per year occurred in the hummock zone for *D. spicata* (1998=1.45, 1999=2.06) and *S. patens* (1998=1.49, 1999=1.65) (Table 35). For comparison, I calculated turnover of *S. patens* from Waits (1967) who reported production (1296 g m^{-2} yr^{-1}) and peak standing stock values (640 g m^{-2}) from a North Carolina marsh, turnover of *S. patens* in a North Carolina marsh would have been 2.03. If Hopkinson and co-workers (1980) calculated turnover from production (1967 g/m^{-2}/yr^{-1}) and standing stock values (505g/m^{-2}), turnover of *D. spicata* in a Louisiana marsh would have equaled 3.9.

It would have been convenient for future ANPP estimates if the estimated turnover of each species in each zone were not as variable as between 1998 and 1999. The average turnover for each species at each zone could then be used to multiply with future EOYB taken in September and result in an accurate estimate of ANPP (e.g. $ANPP_{zone}$=($EOYB_{living}$*Mean turnover). However, turnover of each species in upper Phillips creek can vary between zones and between years, especially for *D. spicata* (Table 35). The end result of using an average turnover for each species would be an overestimate of ANPP one year and an underestimate another year (Figure 33).

This research is a short-term contribution to a long term ecological research site that will likely monitor multiple conditions in the high marsh of upper Phillips Creek for years to come. For future estimates of ANPP, I suggest harvesting EOYB in August, in addition to assessing culm mortality with previously tagged culms that year (50-100/zone). If production will be estimated in different zones, it will be necessary to

Table 35. Estimated turnover rates (yr^{-1}) of each species by zone and year.

	YEAR			
	1998		1999	
	Species		Species	
	D. spicata	*S. patens*	*D. spicata*	*S. patens*
	Mean	Mean	Mean	Mean
Creek	1.30	1.47	1.91	1.90
Non-hummock	1.28	1.28	1.71	1.23
Hummock	1.45	1.49	2.06	1.65

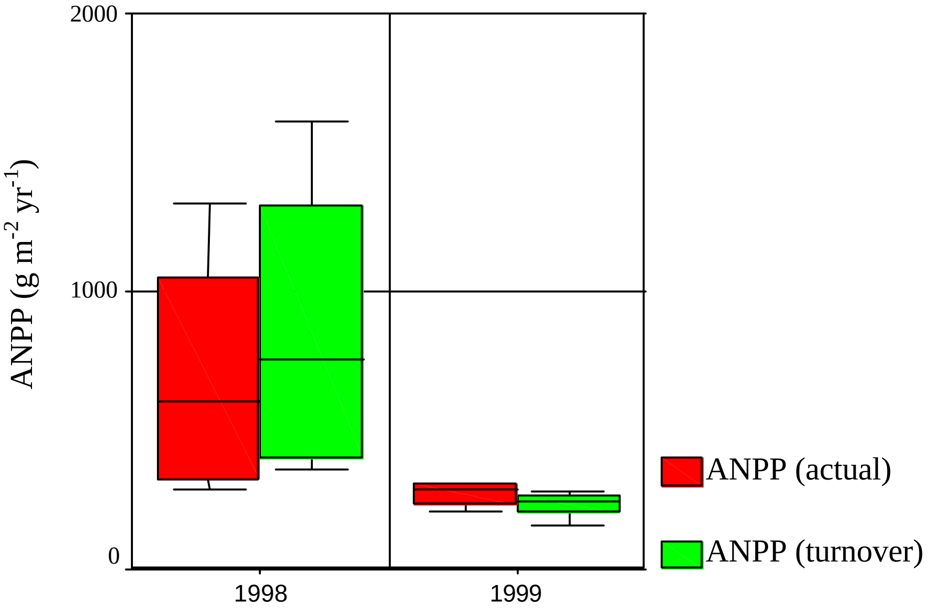


Figure 33. Actual ANPP of *D. spicata* vs. ANPP estimated from mean turnover in Creek zone.

monitor mortality through August in each zone. By harvesting one month earlier and assessing mortality in each zone, correction factors and potential error will be reduced, ultimately resulting in a more accurate estimate of ANPP.

The mass that dies prior to August via culm mortality should be estimated by the following equation: Mass of future culm mortality (g) = The number of dead culms prior to August (m^{-2}) * (harvested green mass (g)/harvested density (m^{-2}).

Leaf loss of each species typically occurs when a leaf on a stem dies, becomes brittle over time, and falls to the ground. The need for monitoring culms on a regular basis to assess relatively small amounts of mass lost in leaves is not as vital to ANPP estimates as the need to assess culm mortality. This is seen when the estimates of production at each site are broken down into their 3 components (Figures 21a-b). For future estimates I suggest leaf loss be estimated from the regression equations of mass lost in leaves vs. mass lost in culm mortality in each species in 1998 (Figures 21c-d). This would save significant amounts of field work for results that contribute relatively little to the overall estimate.

Future ANPP estimates should be calculated for each species at each zone by the following equation: ANPP ($g\ m^{-2}\ yr^{-1}$) = Biomass produced by August (EOYB) ($g\ m^{-2}\ yr^{-1}$) + Mass of culm mortality ($g\ m^{-2}\ yr^{-1}$) + Mass of leaf loss ($g\ m^{-2}\ yr^{-1}$).

This method could be applied in other marshes, or perhaps other zones in upper Phillips Creek marsh in which these species grow. It would be essential to assess mortality prior to peak standing stock and to harvest EOYB at the time of the peak standing stock. Other studies indicate that time of peak standing stock may depend on geographical location (Turner 1976, Pennings and Bertness 1999b)

5.4. Evaluation of the Creek zone

I discuss results from the Creek zone separately from Hummock and Non-hummock zones because it represents a high marsh to low marsh transition zone that is more directly affected by the encroachment of Phillips Creek. There appear to be advantages and disadvantages for both species growing adjacent to the creek, where species co-exist. Density and production of *D. spicata* in the Creek zone appears to be limited, but not excluded, by competition with *S. patens*. *S. patens* appears to out-compete *D. spicata* at upper Phillips Creek in this area. This environment appears to benefit from what is known as the streamside effect, which has been studied primarily on marshes dominated by *S. alterniflora* (Delaune *et al*. 1983, Mendehlsson and McKee 1992).

The Creek zone is potentially the most productive zone in the high marsh for several reasons. Benefits in this area include soil drainage, which decreases soil toxicity and increases soil redox potential, and tidal deposition of inorganic nutrients (Burdick *et al.* 1989, Pennings and Bertness 1999a). When ground water data were collected during the growing season, other zones at upper Phillips creek experienced aboveground flooding until at least June of 1998 and May of 1999, but I never mesured groundwater above 0 cm in the Creek zone. Therefore the potential for lower soil toxicity in the creek zone likely played a role in the overall success of each species. Additionally, it is not uncommon to walk around the border of the Creek zone and cave in the turf. Local tunneling by muskrats (*Ondatra zibethicus*) is the likely contributor (personal observation). Tunneling has been shown to increase nitrogen mineralization and nitrification rates at the creekbank by soil aeration and decreasing uptake by plants because of herbivory (Connors *et al*.2000).

ANPP estimates were most variable at the creek . I suggest the patchiness in ANPP seen here is influenced by "cowlicks". Cowlicks form as a result of incoming tides that cause culms to lean over on adjacent culms. When these culms (that average 40 cm or more) lean over, they shade out their neighbors. Thus, if a 0.0625 m^2 quadrat were randomly placed under a cowlick for harvesting, production estimates would be diminished as a result.

Although the Creek zone can be highly productive, cowlicks are not the only potential limiting factor. Another potential cause of stress is that this zone experiences low groundwater during the growing season, at least down to 25 cm below the marsh surface (Figure 9, Table 9). Therefore, when this zone is inundated by salty creek water up to 36 ppt (Appendix 2), salinities my be stressful (Warren and Brockelman 1989, Broome *et al* 1995.

5.5. Background on Hummock and Non-hummock zones

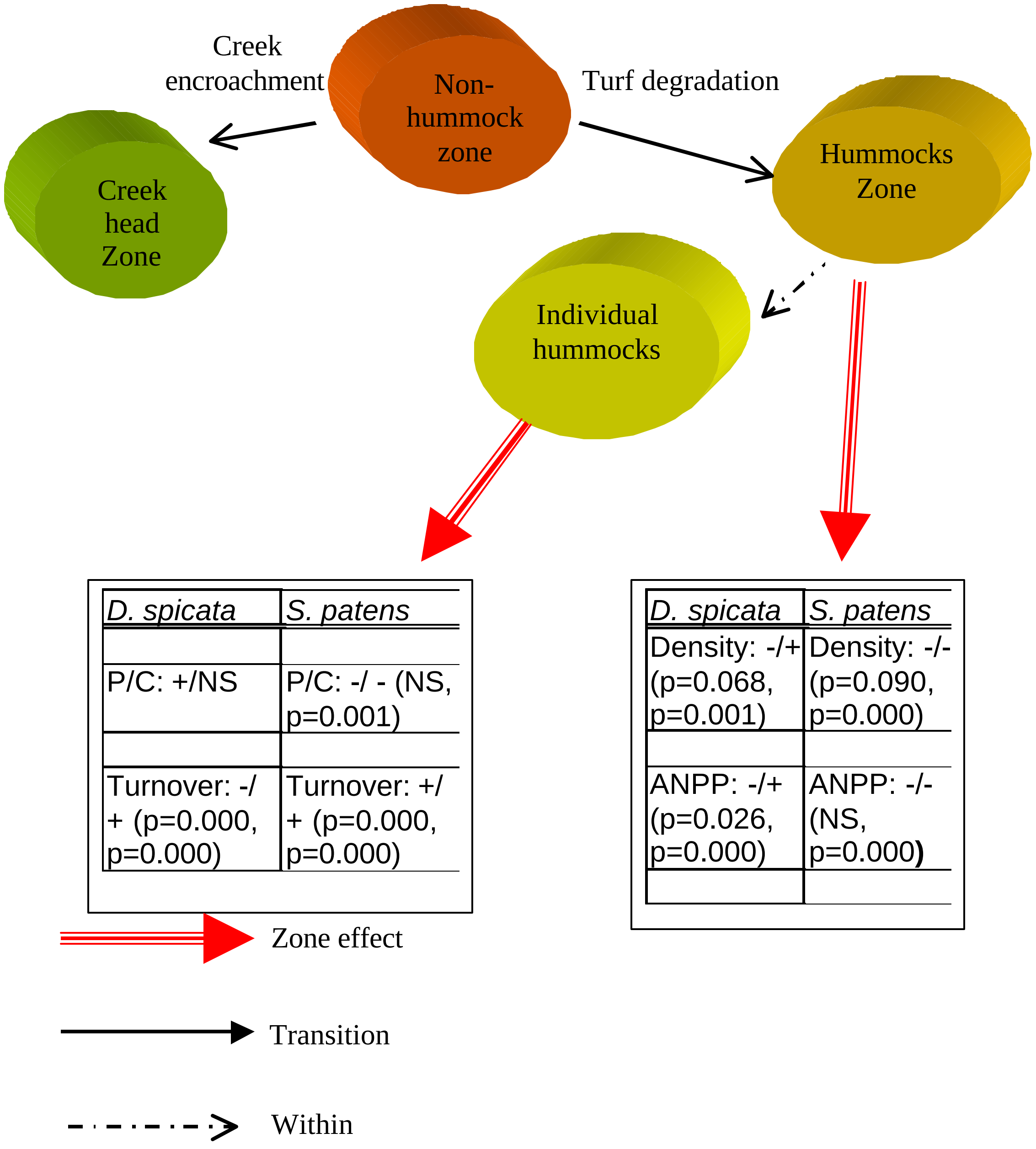
The Hummock zone was shown to have higher groundwater than the Non-hummock zone partly as a result of slightly lower elevations (Appendix 1, Figures 9a-b). The Hummock zone additionally had higher groundwater salinities. (Figures 10a-b).

Both water table height and salinity have been shown to stress *S. patens* more than *D. spicata* (Smart and Barko 1978, Kemp and Cunningham 1981, Bandyopadhyay *et al*. 1993, Broome *et al*. 1995).

Patchiness of ANPP from cowlicks can occur in the Non-hummock zone (Figure 27b, Figure 28b). However, patchiness that occurred in Hummock areas was a result of hollows that experienced longer periods of ponding than hummocks (personal observation). This is why growth in the Hummock zone was analyzed on 2 scales, the Hummock and hollow zone, and individual hummocks. Based on observations of higher stress and less surface area for culms to colonize in the Hummock zone, I developed the first two hypotheses.

5.5.1. Evaluation of H1: *S. patens* will out-produce *D. spicata* in the Non-hummock zone, and *D. spicata* will out-produce *S. patens* in the Hummock zone.

Results indicate Non-hummock areas were typically more desirable for both species than Hummock areas at upper Phillips Creek marsh (Figure 34). *S. patens* easily out-produced *D. spicata* in the Non-hummock zone as hypothesized. However, if *D. spicata* were given an opportunity to colonize Non-hummock areas without the presence of *S. patens*, it would likely be more productive due to a release from interspecific competition in this zone as found by Bertness (1991b) in a New England marsh. ANPP of *S. patens* was lower in the Hummock than Non-hummock zone. This was a result of lower densities and shorter culms (Figure 28a, Figure 28c). This supports findings made by Broome and co-workers (1995), Morris (1984), and Burdick and co-workers (1989)



D. spicata	*S. patens*
P/C: +/NS	P/C: -/ - (NS, p=0.001)
Turnover: -/+ (p=0.000, p=0.000)	Turnover: +/+ (p=0.000, p=0.000)

D. spicata	*S. patens*
Density: -/+ (p=0.068, p=0.001)	Density: -/- (p=0.090, p=0.000)
ANPP: -/+ (p=0.026, p=0.000)	ANPP: -/- (NS, p=0.000**)**

Figure 34. Species response to zone in the context of high to low marsh state change. P/C = production per culm, ANPP = Aboveground Net Primary Production, NS = not significant. The first sign indicates hypothesized response in the Hummock zone relative to the Non-hummock zone, while the sign on the opposite other side of the slash is the response found. A positive means higher value in the Hummock zone than the Non-hummock zone. The first value in parentheses represents 1998 data, while the second value indicates 1999 data.

that *S. patens* is limited by saturated soils (as in the high water table of hummock areas).

D. spicata was generally more productive in the Hummock zone than *S. patens* as hypothesized, but higher turnover was an indication of stress relative to the Non-hummock zone. *D. spicata* appeared to experience higher production in this zone as a result of *S. patens*' lack of ability to colonize stressed areas as found by Bertness (1991b). It is probably because of less inter-specific competition from *S. patens* that *D. spicata* had higher production in the Hummock zone than the Non-hummock zone. This occurred regardless of the generally stressed nature of Hummock areas. Therefore, I conclude that competition with *S. patens* in the Non-hummock zone may limit *D. spicata* more than stressing edaphic conditions.

5.5.2. Evaluation of H2: Hummock zones will have negative effects on growth per unit area, and positive effects on growth of *D. spicata* only on Hummocks.

As predicted, *S. patens* showed negative effects on growth characteristics that occurred on a per unit area scale (i.e. ANPP and density) in addition to the hummock scale (i.e. production per culm and turnover). However, results found for *D. spicata* in Hummock zone were not as predictable. In fact, Hummock zones actually had positive effects on *D. spicata* ANPP and density relative to the Non-hummock zone, while having negative effects on the hummock scale by having higher turnover (Figure 34).

From these findings two conclusions can be made. The first is that the Hummock zone is stressful for all aspects of growth of *S. patens*. The second is that although *D. spicata* may benefit from a decreased competition with *S. patens* by having higher production and density in the Hummock zone, it too can be stressed as indicated by having a higher turnover. Therefore, because of a higher turnover of *D. spicata* in the Hummock zone (Table 35), I conclude that culms of *D. spicata* in Hummock areas appear to show signs of stress from high groundwater and groundwater salinities through turnover, rather than by a significant reduction in ANPP. Based on the results found on the four aspects of growth measured, the hypothesis is not accepted for *D. spicata*, but is accepted for *S. patens* (Figure 34).

5.6. Background to ponding experiment

The purpose of simulating spring tides during the growing season was to assess the effects of sea level rise on the growth of *D. spicata* and *S. patens* in Hummock and Non-hummock areas. The goals of this short-term study are in keeping with the focus of the long-term ecological research occurring at the Virginia Coast Reserve examining impacts of sea level rise on coastal areas (Hayden *et al*. 1991).

When compared to 1998, high creek salinities (Figure 14) in 1999 were a result of a lower precipitation earlier in the growing season. In fact, more precipitation fell by from March to June of 1998, than from March to August of 1999 (Figure 13). Thus any short-term effects of increased inundation on the high marsh community would have likely been more discernible in a year with low precipitation such as 1999.

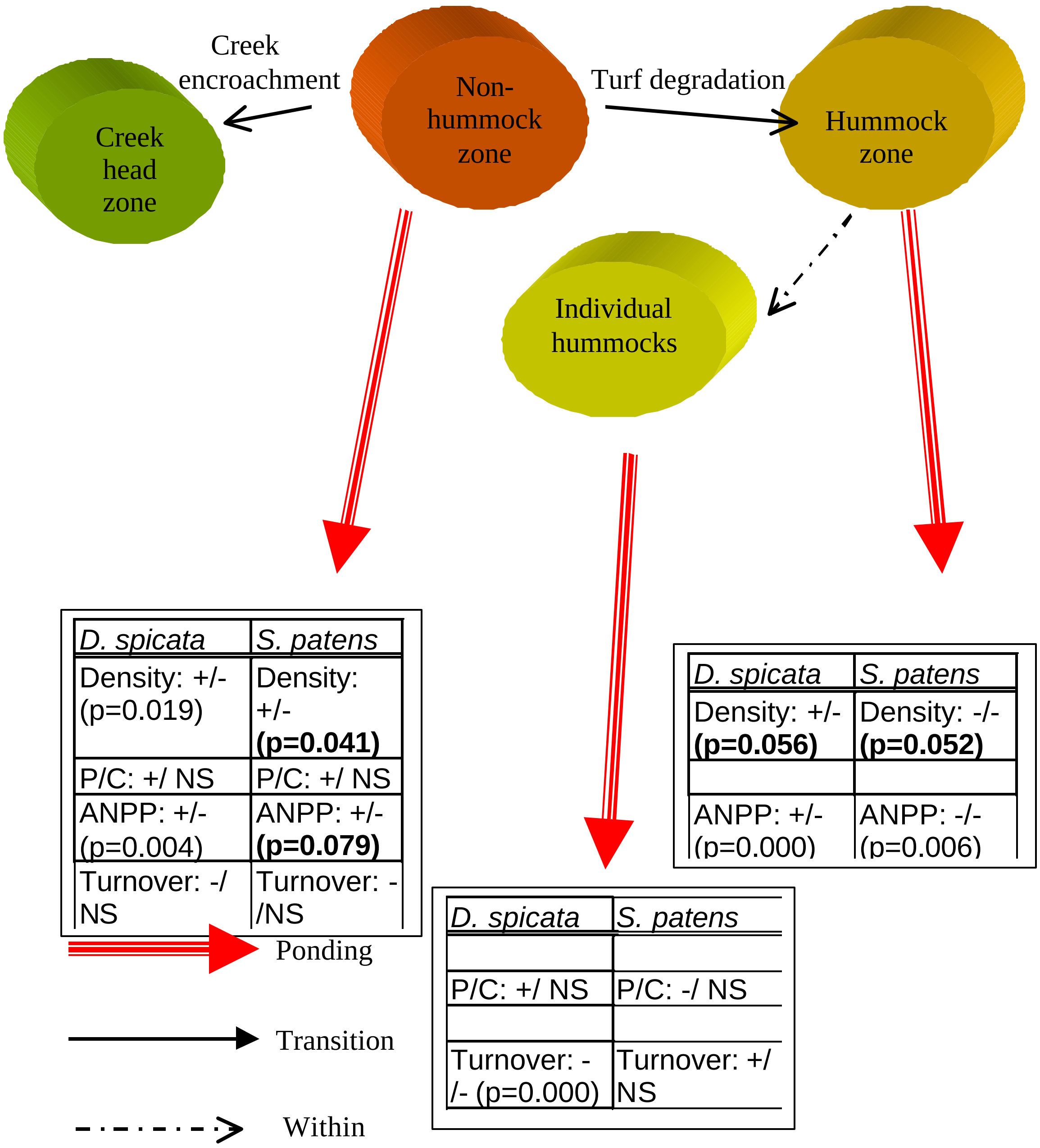
The belowground border at times showed similar effects as ponding. Therefore, some effects of ponding may have been masked by the subsurface border. It is likely the belowground border restricts groundwater movement and may damage the underground rhizomes upon insertion.

5.6.1. Evaluation of H3: Monthly tidal simulations (i.e. ponding) will have an overall positive effect on growth characteristics of each species in the Non-hummock zone.

Ponded water from pumping was absorbed relatively quickly (between 45-65 minutes), so I did not forsee ponding to cause limiting or low redox conditions. Instead, I predicted adding water to Non-hummock areas during summer months when a lack of water would be greatest would ultimately benefit *D. spicata* and *S. patens.*

Stress observed from ponding on ANPP of *D. spicata* in the Non-hummock zone could not be discerned from stress observed with an underground border. Ponding reduced *D. spicata* density. However, a similar pattern occurred in the subsurface control. Therefore, I could not attribute negative effects on density solely to a ponding effect. I conclude that ponding did not have a positive effect on *D. spicata* in the Non-hummock zone as originally hypothesized, and further conclude that altering the belowground hydrology by inserting a plywood border 10 cm belowground may have altered aboveground characteristics of *D. spicata* more than ponding in this second year of study (Figure 35).

Contrary to the hypothesis, aspects of *S. patens* growth showed no positive response to ponding in the Non-hummock zone. In fact, negative effects were found through density and ANPP variables of *S. patens*. *S. patens* aboveground and belowground production have been shown to be reduced in low salinity ($\leq$15 ppt)



D. spicata	*S. patens*
Density: +/- (p=0.019)	Density: +/- **(p=0.041)**
P/C: +/ NS	P/C: +/ NS
ANPP: +/- (p=0.004)	ANPP: +/- **(p=0.079)**
Turnover: -/ NS	Turnover: -/NS

D. spicata	*S. patens*
Density: +/- **(p=0.056)**	Density: -/- **(p=0.052)**
ANPP: +/- (p=0.000)	ANPP: -/- (p=0.006)

D. spicata	*S. patens*
P/C: +/ NS	P/C: -/ NS
Turnover: -/- (p=0.000)	Turnover: +/ NS

Figure 35. Species response to ponding in the context of high to low marsh state change. P/C = production per culm, ANPP = Aboveground Net Primary Production, NS = not significant. The first sign indicates hypothesized response, while the sign on the opposite other side of the slash is the response found. The p-value <0.10 are reported. P-values in bold font indicate a similar pattern was not found in subsurface control plots.

and flooded conditions (Naidoo *et al*. 1992, Bandyopadhyay *et al*. 1993). Smart and Barko (1978) suggested that *S. patens* is stressed in high sediment salinties. Bandyopadhyay and co-workers (1993) suggested that *S. patens* roots are more affected by hypoxia, but high salinities can also stress the plant. Therefore, I attribute the negative response of *S. patens* to pumping high salinity creek water on these plots (Figure 14).

5.6.2. Evaluation of H4; *S. patens* in the Hummock zone will show signs of stress to ponding, (b) *D. spicata* in the Hummock zone will respond positively if competition with *S. patens* is reduced.

The acceptance of H2 suggests *S. patens* in the Hummock area appears to be more stressed than *D. spicata.* H4 develops this idea further in saying that ponding in this already stressed area will also have a negative affect on *S. patens* growth. Given the expected negative response of *S. patens*, in addition to *D. spicata* being more resilient to the increased ponding (Baldwin and Mendehlssohn 1998); one might expect *D. spicata* to benefit from a decreased competition with *S. patens* as proposed by Bertness (1991b). As before, only trends or significant results of ponding that were not negated by results found for subsurface controls will be discussed (Figure 35).

S. patens showed negative trends to ponding in forms of lower density and ANPP as may be expected based on results by Broome and co-workers (1995) and evaluation of my second hypothesis. However, ANPP was also negatively affected by belowground borders and will not be discussed as ponding effects. *S. patens* showed no significant sign of stress to ponding in the Hummock zone through production per culm or turnover.

The hypothesis is partially accepted for *S. patens* because it did show a sign of stress from ponding in the Hummock zone through decreased density (Figure 35).

D. spicata showed signs of stress to ponding through density, ANPP, and turnover variables. However, ANPP and turnover were also affected by the belowground border. There was a trend found towards lower density (p=0.056) (Figure 30a). There was no positive growth response to ponding by *D. spicata* in the Hummock zone as hypothesized, and a questionable slight response through decreased density. This is likely due to adding relatively high salinity water (> 30 ppt) to a saturated zone during the growing season. From these findings I conclude that increased inundation in the Hummock zone had more of a negative effect on *D. spicata* than the reduction of competition with *S. patens* had as a positive effect.

5.7. Interannual comparisons

Interannual comparisons of growth variables of each species were examined. De Leeuw and co-workers (1990) and Morris and Haskin (1990) each found that lower precipitation patterns during the growing season have negative effects on vegetative growth in a salt marsh. More precipitation was received from March to June of 1998 than by from March to August of 1999 in upper Phillips Creek marsh, signifying a lack of precipitation during the crucial months of growth in 1999. Lower precipitation, in turn, decreased groundwater depth, increased groundwater salinities, and increased creek salinities in 1999 relative to 1998 (Figures 9, 10, and 14).

These cumulative effects were likely the driving forces behind lower production per culm and higher turnover *of D. spicata* in 1999 compared to 1998 (Figures 30 a-b,

Table 34). These effects also likely influenced significantly lower ANPP in *S. patens* and a trend towards lower production per culm in 1999 compared to 1998. (Figures 31 a, c, Table 34).

An interesting pattern appeared in Hummock areas where ANPP of *S. patens* declined considerably in hummock areas in 1999 compared to 1998. Meanwhile, ANPP and turnover of *D. spicata* increased from 1998 to 1999 (Figure 32). This, along with other findings of this study suggest that *D. spicata* ANPP may benefit from a lack of competition with *S. patens*. However, *D. spicata* will show signs of being stressed through turnover. These results indicate competition with *S. patens* may limit *D. spicata* more than the stresses found in Hummock areas. To my knowledge, these findings have never before been reported in the literature.

When interannual variation in this study is considered, ANPP of Hummock zones that are dominated by *D. spicata* can be comparable to ANPP of Non-hummock zones that are dominated by *S. patens* (Figure 36). This finding is comparable to that of Nyman and co-workers (1994) who found no difference in aboveground biomass of *S. patens*, (the dominant species), in "broken" and "unbroken" (i.e. hummock and non-hummock) parts of a Louisiana marsh. This finding, in turn, forced them to reject the hypothesis that marsh loss was related to vegetation change.

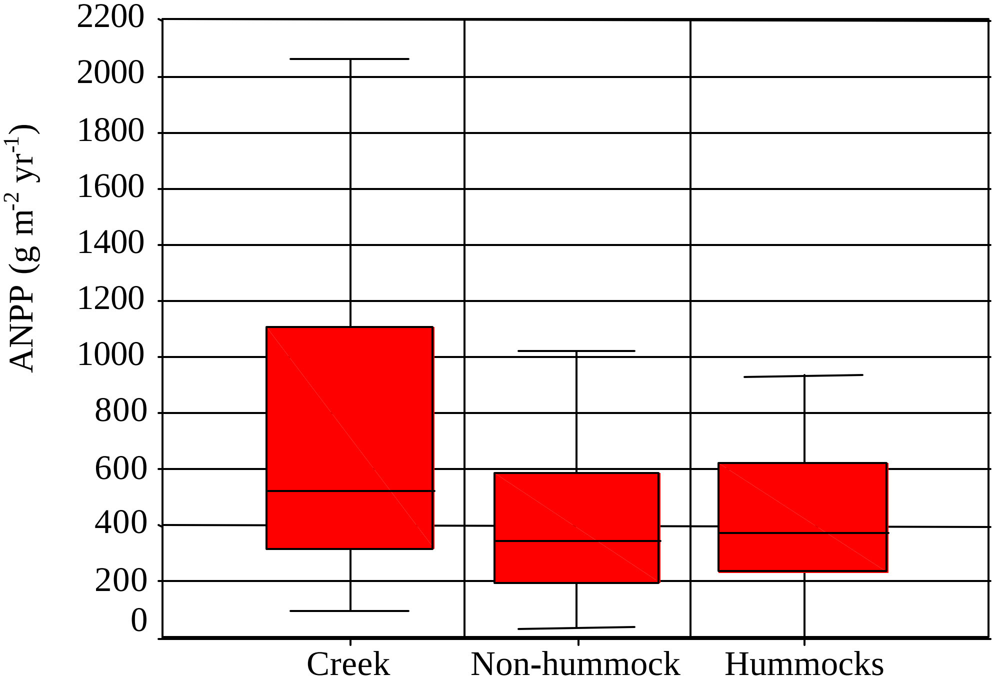


Figure 36. Average total ANPP by zone.

5.8. Relationship to state change model of Brinson and co-workers (1995) and Christian and co-workers (2000)

Results of this study indicate an increase in sea level and frequency of inundation in a high marsh will likely facilitate a decrease in production of *S. patens*, and eventually a decrease in production of *D. spicata.* This limited production will likely facilitate subsidence and result in an increase in ponding in these areas. This would facilitate the positive feedback loop identified by Nyman and co-workers (1993) and DeLaune and co-workers (1994) for Louisiana marshes.

Over the long-term, one might expect these hollows to enlarge and coalesce due to a combination of vegetative dieback (DeLaune *et al*.1994) and erosion at the sediment water interface (Nyman *et al*. 1994) in the high marsh because of the positive feedback loop. This would facilitate the process of the high marsh becoming connected to tidal creeks. Once connected, the area that was once originally a functional high marsh, would become an intertidal low marsh via the development of the hummock and hollow area as proposed by Brinson *et al*. (1995) and Christian and co-workers (2000).

6. CONCLUSIONS

D. spicata and *S. patens* produce a significant amount of aboveground biomass during the growing season that is not a component of September EOYB harvests. Estimating ANPP from EOYB can be an underestimate by not accounting for processes such as leaf loss, culm mortality, dissolved organic matter export, and herbivory. In this study, I quantified the amount of biomass lost to leaf fall and culm mortality to better estimate ANPP of these species in 1998 and 1999. I suggest future ANPP estimates be derived from harvesting EOYB in August, in addition to assessing mortality through a modest effort in tagging, and estimating mass lost in leaves from a significantly positive relationship with the mass lost in culm mortality.

I am unaware that turnover of *D. spicata* and *S. patens* has ever been directly reported in the primary literature. In 1998 and 1999 in upper Phillips Creek marsh, *D. spicata* had a turnover range of 1.25-1.89 per year, while *S. patens* had a turnover range of 1.25-1.74 (Table 21). End of year biomass accounted for 54-70% of an ANPP of *D. spicata* which ranged from 400-450 g m^{-2} yr^{-1}, and 70-72% of ANPP in *S. patens* that ranged from 425-775 g m^{-2} yr^{-1} between 1998 and 1999 (Table 20).

The observational hypotheses were created in context of aboveground response of each species to stages of high marsh transition to low marsh. Based on prolonged ponding during the growing season and less surface area for culms to establish because of hollow areas, I predicted ANPP would be lower in the Hummock zone. I also predicted *D. spicata* to be the dominant species in the Hummock zone since *S. patens* lacks vital arenchyma (Naidoo *et al.* 1992) and is believed to be less adapted to stressful conditions

(Bertness 1991b). I further predicted production of each species would be higher in the Non-hummock zone. I treated the creek bank zone separate from other zones since it was located adjacent to Phillips Creek and possessed both advantages and disadvantages unique to this zone.

The Creek zone was found to be most productive but most variable due to patchiness that occurs as a result of cowlicks. It appears both species are successful at the Creek zone. Here, each species is flooded more often, yet experiences a lower water table as result of water draining into the creek.

D. spicata was the dominant species in the Hummock zone as hypothesized. However, average total production per zone indicated Hummock zones can be just as productive as Non-hummock zones, where *S. patens* was found to be more dominant. This collectively is consistent with my conclusion that *S. patens* limits success of *D. spicata* through competition more than do stresses present in the Hummock zone.

Experimental hypotheses were formed in context of aboveground species response to a gradual rise in sea level at each high marsh transitional stage. I assumed production of these species at upper Phillips Creek was limited by water and nutrients during summer and predicted simulating high tide events during each month of the growing season in 1999 would increase ANPP.

Inserting a border around plots and ponding plots to simulate high tide events during the growing season had an overall negative effect on density and ANPP of each species in Hummock and Non-hummock areas. However, results found in subsurface control plots were similar to those of ponding in half of these findings. Therefore, ponding alone may not have been responsible for the found effects.

It does appear ponding had a negative effect on density and ANPP of *S. patens* in Non-hummock areas, but the negative trend found on density of *D. spicata* in the Hummock zone is questionable. Given this, I conclude *D. spicata* will become the dominant species in Non-hummock areas as sea level rises and stresses *S. patens*, regardless of whether Non-hummock areas remain intact or develop into Hummock areas. However, possible negative effects of ponding on *D. spicata* density in Hummock zone indicate *D. spicata* will eventually be negatively affected by sea level rise.

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APPENDIX A. SITE ELEVATIONS

Site	Mean Elevation (m)	Std Deviation (m)
1	1.03	0.06
2	1.03	0.02
3	1.05	0.05
4	1.09	0.06
5	1.01	0.03

APPENDIX B. 1998-1999 PUMPING DATA.

Year	Date	Plot	Creek salinity (ppt)	Plot salinity (ppt)	1st Pump duration (min)	Depth lost (cm)	Volume absorbed (L)	2nd Pump duration (min)
1998	29-Jun	2P1	NR	NR	NR	NR	NR	NA
1998	29-Jun	2P2	NR	NR	NR	NR	NR	NA
1998	29-Jun	4P1	NR	NR	NR	NR	NR	NA
1998	29-Jun	4P2	NR	NR	NR	NR	NR	NA
1998	29-Jun	5P1	NR	NR	flooded	flooded	flooded	flooded
1998	29-Jun	5P2	NR	NR	flooded	flooded	flooded	flooded
1998	24-Jul	2P1	15	24	5	NR	NR	NA
1998	24-Jul	2P2	15	24	6	NR	NR	NA
1998	25-Jul	4P1	15	22	7	NR	NR	NA
1998	25-Jul	4P2	15	21	7	NR	NR	NA
1998	25-Jul	5P1	15	18	6	NR	NR	NA
1998	25-Jul	5P2	15	20	5	NR	NR	NA
1998	22-Aug	2P1	30	32	4	NR	NR	NA
1998	22-Aug	2P2	30	32	4	NR	NR	NA
1998	22-Aug	4P1	30	30	6	NR	NR	NA
1998	22-Aug	4P2	30	30	4	NR	NR	NA
1998	22-Aug	5P1	30	30	7	NR	NR	NA
1998	22-Aug	5P2	30	31	6	NR	NR	NA
1998	23-Aug	2P1	30	32	5	3.2	387	2.5
1998	23-Aug	2P2	30	33	5	3.2	387	1.25
1998	23-Aug	4P1	30	33	5	7.2	871	NA
1998	23-Aug	4P2	30	32	4	3.9	472	NA
1998	23-Aug	5P1	30	27	7	2	242	1.5
1998	23-Aug	5P2	30	32	6	2	242	1.5
1998	26-Sep	2P1	20	NR	3	2	242	1
1998	26-Sep	2P2	20	NR	4	4	484	1
1998	26-Sep	4P1	20	NR	5	0.5	61	NA
1998	26-Sep	4P2	20	NR	3	0.65	79	NA
1998	26-Sep	5P1	20	NR	5	<2	NA	NA
1998	26-Sep	5P2	20	NR	4	<2	NA	NA
1998	27-Sep	2P1	20	NR	4	<2	NA	NA
1998	27-Sep	2P2	20	NR	3.5	2.6	315	NA
1998	27-Sep	4P1	20	25	5	<2	NA	NA
1998	27-Sep	4P2	20	24	5	<2	NA	NA
1998	27-Sep	5P1	20	23	4	1.3	157	NA
1998	27-Sep	5P2	20	24	4	<2	NA	NA
1999	11-May	2P1	22	24	5	1.3	157	1
1999	11-May	2P2	22	24	5	0.6	73	1.5

Apendix B, continued

Year	Date	Plot	Creek salinity (ppt)	Plot salinity (ppt)	1st Pump duration (min)	Depth lost (cm)	Volume absorbed (L)	2nd Pump duration (min)
1999	11-May	4P1	22	22	8	1	121	na
1999	11-May	4P2	22	22	5	0.6	73	na
1999	11-May	5P1	22	11	flooded	flooded	flooded	flooded
1999	11-May	5P2	22	11	flooded	flooded	flooded	flooded
1999	12-May	2P1	22	20	3.5	1	121	NA
1999	12-May	2P2	22	20	4	0.6	73	NA
1999	12-May	4P1	22	22	5	0.6	73	NA
1999	12-May	4P2	22	22	4	1	121	NA
1999	12-May	5P1	22	11	flooded	flooded	flooded	flooded
1999	12-May	5P2	22	11	flooded	flooded	flooded	flooded
1999	8-Jun	2P1	31	35	7	2	242	3
1999	8-Jun	2P2	31	36	6	2	242	2
1999	8-Jun	4P1	31	33	10	<2	NA	NA
1999	8-Jun	4P2	31	35	6	<2	NA	NA
1999	8-Jun	5P1	31	34	8	2.5	303	1.5
1999	8-Jun	5P2	31	34	7	2.5	303	1.5
1999	9-Jun	2P1	31	30	4	2	242	0.5
1999	9-Jun	2P2	31	36	6	2.5	303	2
1999	9-Jun	4P1	31	34	6	<2	NA	NA
1999	9-Jun	4P2	31	35	7	<2	NA	NA
1999	9-Jun	5P1	31	32	1	<2	NA	NA
1999	9-Jun	5P2	31	32	1	<2	NA	NA
1999	7-Jul	2P1	34	33	6	2.5	303	3
1999	7-Jul	2P2	34	33	6	2.5	303	3
1999	7-Jul	4P1	34	32	5	<2	NA	NA
1999	7-Jul	4P2	34	31	6	<2	NA	NA
1999	7-Jul	5P1	34	31	6	2	242	2.25
1999	7-Jul	5P2	34	32	5	2	242	2
1999	8-Jul	2P1	34	35	5	2.5	303	3
1999	8-Jul	2P2	34	34	5	3	363	2.5
1999	8-Jul	4P1	34	32	4.25	<2	NA	NA
1999	8-Jul	4P2	34	33	4.5	<2	NA	NA
1999	8-Jul	5P1	34	30	5	<2	NA	NA
1999	8-Jul	5P2	34	32	4.25	<2	NA	NA
1999	5-Aug	2P1	33	35	4	2.5	303	2
1999	5-Aug	2P2	33	36	4	2	242.06	2
1999	5-Aug	4P1	33	33	5	<2	NA	NA
1999	5-Aug	4P2	33	35	4.5	<2	NA	NA
1999	5-Aug	5P1	33	35	5	2	242	1
1999	5-Aug	5P2	33	35	5	2	242	1

Appendix B, continued

Year	Date	Plot	Creek salinity (ppt)	Plot salinity (ppt)	1st Pump duration (min)	Depth lost (cm)	Volume absorbed (L)	2nd Pump duration (min)
1999	6-Aug	2P1	34	33	6.25	2	242	2.5
1999	6-Aug	2P2	34	33	6	2	242	2.25
1999	6-Aug	4P1	34	39	4.75	<2	NA	NA
1999	6-Aug	4P2	34	36	4.5	<2	NA	NA
1999	6-Aug	5P1	34	34	5.15	<2	NA	NA
1999	6-Aug	5P2	34	32	6	<2	NA	NA
1999	10-Sep	2P1	33	35	4.25	2.2	266	2
1999	10-Sep	2P2	33	35	3.75	2	242	2.25
1999	10-Sep	4P1	33	34	4	<2	NA	NA
1999	10-Sep	4P2	33	34	4	<2	NA	NA
1999	10-Sep	5P1	33	35	4	<2	NA	NA
1999	10-Sep	5P2	33	36	3	<2	NA	NA
1999	11-Sep	2P1	33	35	4	2	242	2
1999	11-Sep	2P2	33	35	3	2	242	2
1999	11-Sep	4P1	33	34	4	<2	NA	NA
1999	11-Sep	4P2	33	34	4	<2	NA	NA
1999	11-Sep	5P1	33	35	4	<2	NA	NA
1999	11-Sep	5P2	33	36	3	<2	NA	NA

NR = not recorded, NA = not applicable

APPENDIX C. DESCRIPTIVE STATISTICS OF GROUNDWATER DEPTH (GW) (CM) AND SALINITY (PPT) FROM CONTROL PLOTS.

				1998		1999	
				Mean	Std Deviation	Mean	Std Deviation
March	SITE	1	GW	-9	4	-12	4
			SALINITY	5	1	15	9
		2	GW	-1	1	-1	1
			SALINITY	9	1	6	4
		3	GW	6	1	6	1
			SALINITY	5	1	4	3
		4	GW	2	3	2	1
			SALINITY	9	0	12	1
		5	GW	7	3	10	6
			SALINITY	17	2	13	3
April	SITE	1	GW	-7	5	-14	0
			SALINITY	12	2	3	0
		2	GW	-1	3	-1	2
			SALINITY	12	0	4	1
		3	GW	6	2	6	0
			SALINITY	11	1	4	2
		4	GW	2	2	2	2
			SALINITY	24	2	21	6
		5	GW	7	3	7	3
			SALINITY	20	3	12	4
May	SITE	1	GW	-5.7	3.9	-19	1
			SALINITY	19	1	19	1
		2	GW	1	0	-6	3
			SALINITY	16	0.7	18	2.8
		3	GW	7	1	0	4
			SALINITY	21	1	24	6
		4	GW	4	3	-2.	2
			SALINITY	19	1	24	5
		5	GW	8	2	5	0
			SALINITY	17	2	16	1
June	SITE	1	GW	-8	1	-25	0
			SALINITY	8	1	0	0
		2	GW	2	1	-6	1
			SALINITY	9	1	30	6
		3	GW	6	1	-10	0
			SALINITY	8	1	30	0
		4	GW	3	2	-7	2
			SALINITY	16	1	33	1
		5	GW	7	2	-11	3

Appendix C, continued

				1998		1999	
				Mean	Std Deviation	Mean	Std Deviation
			SALINITY	18	2	24	2
July	SITE	1	GW	-11	3	-25	0
			SALINITY	6	1	0	0
		2	GW	-6	6	-11	9
			SALINITY	8	2	27	1
		3	GW	-3	10	-4	0
			SALINITY	6	2	26	0
		4	GW	-5	8	-19	3
			SALINITY	23	4	32	0
		5	GW	4	3	-5	3
			SALINITY	18	1	25	1
August	SITE	1	GW	-18	2	-18	8
			SALINITY	22	1	11	6
		2	GW	-15	5	-6	8
			SALINITY	22	4.1	24	7.6
		3	GW	-15	4	3	6
			SALINITY	12	1	20	9
		4	GW	-11	7	-4	7
			SALINITY	24	9	36	5
		5	GW	-15	6	3	8
			SALINITY	21	3	27	2
September	SITE	1	GW	-16	6	-20	1
			SALINITY	15	2	12	3
		2	GW	-9	3	4	0
			SALINITY	18	2	17	4
		3	GW	-1	1	10	0
			SALINITY	14	1	15	0
		4	GW	-3	4	5	1
			SALINITY	29	4	33	3
		5	GW	0	3	10	3
			SALINITY	21	2	27	2

APPENDIX D. DESCRIPTIVE STATISTICS OF GROUNDWATER DEPTH (GW) (CM) AND SALINITY (PPT) BY TREATMENT.

			1998		1999	
			Mean	Std Deviation	Mean	Std Deviation
March	Control	GW	3	4	4	6
		SALINITY	13	4	10	4
	Ponded	GW	4	6	5	6
		SALINITY	14	4	13	2
	Subsurface control	GW	4	5	5	5
		SALINITY	14	4	10	5
April	Control	GW	2	4	2	4
		SALINITY	19	5	12	8
	Ponded	GW	4	6	4	6
		SALINITY	19	4	13	7
	Subsurface control	GW	4	5	3	5
		SALINITY	19	5	11	8
May	Control	GW	4	3	-1	5
		SALINITY	17	2.0	19	4.8
	Ponded	GW	5	5	0	6
		SALINITY	19	2	19	3
	Subsurface control	GW	6	5	-1	7
		SALINITY	18	2	19	2
June	Control	GW	4	3	-8	3
		SALINITY	14	4	29	5
	Ponded	GW	5	5	-9	5
		SALINITY	16	2	30	5
	Subsurface control	GW	4	4	-11	4
		SALINITY	14	4	28	5
July	Control	GW	-2	7	-12	8
		SALINITY	16	7	28	3
	Ponded	GW	-2	10	-14	10
		SALINITY	17	6	28	5
	Subsurface control	GW	-1	9	-13	7
		SALINITY	16	6	30	5
August	Control	GW	-13	6	-2	8
		SALINITY	22	5	29	7
	Ponded	GW	-12	6	-2	8

Appendix D, continued

			1998		1999	
			Mean	Std Deviation	Mean	Std Deviation
		SALINITY	25	6	29	5
	Subsurface control	GW	-14	6	-1	8
		SALINITY	22	6	28	8
September	Control	GW	-4	5	6	3
		SALINITY	23	5	25	7
	Ponded	GW	-2	6	7	5
		SALINITY	23	3	26	4
	Subsurface control	GW	-3	5	6	3
		SALINITY	22	4	25	7

APPENDIX E. 1999 MEAN AND SD OF CULM HEIGHT (CM), HEIGHT TO FIRST LEAF FROM CULM BASE (CM), HEIGHT TO UPPERMOST (LAST) LEAF (CM),AND NUMBER OF GREEN AND BROWN LEAVES PER CULM FOR *D. SPICATA* AND *S. PATENS.*

		SPECIES			
		D. spicata		*S. patens*	
		Mean	Std Deviation	Mean	Std Deviation
April	Height	9.6	4.1	9.6	4.0
	Height to 1st leaf	NR	NR	NR	NR
	Height to last leaf	NR	NR	NR	NR
	# of green leaves	NR	NR	NR	NR
	# of brown leaves	0.0	0.0	0.0	0.0
	Leaf fall	NR	NR	NR	NR
May	Height	21.8	6.5	27.2	7.1
	Height to 1st leaf	NR	NR	NR	NR
	Height to last leaf	NR	NR	NR	NR
	# of green leaves	5.3	1.5	3.5	0.7
	# of brown leaves	0.0	0.2	0.0	0.2
	Leaf fall	NR	NR	NR	NR
June	Height	29.0	7.9	34.2	9.6
	Height to 1st leaf	8.6	2.8	8.4	2.7
	Height to last leaf	19.6	5.9	16.2	4.8
	# of green leaves	6.8	2.0	3.4	0.8
	# of brown leaves	0.7	0.8	0.6	0.7
	Leaf fall	0.1	0.0	0.1	0.0
July	Height	29.1	8.6	39.0	9.2

Appendix E, continued

		D. spicata		*S. patens*	
		Mean	Std Deviation	Mean	Std Deviation
	Height to 1st leaf	7.9	2.9	8.4	2.8
	Height to last leaf	21.9	7.2	19.8	5.8
	# of green leaves	6.4	2.8	3.2	0.9
	# of brown leaves	1.9	1.5	1.3	0.9
	Leaf fall	0.2	0.1	0.1	0.1
August	Height	32.0	8.3	40.6	9.3
	Height to 1st leaf	8.5	3.1	8.5	3.5
	Height to last leaf	25.1	7.5	21.0	6.2
	# of green leaves	7.1	2.6	3.4	4.3
	# of brown leaves	3.3	1.8	2.0	1.0
	Leaf fall	0.3	0.2	0.3	0.1
September	Height	35.4	9.3	38.9	11.5
	Height to 1st leaf	9.8	3.8	10.1	4.3
	Height to last leaf	29.1	9.0	21.7	7.4
	# of green leaves	5.6	3.1	2.6	1.2
	# of brown leaves	6.5	3.3	2.9	1.3
	Leaf fall	0.7	0.3	0.3	0.1

(NR=not recorded)

APPENDIX F. DESCRIPTIVE STATISTICS OF MASS (G M^{-2}) AND DENSITY (# M^{-2}) IN 1999 OF CONTROL PLOTS USED IN SEPTEMBER.

		Live *D. spicata.*		Live *S. patens*		Dead *D. spicata*		Dead *S. patens*	
		Mean	Std Dev	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
Apr	Mass	18	12	18	17	366	272	755	339
	Density	538	433	700	883	1648	1263	3050	1233
May	Mass	75	33	137	73	372	159	675	292
	Density	1782	835	2563	1524	2157	1055	2346	1115
Jun	Mass	231	109	268	139	717	379	822	421
	Density	2392	1507	2915	1738	2380	1239	2597	1418
Jul	Mass	221	62	447	242	490	254	798	584
	Density	2010	702	3384	1138	2146	1299	3216	1666
Aug	Mass	252	111	496	192	257	172	322	136
	Density	1809	749	3417	1447	1233	582	1725	811
Sep	Mass	219	158	326	228	421	202	406	322
	Density	2084	1393	2891	1698	2489	1495	1969	991

APPENDIX G. COMPONENTS OF ANPP IN 1998 AND 1999.

				1998		1999	
				Mean (g m^{-2})	Std Deviation	Mean (g m^{-2})	Std Deviation
D. spicata	SITE	1	EOYB	536	312	145	30
			Mass in mortality	134	78	100	21
			Leaf loss	27	17	28	9
		2	EOYB	226	124	152	92
			Mass in mortality	43	23	75	45
			Leaf loss	12	4	23	17
		3	EOYB	437	142	413	255
			Mass in mortality	170	55	286	177
			Leaf loss	28	8	75	39
		4	EOYB	154	46	130	30
			Mass in mortality	38	11	80	18
			Leaf loss	10	3	22	5
		5	EOYB	237	182	256	46
			Mass in mortality	92	70	256	46
			Leaf loss	15	12	57	9
S. patens	SITE	1	EOYB	876	499	425	300
			Mass in mortality	340	194	99	70
			Leaf loss	62	33	77	41
		2	EOYB	337	130	437	212
			Mass in mortality	64	24	45	22
			Leaf loss	17	5	43	20
		3	EOYB	632	604	150	61
			Mass in mortality	246	235	47	19
			Leaf loss	20	10	33	11
		4	EOYB	665	217	489	136
			Mass in mortality	166	54	54	15
			Leaf loss	37	7	63	11
		5	EOYB	161	125	130	51
			Mass in mortality	75	58	60	24
			Leaf loss	14	11	34	13

EOYB = End of Year Biomass.

APPENDIX H. COMPONENTS OF DEAD MATERIAL HARVESTED IN SEPTEMBER.

				1998		1999	
				Mean (g m^{-2})	Std Deviation	Mean (g m^{-2})	Std Deviation
D. spicata	SITE	1	Leftover	448	355	396	135
			Culm mortality	134	78	100	21
			Leaf loss	27	17	28	9
		2	Leftover	214	110	171	154
			Culm mortality	43	23	75	45
			Leaf loss	12	4	23	17
		3	Leftover	309	206	276	205
			Culm mortality	170	55	286	177
			Leaf loss	28	8	75	39
		4	Leftover	258	91	125	96
			Culm mortality	38	11	80	18
			Leaf loss	10	3	22	5
		5	Leftover	272	147	128	57.23
			Culm mortality	92	70	256	46.83
			Leaf loss	15	12	57	9
S. patens	SITE	1	Leftover	472	272	176	72
			Culm mortality	340	194	119	57
			Leaf loss	62	33	89	31
		2	Leftover	566	271	750	490
			Culm mortality	64	24	45	22
			Leaf loss	17	5	43	20
		3	Leftover	137	68	183	73
			Culm mortality	246	235	47	19
			Leaf loss	20	10	33	11
		4	Leftover	549	178	287	197
			Culm mortality	166	54	54	15
			Leaf loss	37	7	63	11
		5	Leftover	146	145	75	53
			Culm mortality	75	58	60	24
			Leaf loss	14	11	34	13

Leftover= material leftover from the previous year, Culm mortality = mass lost in culms produced during the growing season, and Leaf loss = mass lost in leaves during the growing season.

APPENDIX I. DESCRIPTIVE STATISTICS OF GROWTH MEASURES BY ZONE AND YEAR. P/C = PRODUCTION PER CULM.

			1998		1999	
			Mean	Std Deviation	Mean	Std Deviation
D. spicata	Creek	Density (# 0.0625 m^{-2})	225	135	94	32
		P/C (g culm^{-1})	0.16	0.00	0.13	0.07
		ANPP (g m^{-2} yr^{-1})	697.86	408.01	274.45	47.68
		Turnover (yr^{-1})	1.30	0.01	1.91	0.11
	Non-hummock	Density (# 0.0625 m^{-2})	82	37	83	48
		P/C (g culm^{-1})	0.15	0.02	0.13	0.04
		ANPP (g m^{-2} yr^{-1})	242.47	118.22	242.49	110.50
		Turnover (yr^{-1})	1.28	0.04	1.71	0.10
	Hummock	Density (# 0.0625 m^{-2})	145	78	194	97
		P/C (g culm^{-1})	0.15	0.01	0.12	0.02
		ANPP (g m^{-2} yr^{-1})	490.93	272.38	673.74	341.72
		Turnover (yr^{-1})	1.45	0.01	2.06	0.18
S. patens	Creek	Density (# 0.0625 m^{-2})	429	230	319	111
		P/C (g culm^{-1})	0.13	0.02	0.11	0.02
		ANPP (g m^{-2} yr^{-1})	1280.17	727.19	719.73	328.84
		Turnover (yr^{-1})	1.47	0.01	1.42	0.05
	Non-hummock	Density (# 0.0625 m^{-2})	224	97	213	74
		P/C (g culm^{-1})	0.14	0.01	0.15	0.04
		ANPP (g m^{-2} yr^{-1})	644.75	319.98	567.00	204.62
		Turnover (yr^{-1})	1.28	0.03	1.23	0.04
	Hummock	Density (# 0.0625 m^{-2})	128	96	100	36
		P/C (g culm^{-1})	0.18	0.13	0.10	0.02
		ANPP (g m^{-2} yr^{-1})	575.83	675.69	228.32	84.96
		Turnover (yr^{-1})	1.49	0.07	1.65	0.12

APPENDIX J. DESCRIPTIVE STATISTICS OF TREATMENT ON GROWTH CHARACTERISTICS IN 1999.

		D. spicata		***S. patens***	
		Mean	Std Deviation	Mean	Std Deviation
Control	Density (# 0.0625 m^{-2})	106	52	173	85
	P/C (g $culm^{-1}$)	0.13	0.03	0.14	0.04
	ANPP (g m^{-2} yr^{-1})	352.10	190.49	453.18	238.38
	Turnover (yr^{-1})	1.88	0.26	1.40	0.25
Ponding	Density (# 0.0625 m^{-2})	79	57	125	73
	P/C (g $culm^{-1}$)	0.12	0.04	0.13	0.04
	ANPP (g m^{-2} yr^{-1})	210.88	147.61	299.68	195.07
	Turnover (yr^{-1})	1.70	0.30	1.34	0.18
Subsurface control	Density (# 0.0625 m^{-2})	68	37.57	158	92
	P/C (g $culm^{-1}$)	0.14	0.04	0.12	0.05
	ANPP (g m^{-2} yr^{-1})	197.69	94.69	536.47	369.27
	Turnover (yr^{-1})	1.58	0.46	1.94	0.67

P/C = production per culm.