Mark Keusenkothen. THE EFFECTS OF DEER TRAMPLING IN A SALT MARSH (Under the direction of Dr. Robert R. Christian) Department of Biology. September 2002.

The goals of the study were to determine (1) the extent of deer trails in a salt marsh, (2) the effects of trampling within the trails on four different salt marsh communities, (3) differences in effects from community to community, and (4) the role trampling may play in facilitating ecosystem state change in a salt marsh. The study was done in a mainland marsh on the Delmarva Peninsula of Virginia in the *Juncus roemerianus*, *Distichlis spicata/Spartina patens*, low marsh, and creek bank communities. Nearly 24 km of deer trails covered approximately 6876 m^2, or 0.23%, of the total study site area. Live above ground plant biomass was significantly reduced in on-trail areas relative to off-trail areas in all four communities. Reductions in the plant canopy allowed significantly more light to reach the marsh surface in on-trail areas of all communities relative to off-trail areas. Significant differences were found between on- and off-trail soil characteristics in the four marsh communities. The relative elevations of on-trail areas were significantly lower than that of off-trail areas in all marsh communities except the *D. spicata/S. patens* community. These changes in the ecosystem altered primary producer community composition. Further, significantly more *Ilyanassa obsoleta* were found in on-trail areas of the low marsh and creek bank communities than in off-trail areas. Trampling may facilitate ecosystem state change differently in the various communities, but the effects tend to be localized.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Continual trampling by deer, and perhaps other vertebrates such as raccoon, may create networks of trails throughout salt marshes. Trampling has been shown to modify physical characteristics of soils such as bulk density, organic content, and elevation in a wide variety of environments (Jeffreys 1917, Bates 1935, Edmond 1964, Frissell and Duncan 1965, Chappell et al. 1971, Dale and Weaver 1974, Liddle and Greig-Smith 1975, Weaver and Dale 1978, Manning 1979, Hole 1981, Hylgaard and Liddle 1981, Liddle and Chitty 1981, Cole 1987, Trimble and Mendel 1995, Kozlowski 1999), and may alter these same soil characteristics in salt marshes. Trampling has also been shown to reduce above-ground plant biomass in a wide variety of environments (Edmond 1964, Burden and Randerson 1972, Weaver and Dale 1978, Hylgaard and Liddle 1981, Cole 1995a, Whinam and Chilcott 1999), and may reduce above-ground plant biomass in salt marshes as well. Disturbance induced reductions in vegetation cover in salt marshes have been demonstrated to increase light intensity at the soil surface, increase the range of soil temperatures, and increase soil salinities (Siira 1970, Chappell et al. 1971, Bakker and Ruyter 1981, Bertness 1991b, Bertness et al. 1992, Meyer et al. 1995, Srivastava and Jefferies 1996). These aforementioned alterations in the marsh environment may in turn, alter plant and animal population distribution patterns (van Raalte 1976, Bertness 1991b, Chandrasekara and Frid 1996, Tolley 1996, and Tolley and Christian 1999, Williams et al. 2001).

Ecosystem state change may occur in salt marshes as sea level rises (Brinson et al. 1995). Ecosystem states are characterized by particular " . . . plant community dominants and soil/sediment characteristics" (Brinson et al. 1995). It follows then, that ecosystem state change is an alteration in these characteristics. Disturbance, such as trampling, may facilitate state change (Brinson et al. 1995). Elevation changes brought about by trampling may contribute to the hummock and hollow topography of the high marsh. Hummock and hollow areas are characterized by raised areas (hummocks) and depressions (hollows) in the surface of the high marsh. Also, trampling may facilitate the replacement of high marsh vegetation with low marsh vegetation in a manner similar to that of wrack deposition. In the low marsh the removal of plant biomass may reduce the amount of sediment trapped by vegetation (Steers 1977, Gleason et al.1979). These changes to the marsh ecosystem may help break down marsh resistance to sea-level rise, thus facilitating ecosystem state change – areas of high marsh become areas of low marsh and areas of low marsh become open water benthic systems (sensu Brinson et al. 1995).

The purposes of this study were to determine (1) the extent of animal trails in a salt marsh, (2) the effects of trampling in the trails on four different salt marsh communities, (3) whether these effects varied in significance from community to community, and (4) whether trampling plays a role in facilitating ecosystem state change in a salt marsh. This work was done within the context of a conceptual model of interacting conditions and processes to be described later (Figure 1).

LITERATURE REVIEW

Disturbance

White and Pickett (1985) defined disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." Trampling by deer in a salt marsh may be such a disturbance. Trampling is a discrete event that may disrupt community and population structure both directly, by physically damaging vegetation, and indirectly, by changing such soil characteristics as salinity, bulk density, and organic content.

Disturbance may be caused by either physical or biological processes (Sousa 1984). Physical processes of disturbance include fire, large waves, wind, drought, landslides, ice storms, floods and desiccation stress (Sousa 1984). A major source of physical disturbance in salt marshes is wrack deposition (Hartman et al. 1983, Bertness and Ellison, 1987). Biological processes of disturbance include herbivory, predation, digging, burrowing (Sousa 1984), manuring (Gillham 1956), wallowing (Butler 1995) and trampling (Bates 1935, Davies 1938, Gillham 1956). Trampling by vertebrates is a biological disturbance in many salt marshes.

Natural communities are both dynamic and spatially heterogeneous. They are dynamic in that the relative abundances of species, densities, and age-structures of populations change over time. Local extinctions of populations are commonplace (Connell and Sousa 1983). Sousa (1984) inferred from published literature that communities are spatially heterogeneous. Across any landscape there exists a mosaic of patches identified by spatial discontinuities in the distributions of populations. This spatial heterogeneity is exemplified in the salt marshes along the eastern seaboard of the United States. For instance, in the salt marshes of New England, striking plant zonation exists between areas dominated by *Spartina alterniflora* Loisel. and areas dominated by *Spartina patens* (Ait.) Muhl. (Bertness 1991a). Discrete patch boundaries may reflect the differing abilities of species to endure steep gradients in the physical environment (Sousa 1984) and/or competition and other biotic interactions (Bertness 1991a, Hacker and Bertness 1999). In the salt marsh example, zonation appears to be linked with elevation and the mean high water line (Chapman 1974, Nixon 1982, Bertness and Ellison 1987, Bertness and Pennings 2000). *S. patens* is generally found in high marshes above the mean high water line, while *S. alterniflora* is generally found in low marshes below the mean high water line. The low marshes are subjected to daily flooding while the high marshes are not (Nixon 1982). This difference in flooding regime creates environmental gradients. For instance, in a New England salt marsh, substrate redox increases, and salinity decreases with increasing marsh elevation (Bertness and Ellison 1987). Bertness and Ellison (1987) noted that most researchers credit these physical gradients as the primary determinants of plant zonation in salt marshes.

However, gradients in the physical environment are not the only determinants of spatial heterogeneity (Greig-Smith 1979, Sousa 1984, Bertness and Ellison 1987). Sousa suggested that disturbance is also a major contributor to both temporal and spatial heterogeneity of natural communities. Additionally, Sousa noted several studies that demonstrate the important influence disturbance has upon ecosystem-level processes such as primary and secondary production, biomass accumulation, energy flow, and nutrient cycling. In salt marshes, wrack (dead plant material) deposition has been demonstrated to influence both spatial and temporal heterogeneity (Hartman et al. 1983, Bertness and Ellison 1987, Tolley and Christian 1999, Fischer et al. 2000). Wrack, deposited by tides, buries and kills marsh plants creating bare areas. In high salt marshes, two species are commonly associated with colonizing disturbed areas and altering the marsh community mosaic – *Distichlis spicata* (L.) Greene and *Salicornia europaea* L. (Bertness and Ellison 1987, Brewer et al. 1998, Tolley and Christian 1999).

According to Sousa (1984), the view of disturbance put forward by White (1979) and Karr and Freemark (1984) suggests that disturbances are uncommon, irregular events that cause abrupt structural changes in natural communities and move them away from static, near equilibrium conditions. Sousa (1984) posited that this view has little utility for several reasons. At a local scale, few natural populations or communities persist at or near equilibrium condition (Connell and Sousa 1983). Additionally, changes caused by a particular force may vary from negligible to extreme, depending upon both the intensity of the disturbance and the nature of the populations affected. Sousa noted that it is difficult to objectively determine what degree of change, along this continuum, should be labeled disturbance. Sousa used perennial species response to seasonal change to illustrate this point. When precipitation and temperature fluctuate near their long-term seasonal averages, organisms are able to react physiologically and/or behaviorally to survive environmental change. However, when seasonal precipitation and temperature fluctuate widely beyond seasonal averages, organism physiological and behavioral reactions may become insufficient for survival. Individuals may die and populations may become extinct. Thus, depending upon the magnitude of variation in the same natural phenomena, responses ranging from acclimatization to death may be elicited in organisms. At what point do seasonal fluctuations become disturbances? As Karr and Freemark (1984) put it, the "objective definition of a threshold at which a periodicity becomes a disturbance is difficult at best." Sousa (1984) propounded an alternative view of disturbance. He defined disturbance as "a discrete punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly create an opportunity for new individuals (or colonies) to become established."

However, disturbance may also alter certain parameters in the physical environment – with or without killing or damaging individuals - such that opportunities for new individuals to become established may occur. For instance, Brokaw (1985) reported that both the intensity and duration of light increase in forest gaps created by windfall. Also humidity levels may decrease while air and soil temperatures rise dramatically. These changes in the physical environment of the forest alter successional patterns and community composition – thus contributing to temporal and spatial heterogeneity in the forest.

Influence of animals on ecosystems

In recent years, a great deal of literature has been produced that examines the influence of animals on ecosystems. A common theme among these works is the decrying of the previous lack of emphasis on the " . . . role that many organisms play in the creation, modification, and maintenance of habitats" (Jones et al. 1994). Animals influence ecosystems in a wide variety of ways.

Butler (1995) examined the role of animals as geomorphic agents. He coined the term *zoogeomorphology*, which is the study of the geomorphic effects of animals (Butler 1992). The geomorphic effects of animals include " . . . eroding, transporting, and/or depositing or causing the deposition of rock, soil, and unconsolidated sediments (Butler 1995)." Much of the work is concerned with the activities of mammals which, in particular, have a " . . . widespread influence and variety of geomorphic influences . . . (Butler 1995)," although the influences of invertebrates, ectothermic vertebrates, and birds are also addressed. Some of the geomorphic effects of mammals result from digging for and caching food, wallowing, and burrowing. Butler (1995) provided numerous examples from the literature. He estimated that over the last one hundred years in Glacier National Park, Montana, grizzly bears displaced a minimum of 30,000 m^3 of sediment by digging on steep slopes in their efforts to find plant bulbs (Butler 1992). Wallowing and geophagy by large ungulates in Africa contribute to the formation of waterholes (Flint and Bond 1968). The animals dig up and eat the salty soil, leaving excavations that trap water. Animals are drawn to the water, and their trampling around the water holes creates a clay seal that further increases water retention (Goudie and Thomas 1985). Animals then use these waterholes for wallowing. According to Flint and Bond (1968), an individual elephant removes approximately 0.3-1.0 m^3 of sediment with each wallow.

Geomorphic effects also arise from trampling by mammals (Butler 1995). For instance, Higgens (1982) found that trampling by domestic animals could contribute to the formation of “terracettes”, which are stepped terraces found on moderately steep slopes. Prior to this it had been thought that abiotic forces created terracettes. He observed sheep grazing on previously ungrazed slopes with no terracettes, and found that over a six-week period, trails appeared. The trails were 20–320 cm wide, bare of vegetation, and followed the contour of the slope. Similarly, he found that cattle also created trails on a previously smooth slope (Higgens 1982). If trampling by deer in salt marshes contributes to lowering the elevation of trails relative to the surrounding marsh surface, then it too may be considered an example of zoogeomorphology.

Butler (1995) concluded his work by noting that, although the geomorphic effects of particular species may be quite localized, “ . . . the shear ubiquity of geomorphic accomplishments by animals *collectively as a group* . . . ” (Butler’s emphasis) is significant and should not be underestimated.

Jones et al. (1994) developed the concept of ecosystem engineers. They defined ecosystem engineers as “ . . . organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and create habitats.” Two types of engineers were defined. Autogenic engineers alter the ecosystem with their own living or dead tissue. Thus the engineer remains part of the engineered environment (Jones et al.

1997). Examples include corals and trees in a forest. These provide physical structures which alter the environment and ". . . modulate the distribution and abundance of many other resources" (Lawton and Jones 1995). Allogenic engineers alter living or nonliving materials from one physical state to another, however the engineer is not part of the permanent physical ecosystem structure (Jones et al. 1997). Beaver are excellent examples of allogenic ecosystem engineers. To build dams with trees, beavers ". . . take materials in the environment, and turn them (engineering them) from physical state 1 (living trees) into physical state 2 (dead trees in a beaver dam)" (Lawton and Jones 1995). Likewise, the creation of trails by deer in a salt marsh may be an example of allogenic ecosystem engineering. Trampling may reduce above-ground biomass. Again, an area goes from physical state 1 (heavily vegetated) to physical state 2 (relatively unvegetated). In both cases, the availability of resources for other organisms is modified. Beaver dams alter stream hydrology. This in turn changes stream sedimentation rates, the standing stock of carbon, soil redox conditions, and chemical processes such as nitrogen and phosphorus cycling (Pollock et al. 1995). Reductions in above-ground plant biomass caused by trampling may change the amount of sunlight reaching the marsh surface, perhaps altering the amount of energy available to benthic microalgae. This change in the resource availability for other organisms is a "critical characteristic of ecosystem engineering" (Lawton and Jones 1995).

Hobbs (1996) stated that ungulates may be ". . . important regulators of ecosystem processes at several scales of time and space." He conducted an extensive review of the effects of ungulates on ecosystems, concentrating on effects ". . . that modify conditions for other organisms above- and below-ground" - specifically, "alteration of nutrient cycles, influences on net primary production, and modification of abiotic disturbance, particularly fire regimes" (Hobbs 1996). Ungulates accelerate nutrient turnover by urinating and defecating. In this way, a large portion of the nitrogen in food eaten by ungulates returns to the soil in a form more readily decomposed than litter (Ruess and McNaughton 1987). Hobbs noted that nitrogen is not excreted evenly across an animal's home range. Ungulates do not use their environments uniformly (Hilder and Motershead 1963). Therefore, nitrogen that may be ingested over large areas might become concentrated in much smaller areas (Ruess 1987). In such a case, ungulates act as 'conduits' for nutrient movement (Hobbs 1996).

Herbivory by ungulates may also affect primary production. McNaughton (1976, 1979, 1983) suggested that herbivory by ungulates may increase net annual primary production (NAPP) in plants in grassland ecosystems. This occurs as a ". . . result of grazing-induced feedbacks among individual plants, plant communities, and the soil environment" (Hobbs 1996). The idea that herbivores can increase NAPP has become known as the "grazing optimization hypothesis" (See Dyer et al. 1993 for the history of the use of this phrase). Hobbs noted that the grazing optimization hypothesis has ". . . been verified empirically in several ecosystems (McNaughton 1979, 1985, Page and Whitham 1987, Dyer et al. 1991, Frank and McNaughton 1993, Turner et al. 1993)," but also that ". . .the interpretation of empirical results showing increased NAPP in response to grazing has been questioned (Belsky 1986, 1987, Verkaar 1986)." Whether or not plants experience compensatory growth after grazing by ungulates depends on a variety of factors. Plants that evolved with pressure from ungulate herbivory seem to have the capacity to regrow after defoliation better than plants that did not evolve with ungulate herbivory pressure (Mack and Thompson 1982). According to Coughenour (1985), plant adaptations that facilitate regrowth include: low stature, deciduous leaves, linear leaf elongation from intercalary meristems, rhizomatous growth, high shoot density, below-ground nutrient reserves, and rapid transpiration and photosynthetic rates. Hobbs (1996) also noted that the grazing and browsing of ungulates plays an important role in controlling the ". . . spatial and temporal dynamics of fire." Ungulates reduce the standing crop of biomass and thereby ". . . reduce the frequency, extent, and intensity of grassland fires" (Hobbs 1996). For instance, McNaughton (1992) found that most of the plains of the Serengeti burned when populations of wildebeest fell below 600,000. However, when populations increased above this number less than 20% of the plains burned. The proportion of plains that burned was asymptotically related to the numbers of wildebeest present (McNaughton 1992).

Hobbs (1996) did not include the effects of trampling by ungulates in his discussion. Trampling may be another way ungulates modify conditions for other organisms. As previously discussed, trampling by deer in salt marshes may alter community structure both directly, by damaging plants and reducing biomass, and indirectly, by altering the abiotic environment.

Trampling

Trampling by vertebrates influences both the biotic and abiotic components of ecosystems. Both Chandrasekara and Frid (1996) and Liddle (1975) credited Bates

(1935) for being the first scientist to investigate the effects of trampling systematically. Bates' studies revealed that trampling can suppress plants so that more light reaches the soil (see also Kobayashi et al. 1997), that trampled areas are often wetter than non-trampled areas, that trampled soils may be compacted, and that trampling changes community composition (see also Davies 1938, Jensen 1985, Andersen 1995, Manseau 1996, Hewitt 1997).

Since Bates, many other effects of trampling in a wide variety of ecosystems have been documented. For instance, changes to plant canopies, which allow more solar radiation to reach the soil, may lead to increased evaporation, soil temperature (Kobayashi et al. 1997), decomposition rates (Lynch et al. 1947), and soil salinity (Bertness et al. 1992). Soil compaction increases soil bulk density, mechanical resistance to penetration, and moisture runoff, while reducing soil aeration and moisture infiltration rates (McNaughton and Sabuni 1988). Trampling reduces net annual primary production (NAPP) (Turner 1987), biomass and seedling establishment (Reimold et al. 1975), and plant regeneration (Chabreck 1968, Jensen 1985).

Much of the published work examining the effects of animals in salt marshes has focused on grazing. Grazing effects actually arise from several distinct activities, as Edmond (1963) made clear when he said "an animal exerts three main influences on pasture - it treads, removes leaves (defoliates), and excretes upon it". Published studies that have examined the effects of grazing on salt marshes often do not distinguish between effects arising from these separate activities (i.e. Ranwell 1961, Bakker 1985, Wood et al. 1987, Furbish and Albano 1994, Neuhaus 1994, Meyer et al. 1995, Kiehl et al. 1996, Olff et al. 1997, Ford and Grace 1998, Laffaille et al. 2000).

Bakker (1985) compared the effects of mowing to the effects of grazing in a salt marsh on the Dutch Frisian Island of Schiermonnikoog. Bakker (1985) found that grazing, rather than mowing, is associated with the appearance of low marsh vegetation in high marsh areas. The formation of bare areas created by grazing facilitated this change. Though Bakker did not specifically credit trampling by grazers for creating bare spots, the finding that grazing rather than mowing facilitates the creation of bare spots suggests that it is trampling, rather than the cropping action of feeding, which is responsible for the change.

Kiehl et al. (1996), studying the effects of sheep grazing on a salt marsh in Germany, concluded that "grazing causes an upward shift of zonation boundaries between lower, mid and upper salt marsh vegetation." Research plots, located in the ". . . lower and middle salt marsh. . .", were subjected to various grazing intensities over a 13 year period (Kiehl et al. 1996). Heavily grazed plots were dominated by *Puccinellia maritima,* a low marsh species. However, in moderately grazed and ungrazed plots, *P. maritima* was partly replaced by *Festuca rubra*, a plant less well adapted to low marsh conditions than *P. maritima*. Kiehl et al. (1996, after Schmeisky 1974 and Hansen 1982) credited ". . . increasing salinities and soil compaction due to grazing and trampling. . . as prime reasons for the competitive advantage of lower salt marsh species in higher zones."

Reimold (1975) conducted a study in Georgia comparing marshes that had never been grazed to marshes that had been grazed by domestic ungulates for 30 years. He examined the effects of presumed trampling on the populations of the fiddler crab *Uca pugnax.* Reimold (1975) found that "there were significantly fewer crabs (per square meter) in the grazed than in ungrazed marshes." He concluded that "presumably the trampling effects… led to the depletion of crabs in the grazed areas."

Turner (1987) examined the effects of grazing by feral horses in a *S. alterniflora* marsh in Georgia. Turner set up a variety of experimental *S. alterniflora* plots and subjected them to different treatments. In one treatment she used a trowel to simulate horse trampling. In another treatment she clipped plants to simulate feeding. In a third treatment she combined the trampling and clipping treatments. Horses were allowed to graze in a fourth treatment. She then compared NAPP among the treatments. Clipping alone did little to affect NAPP, but the "trampled only" plots showed a marked drop in NAPP. The "trampled only" and plots grazed by horses were nearly equal to each other in NAPP. The plots that were both clipped and trampled registered the lowest NAPP. Turner (1987) concluded that "…trampling may be the more destructive component of grazing by large ungulates in the marsh."

Andersen (1995), working in a salt marsh in Denmark, compared the vegetation of a human made path to undisturbed vegetation off the path. He analyzed the areas with respect to the total number of species and vegetation cover. He found that species diversity was unaffected but total vegetation cover was reduced on the path. Andersen noted that the salt mash vegetation at the study site was dominated by hemicryptophytes (plants which survive unfavorable seasons by developing buds at the soil surface), and that hemicryptophytes are less susceptible to trampling than either geophytes (plants that survive unfavorable seasons by developing buds below the soil surface) or therophytes (plants that survive unfavorable seasons as seeds). He categorized the trampling on the path as “light” though he did not count the number of passages (according to Schofield (1967) 7,500 passages per year would cause complete loss of vegetation in salt marshes). Interestingly, Andersen found that the annual *Spergularia marina* was able to colonize bare patches created by trampling. The plant, which is unable to establish itself in dense, saturated communities, was found nowhere else in the salt marsh. Andersen (1995) concluded that trampling can create open spaces for new species to become established.

Chandrasekara and Frid (1996) conducted a study to determine the effects of human trampling on tidalflat infauna. The study sites were at two footpaths in the Lindisfarne National Nature Reserve along the northeast coast of England. One path, the PilgrimsWay, leads to the island of Lindisfarne across an unvegetated tidal flat. This island, which is a holy site, is separated from the mainland at high tide. During the summer, people make pilgrimages to the holy site along the path. The other footpath, the Old Track, runs through heavily vegetated emergent marsh and is used primarily by bait collectors and naturalists. Chandrasekara and Frid sampled from one transect at each site during summer and winter. The two transects ran perpendicular to the two paths. Analysis of the summer samples for Pilgrims Way showed significant differences between on and off-path infauna community composition. Analysis of the winter samples for the same path did not show these differences. The response of individual species to summer trampling on the path varied. Abundances of some species decreased while abundances of others increased. During winter, when trampling disturbance nearly stopped, the infauna communities on Pilgrims Way reverted to a structure similar to that of adjacent untrampeled areas. Analysis of the summer and winter Old Track samples did not reveal any differences between on and off-path community composition. Species abundance did not differ between the winter and summer or the on and off-path samples. Chandrasekara and Frid proffered several explanations for the absence of any measurable effects of repeated trampling on Old Track. They noted that a substantial part of the path was covered by low growing, trampling resistant vegetation. This vegetation may have mitigated the effects of trampling pressure by cushioning the impact on fauna in the sediment. However, it was concluded that, while vegetation may protect infauna from the effects of trampling, high levels of trampling on unvegetated mudflats lead to changes in tidalflat infaunal population and community structure. But these changes will disappear quickly once the intensity of trampling becomes less. Finally, the susceptibility of infauna to human trampling depends upon both the nature of the habitat and the intensity of trampling (Chandrasekara and Frid 1996).

Trails

According to Butler (1995) "Natural animal trails produced by trampling are widespread . . . " Deer, raccoons, and humans may create numerous trails throughout salt marshes. It seems unlikely that trampling by deer in salt marshes occurs in conjunction with grazing. Deer rarely graze in salt marshes (Pfeiffer and Wiegert 1981, Newsome 1984), although Turner and Bratton (1987) stated that " . . . deer intensively graze the . . . upper edges of the salt marsh . . ." on a Georgia barrier island. Keiper (1985) analyzed deer fecal samples collected in the late fall on Assateague Island, Maryland. *S. patens* and *S. alterniflora*, while present in 5% of the samples, contributed only 0.14% to the relative density of fecal samples. *D. spicata* was not present in any of the samples. It may be the case then, that deer create trampling disturbance in the marshes primarily from transiting between habitats, rather than from grazing in the marsh. The naturalist Rue (1989) reported that when deer are moving to feeding areas they generally choose direct paths that offer the least resistance. Also, Servinghaus and Cheatum (1956) reported that ". . . deer take the paths of least resistance, going around obstructions whenever encountered." This seems to be the case in salt marshes, where deer tend to travel the same routes and create trail from repeated trampling.

Ecosystem state change and the salt marshes of mainland Virginia

An ecosystem state change is a transformation from one ecosystem class to another driven by disturbance or alterations in some external controlling force that changes the endpoint of succession in ecosystems (Brinson et al. 1995). Internal controlling forces may also play a role in such a transformation (R. Christian, 2001, East Carolina University, *personal communication*.). Hayden et al. (1991) suggested that "under certain intensities of disturbance, systems are displaced sufficiently that their dynamics track a different terminal state." Along the mainland coast of Virginia, "rising sea level is acknowledged as the master variable that forces the process of [state] change overall" (Brinson et al. 1995). Brinson et al.(1995) recognized five ecosystem classes in this area involved in state change. The classes are forest, organic high marsh, intertidal mineral low marsh, autotrophic benthic systems, and heterotrophic benthic systems. Each class is characterized by specific plant community dominants and soil/sediment characteristics (Brinson et al. 1995). Most salt marshes along the mainland of the Delmarva Peninsula appear to be eroding on the seaward edge and migrating overland on the landward edge. Expressed in terms of state change, this means that forested areas are becoming organic high marshes, organic high marshes are becoming mineral low marshes, mineral low marshes are changing to autotrophic benthic systems, and autotrophic benthic systems are becoming heterotrophic benthic systems (Brinson et al. 1995, Ricker 1999) (However, it should be noted that Ricker (1999) found that "…not all high marshes developed organic rich horizons" and that "…soil organic matter was not always lost as high marsh was replaced by low marsh."). Though rising sea level appears to be the key force driving these state changes, disturbance or exposure to acute stress also facilitates transitions between classes (Brinson et al. 1995). Disturbances may include wrack deposition and erosion. Stresses may include the osmotic effects of salt, low redox conditions due to flooding, and the accumulation of chemicals, such as hydrogen sulfide, that are toxic to plants (Brinson et al. 1995). These disturbances or stresses help overcome resistance created by self-maintaining properties inherent in each ecosystem class and facilitate plant species replacement and alter sediment conditions (Brinson et al. 1995).

Conceptual model of trail effects

As detailed in Figure 1, trampling disturbance may alter conditions in the marsh such that ecosystem state change is facilitated. For instance, soil compaction from trampling and associated reductions in soil moisture infiltration rates may cause ponding on the marsh surface. Brinson et al. (1995) hypothesized that ponding in high marshes may be one factor that hastens state change to low marsh. Ponding may lead to deterioration in marsh production, which could in turn lead to subsidence, as observed in the Mississippi

River Delta (McKee and Mendelssohn 1989). Ponding heightens levels of anoxia in the soil, which may further decrease NAPP. These reductions in biomass and NAPP may lead to subsidence as soil organic matter content declines because of reduced input.

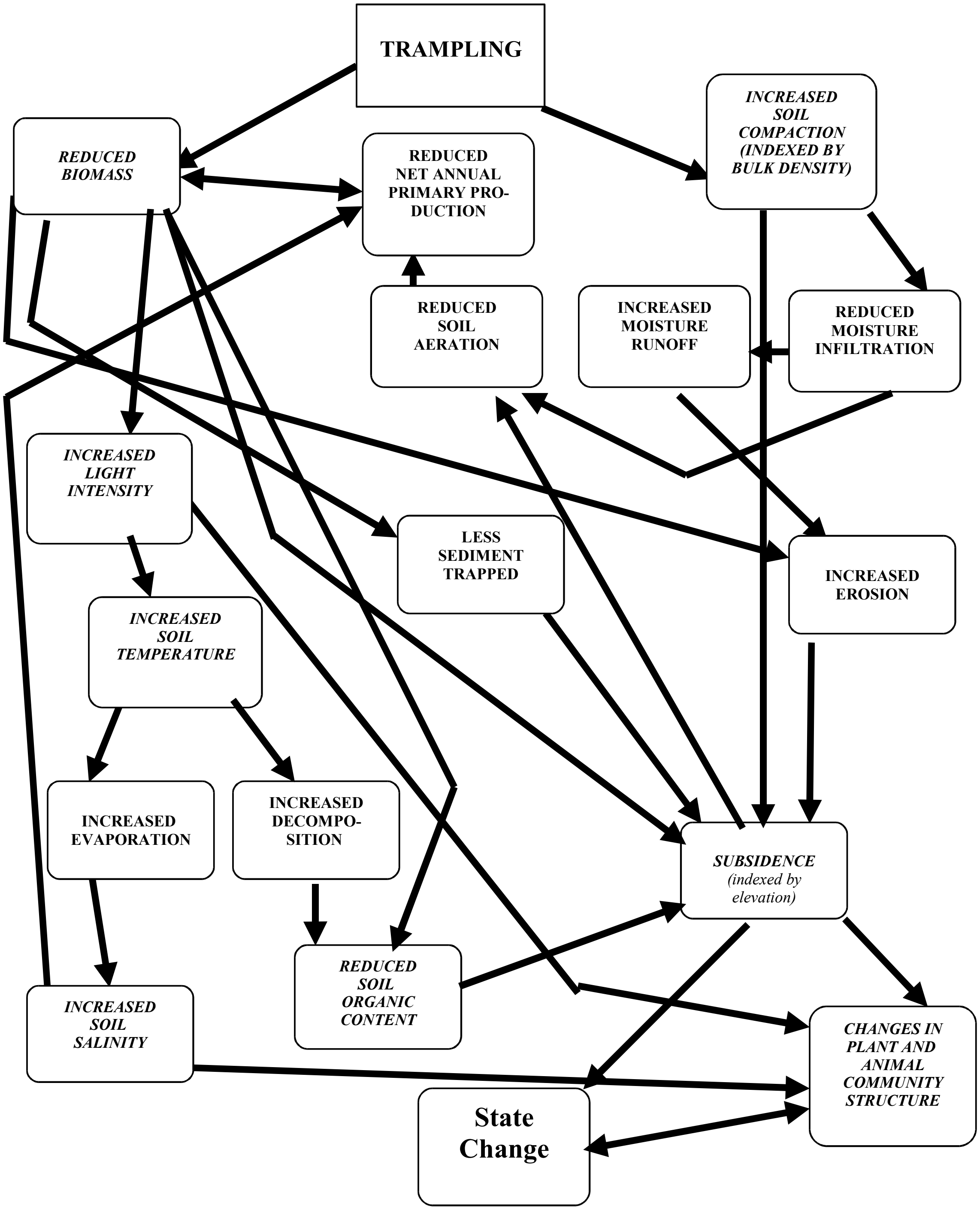

Figure 1. The possible effects of trampling disturbance on a salt marsh. Effects in italics were examined in study.

following periods of flooding (Brinson and Christian 1999). Trampling disturbance may increase evaporation rates and decomposition rates. Trampling reduces biomass and creates bare areas. More solar energy reaches the soil so both temperature and associated evaporation rates may increase. Increased temperatures and greater soil oxidation may increase decomposition rates. Increased decomposition rates may lead to subsidence. As patches of organically rich soil subside, hummock and hollow topography may be formed (Brinson et al. 1995, Brinson and Christian 1999). Subsidence lowers the surface elevation of the high marsh and facilitates the exposure of surfaces to tidal inundation and the transport of sediments (Brinson et al. 1995). State change from high marsh to low marsh may therefore occur.

Trampling disturbance may also play a role in state change from low marsh to autotrophic benthic system. Trampling in low marshes reduces both biomass and NAPP of *S. alterniflora*. This may facilitate the creation of bare areas. Reidenbaugh and Banta (1980) gathered from Varricchio et al. (in publication at time of reference) that bare areas resulting from wrack deposition contribute to sediment erosion in the low marsh. Erosion in bare areas of the low marsh “probably occurs from increased tidal and wind scouring in devegetated areas, and from decreased interference with the water column to cause settling of suspended particles” (Reidenbaugh and Banta 1980). It is possible that plant biomass and NAPP reductions caused by trampling also contribute to increased erosion and reductions in sediment deposition in the low marsh (Fig. 1). Increased erosion and decreased sediment deposition may lower the marsh surface. Brinson et al. (1995) stated that “further deepening at the original reference point below mean low tide results in subtidal conditions, either as open water of a lagoon or tidal creek.”

Deer in Virginia

The density of deer in Virginia has varied considerably over time. According to the Virginia Department of Game and Inland Fisheries' Deer Management Plan (DMP) (2002), white tailed deer had been nearly extirpated in many parts of Virginia by the 19th century. An estimated pre-colonial population of 400,000 animals had been reduced to approximately 25,000 statewide by 1931. Over-harvesting is believed to be the primary cause for this population reduction, although habitat loss also played a role. The population began to rebound by the early to mid 20th century because of reforestation, farm abandonment, protective game laws, law enforcement, and restocking (DMP 2002). By 1987, the population of deer in the state was estimated at 575,000 animals. Estimates in 1988 placed the density of deer in Northampton County, the county in which the study site was located, at between 0.06-0.12 individuals per ha. However, the density of deer in the study site area may be somewhat less. According to Newsom (1984), "Salt marshes support low populations [of deer] primarily because of a lack of available deer food." Also ". . . deer generally are limited to higher elevations" in coastal marsh areas, so ". . . the total amount of occupied habitat usually is small and the deer populations are low" (Newsome 1984).

Study objectives

The goals of my research were to determine (1) the extent of animal trails in a salt marsh, (2) the effects of trampling on these trails in four different salt marsh communities, (3) whether these effects varied in significance from community to community, and (4) whether trampling plays a role in facilitating ecosystem state change in a salt marsh. To this end, biotic and abiotic components of four marsh communities were examined to determine how they were affected by trampling. My expectations are based on the conceptual model summarized in Figure 1. If trampling reduces plant biomass and NAPP in the high marsh, and these reductions in turn lead to increased soil temperature, increased decomposition, compaction, and subsidence, then it is possible that trampling helps facilitate state change in the high marsh. If trampling reduces plant biomass and NAPP in the low marsh, then it is possible that sediment deposition rates decrease, and erosion rates increase, such that subsidence of the marsh surface occurs. Therefore, if subsidence occurs from these effects, then trampling may help facilitate ecosystem state change in both the high and low areas of the salt marsh (Figure 1).

To accomplish the aforementioned goals, the following were performed:

1. Trails were mapped and characterized.
2. Trail usage was monitored.
3. On- and off-trail above-ground plant biomass was measured in four marsh communities.
4. On- and off-trail community composition was compared in four marsh communities.
5. Light intensities, soil temperatures, trail elevation, soil salt content, soil

percent organic content, and soil bulk density were measured in on- and off-trail areas in four marsh communities.

6. On- and off-trail distributions of *Ilyanasa obsoleta*, the eastern mud snail, were compared.
7. On- and off-trail levels of chlorophyll *a*, an index for benthic microalgae biomass, were measured in four marsh communities.

Inter- and intra-community statistical comparisons were then made using the above observations and measurements. The hypothesized directions of comparisons are listed in Table 1.

Table 1. Summary of expected direction of analyses performed.

On-trail to Off-trail comparison	Expected direction of comparison
Above-ground plant biomass	Biomass less on-trail
Plant community composition	On-trail increase in disturbance tolerant species - increased presence of low marsh species in on-trail areas in high marsh
Light intensity	Light intensity higher on-trail
Soil temperature	Temperatures higher on-trail
Elevation	Elevation lower on-trail
Soil salt content	Soil salt content higher on-trail
Soil % organic content	Organic content lower on-trail
Soil bulk density	Bulk density higher on-trail
Densities of *I. obsoleta*	More *I. obsoleta* on trails
Benthic chlorophyll *a* concentration	More chlorophyll *a* on trails

METHODS AND MATERIALS

Site description

This study was undertaken at the Virginia Coast Reserve Long-term Ecological Research site (VCR-LTER), which is located on the Atlantic side of the southern end of the Delmarva Peninsula (32° 27'N, 75° 50'W) (See Figure 2). The research was performed in the Brownsville Marsh complex, a mainland salt marsh. The marsh was divided into four communities based upon the dominant plant species occurring in each. Organic high marsh areas, flooded only by storm tides, spring tides, or precipitation (Stasavitch 1998), contained two communities. The *Juncus roemerianus* community was dominated primarily by monocultures of *Juncus roemerianus* Scheele, whereas the *D. spicata*/*S. patens* community was dominated by both *D. spicata* and *S. patens*. These plants grew either interspersed with each other or in distinct patches. Mineral low marsh areas were regularly flooded by diurnal tides and were dominated by *S. alterniflora*. The creek bank community occurred along tidal creeks eroding into both low and high marsh areas. This community was dominated by tall form *S. alterniflora*. Trails were present in all four communities.

Analyses conducted

Trail extent

Trails were defined as places where plants were trampled so that biomass was visibly less than surrounding areas. Trails were considered to be separate when they were more than approximately 2 m apart. Trails leading to experimental sites were considered to be of human origin and were not included in the study. All trails in the designated study site

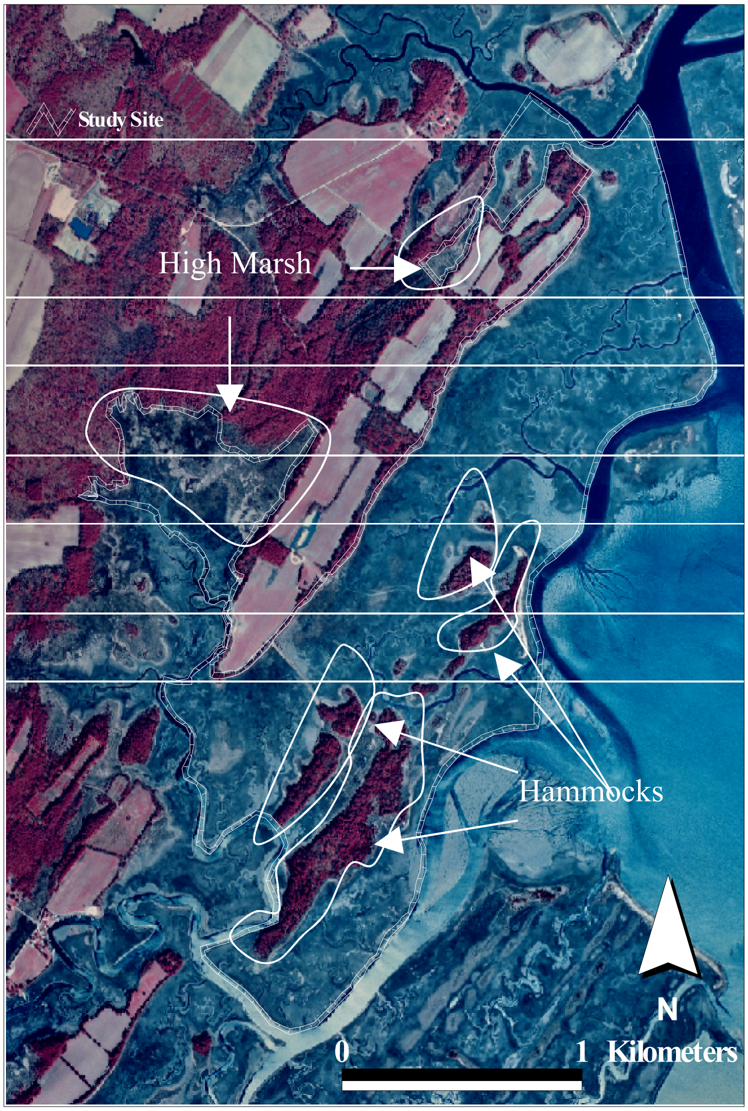

Figure 2. 1994 USGS aerial photo showing study site. The study site is bounded by double white line. The hammocks and high marsh areas are bounded by single white lines (the lines do not designate exact borders). Areas within the study site not bounded by single white lines are low marsh.

were walked and Global Positioning System (GPS) points were taken during 2001 using a hand held Magellan GPS 315 receiver. Points were then plotted, using ARCVIEW Geographic Information System (GIS) software, on a 1994 United States Geographical Survey (USGS) aerial photo of the designated study site. Trail lengths, the areas of the various communities studied, and the area of the designated study site itself, were calculated using this software. Trail widths were measured in the field using a meter stick. Average trail widths were calculated for the low marsh community, and for creek bank communities occurring along creek banks eroding into the low marsh community. Values were collected by measuring trail widths every four to five meters along trails in those respective communities. Average trail widths for trails in the *J. roemerianus and D. spicata/S. patens* communities were extrapolated from the average widths of the six study trails within those two communities.

Study trails

Generally, analyses were conducted along three trails in each of the four marsh communities (Figure 3, Figure 4). Plant heights, species composition, and trail lengths were observed and recorded in summer 2001 and Spring 2002. The presence or absence of scat and evidence of trail as a flow path were noted and recorded periodically from June 2001 - March 2002. The trails varied in their characteristics (Table 2). They ranged in length from a high of 92m in the low marsh community, to lows of between 2-3.5 m in the creek bank community. The narrowest trails were found in the *D. spicata/S. patens* community, and the widest trails were found in the creek bank community. Deer or raccoon scat was never on any trail other than *J.*

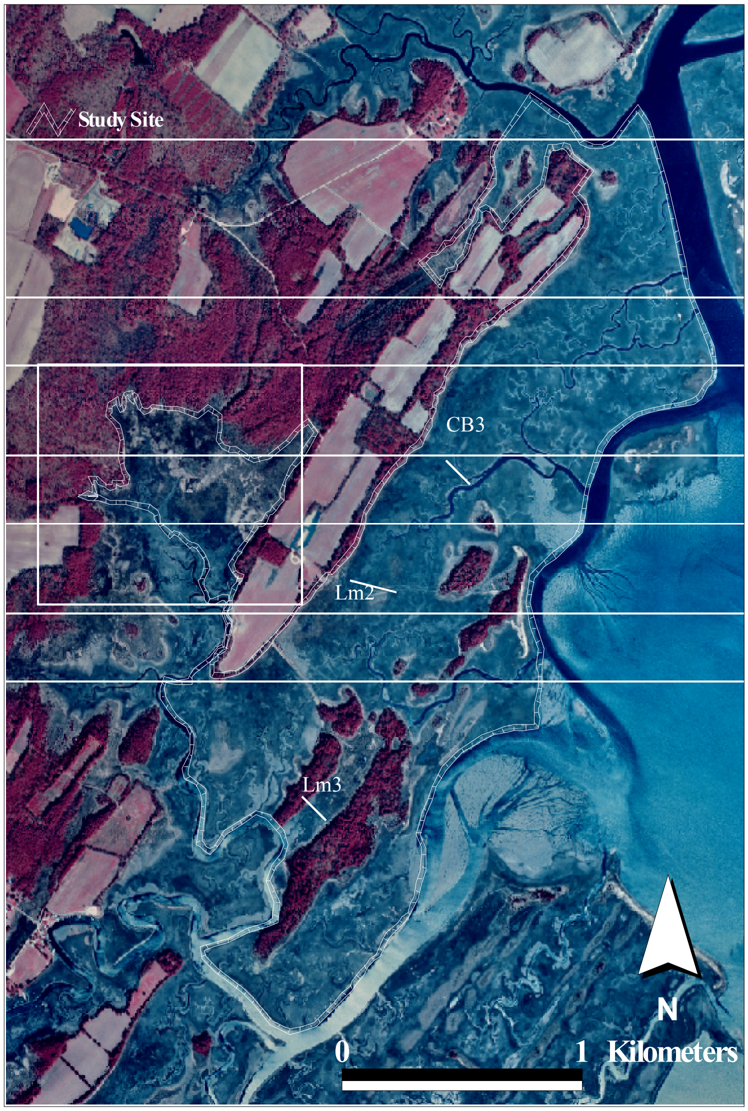

Figure 3. 1994 USGS aerial photo showing the location of study trails in Brownsville Marsh. LM2 and LM3 identify the positions of low marsh trails 2 and 3. CB3 identifies the position of creek bank trail 3. See Figure 4 for study trails in area bounded by square. Note that the lengths of the lines indicating trail position are not related to actual trail length.

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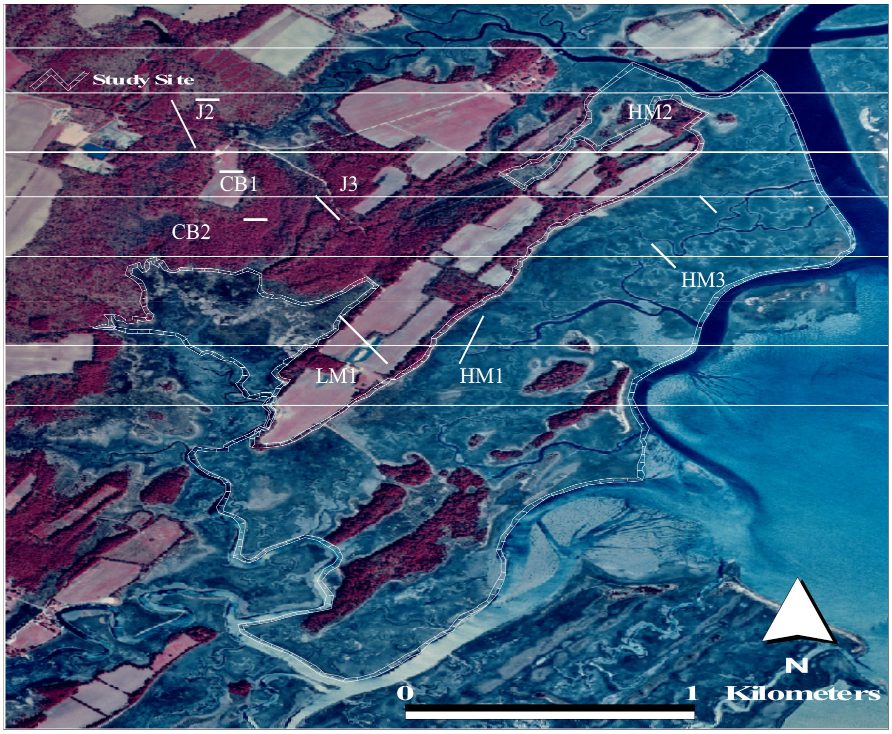

Figure 4. 1994 United States Geographical Survey aerial photo showing location of study trails in Brownsville Marsh. J2, J3, and J4 indicate the positions of *J. roemerianus* trails 1 - 3. HM1, HM2, and HM3 indicate the positions of *D. spicata/S. patens* trails 1 - 3. LM1 indicates the position of low marsh trail 3. CB2 and CB3 indicate the position of creek bank trails 2 and 3. Note that the lengths of the lines indicating trail position are not related to actual trail length.

Table 2. Study trail characteristics. Refer to Table 3 for symbol identification.

Trail	Trail length (m)	Average trail width (m)	On- and off-trail species composition	Average off-trail plant height (m)	Off-trail plant height range (m)	Presence of scat on-trail
J1	21	0.26	*J. roemerianus* *D. spicata* *S. patens*	1.3	0.6-1.6	Yes
J2	26	0.39	*J. roemerianus* *D. spicata* *S. patens* *S. alterniflora* *Pluchia* spp.	1.3	1.0-1.6	No
J3	29	0.35	*J. roemerianus* *D. spicata* *S. patens*	1.2	1.0-1.5	No
HM1	80	0.16	*D. spicata* *S. patens*	0.4	0.3-0.5	No
HM2	22	0.13	*D. spicata* *S. patens*	0.5	0.3-0.6	No
HM3	20	0.12	*D. spicata* *S. patens*	0.4	0.3-0.6	No
LM1	92	0.29	*S. alterniflora* *D. spicata*	0.3	0.2-0.5	No

Table 2. cont.

Trail	Trail length (m)	Average trail width (m)	On- and off-trail species composition	Average off-trail plant height (m)	Off-trail Plant height range (m)	Presence of scat on-trail
LM2	90	0.26	*S. alterniflora*	0.3	0.2-0.5	No
LM3	51	0.22	*Salicornia* spp. *S. alterniflora* *Salicornia* spp. *D. spicata*	0.3	0.1-0.5	No
CB1	2.0	0.55	*S. alterniflora*	0.7	0.7-0.8	No
CB2	5.0	0.56	*S. alterniflora*	1.0	1.0-1.2	No
CB	6.0	2.60	*S. alterniflora*	0.7	0.6-0.8	No

roemerianus trail 1. Scat was observed at several locations along the trail in December and January 2001. Two trails appeared to act as flow paths: low marsh trails 1 and 3. Water appeared to be flowing off the marsh surface on trail 3 in September 2001, and on trail 1 in January 2002.

Deer movement and general trail observations

One-meter strips of sand were spread along each of the twelve study trails. Sand was periodically observed from June 2001 – March 2002, and any visible prints were recorded. The sand was then spread smooth. Prints occurring in soft mud of trails were also identified and recorded. The frequency of prints found on trails was identified at three different levels: L = low frequency – one set of prints on trail, M = medium frequency – more than one set of prints on trail, but sets of prints still individually discernable, H = high frequency – multiple sets of prints so that individual sets of prints no longer discernable. A Chi-square test was used to compare the frequency of trail use in the four marsh communities. The test was considered to be statistically significant at p value ≤ 0.05.

An effort was made to monitor trail usage using an infrared Trailmaster 1500 trail monitor. The trail monitor was composed of two parts - a transmitter and a receiver. Each was mounted on 8.9 cm PVC and placed on either side of a given trail. The trail monitor was moved to different trails periodically from February 2001 through January 2002. The monitor was placed generally around 2-3 m on either side of the trail at an approximate height of 69.7 cm per manufactures recommendation. Unfortunately, the results seemed to be unreliable. On some occasions the monitor indicated that thousands of passages had occurred, and on at least one occasion hoof prints were observed in the sand of a trail being monitored yet the monitor registered no passages. Part of the difficulty may have had to do with the necessity for mounting the monitor on relatively unstable PVC rather than on a more stable tree as recommended by the manufacturer. It is possible that wind generated movement caused the improbable number of marks routinely registered on the monitor.

An attempt was also made to monitor trail usage with a Trailmaster TM550 passive infrared trail monitor. The monitor registered any movement by warm blooded animals within a field of sensitivity. Unfortunately if was impossible to discern whether movements registered were actually made on the trails. Results from the TM550 were considered unreliable.

Other trail observations and measurements were made when sand was examined for the presence or absence of prints. These included inspecting trails for the presence or absence of any scat, noting plant species composition alongside trails, the measurement of plant height along trails with a meter stick, and finally, looking for evidence of the flow of water along trails.

Above-ground plant biomass – August 24 and 25, 2000

Live and dead above-ground plant biomass was collected from three randomly selected locations on each study trail, and from three locations 1m off-trail from each sampled location. Biomass was clipped down to the marsh surface within a quadrat measuring 0.25 m on a side and encompassing 0.0625 m^2 in area. The collected biomass was then kept frozen until it was sorted. Following that, live and dead biomass was separated, sorted into species and then dried to a constant mass at 85 °C.

Above-ground plant biomass – August 17 and 18, 2001.

Biomass was collected in August 2001 and processed in the same manner as August 2000 biomass (see above) with one exception. Some trails were narrower than the 0.25 m length of the quadrat used in August 2000, and some biomass along the edge of the trail was included in on-trail samples. Therefore quadrat shape was altered for this collection period to minimize the inclusion of off-trail biomass in on-trail samples. The quadrat used in this collection period was 0.5 m x 0.125 m so it fit more neatly within narrow trails.

August 2000 and August 2001 plant community composition

Community composition was determined by calculating the percent of total live biomass for each species sampled in quadrats in both on- and off-trail areas.

Light Intensity

The intensity (photon flux) of photosynthetically active radiation (PAR) (400 - 700 nm) was measured in $\mu E/(m^2 \times sec)$ using a Licor Quantum radiometer/photometer (Li-185B) and flat Licor Quantum sensor (Li-190SB) on 21 August 2001. Both diffuse and direct light was measured, though no distinction was made between the two types of light. Measurements were made at the marsh surface at five on-trail locations and at five paired locations 1m off-trail at each trail sampled. Although measurements were made throughout the day, on- and off-trail paired samples on any given trail were always taken within minutes of each other.

Temperature

Temperature was measured using a Yellow Springs Instrument Co., Inc. Telethermometer in on- and off-trail areas over two days in August 2000, and on one day in March 2002. Temperatures were measured on the surface and at depths of 5 cm in all communities in both sampling periods. In August 2000, temperatures were measured at three randomly selected paired on- and off-trail locations at each of the three study trails in the *J. roemerianus*, low marsh and creek bank communities. Five paired locations were sampled at each of the sample trails in the *D. spicata/S. patens* community. In the March 2002 sampling period, five on- and off-trail paired locations were sampled at each of the trails in all four marsh communities. As with the collection of light intensity data, although temperatures were taken at different times throughout the sampling days, on- and off-trail paired samples on any given trail were always taken within minutes of each other.

Elevation

Trail elevations were measured using a Marksman Rl-50A rotating laser level and stadia rod in July 2001. Five randomly selected paired on- and off-trail locations were measured at each study trail in the *J. roemerianus, S. patens/D. spicata*, and low marsh trails. Fewer samples were taken at two of the creek bank trails because the softness of the substrate made use of the stadia rod exceedingly difficult. Six measurements were made at each paired on- and off- trail sampling location. One measurement was made in the center of the trail and two measurements were made 10 cm on either side of the center. Then one measurement was made 1m from the center of the trail and two measurements were made 10 cm on either side of that.

Soil analyses

Soil cores with a length of 10 cm and a diameter 7.62 cm in diameter were extracted from three randomly selected on-trail locations and three paired sampling locations 1m off-trail at each sample trail in four marsh communities. Samples were collected in July 2001. Cores were stored at approximately 5 °C until processing. The cores were then cut into four sections: 0-1, 1-3, 3-5, and 5-10 cm from the surface of the soil. Each section was quartered. One quarter from each section was used to calculate soil salt content, another quarter was used to calculate percent organic matter, the third was used to calculate soil bulk density, and the final quarter was stored as a reserve.

Soil salt content

The soil samples were allowed to air dry to a constant mass. Following that, the samples were weighed and a known volume of water was added to them (generally either two or five times the sample mass). Next, samples were mechanically shaken for one hour. Then they were filtered through a Whatman 934-AH glass fiber filter of 1.5 μm effective pore size and a Gelman Sciences GN-4 membrane of 0.8 μm effective pore size. Finally, salinity of the filtrate was measured in parts per thousand (ppt) with a Reichert T/C refractometer. The following formula was used to calculate the mg salt/g soil: mg salt/g soil = ppt x (ml of water added)/sample mass (Rhoades and Oster 1986, Rhoades 1996).

Percent organic matter content of soil

Samples were dried at 105 °C until a constant mass was reached. The samples were then crushed by hand to an exceedingly fine powder using a mortar and pestle. The dry mass of the samples was determined to the nearest 0.00001 g, and the samples were burned in a muffle furnace at 480 °C for 3 hours and reweighed. The difference between the initial dry mass and the post-burning mass was considered to be the mass of organic matter in the sample. The percent organic matter was then calculated by dividing the mass of organic matter by the initial dry mass of the sample and multiplying by 100 (Grimshaw 1989).

Soil bulk density

A known volume of soil (see section 3.2.10) was dried in a drying oven at 105 °C to a constant mass. The dried mass of the sample was then divided by volume of the sample to calculate soil bulk density in g/cm^3 (Klute 1986, Grimshaw 1989).

Distribution of *Ilyanassa obsoleta* Say

An area of low marsh and creek bank communities was examined for the presence or absence of *I. obsoleta*, the eastern mud snail, by walking along the upper border of the low marsh community, at low tide, until trails were found. Trails were then followed across the marsh until either the trail ended or snails were found. If snails were indeed present on a given trail a series of counts and measurements was initiated. First, the distance from any creek bank present on the trail to the farthest snail or snails was measured. The creek bank was considered to be where the growth of vegetation began along the creek. Next all snails present within a quadrat of 0.0625 m^2 at this farthest location were counted. A quadrat of the same area was then examined for the presence or absence of snails at a distance of 1 m and 2 m perpendicular to the trail. If snails were present at either location they were counted. Following that, three randomly selected areas between the farthest snails and the end of the trail at the creek bank were assessed for snails. Again, samples were taken at on-trail, 1 m, and 2 m off-trail locations. Finally, both on-and off-trail samples were taken at the end of the trail at the creek bank.

Chlorophyll *a*

Similarly to Lukatelich and McComb (1986), Duffy et al. (1997), MacIntyre et al. (1996), concentrations of benthic chlorophyll *a* were used as a proxy for microalgae biomass in sediments. In September 2001, nine - 8.04 cm^2 cores were collected to a depth of 1 cm from randomly selected on-trail locations at each sample trail. Cores were also taken from nine paired locations 1 m off-trail from each on-trail sample location. These cores were kept out of the light and frozen until processing. The samples were each placed into centrifuge tubes and 10 ml solution of 45% acetone, 45% methanol, and 10% distilled water was added. The samples were then mechanically shaken for ten seconds, and placed in a 7.2 °C cooler for a period that varied from 12-20 hours. After cooling, the samples were spun down in a centrifuge for 10 min at 2377.5 relative centrifugal force. Samples were then pipetted from the centrifuge tube and read on a Turner Designs TD-700 fluorometer. Data was analyzed according to the methods propounded by Arar and Collins (1992). Acid was added to the samples in order to determine the amount of phaeopigments as well (see appendix).

Experimental method and statistical analyses

For the most part, each of the different analyses was conducted at various locations on the trails, and at corresponding paired locations 1m off the trails. One-tailed Wilcoxon Signed Ranks tests were used to compare on-trail data to corresponding off-trail data (See Table 1 for the expected direction of one-tailed Wilcoxon Signed Ranks tests). Wilcoxon Signed Ranks tests were used because much of the data did not meet the assumptions of parametric testing. One-tailed tests were performed because the direction of differences between on- and off-trail conditions was postulated. Tests were considered to be statistically significant at p value ≤ 0.05. If differences between on- and off-trail conditions were found to be statistically significant in a particular community, then the ratio of the on-trail to off-trail condition was calculated (on-trail condition/off-trail condition) for each pair of sampled locations. Note that ratios equal to one indicate that the on- and off-trail values are relatively equivalent. Ratios greater than one indicate that the on-trail values are larger relative to off-trail values. Ratios less than one indicate that the on-trail values are lesser relative to off-trail values. Ratios from each community were then compared using the non-parametric Kruskal- Wallis test in order to determine whether the degree to which on- and off-trail differences occurred differed from community to community.

Box plots were used to graphically display on- and off-trail data. The box in the plots represents the interquartile range, which contains 50% of the values. The line in the box indicates the median value. The whiskers extend to the highest and lowest values excluding outliers and extreme values. Outliers are indicated by a circle and are values 1.5 – 3 box lengths from the upper or lower edge of the box. Extreme values are indicated by a star and are more than 3 box lengths from the upper or lower edge of the box.

RESULTS

The following are results for various analyses conducted in both trampled on-trail areas and untrampled off-trail areas in *J. roemerianus*, *D. spicata*/*S. patens*, low marsh, and creek bank communities. Other than sections 4.1 and 4.2, each section contains comparisons between on- and off-trail data from within each community, as well as, when appropriate, intercommunity comparisons. Generally each section contains a table that provides means, medians, and the results of inferential statistical tests that have been performed. Following that are figures containing boxplots that indicate variation found within each dataset. Other tables and figures may be provided if intercommunity comparisons are appropriate.

Table 3 contains an explanatory list of the symbols that will be used in tables and figures. Appendices A - S contain all data collected.

Extent of trails

Trails were present throughout all marsh communities within the 3 km^2 study site. However, the distribution and structure of the trails varied among communities (Table 4, Figure 5). I identified 380 individual trails, the total lengths of which were approximately 23.9 km. Almost 90% of the study site was low marsh community, while just over 10% was high marsh. 80% of the study site total trail length was found in the low marsh, while 20% was found in the high marsh. Trail lengths in the creek bank community were not calculated separately. Rather, they were incorporated into the trail length totals calculated for other marsh communities containing tidal creek banks. The amount of study site covered by trails was estimated as 6876 m^2, or 0.23%, of the

Table 3. List of symbols commonly used in figures and tables.

Symbol	*Meaning*
Community	
J	*J. roemerianus*
HM	*D. spicata/S. patens*
LM	low marsh
CB	creek bank
Trail area	
+	on-trail
-	off-trail
Plant species	
J	*J. roemerianus*
SA	*S. alterniflora*
SL	*Salicornia* spp.
DS	*D. spicata*
SP	*S. patens*

Order of symbols: community, trail area, plant species

Example: "J-SP"

J = *J. roemerianus* community

- = off-trail

SP = *S. patens*

total marsh surface. Trails in both the low marsh, and *D. spicata/S. patens* communities each covered approximately 0.2% of their respective community area.

However, approximately 0.5% of the *J. roemerianus* community area was covered by trails. Trails in the *D. spicata/S. patens* community, which average 15.5 cm in width, were the narrowest trails. Generally, creek bank trails were the widest trails. Furthermore, creek bank trails tended to be wider closer to tidal creeks.

Trail patterns in the marsh appear to be influenced by the layout of upland areas surrounding the marsh. Most trails in the high marsh appear to run in a southeast-northwest direction between upland areas. Most trails in the low marsh seem to run between upland areas and wooded hammock areas in the marsh. Generally, trails are absent if there are no upland areas to which deer could go. In both high and low marshes, trails also appear to run alongside upland areas bordering the marsh.

Deer movement

Although the level of traffic on trails varied somewhat from community to community, these differences were not statistically significant at p value = 0.05 (Tables 5 and 6). The lowest frequency of prints was observed in the *D. spicata/S. patens* community, where prints were observed in only 30% of the observations. The highest frequency of prints was observed in the low marsh, where prints were observed in approximately 60% of observations.

Overall, prints were observed in the twelve study trails on 57, or 47.5%, of the possible 120 observation opportunities. The frequency of traffic along trails seemed to increase beginning in late October, and continuing through early March. Prints were

Table 4. Extent of marsh communities and trails.

Community	Area (km^2)	% of study area	Trail length (m)	% of study site total trail length	Average trail width (cm)	Trail area(m^2)	% of community area covered by trails
J	0.08	2.7	1192	5.0	33.5	399	0.5
HM	0.23	7.5	3488	14.6	15.5	537	0.2
LM	2.69	89.8	19220	80.4	30.9	5939	0.2

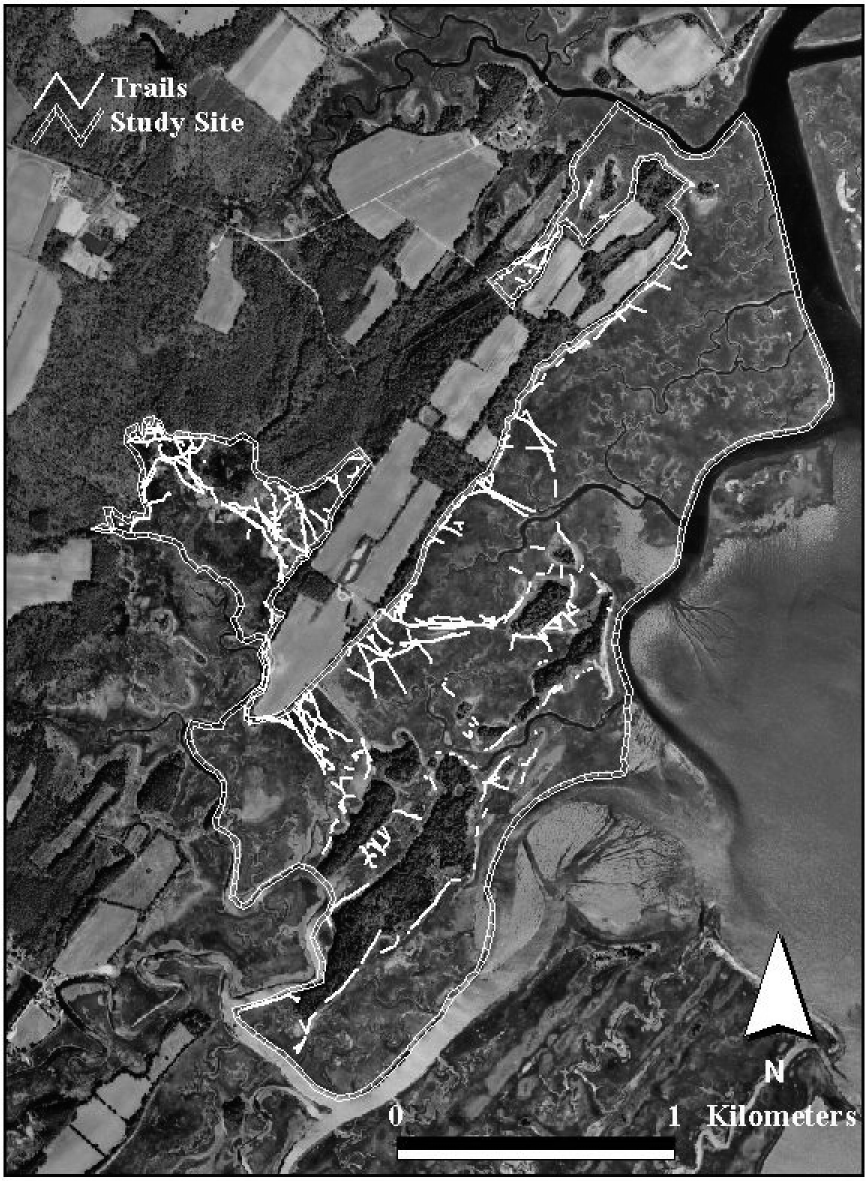

Figure 5. 1994 United States Geographical Survey aerial photo of Brownsville marsh complex showing study site and trails.

observed in only 27% of the five observations periods made between June and September. In the five observation periods occurring between October and March, prints were observed on more than 68% opportunities possible. Additionally, all of the traffic observations characterized as “high” occurred between mid-November and early March. The greatest frequency of traffic occurred in late November, when prints were observed on eleven of twelve trails, while the lowest frequency occurred in early September, when no prints were observed on any trail.

Generally, deer and raccoon were the only mammals to leave prints in sand placed on the twelve study trails (Table 7). Of the 57 occasions when prints of any sort were observed, 63% of the observations were of deer prints alone, 26% were of deer prints occurring together with raccoon prints, and 11% were of raccoon prints alone. On one occasion, prints of a bird’s webbed feet were observed on a low marsh trail.

Plant biomass

August 2000 above-ground plant biomass

The influence of trampling on biomass varied in the four different marsh communities. Median live biomass in undisturbed off-trail areas ranged from a low of 496.0 g/m^2 in the low marsh to a high of 1084.8 g/m^2 in the *J. roemerianus* community. Trampling significantly lowered live biomass in all communities (Table 8, Figure 6). However, the degree to which biomass was reduced on trails, as reflected in the on-trail percentage of off-trail biomass (on-trail biomass/off-trail biomass x 100), differed significantly from community to community (Table 8, Figure 7). Biomass losses were greatest in the creek bank community, which retained only 4.8% of live off-trail biomass. Biomass was

Table 5. Frequency of animal prints observed on 12 trails in four marsh communities. L = low frequency – one set of prints on trail. M = medium frequency – more than one set of prints on trail, but sets of prints still individually discernable. H = high frequency – multiple sets of prints so that individual sets of prints are no longer discernable.

	25JUN01	03JUL01	21JUL01	03SEP01	22SEP01	15OCT01	25NOV01	12DEC01	29JAN02	09MAR02
J1		L					M		L	
J2		L		L		L	H	L	M	H
J3							M	L		M
HM1		L				L	H	L	L	
HM2			L				L			M
HM3								L		
LM1	L	L	L				H	H		L
LM2			M	L		L	H	H	H	H
LM3		M		L		L	H	M		H
CB1						L	M	M		L
CB2		L				L	H	M	H	H
CB3	L	L		L			H		H	H

Table 6. Chi square contingency table and results of 2-sided Chi-square test used to compare the presence or absence of prints on trails in four marsh communities from June 2001 – March 2002. See Table 3 for symbol identification.

Community		No prints	Prints	Total
J	Count	17	13	30
	%	56.7%	43.3%	100%
HM	Count	21	9	30
	%	70%	30.0%	100%
LM	Count	11	19	30
	%	36.7%	63.3%	100%
CB	Count	14	16	30
	%	46.7%	53.3%	100%
Total	Count	63	57	120
	%	52.5%	47.5%	100%

	Value	Sig. (p value)
Pearson chi-square	7.318	0.062

Table 7. Animal prints observed on 12 trails in four marsh communities. D = deer. R = raccoon. B = bird.

	25JUN01	03JUL01	21JUL01	03SEP01	22SEP01	15OCT01	25NOV01	12DEC01	29JAN02	09MAR02
J1		R					D		D	
J2		D		D		D	D	D	D	D/R
J3							D	D		D
HM1		D				D	D	D	D	
HM2			D				D			D
HM3								D		
LM1	D	D	D				D/R	D		R
LM2			D/R/B	D		D	D/R	D	D/R	D
LM3		D/R		R		R	D/R	D/R		D/R
CB1						D	D	D/R		D
CB2		D				D	D/R	D	D	D/R
CB3		**D**	**R**	**R**			**D/R**	**D/R**	**D/R**	

reduced the least in the *D. spicata/S. patens* community. These areas retained as much as 54.5% of off-trail biomass.

The examination of both dead and total biomass also revealed similar trends in community response to trampling, but these data are not shown (see appendix).

August 2000 - plant community composition

Based upon the examination of live biomass, community composition in trampled on-trail areas did not differ significantly from community composition in untrampled off-trail areas in any community except *J. roemerianus* (Table 9, Figures 8-11). On-trail areas in that community contained a significantly higher percentage of *D. spicata* than off-trail areas (Table 8, Figure 9). In off-trail areas, *D. spicata* only made up 1.1% of live plant biomass, while in on-trail areas the plant made up 17.3% of live biomass.

August 2001 above-ground plant biomass

As in 2000, the influence of trampling on biomass varied from community to community. Median live above-ground plant biomass in untrampled off-trail areas was least in the low marsh community at 323.2 g/m^2, and highest in the *J. roemerianus* community at 1144.0 g/m^2. Biomass was significantly lower in on-trail areas than in off-trail areas in all communities (Table 10, Figure 12). The percentage by which biomass was reduced varied significantly from community to community (Table 10, Figure13). Live biomass was reduced most in the creek bank community, where only 3.4% of off-trail biomass was retained, and least in the *D. spicata/S. patens* community, where 20.6% of off-trail biomass was retained.

The examination of both dead and total biomass also revealed similar trends in

Table 8. August 2000 – On- and off-trail means and medians for live plant biomass in four marsh communities. Results of one-tailed Wilcoxon Signed Ranks tests used to compare live biomass from on- and off-trail areas in four marsh communities. Results of Kruskal-Wallis test used to compare the on-trail percentage of off-trail biomass from each marsh community. See Table 3 for symbol identification. Tests were significant at p value ≤ 0.05.

Area	Mean (g/m^2)	Median (g/m^2)	Wilcoxon Z score	Wilcoxon Sig. (p value)	Mean % on of off	Median % on of off	Kruskal-Wallis Chi-square value	Kruskal-Wallis Sig. (p value)
J+	179.3	73.6	-2.666	0.0038	20.6	6.0	14.691	0.002
J-	1062.8	1084.8						
HM+	308.8	313.6	-2.547	0.0054	54.5	52.0		
HM-	706.5	526.4						
LM+	199.1	192.0	-2.547	0.0054	45.7	49.0		
LM-	464.2	496.0						
CB+	33.1	3.2	-2.666	0.0020	4.8	0.8		
CB-	**624.4**	**675.2**						

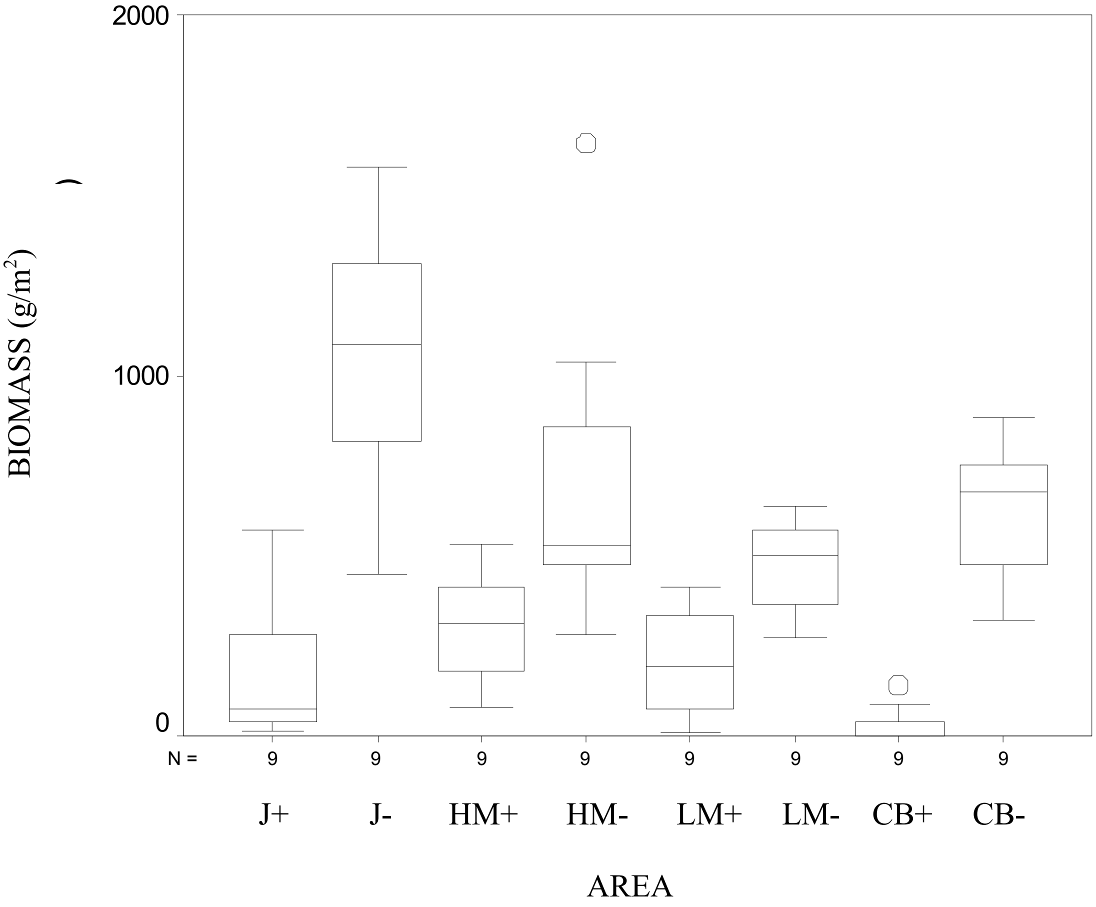

Figure 6. August 2000 - Box plots representing on- and off- trail live plant biomass in four marsh communities. Each box represents the interquartile range, which contains 50% of the values. The line in the box indicates the median value. The whiskers extend to the highest and lowest values excluding outliers and extreme values. Outliers are indicated by circles, extreme values by stars. N = number of samples. See Table 3 for symbol identification.

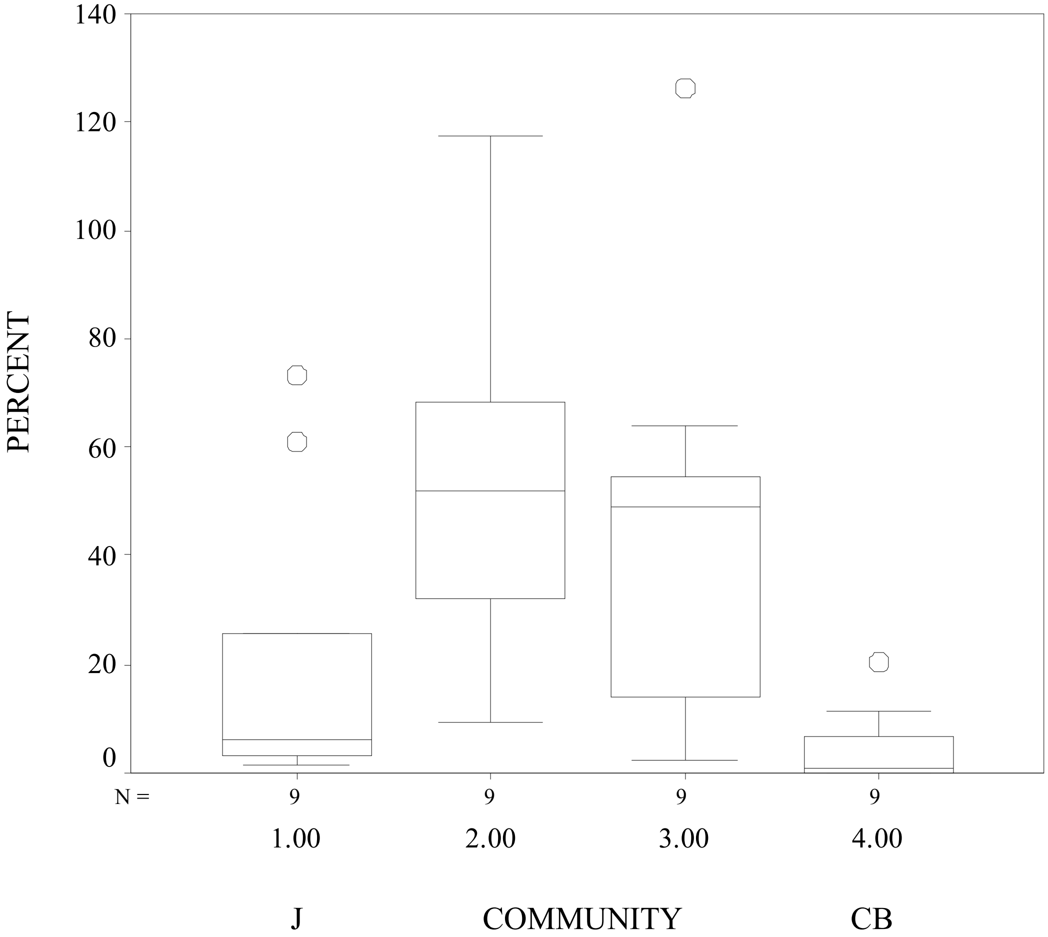

Figure 7. August 2000 [illegible] of off-trail biomass in four marsh communities. See Table 3 for symbol identification.

Table 9. August 2000 plant community composition. Mean and median percent live biomass/m^2 by species and marsh community. Results of one-tailed Wilcoxon Signed Ranks tests used to compare percent biomass/species/m^2 per marsh community. See Table 3 for symbol identification. Test significant at p value ≤ 0.05.

Area and Sp.	Mean (%/m^2)	Median (%/m^2)	Z score	Sig. (p value)
J+SP	6.3	4.0	0.9435	0.2188
J-SP	6.2	0		
J+DS	17.3	5.9	2.100	0.0195
J-DS	1.1	0.9		
J+SA	none	none		
J-SA	none	none		
J+J	76.4	80.1	-1.680	0.0547
J-J	93.1	99.6		
HM+SP	58.5	58.0	1.362	0.1016
HM-SP	44.7	41.9		
HM+DS	41.5	42.0	-1.362	0.1016
HM-DS	55.3	58.1		
HM+SA	none	none		
HM-SA	none	none		
LM+SA	98.2	100.0	1.461	0.1250
LM-SA	91.7	100.0		
LM+SL	1.8	0	-1.461	0.1250
LM-SL	8.3	0		
LM+SP	none	none		
LM-SP	none	none		
LM+DS	none	none		
LM-DS	none	none		
CB+SA	100.0	100.0		
CB-SA	100.0	100.0		

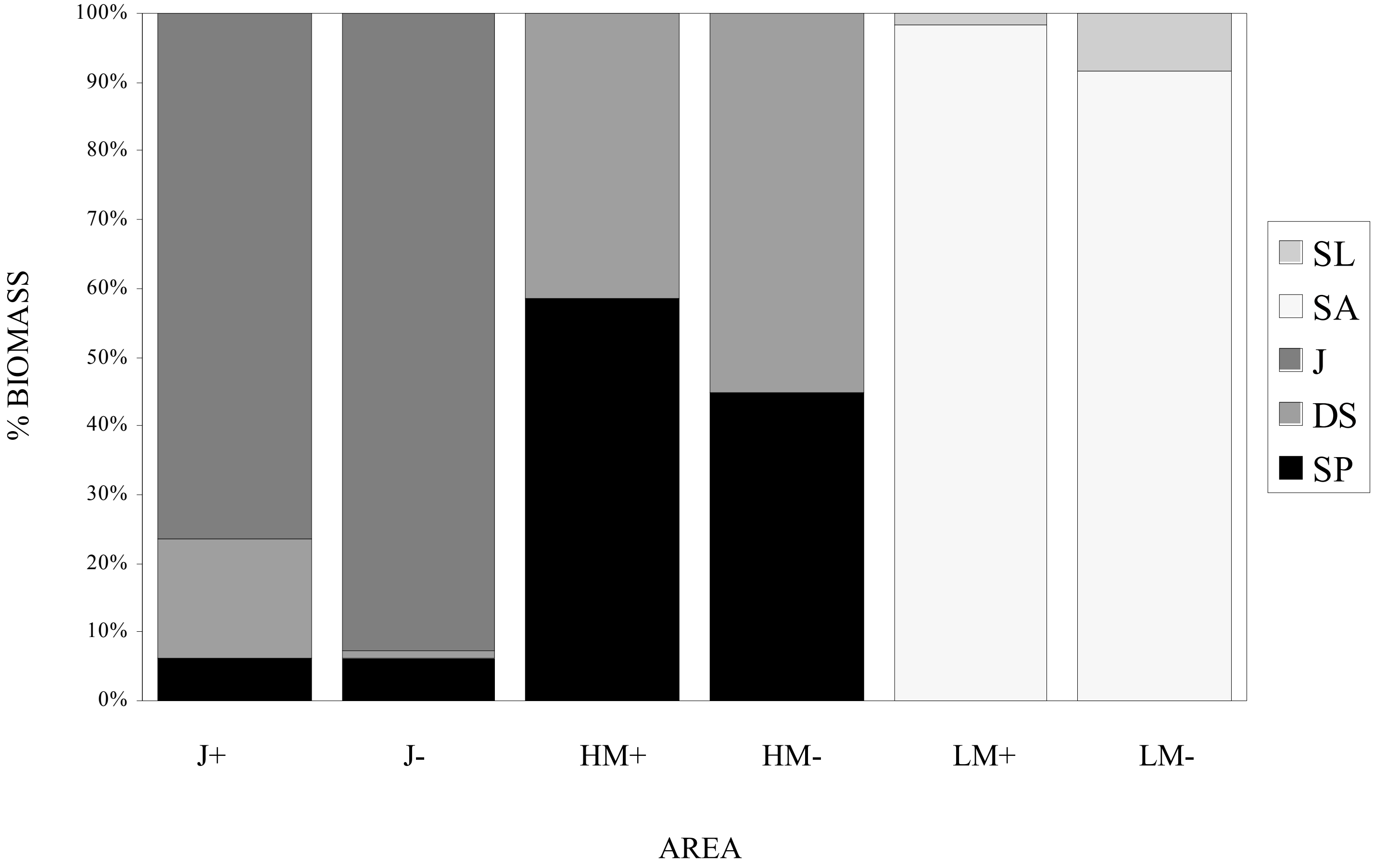

Figure 8. August 2000 – percent live biomass per species from on- and off-trail areas in four marsh communities. The creek bank community composition is not shown because only *S. alterniflora* was present in either on- or off-trail areas. See Table 3 for symbol identification.

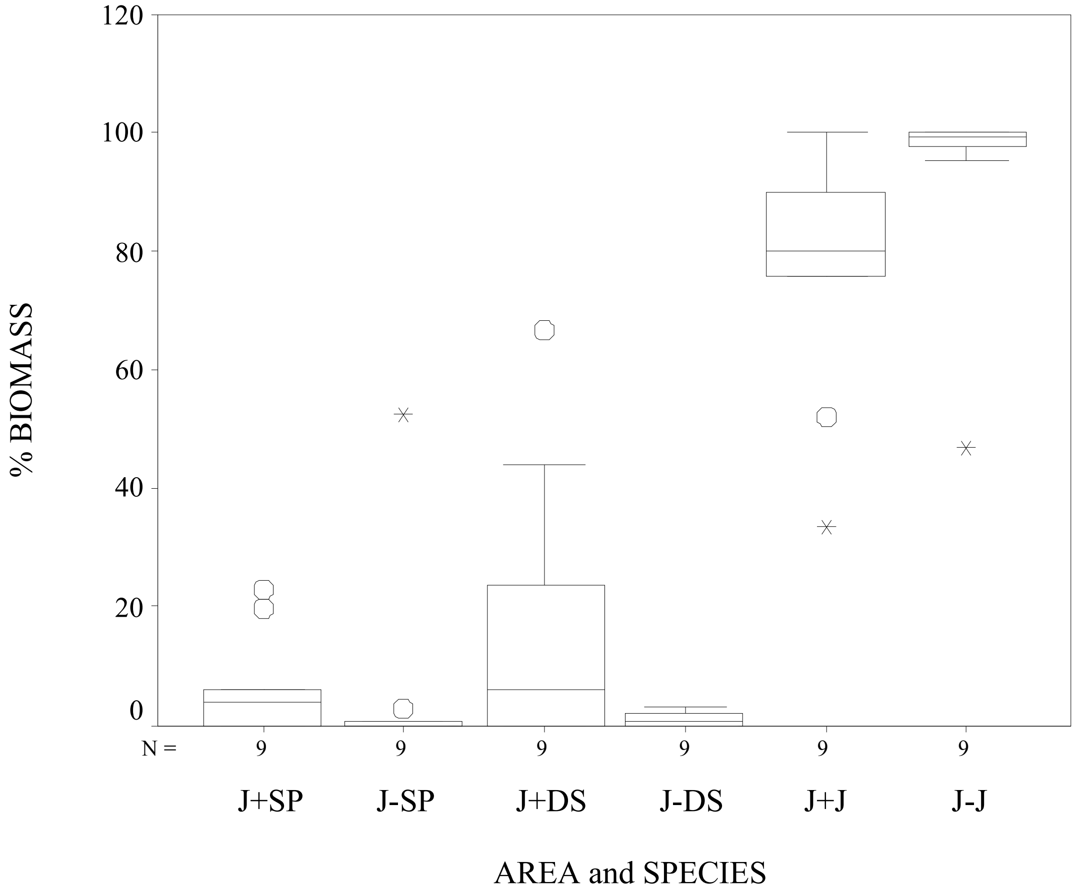

Figure 9. August 2000 - percent live biomass for different species in both on- and off-trail *J. roemerianus* areas. See Table 3 for symbol identification.

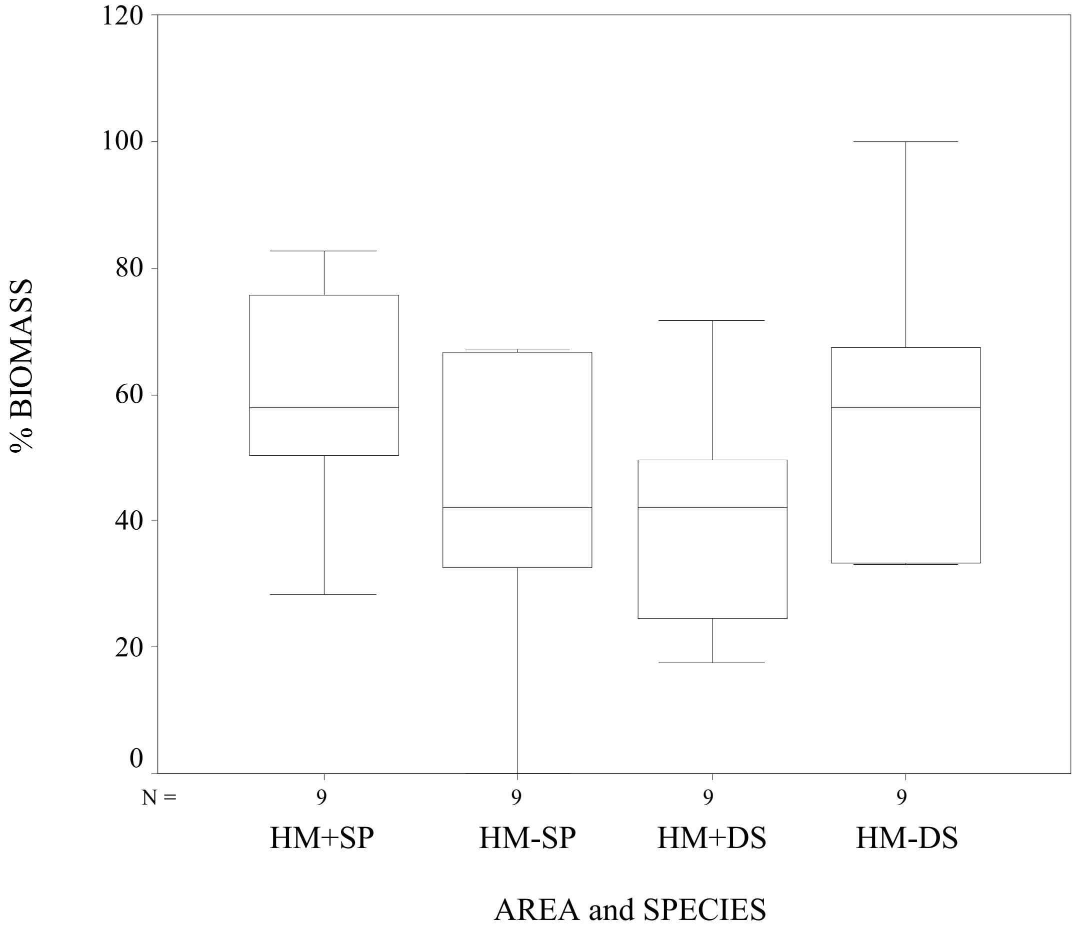

Figure 10. August 2000 - percent live biomass for different species in both on- and off-trail *D. spicata/S. patens* areas. See Table 3 for symbol identification.

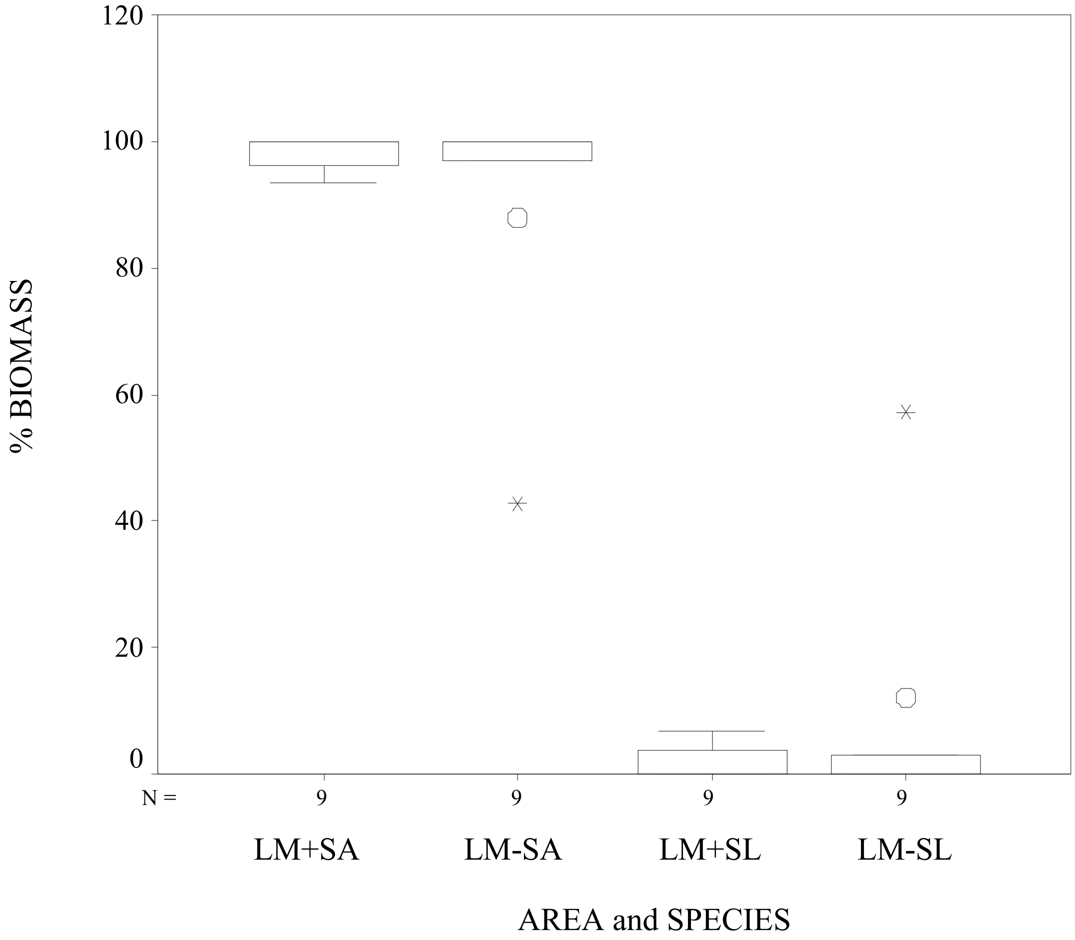

Figure 11. August 2000 - percent live biomass for different species in both on- and off-trail low marsh areas. See Table 3 for symbol identification.

community response to trampling, but these data are not shown (see appendix).

August 2001 – plant community composition

Plant community composition in on-trail areas differed significantly from plant community composition in off-trail areas in the *J. roemerianus*, *D. spicata/S. patens*, and low marsh communities (Table 11, Figures 14-17), but not in the creek bank community. Off-trail live biomass in the *J. roemerianus* community consisted of 3.0% *D. spicata* and 91.8% *J. roemerianus*, but in on-trail areas the percentage of *J. roemerianus* fell to 56.9%, while the percentage of *D. spicata* rose to 23.6%. Percentages of *S. alterniflora* and *S. patens* in this community did not differ significantly between on- and off-trail areas. Off-trail live biomass in the *D. spicata/S. patens* community was composed of 33.5% *S. patens*, but in on-trail areas, *S. patens* was only 6.5% of biomass – a significant difference. Furthermore, *D. spicata* made up only 66.5% of live off-trail biomass, but fully 88.7% of live on-trail biomass – again, a significant difference in community composition. On- and off-trail percentages of live *S. alterniflora* biomass in the *D. spicata/S. patens* community did not differ significantly.

Live biomass in off-trail low marsh areas was composed of 19.6% *D. spicata.* However, this species was entirely absent from on-trail areas in the low marsh. This was a significant difference in community composition. No significant differences in percentage of on- and off-trail biomass were found for *S. alterniflora*, *S. patens,* or *Salicornia* spp.

The only species present in either on- or off-trail areas in the creek bank community was *S. alterniflora*.

Table 10. August 2001 - On- and off-trail means and medians for live plant biomass in four marsh communities. Results of one-tailed Wilcoxon Signed Ranks tests used to compare live biomass from on- and off-trail areas in four marsh communities. Results of Kruskal-Wallis test used to compare the on-trail percentage of off-trail biomass from each marsh community. See Table 3 for symbol identification. Tests were significant at p value ≤ 0.05.

Area	Mean (g/m^2)	Median (g/m^2)	Wilcoxon Z score	Wilcoxon Sig. (p value)	Mean % on of off	Median % on of off	Kruskal-Wallis Chi-square value	Kruskal-Wallis Sig. (p value)
J+	125.3	73.6	-2.666	0.0020	13.9	10.0	11.070	0.011
J-	1209.6	1144.0						
HM+	95.3	48.0	-2.666	0.0020	20.6	17.4		
HM-	537.4	486.4						
LM+	18.5	12.8	-2.666	0.0020	6.7	4.9		
LM-	328.9	323.2						
CB+	18.6	0	-2.666	0.0020	3.4	0		
CB-	1092.3	992.0						

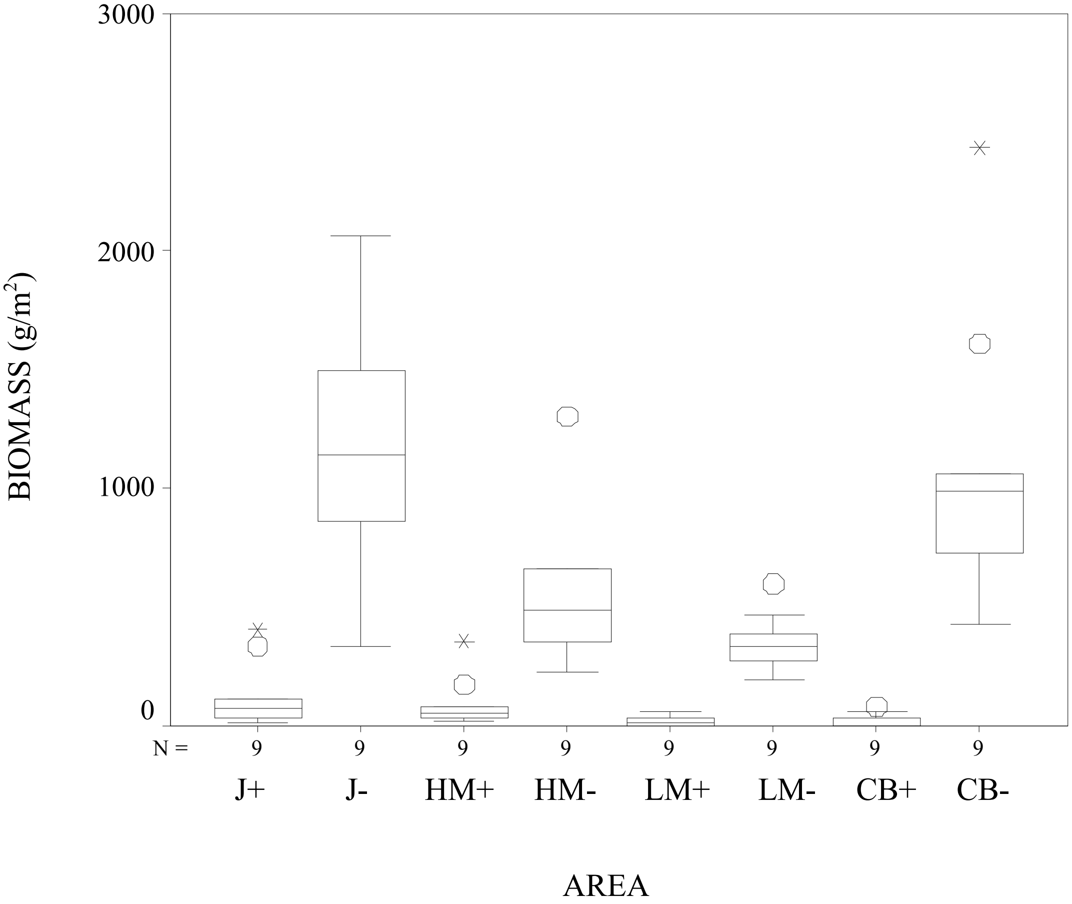

Figure 12. August 2001 – Box plots representing on- and off- trail live plant biomass in four marsh communities. See Table 3 for symbol identification.

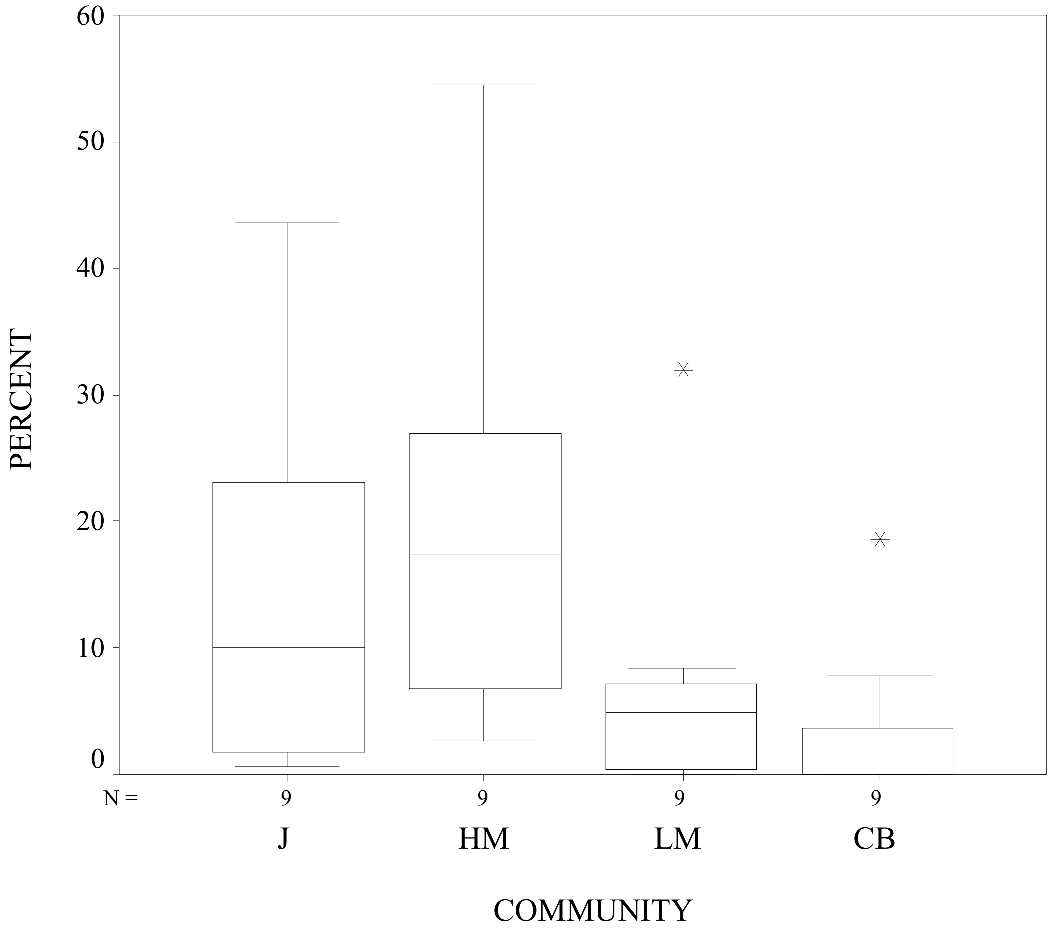

Figure 13. August 2001 - On-trail percentage of off-trail biomass in four marsh communities. See Table 3 for symbol identification.

Table 11. August 2001 plant community composition. Mean and median percent live biomass/m^2 by species and marsh community. Results of one-tailed Wilcoxon Signed Ranks tests used to compare percent biomass/species/m^2/ per marsh community. See Table 3 for symbol identification. Tests were significant at p value ≤ 0.05.

Area and Sp.	Mean (% m^2)	Median (% m^2)	Z score	Sig. (p value)
J+SP	1.6	0	-1.753	0.0625
J-SP	5.2	4.3		
J+DS	23.6	6.8	2.366	0.0078
J-DS	3.0	0.3		
J+SA	17.8	0	1.342	0.2500
J-SA	0.1	0		
J+J	56.9	42.9	-2.197	0.0156
J-J	91.8	93.6		
HM+SP	6.5	1.8	-2.380	0.0078
HM-SP	33.5	29.4		
HM+DS	88.7	95.5	1.718	0.0488
HM-DS	66.5	70.6		
HM+SA	4.8	0	1.000	0.5000
HM-SA	0	0		
LM+SA	91.1	100.0	1.014	0.1875
LM-SA	52.7	52.1		
LM+SL	8.9	0	-1.214	0.1563
LM-SL	25.4	9.2		
LM+SP	0	0	-1.000	0.5000
LM-SP	2.3	0		
LM+DS	0	0	-2.023	0.0313
LM-DS	19.6	1.3		
CB+SA	100.0	0		
CB-SA	100.0	100.0		

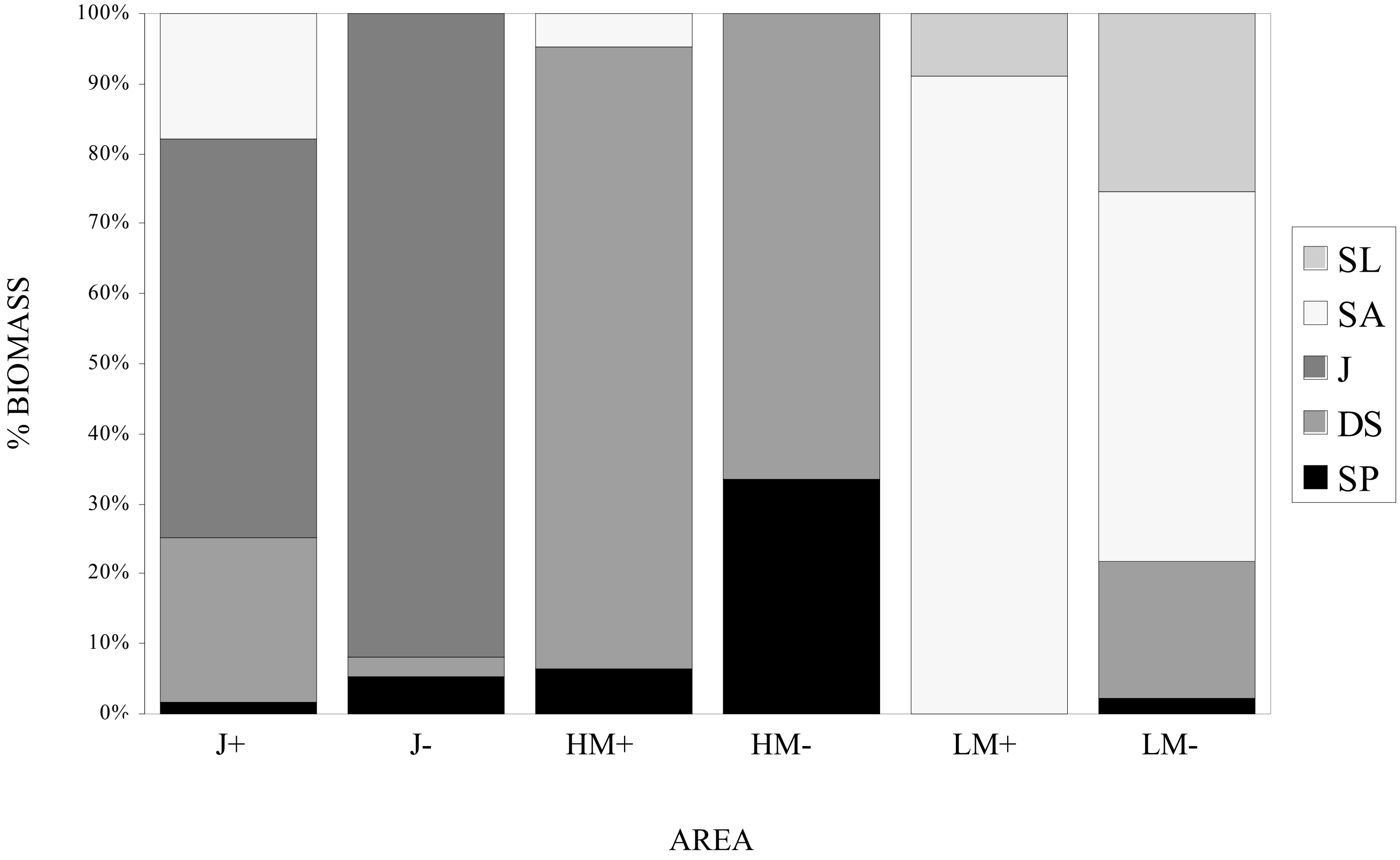

Figure 14. August 2001 – percent live biomass per species from on- and off-trail areas in four marsh communities. The creek bank community composition is not shown because only *S. alterniflora* was present in either on- or off-trail areas. See Table 3 for symbol identification.

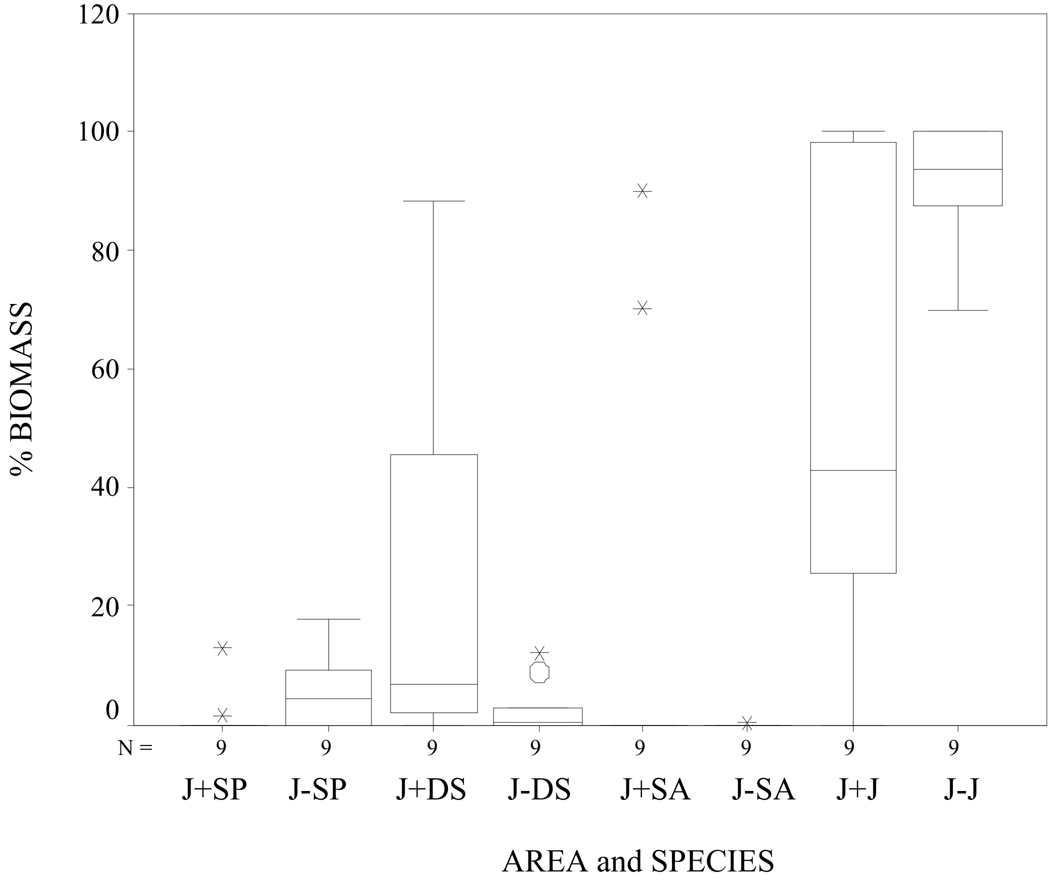

Figure 15. August 2001 - percent live biomass for different species in on- and off-trail *J. roemerianus* areas. See Table 3 for symbol identification.

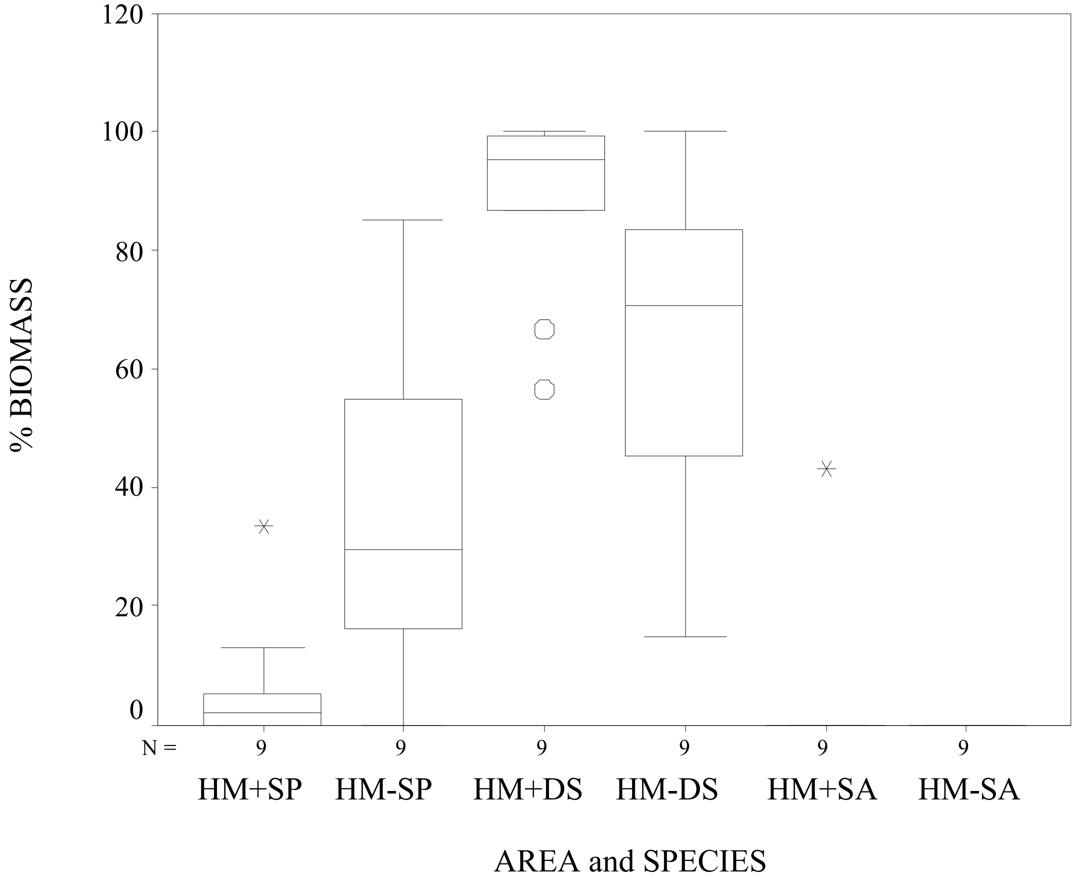

Figure 16. August 2001 - percent live biomass for different species in on- and off-trail *D. spicata/S. patens* areas. See Table 3 for symbol identification.

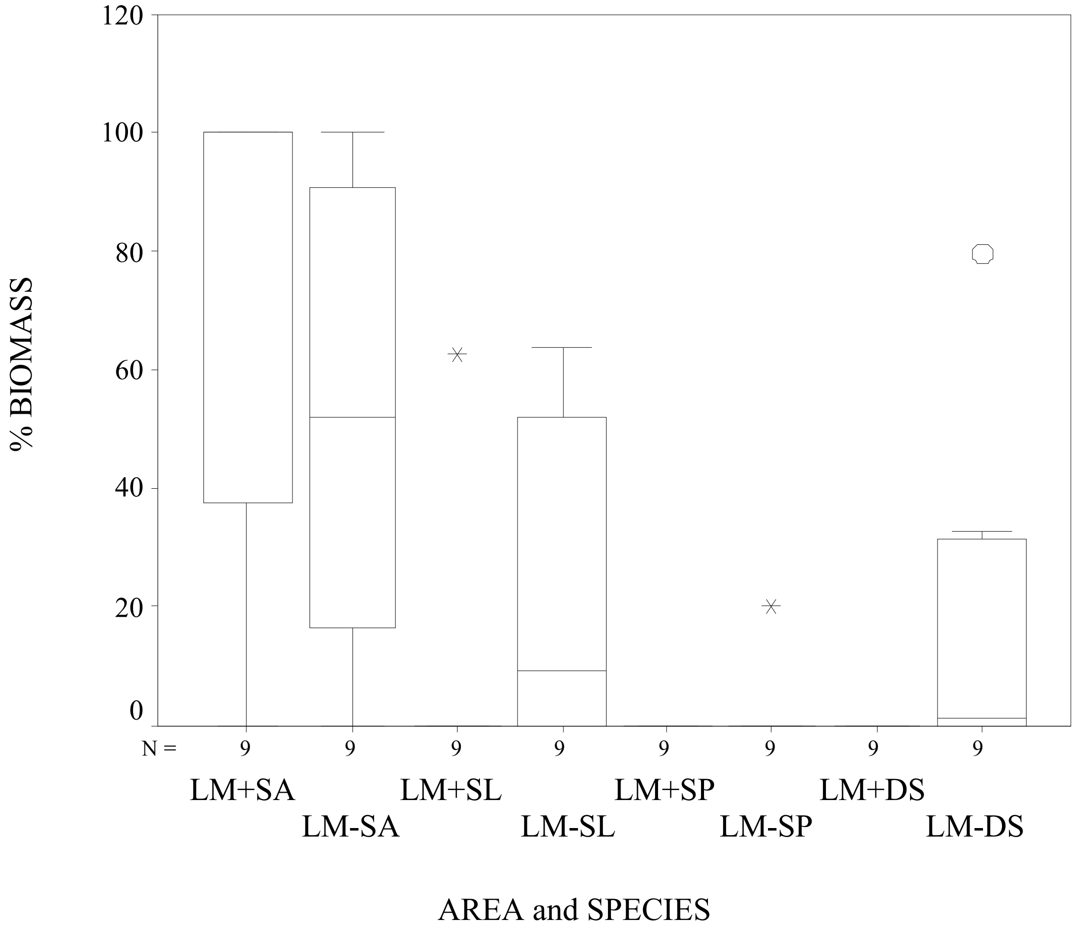

Figure 17. August 2001 - percent live biomass for different species in on- and off-trail low marsh areas. See Table 3 for symbol identification.

Light

Trampling disturbance altered the intensity of light (measured as photon flux of PAR) reaching the marsh surface to varying degrees in the four marsh communities. Light intensities were measured at different times of day in the different communities and, while intercommunity comparisons between ratios of on-trail to off-trail light intensity are appropriate, direct intercommunity comparisons of light intensity are not. Although light intensities at the marsh surface were significantly higher in on-trail areas than in off-trail areas in all communities (Table 12, Figures 18), the degree to which light intensities increased, as reflected in the ratio of on- to off- trail light intensity (on-trail light intensity/off-trail light intensity), varied from community to community (Figure 19). There were significant differences in the ratios of on- to off-trail light intensities in the different communities (Table 12). The largest relative light intensity increases were recorded in on-trail areas in the *J. roemerianus* community. Median light intensity in *J. roemerianus* on-trail areas was measured at 430.0 μE/(m^2 x sec), while median light intensity in off-trail areas was 25.0 μE/(m^2 x sec). The average ratio of on-trail to off-trail light (on-trail light intensity/off-trail light intensity) in the *J. roemerianus* community was 74 to 1. The smallest increases in light intensity were measured in the low marsh community. The median on-trail light intensities in that community were measured at 570 μE/(m^2 x sec) while average light intensities in off-trail areas were measured at 270 μE/(m^2 x sec). The ratio of on- to off-trail light intensity in the low marsh community was 1.6 to 1.

Table 12. Means and medians for on- and off-trail light intensity at ground level in four marsh communities. Results of one-tailed Wilcoxon Signed Ranks tests used to compare light intensities of on- and off-trail areas in each habitat. Results of Kruskal-Wallis tests used to compare the ratio of on-trail light intensity to off-trail light intensity from each marsh community. See Table 3 for symbol identification. Tests were significant at p value ≤ 0.05

Area	Mean *µE/(m^2 x sec)*	Median *µE/(m^2 x sec)*	*Z score*	Wilcoxon *Sig. (p value)*	Mean *ratio*	Median *ratio*	Chi square *value*	Kruskal-Wallis *Sig. (p value)*
J+	455.7	430.0	3.408	0.0000	73.9/1	14.0/1	31.693	0.000
J-	42.3	25.0						
HM+	212.9	200.0	2.387	0.0075	3.1/1	2.2/1		
HM-	137.0	105.0						
LM+	563.3	570.0	3.239	0.0002	1.6/1	1.3/1		
LM-	414.0	270.0						
CB+	673.3	650.0	3.411	0.0000	3.0/1	3.0/1		
CB-	282.0	270.0						

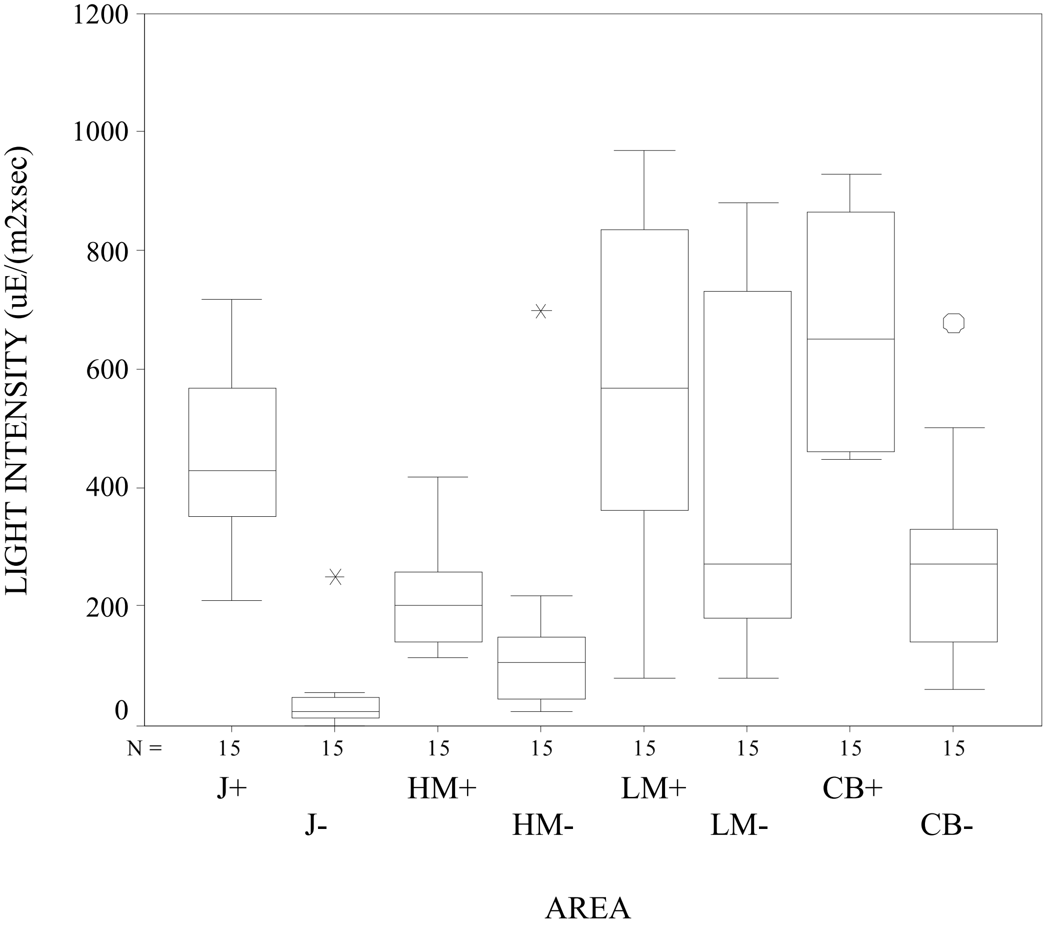

Figure 18. On- and off-trail light intensity (as μE/(m^2 x sec)) in four marsh communities. See Table 3 for symbol identification.

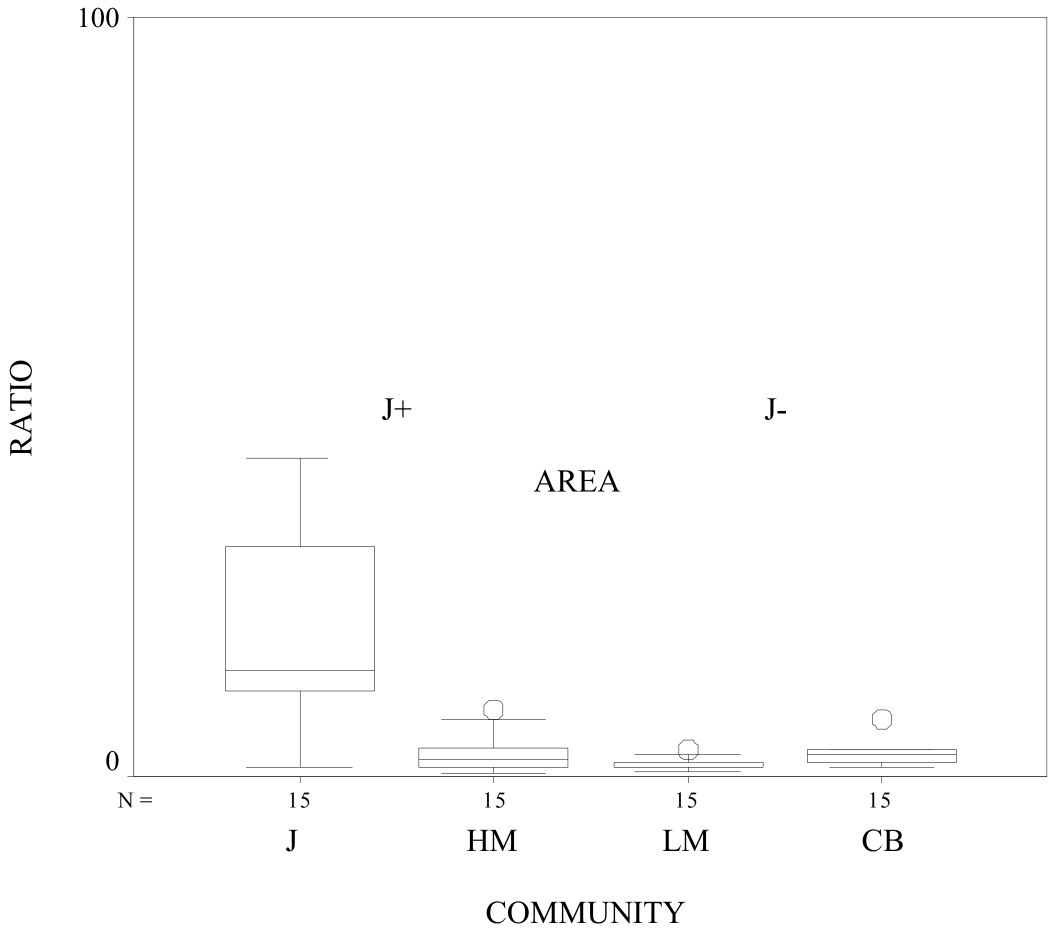

Figure 19. Ratio of on-trail light intensity to off-trail light intensity in four marsh communities. Note: two extreme values from the *J. roemerianus* community are not included in graph. These values are 350/1 and 530/1. See Table 3 for symbol identification.

Temperature

August 2001

Trampling disturbance influenced soil temperatures differently in the four marsh communities. Temperatures were measured at different times of the day in different communities, so direct intercommunity comparisons of temperature are not appropriate – however, comparisons between on- and off-trail temperature ratios are. Mean air temperature in the marsh on 21 and 22 August, the two days during which sampling was performed, were 29.5 °C and 30.3 °C respectively. Surface temperatures in trampled on-trail areas in the *J. roemerianus* and *D. spicata/S. patens* communities were significantly higher than surface temperatures in untrampled off-trail areas (Table 13, Figure 20). On-trail surface temperatures were not significantly higher than off-trail temperatures in either the low marsh or creek bank communities (Table 13, Figure 20). The ratios of on- to off-trail surface temperature (on-trail surface temperature/off-trail surface temperature), did not vary significantly among the four habitats (Table 13, Figure 21). The highest average ratio, 1.04/1, was found in the *J. roemerianus* community. On-trail temperatures at a depth of 5 cm were significantly higher than off-trail temperatures at the same depth in *J. roemerianus*, *D. spicata/S. patens,* and creek bank communities, but not the low marsh (Table 13, Figures 22). Again, as with surface temperature ratios, the on- to off-trail temperature ratio for this depth did not vary significantly among the marsh communities (Table 13, Figure 23). The highest average ratios, 1.05/1, were observed in both the *J. roemerianus* and *D. spicata/S. patens* communities.

Table 13. August 2001 - Means and medians for on- and off-trail temperatures in four marsh communities. Results of one-tailed Wilcoxon Signed Ranks tests used to compare on- and off-trail temperature from each community. Results of Kruskal-Wallis test used to compare the ratio of on-trail temperature to off-trail temperature from each community. Tests were significant at p value ≤ 0.05. Part A displays surface temperature values. Part B displays temperature values taken at a depth of 5 cm. See Table 3 for symbol identification.

	Area	Mean (°C)	Median (°C)	Z score	Wilcoxon Sig. (p value)	Mean ratio	Median ratio	Chi square value	Kruskal-Wallis Sig. (p value)
A.	J+	23.5	23.3	1.973	0.0273	1.04/1	1.05/1	3.894	0.273
	J-	22.5	22.2						
	HM+	22.6	20.3	2.053	0.0215	1.02/1	1/1		
	HM-	22.1	20.0						
	LM+	29.0	29.4	0.7303	0.3125	1.01/1	1/1		
	LM-	28.6	29.4						
	CB+	25.2	25.0	1.511	0.0938	1.01/1	1/1		
	CB-	24.8	24.7						
B.	J+	22.5	22.2	2.552	0.0039	1.05/1	1.05/1	4.123	0.248
	J-	21.5	21.7						
	HM+	22.1	20.6	2.458	0.0054	1.05/1	1.02/1		
	HM-	21.6	20.6						
	LM+	28.0	28.3	1.547	0.0645	1.03/1	1.04/1		
	LM-	27.2	27.8						
	CB+	24.6	24.4	2.201	0.0156	1.02/1	1.02/1		
	CB-	24.0	23.9						

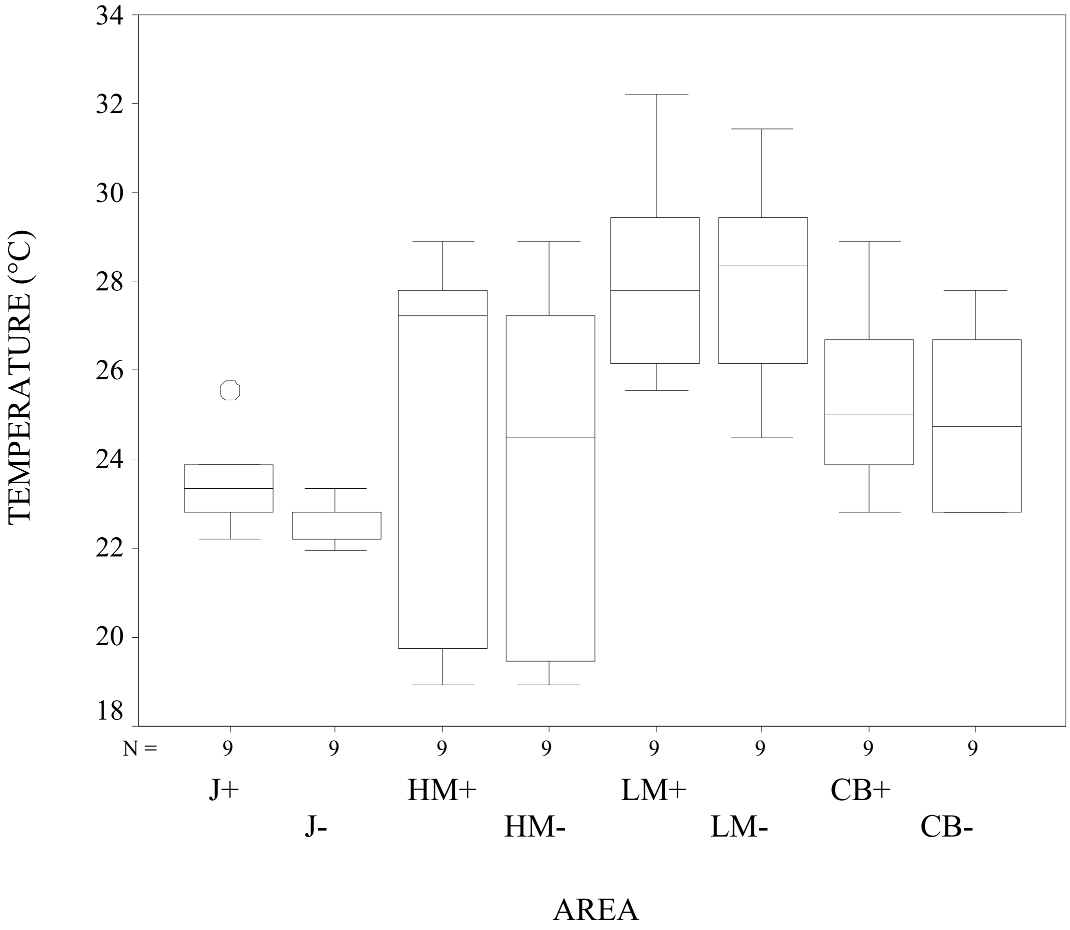

Figure 20. August 2001 - On- and off- trail temperature at the surface in four marsh communities. See Table 3 for symbol identification.

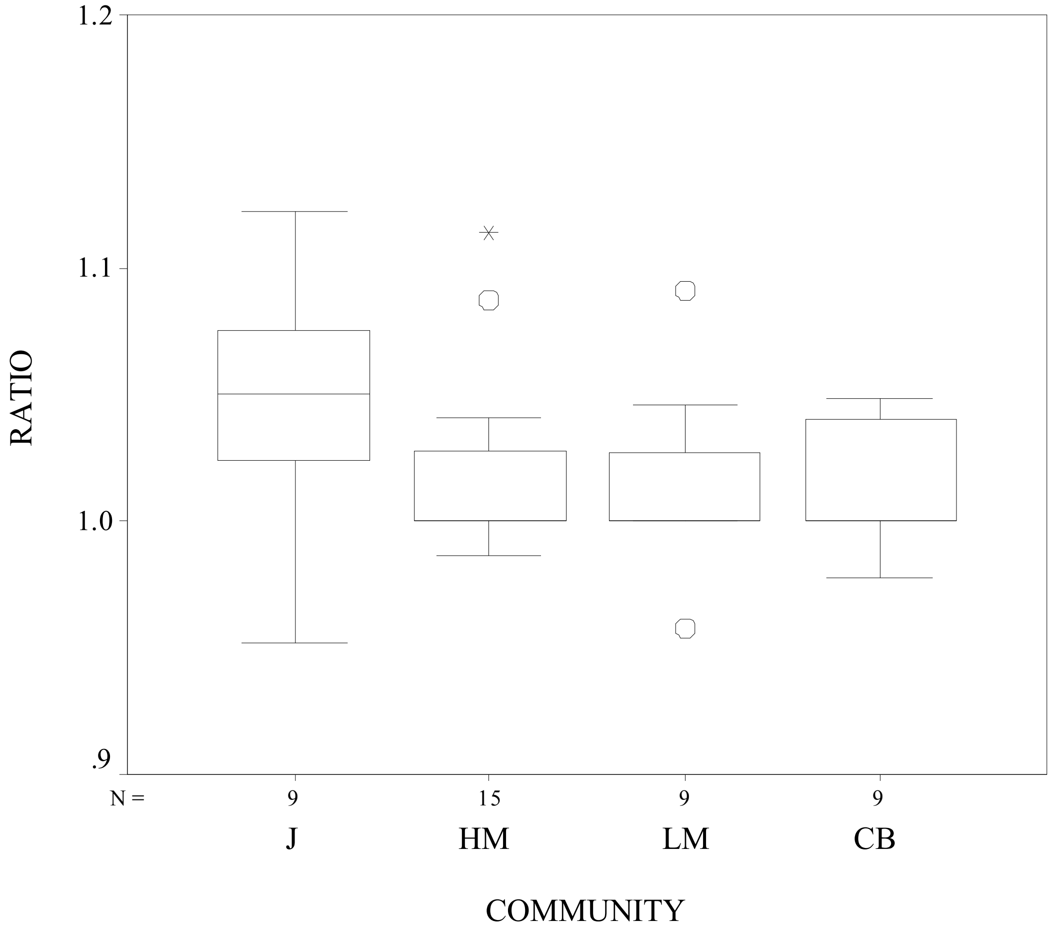

Figure 21. August 2001 – Ratio of on-trail surface temperature to off-trail surface temperature in four marsh communities. See Table 3 for symbol identification.

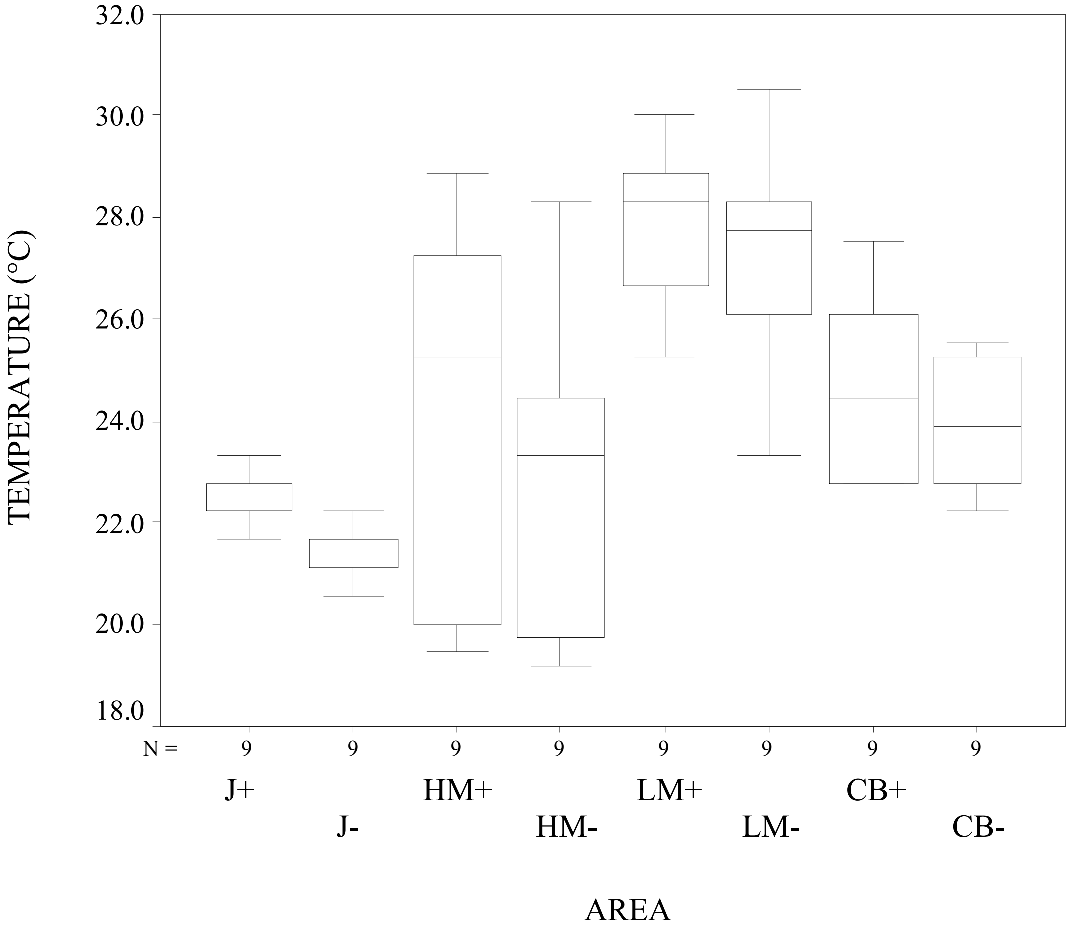

Figure 22. August 2001 - On- and off- trail temperature at a depth of 5 cm in four marsh communities. See Table 3 for symbol identification.

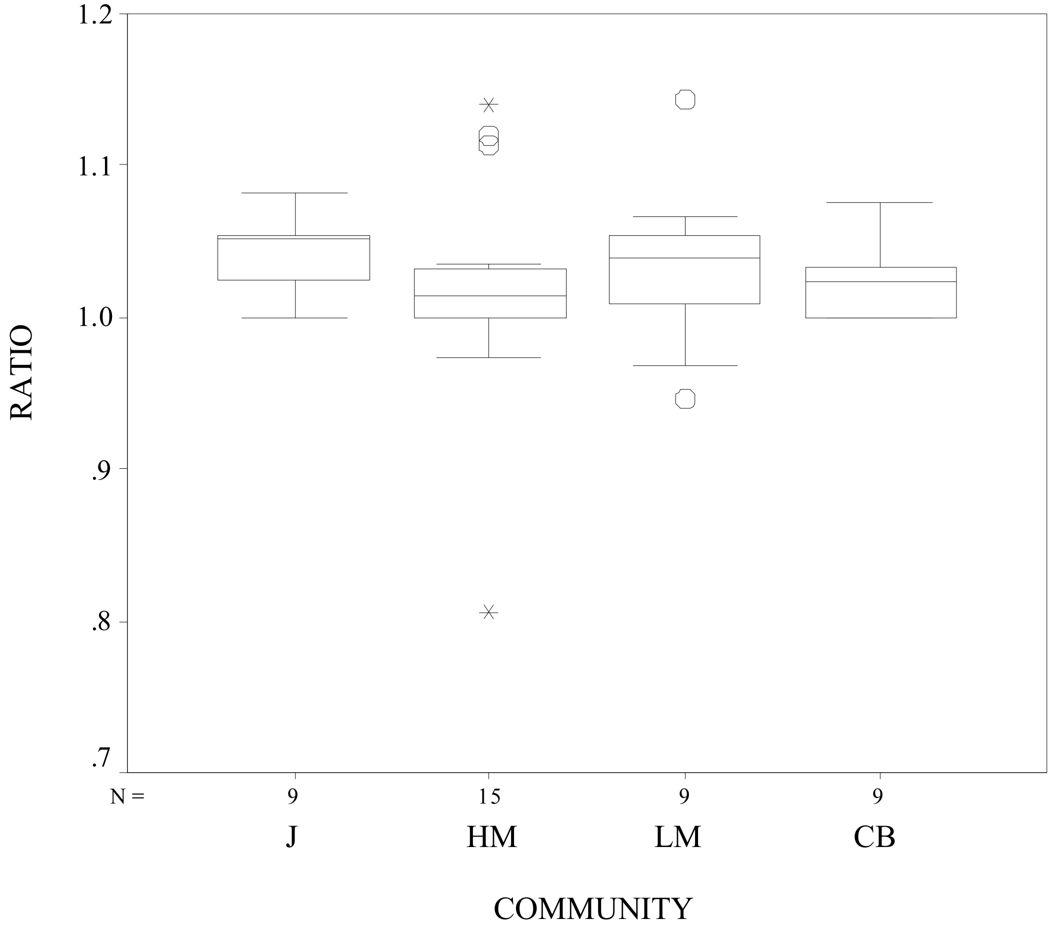

Figure 23. August 2001 – Ratio of on-trail temperature to off-trail temperature at a depth of 5 cm in four marsh communities. See Table 3 for symbol identification.

March 2002

Again, as observed in August 2000, trampling disturbance affected soil temperatures differently in the four marsh communities. Also, as in August 2000, temperatures were measured at different times of the day in different communities, so direct intercommunity comparisons of temperature are not appropriate – however, comparisons between on- and off-trail temperature ratios are. Noon air temperature in the marsh on 9 March, the day sampling was performed, was 21.5°C. On-trail surface temperatures were significantly warmer than off-trail surface temperatures in the *J. roemerianus* and *D. spicata/S. patens* communities. Surface temperatures were not significantly different in the low marsh and creek bank communities. Unlike in the August 2000 surface observations, significant differences were found in the on-trail to off-trail surface temperature ratios calculated for the different marsh communities (Table 14, Figure 24). The largest difference in the average ratio of on- to off-trail surface temperature was 1.06/1 and was observed in the *J. roemerianus* community (Figure 25). The ratio indicating the least difference between on- and off-trail surface temperature was found in the low marsh community and was 0.99/1 (Figure 25). In all communities, on-trail temperatures at a depth of 5 cm were significantly warmer than off-trail temperatures at the same depth (Table 14, Figure 26). Again, as with the on- to off-trail surface temperature ratios, significant differences in the ratios of on- to off-trail temperature at a depth of 5 cm among the marsh communities were found (Table 14, Figure 27). The largest difference in the ratio of on- to off-trail temperature was observed in the *J. roemerianus* community and averaged 1.20/1 (Figure 27). The smallest difference was found to be in the low marsh community where a ratio

Table 14. March 2002 - Means and medians for on- and off-trail temperatures in four marsh communities. Results of one-tailed Wilcoxon Signed Ranks tests used to compare on- and off-trail temperatures from each community. Results of Kruskal-Wallis test used to compare the ratio of on-trail temperature to off-trail temperature from each community. The tests were significant at p value ≤ 0.05. Part A displays surface temperature values. Part B contains temperature values taken at a depth of 5 cm. See Table 3 for symbol identification.

	Area	Mean (°C)	Median (°C)	Z score	Wilcoxon Sig. (p value)	Mean ratio	Median ratio	Chi square score	Kruskal-Wallis Sig. (p value)
A.	J+	13.7	14.0	2.536	0.0039	1.06/1	1.04/1	9.238	0.026
	J-	12.9	13.0						
	HM+	14.2	14.0	1.763	0.0400	1.04/1	1.04		
	HM-	13.6	13.8						
	LM+	16.9	18.0	-1.436	0.0812	0.99/1	0.99/1		
	LM-	17.1	18.2						
	CB+	15.6	14.5	1.436	0.0833	1.03/1	1.02/1		
	CB-	15.1	15.0						
B.	J+	13.1	12.8	3.268	0.0001	1.20/1	1.22/1	11.492	0.009
	J-	11.0	11.0						
	HM+	13.7	14.0	3.235	0.0001	1.13/1	1.13/1		
	HM-	12.1	12.2						
	LM+	16.8	17.5	3.050	0.0004	1.08/1	1.07/1		
	LM-	15.6	17.0						
	CB+	15.7	15.0	3.409	0.0000	1.11/1	1.12/1		
	CB-	14.1	14.0						

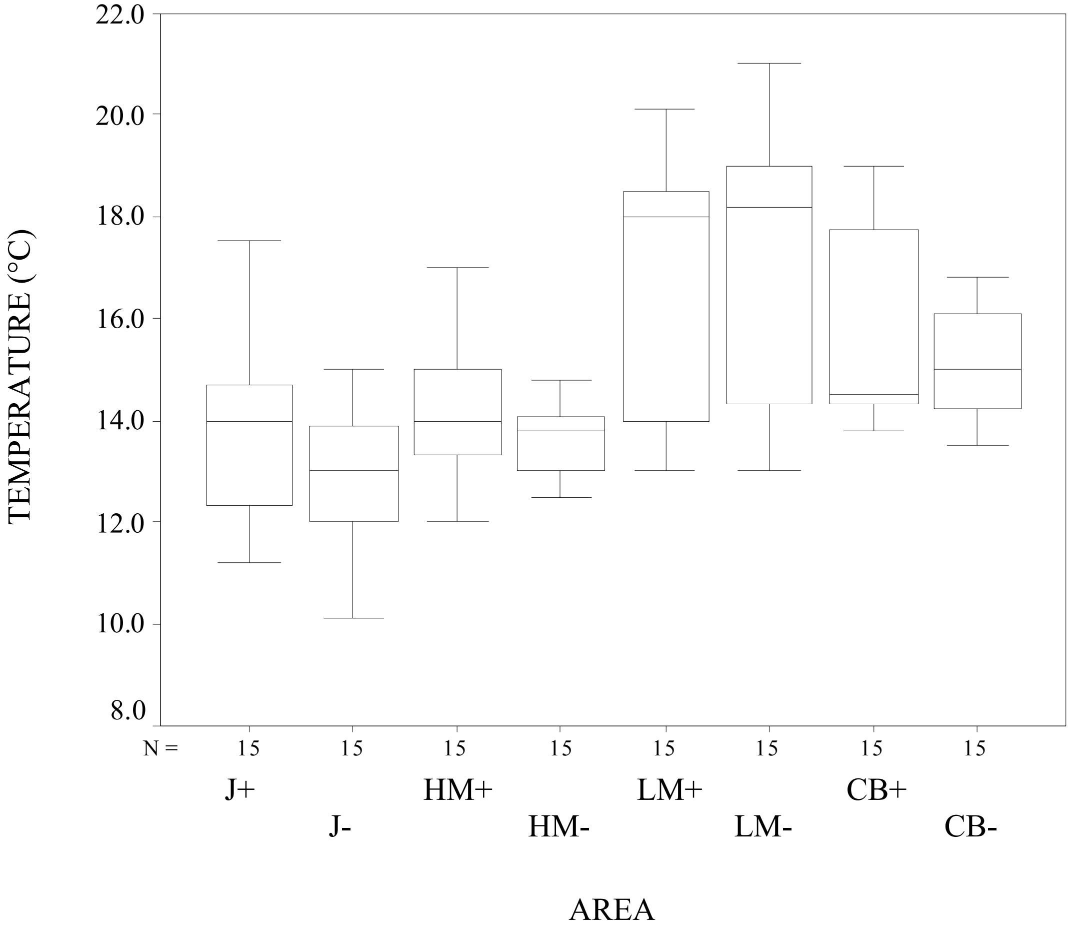

Figure 24. March 2002 - On- and off- trail temperature at surface. See Table 3 for symbol identification.

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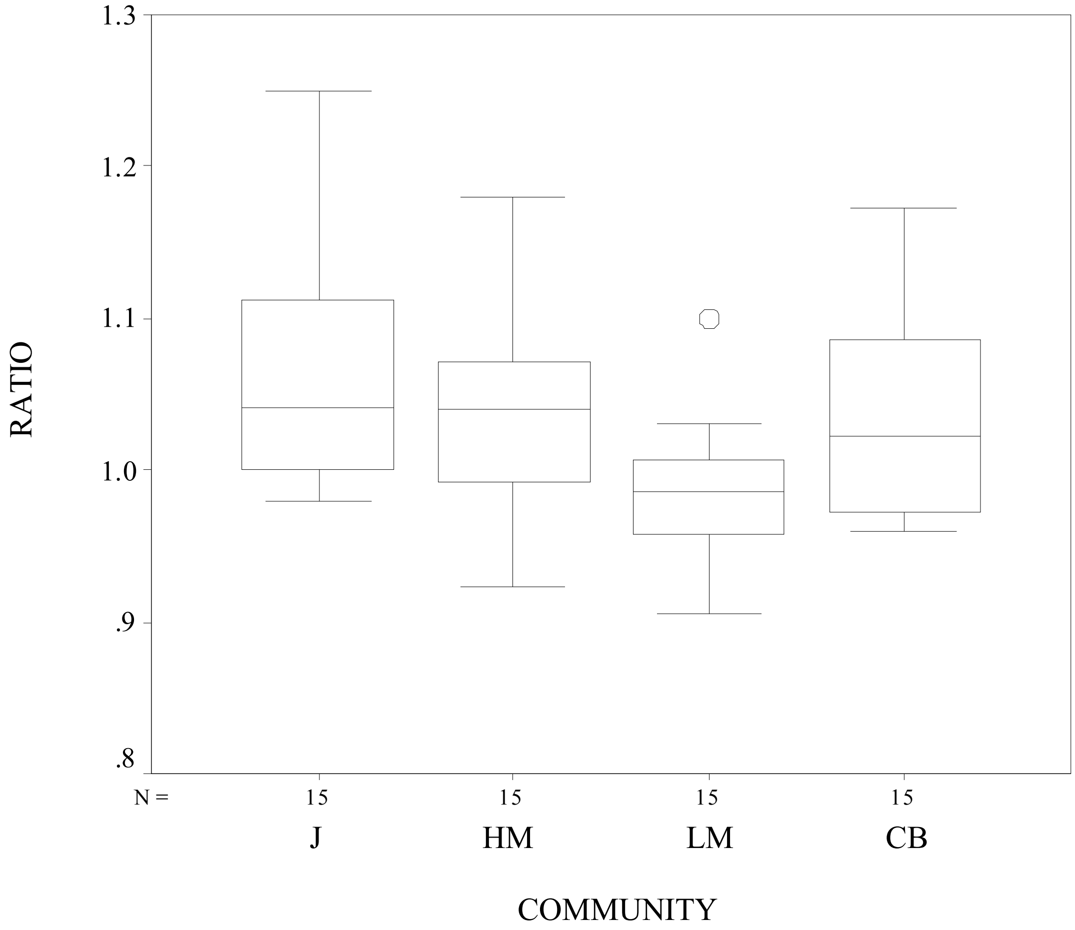

Figure 25. March 2002 – Ratio of on-trail surface temperature to off-trail surface temperature in four marsh communities. See Table 3 for symbol identification.

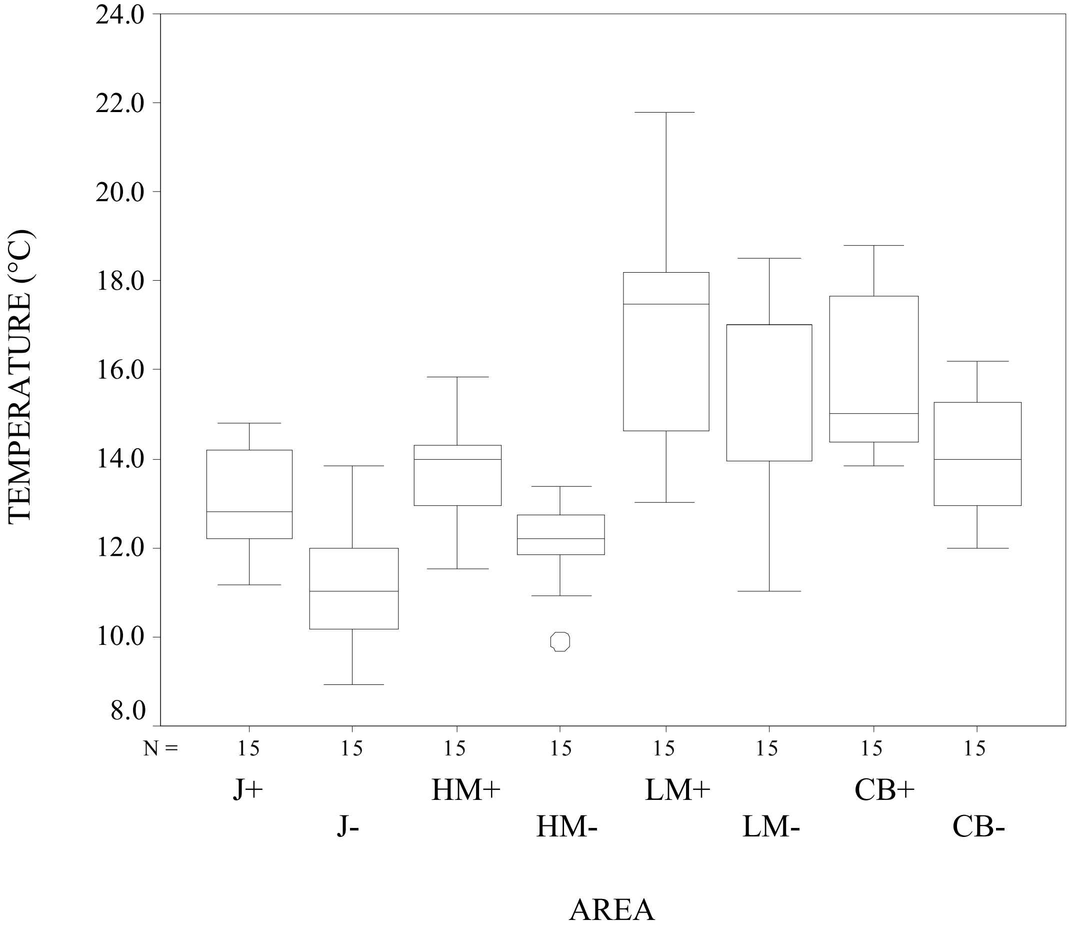

Figure 26. March 2002 - On- and off- trail temperature at a depth of 5 cm. See Table 3 for symbol identification.

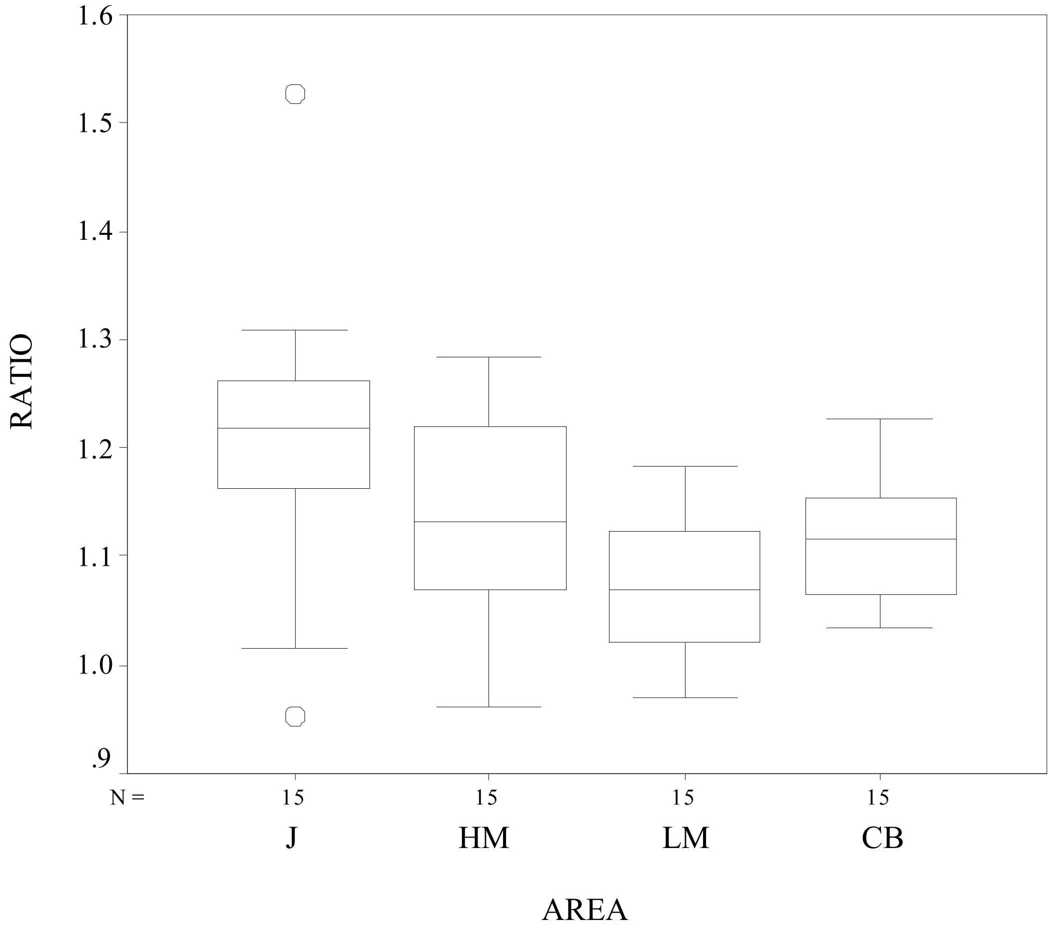

Figure 27. March 2002 – Ratio of on-trail temperature to off-trail temperature at a depth of 5 cm in four marsh communities. See Table 3 for symbol identification.

of 1.08/1 was observed (Figure 27).

Elevation

Trampling disturbance had differential influence on the elevation of the marsh surface in the various communities. Trail elevation measurements were made relative to the lowest points along each trail in each community by subtracting all stadia rod height measurements from the lowest height measurement along each trail - thereby reducing the lowest measurement to zero and rendering all other values relative to that. Though on-trail median elevation was lower than off-trail median elevation in all communities, only on-trail elevations in the *J. roemerianus*, low marsh, and creek bank communities were significantly lower than off-trail elevations in each community. Median on-trail elevation in the *D. spicata/S. patens* community did not differ significantly from the median off-trail elevation (Table15, Figure 28). The largest difference in median on- and off-trail elevation, 0.213 m, was observed in the creek bank community. Differences in median on- and off- trail elevations in the *J. roemerianus* and low marsh communities were 0.021 m and 0.028 m respectively. The smallest difference in on- and off-trail median elevation, 0.014 m, was observed in the *D. spicata/S. patens* community.

Soil salt content

Soil salt concentrations varied from community to community. Median soil salt concentration in the upper 10 cm of soil in off-trail areas ranged from a high of 92.0 mg salt/g soil in the low marsh community to a low of 36.5 mg salt/g soil in the *D. spicata/S. patens* community. On-trail soil salt concentration did not differ significantly from off-trail concentration in any community at any depth (Table 16, Figures 29-33).

Table 15. Elevation means and medians for on- and off-trail areas in four marsh communities. Results of one-tailed Wilcoxon Signed Ranks test used to compare on- and off-trail elevations in each community. Test were significant at p value ≤ 0.05. See Table 3 for_symbol identification.

Area	Mean *elevation (m)*	Median *elevation (m)*	*Z score*	*Sig. (p value)*
J+	0.039	0.045	2.272	0.0103
J-	0.061	0.066		
HM+	0.032	0.024	0.8805	0.1986
HM-	0.046	0.038		
LM+	0.030	0.025	2.101	0.0177
LM-	0.045	0.053		
CB+	0.197	0.054	2.201	0.0133
CB-	0.263	0.267		

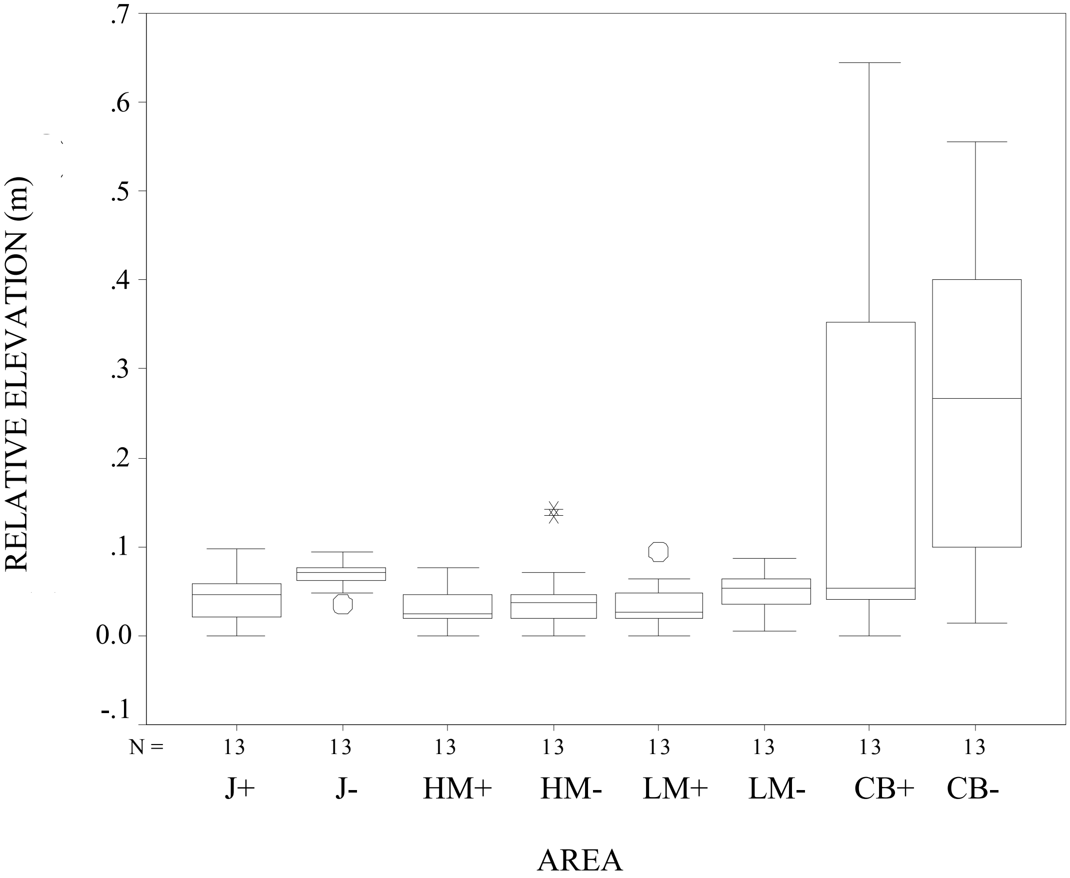

Figure 28. On- and off-trail relative elevation in four marsh communities. See Table 3 for symbol identification.

Percent organic matter content in soil

Percent organic matter content in the soils of the four marsh communities was affected by trampling disturbance in different ways. Median percent organic matter from the upper 10 cm of soil in off-trail areas varied from a high of 72.0 % in the *D. spicata/S. patens* community to a low of 17.8% in the creek bank community. Median percentages in on-trail areas ranged from a high of 58.0% in the *J. roemerianus* community, to a low of 11.8% in the low marsh community (Table 17, Figures 34-38). There were no significant differences in organic matter content in the upper 10 cm of soil between on- and off-trail areas in the *J roemerianus*, low marsh, or creek bank communities. However, percent organic matter content in the on-trail areas of the *D. spicata/S. patens* community was significantly lower than in the off-trail areas. Soil in the off-trail areas was 54.4% organic, while soil in the on-trail areas was only 44.0% organic. Within the upper 10 cm of soil in that community, the significant differences in percent soil organic content occurred at depths from 2-10 cm below the surface (Figure 36).

The average ratio of on- to off-trail % organic matter content (on-trail % organic matter/off-trail % organic matter) in the upper 10 cm of soil in the *D. spicata/S. patens* community was 0.76/1.

Soil bulk density

Soil bulk density varied significantly in the four marsh communities (Table 18, Figure 39-44). Median off-trail bulk density in the upper 10 cm of soil ranged from a high of 0.37 g/cm^3 in the low marsh community to a low of 0.14 g/cm^3 in the *D. spicata/S. patens* community. Median on-trail bulk density ranged from a high of 0.51 g/cm^3 in the low

Table 16. Means and medians for salt content of soil in on- and off-trail areas from four marsh communities. Results of one-tailed Wilcoxon Signed Ranks tests used to compare on- and off-trail soil salt content. Tests were significant at p value ≤ 0.05. Part A displays data from upper 10 cm of soil. Part B displays data from the upper 1cm of soil. Part C displays data from the next 2-3 cm of soil. Part D displays data from the next 3-5 cm of soil. Part E displays data from the next 5-10 cm of soil. See Table 3 for symbol identification.

	Area	Mean (mg salt/g soil)	Median (mg salt/g soil)	Z score	Sig. (p value)
A.	J+	49.5	42.0	-0.1777	0.4551
	J-	47.6	46.0		
	HM+	36.2	26.0	-0.4146	0.3672
	HM-	37.0	36.5		
	LM+	62.0	54.0	-1.244	0.1250
	LM-	76.2	92.0		
	CB+	36.6	37.0	-1.008	0.1719
	CB-	41.7	39.3		
B.	J+1	36.8	40.0	-0.4233	0.3594
	J-1	41.1	40.0		
	J+2	50.4	55.0	0.5355	0.3125
	J-2	47.8	40.0		
	J+3	54.0	40.0	0.7036	0.2695
	J-3	49.4	50.0		
	J+4	49.8	50.0	0.0000	0.5156
	J-4	48.0	45.0		
C.	HM+1	36.7	25.0	0.5108	0.3516
	HM-1	30.3	25.0		
	HM+2	39.7	40.0	-0.1190	0.4688
	HM-2	38.3	35.0		
	HM+3	38.9	35.0	-0.2807	0.4063
	HM-3	41.1	40.0		
	HM+4	33.6	20.0	-0.5927	0.3125
	HM-4	36.2	30.0		

Table 16. Cont.

	Area	Mean (mg salt/g soil)	Median (mg salt/g soil)	Z score	Sig. (p value)
D.	LM+1	65.3	70.0	0.5615	0.3203
	LM-1	64.4	65.0		
	LM+2	61.4	75.0	-0.1777	0.4551
	LM-2	70.1	80.0		
	LM+3	59.6	55.0	-1.185	0.1484
	LM-3	73.0	70.0		
	LM+4	62.6	56.0	-1.481	0.0820
	LM-4	82.3	84.0		
E.	CB+1	40.0	30.0	0.9540	0.2188
	CB-1	34.4	30.0		
	CB+2	45.6	35.0	0.7358	0.2656
	CB-2	41.7	40.0		
	CB+3	36.7	40.0	-1.594	0.0781
	CB-3	42.8	35.0		
	CB+4	32.3	36.0	-1.362	0.1016
	CB-4	42.7	40.0		

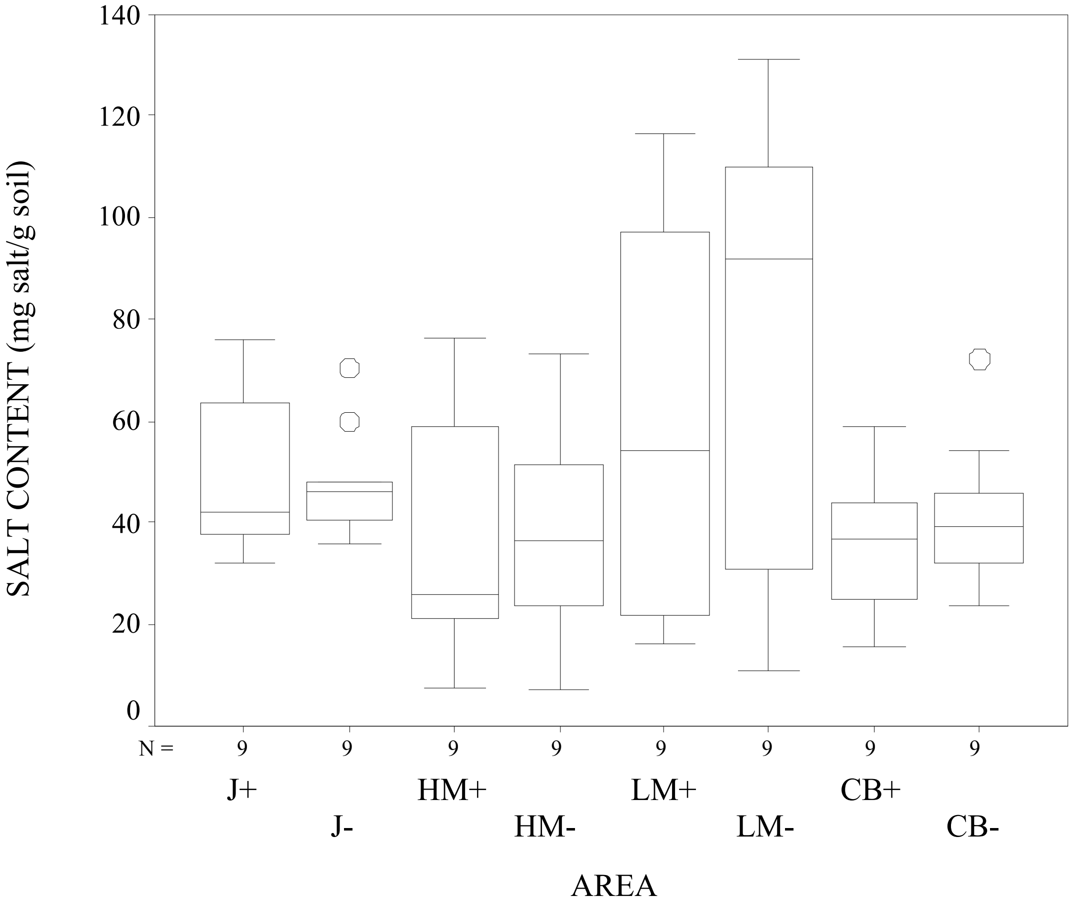

Figure 29. Salt content in upper 10 cm of soil from on- and off-trail areas in four marsh communities. See Table 3 for symbol identification.

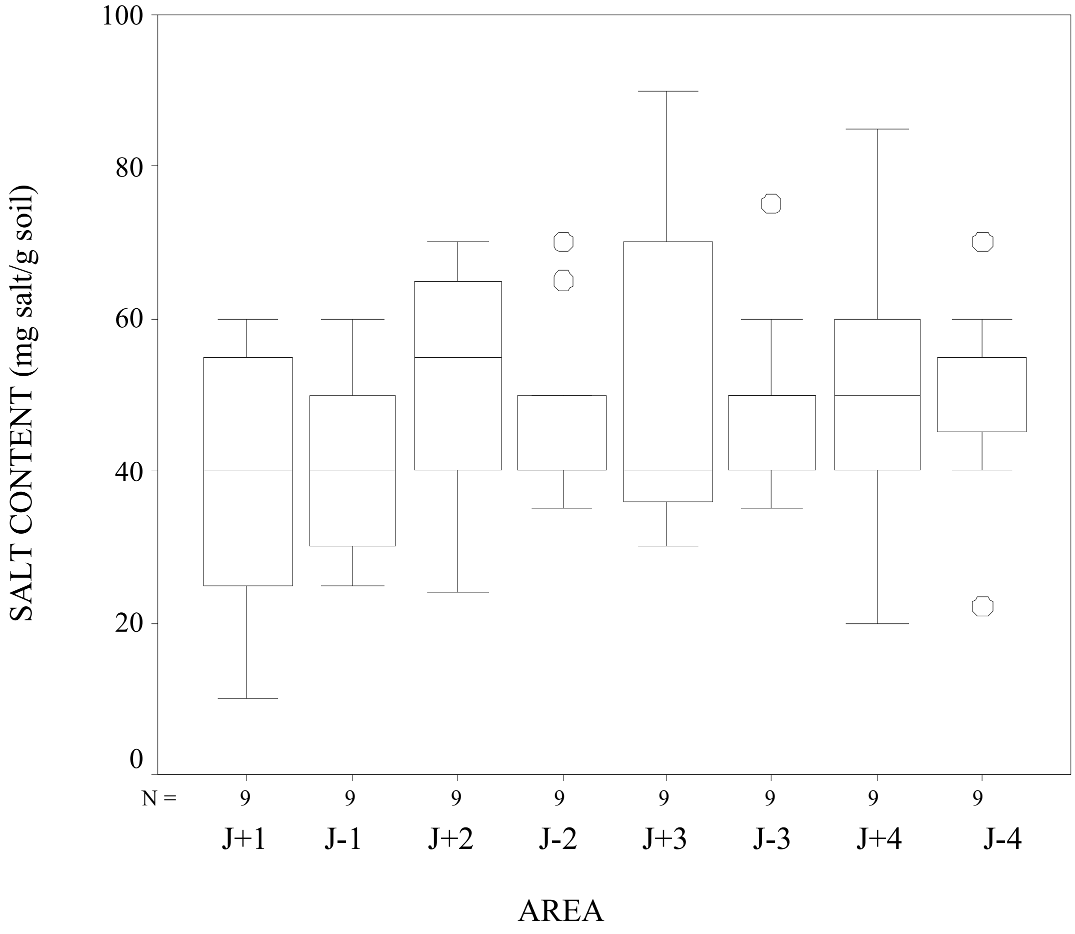

Figure 30. Salt content from various soil depths found in on and off-trail areas in the *J. roemerianus* community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

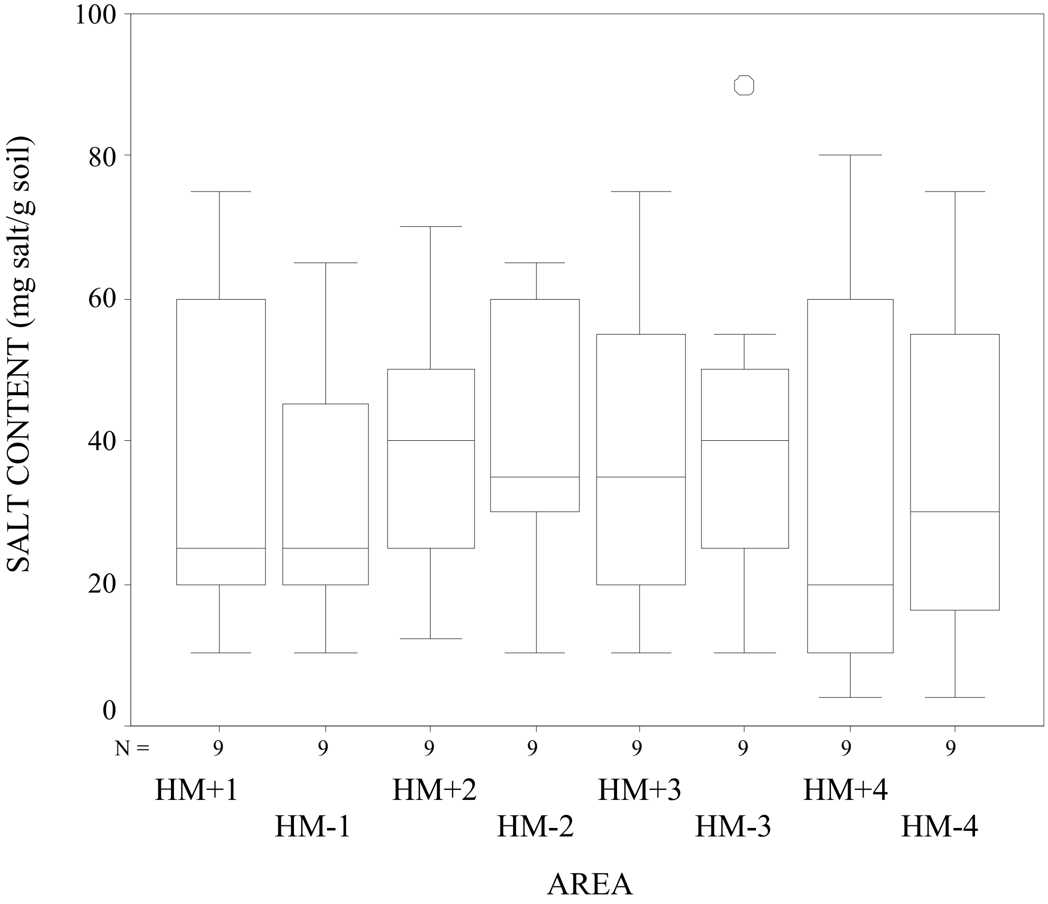

Figure 31. Salt content from various soil depths found in on and off-trail areas in the *D. Spicata/S. patens* community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

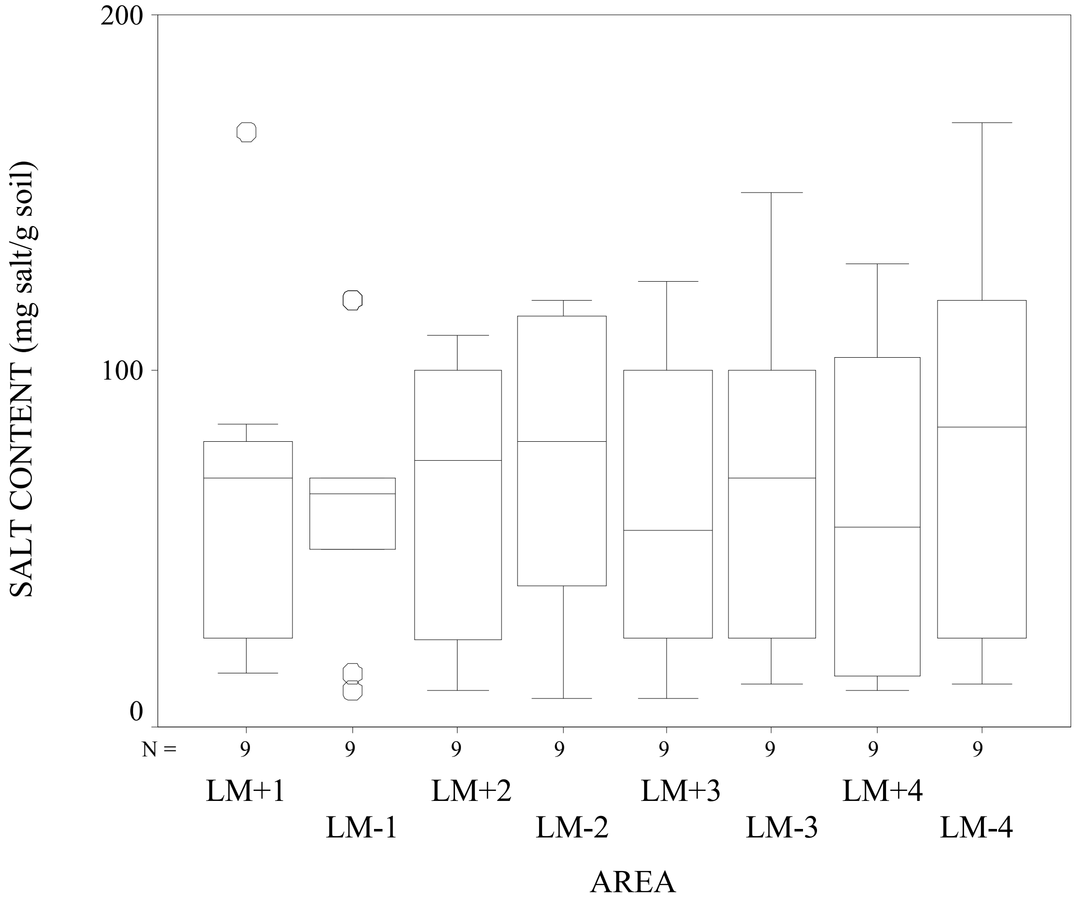

Figure 32. Salt content from various soil depths found in on and off-trail areas in the low marsh community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

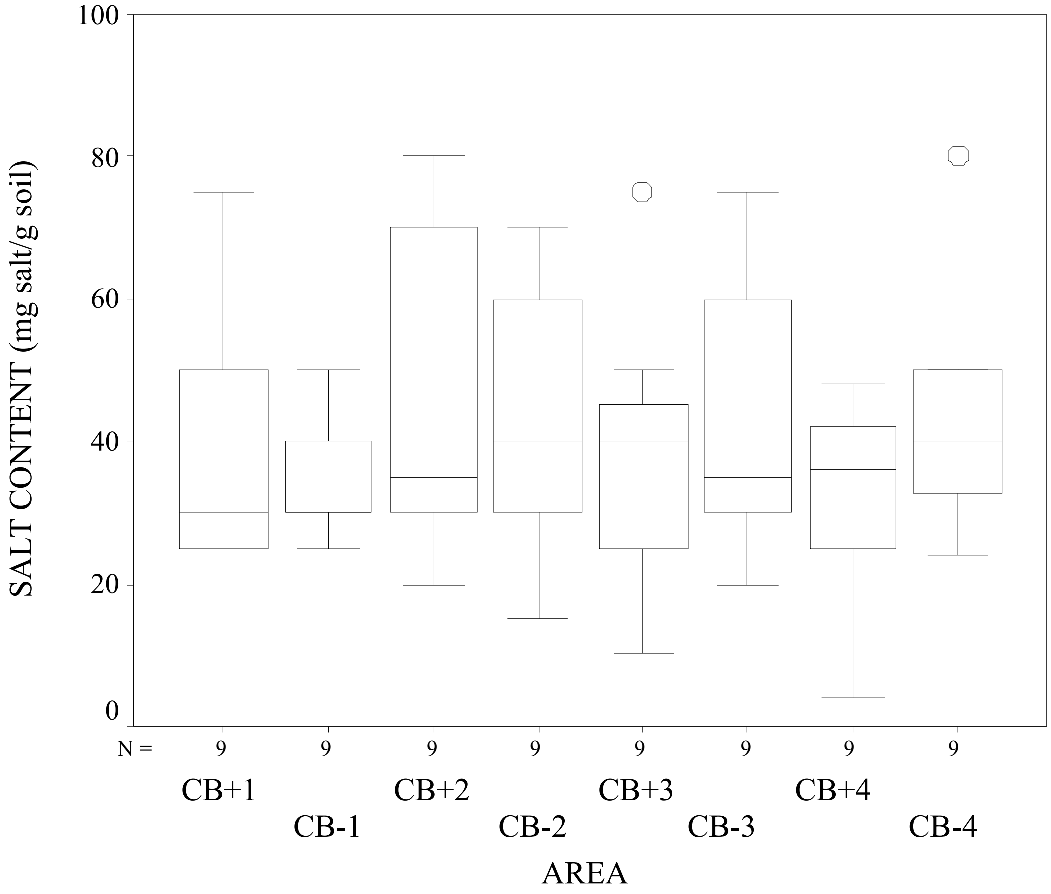

Figure 33. Salt content from various soil depths found in on and off-trail areas in the creek bank community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

Table 17. Mean and median on- and off-trail % soil organic content from four marsh communities. Results of one-tailed Wilcoxon Signed Ranks tests used to compare on- and off-trail % organic content in each community. Tests were significant at p value ≤ 0.05. Part A displays data from the upper 10 cm of soil. Sections B through E display values from different depths of soil from each marsh community. Section 1 is the upper 1 cm of soil. Section 2 is soil from a depth of 2-3 cm. Section 3 is soil from a depth of 3-5 cm. Section 4 is soil from a depth of 5-10 cm. See Table 3 for symbol identification.

Area	Mean %	Median %	Z score	Sig. (p value)
A. J+	57.4	58.0	1.244	0.1250
J-	49.3	55.4		
HM+	44.0	54.4	-2.666	0.0020
HM-	54.4	72.0		
LM+	18.3	18.4	-1.481	0.0820
LM-	28.0	25.4		
CB+	16.6	11.8	-0.1777	0.4551
CB-	*16.7*	*17.8*		
B. J+1	67.4	67.1	1.718	0.488
J-1	52.7	56.3		
J+2	65.3	66.3	1.244	0.1250
J-2	55.9	57.6		
J+3	62.6	65.2	1.481	0.0820
J-3	52.2	52.9		
J+4	50.1	49.8	0.6516	0.2852
J-4	44.8	34.5		
C. HM+1	61.4	75.3	-0.6516	0.2852
HM-1	62.0	78.7		
HM+2	56.2	72.3	-2.547	0.0039
HM-2	64.4	82.7		
HM+3	51.2	69.8	-2.666	0.0020
HM-3	62.0	78.0		
HM+4	32.9	40.2	-2.666	0.0020
HM-4	45.8	63.0		

Table 17. cont.

	Area	Mean %	Median %	Z score	Sig. (p value)
D.	LM+1	20.2	13.9	-0.7701	0.2480
	LM-1	28.7	17.9		
	LM+2	22.1	18.3	-0.4146	0.3672
	LM-2	27.9	27.1		
	LM+3	18.7	16.7	-0.5331	0.3262
	LM-3	25.3	24.3		
	LM+4	16.1	18.1	-1.362	0.1016
	LM-4	26.9	25.6		
E.	CB+1	16.5	13.0	0.6516	0.2852
	CB-1	15.6	14.6		
	CB+2	18.6	13.3	0.2962	0.4102
	CB-2	17.3	17.9		
	CB+3	20.1	13.4	0.6516	0.2852
	CB-3	16.4	14.6		
	CB+4	14.5	10.7	-1.362	0.1016
	CB-4	16.7	18.1		

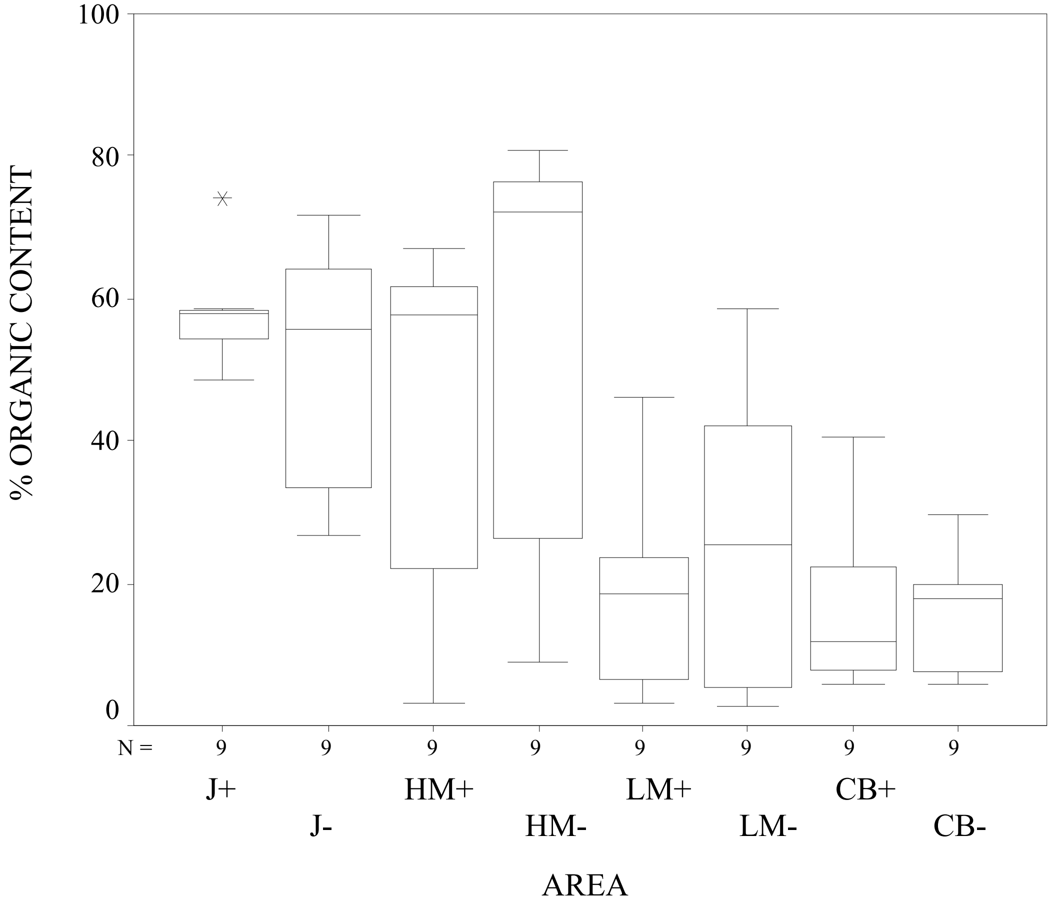

Figure 34. On- and off-trail percent organic matter from upper 10 cm of soil of on- and off-trail areas in four marsh communities. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

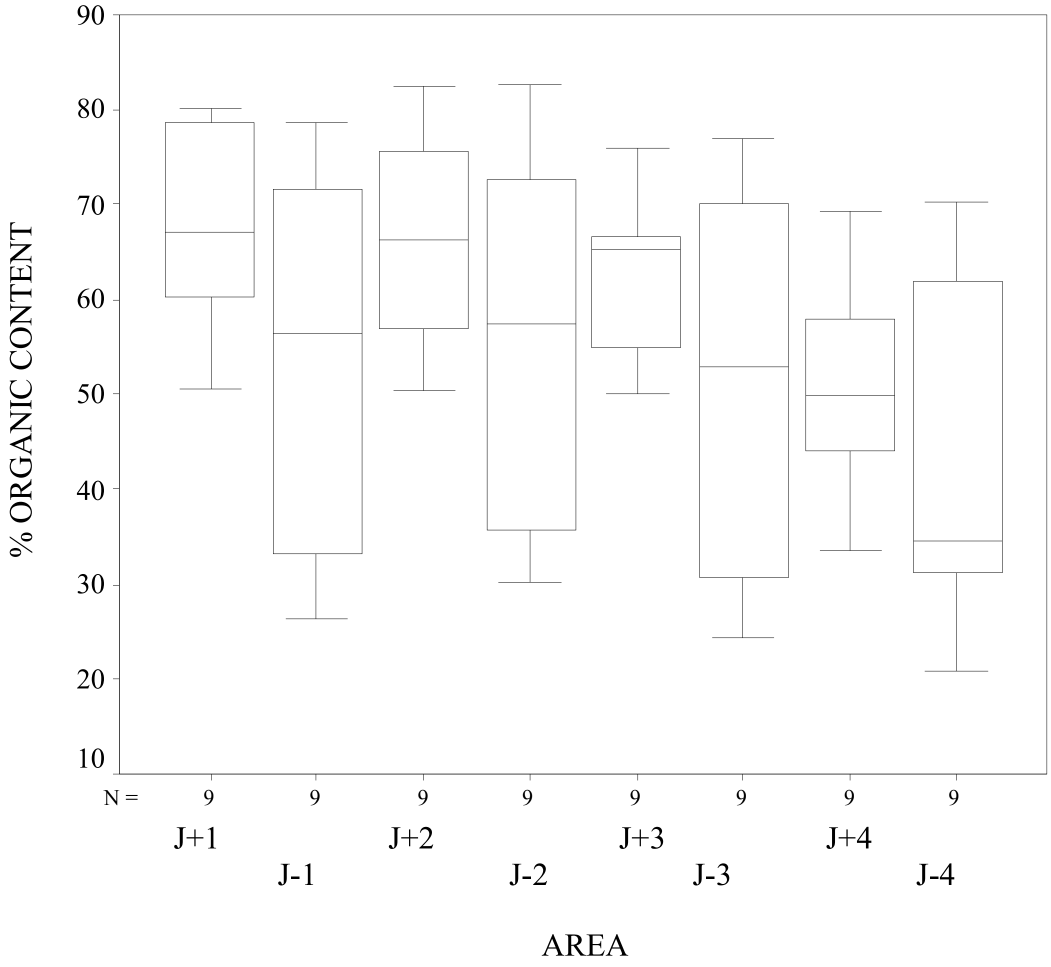

Figure 35. Percent organic matter from various soil depths of on- and off-trail areas in the *Juncus roemerianus* community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

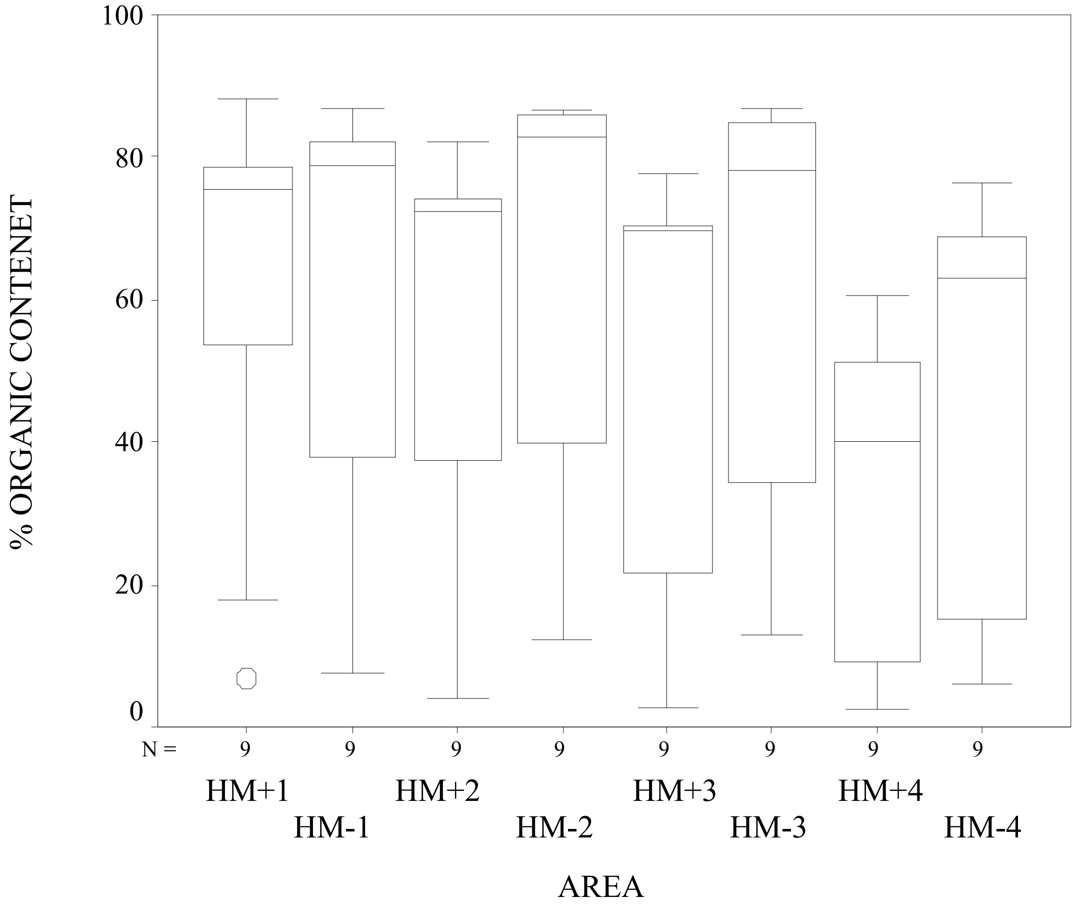

Figure 36. Percent organic matter from various soil depths of on- and off-trail areas in the *D. spicata/S. patens* community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

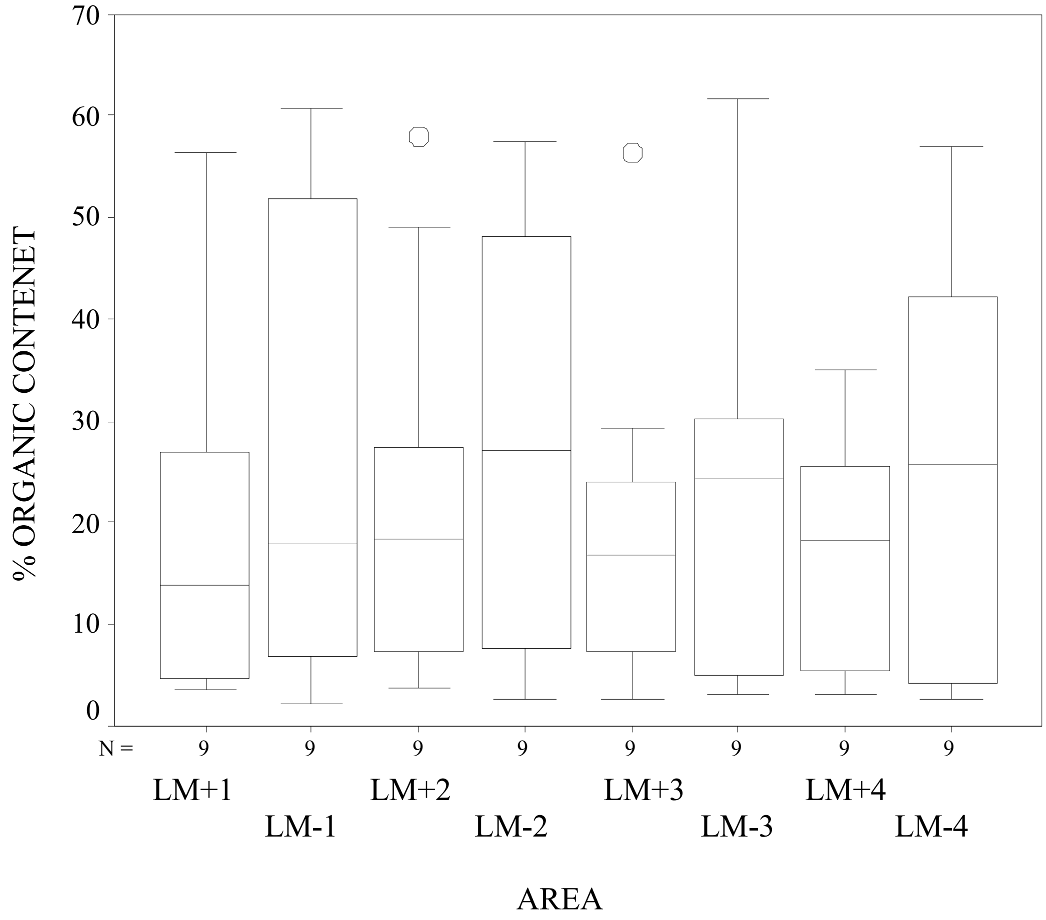

Figure 37. Percent organic matter from various soil depths of on- and off-trail areas in the low marsh community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

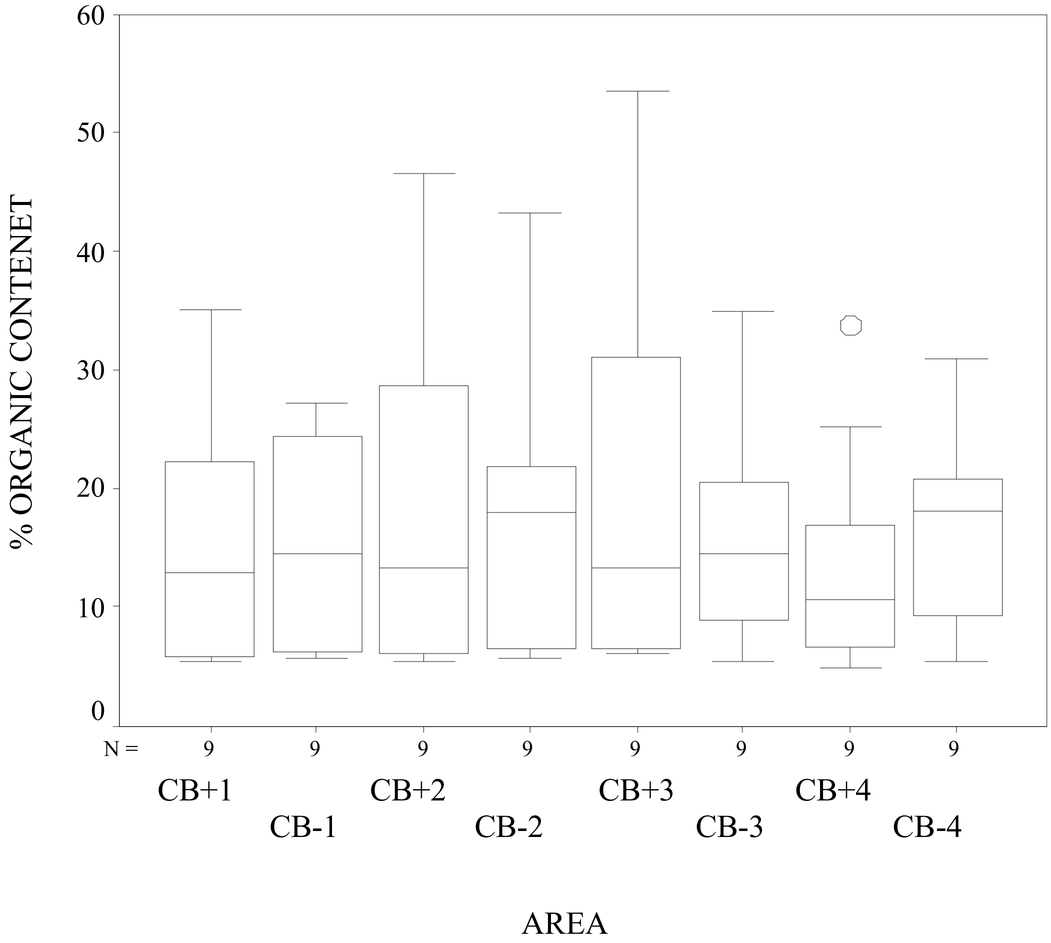

Figure 38. Percent organic matter from various soil depths of on- and off-trail areas in the creek bank community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

marsh community to a low of 0.16 g/cm^3 in the *J. roemerianus* community. On-trail soil bulk density did not differ significantly from off-trail soil bulk density in either the *J. roemerianus* or creek bank communities. However, on-trail soil bulk density was significantly greater than off-trail soil bulk density in both the *D. spicata/S. patens* and low marsh communities. However, the degree to which bulk density was influenced by trampling, as reflected in the ratios of on- to off-trail bulk density (on-trail bulk density/off-trail bulk density), did not differ significantly among the four marsh communities (Table 18, Figure 40). The average ratio of on- to off-trail bulk density was 1.43/1 in the *D. spicata/S. patens* community, and 1.67/1 in the low marsh community. Within the upper 10 cm of soil in the *D. spicata/S. patens* community, the significant differences between on- and off-trail soil bulk density occured at depths of 3-10 cm. In the low marsh community the significant differences between on- and off-trail soil bulk density occurred at depths of 5-10 cm.

Distribution of *Ilyanassa obsoleta*

The distribution of *I. obsoleta* on the marsh surface seemed to be affected by trails (Table 19, Figure 45). *I. obsoleta* were found on 19 of 34 trails examined in the low marsh and creek bank communities. On trails where snails were present, the average distance from tidal creeks to the farthest snails was approximately 28 m. The farthest on-trail snails were approximately 79 m from the nearest tidal creek. Median snail density was 16 individuals/m^2 on trails where snails were present. Median snail densities at both 1 m and 2 m off-trail were 0 individuals/m^2. These off-trail densities were significantly less than on-trail density (Table 19).

Table 18. Means and medians for bulk density of soil in on- and off-trail areas from four marsh communities. Results of one-tailed Wilcoxon Signed Ranks test used to compare on- and off-trail bulk density. Results of Kruskal-Wallis test used to compare ratios of on- to off-trail bulk density in four marsh communities. Tests were significant at p value ≤ 0.05. Part A displays data from upper 10 cm of soil. Part B displays data from the upper 1 cm of soil. Part C displays data from the next 2-3 cm of soil. Part D displays data from the next 3-5 cm of soil. Part E displays data from the next 5-10 cm of soil. See Table 3 for symbol identification.

Area	Mean (g/cm^3)	Median (g/cm^3)	Z score	Wilcoxon Sig. (p value)	Mean ratio	Median ratio	Chi square score	Kruskal-Wallis Sig. (p value)
A. J+	0.18	0.16	0.6516	0.2852	1.11/1	1.12/1	7.432	0.059
J-	0.17	0.15						
HM+	0.46	0.17	2.666	0.0020	1.43/1	1.45/1		
HM-	0.31	0.14						
LM+	0.68	0.51	1.955	0.0273	1.67/1	1.06/1		
LM-	0.57	0.37						
CB+	0.51	0.41	0.7701	0.2480	1.17/1	1.03/1		
CB-	0.44	0.34						
B. J+1	0.14	0.13	-1.362	0.1016				
J-1	0.17	0.15						
J+2	0.14	0.13	-0.1777	0.4551				
J-2	0.14	0.14						
J+3	0.16	0.15	-0.1777	0.4551				
J-3	0.16	0.15						
J+4	0.21	0.19	1.481	0.0820				
J-4	0.19	0.18						

Table 18. cont.

	Area	Mean (g/cm^3)	Median (g/cm^3)	Z score	Sig (p value)
C.	HM+1	0.23	0.11	0.2962	0.4102
	HM-1	0.21	0.11		
	HM+2	0.31	0.13	0.7701	0.2480
	HM-2	0.21	0.11		
	HM+3	0.43	0.15	2.192	0.0137
	HM-3	0.22	0.13		
	HM+4	0.57	0.23	2.666	0.0020
	HM-4	0.42	0.15		
D.	LM+1	0.67	0.55	1.244	0.1250
	LM-1	0.60	0.44		
	LM+2	0.65	0.59	0.1777	0.4551
	LM-2	0.59	0.51		
	LM+3	0.65	0.48	1.362	0.1016
	LM-3	0.54	0.35		
	LM+4	0.71	0.42	1.718	0.0488
	LM-4	0.60	0.28		

Table 18. cont.

	Area	Mean (g/cm^3)	Median (g/cm^3)	Z score	Sig. (p value)
E.	CB+1	0.52	0.52	-0.6516	0.2852
	CB-1	0.58	0.59		
	CB+2	0.48	0.31	0.5331	0.3262
	CB-2	0.44	0.37		
	CB+3	0.47	0.42	0.7114	0.2578
	CB-3	0.38	0.38		
	CB+4	0.53	0.44	0.5331	0.3262
	CB-4	0.44	0.38		

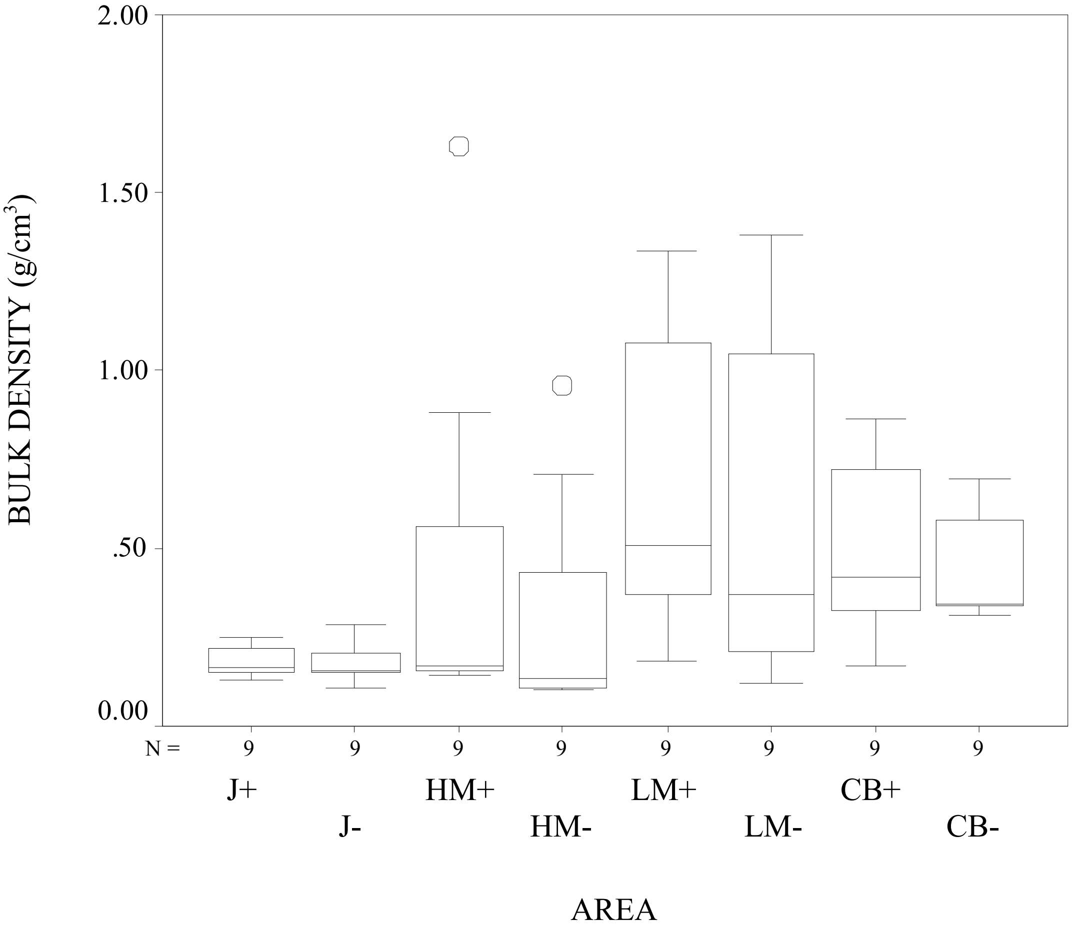

Figure 39. On- and off-trail soil bulk density from upper 10 cm of soil of on- and off-trail areas in four marsh communities. See Table 3 for symbol identification.

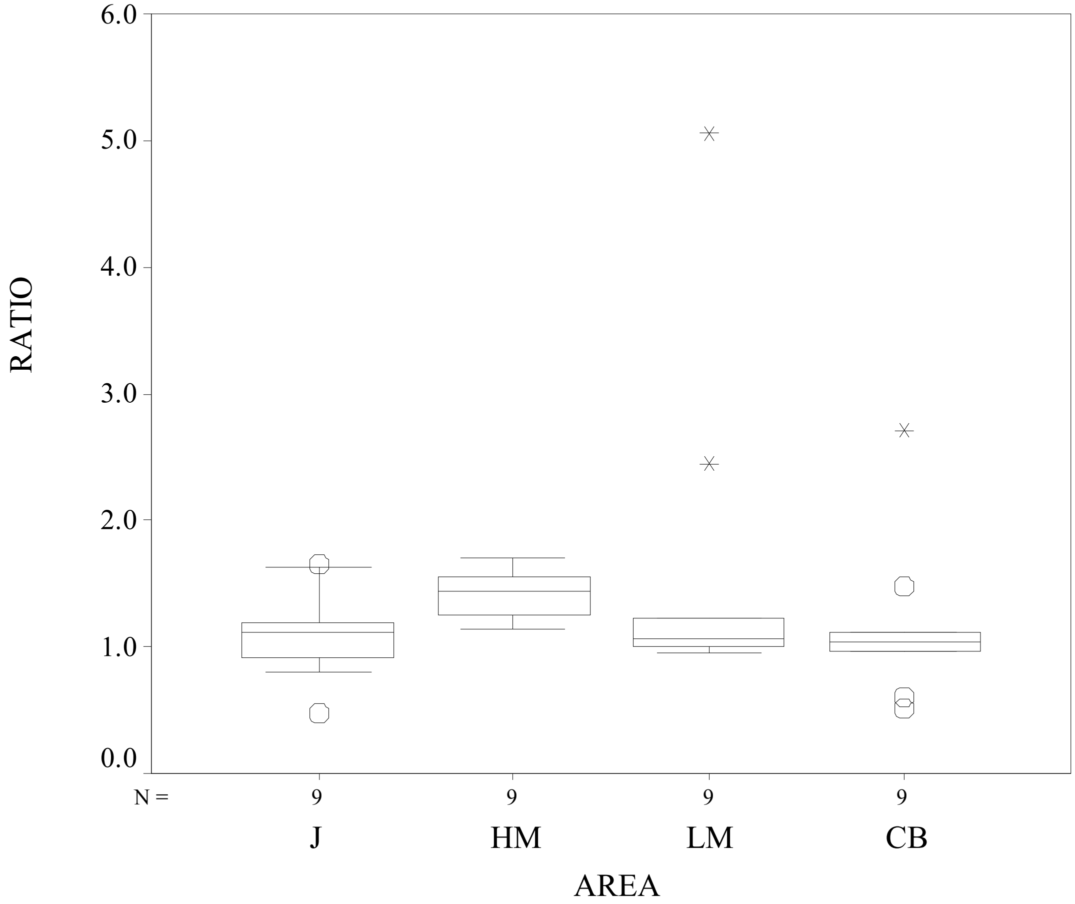

Figure 40. Ratio of on-trail soil bulk density to off-trail soil bulk density in four marsh communities. See Table 3 for symbol identification.

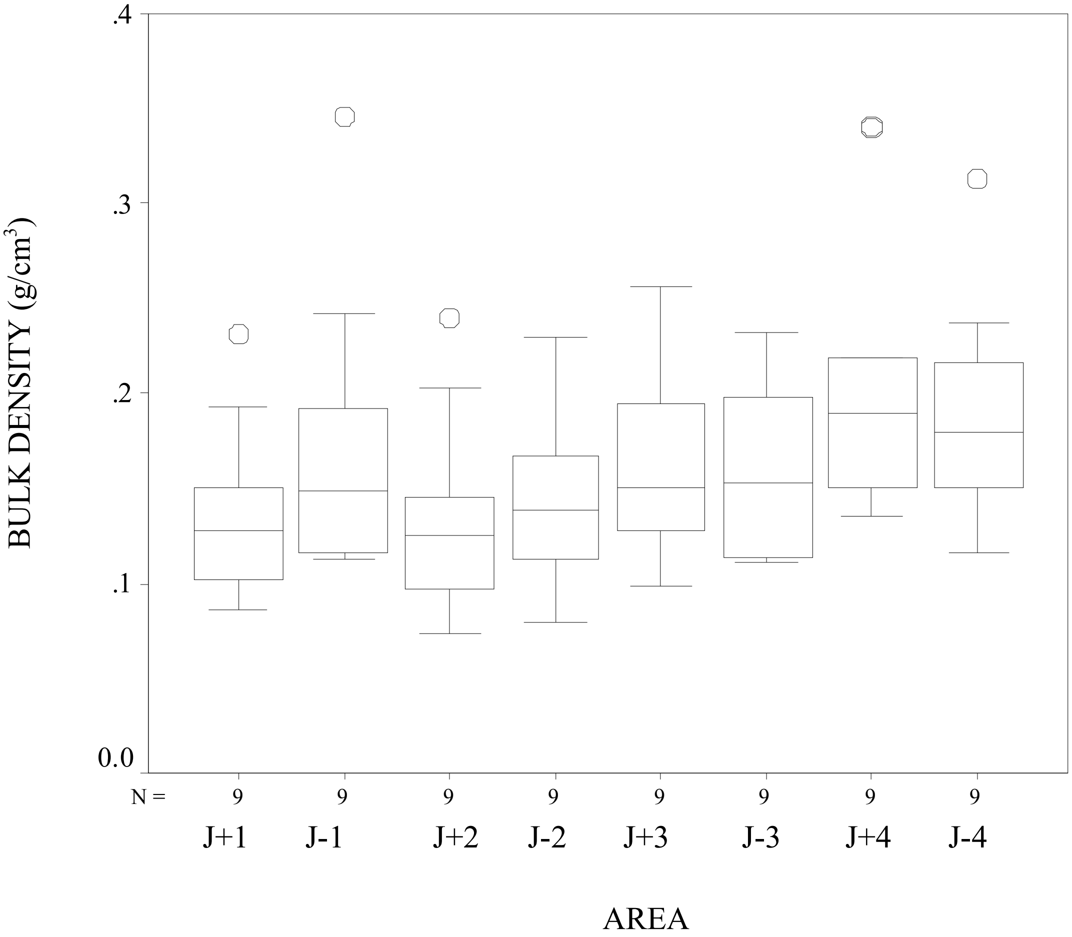

Figure 41. Soil bulk density from various soil depths of on- and off-trail areas in the *Juncus roemerianus* community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

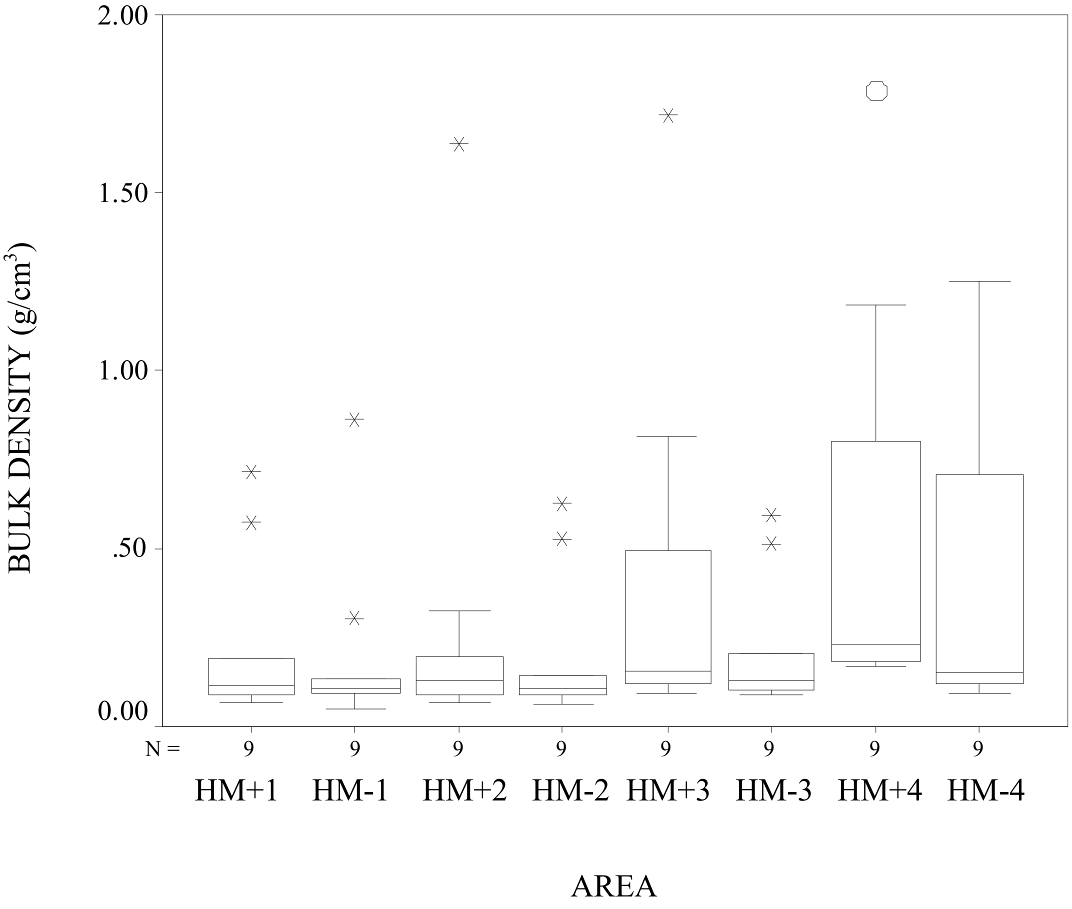

Figure 42. Soil bulk density from various soil depths of on- and off-trail areas in the *D. spicata/S. patens* community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

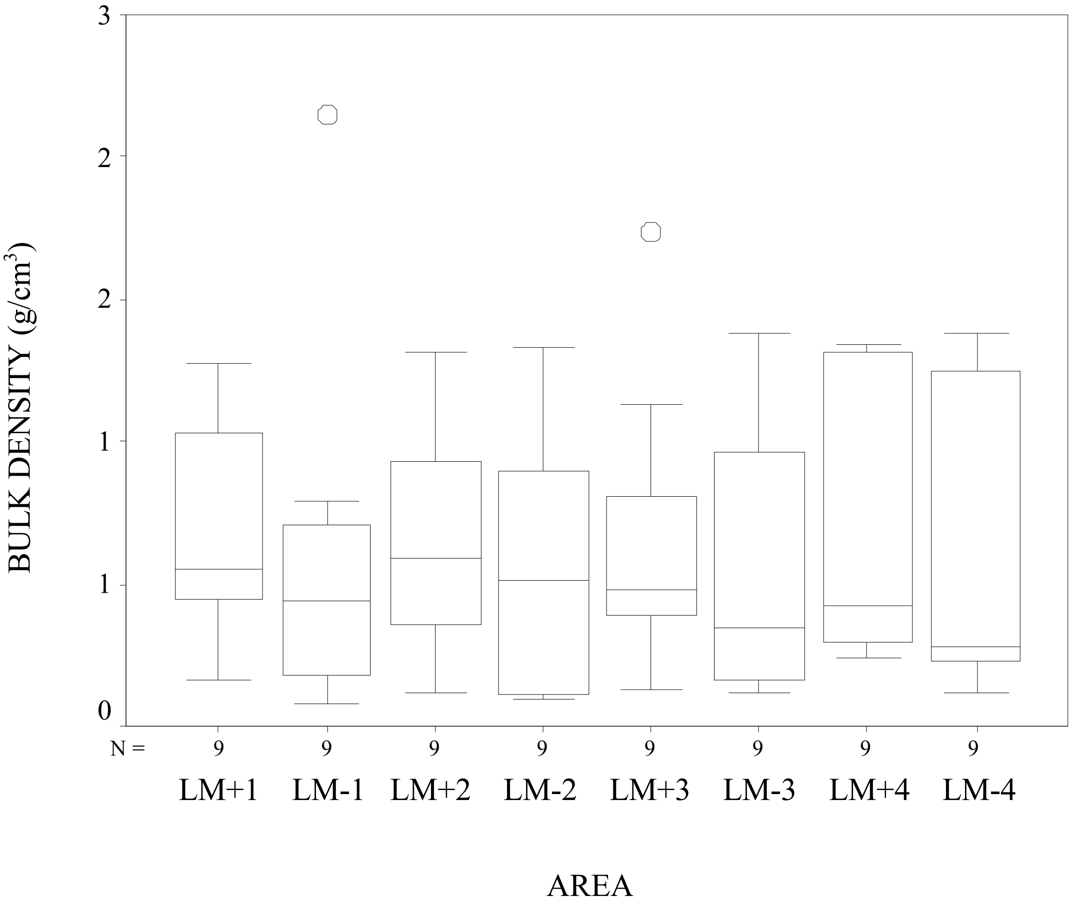

Figure 43. Soil bulk density from various soil depths of on- and off-trail areas in the low marsh community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

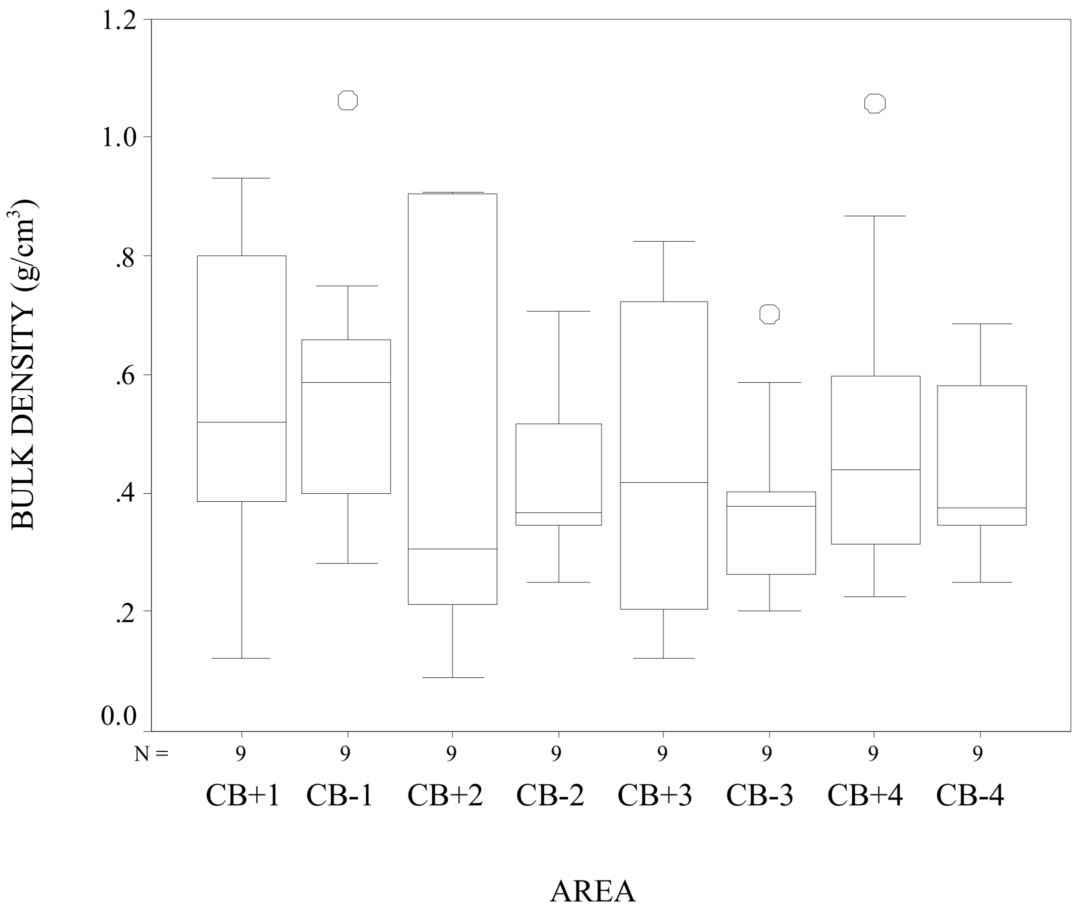

Figure 44. Soil bulk density from various soil depths of on- and off-trail areas in the creek bank community. Soil depths are denoted by various numbers: 1 = upper 1 cm of soil. 2 = depths of 2 – 3 cm of soil. 3 = depths of 3-5 cm of soil. 4 = depths of 5-10 cm of soil. See Table 3 for symbol identification.

Benthic chlorophyll *a*

The quantity of benthic microalgae present in a given area was estimated by the amount of chlorophyll *a* (as mg/m^2). The amount of chlorophyll *a* present in undisturbed off-trail areas varied from community to community (Table 20, Figure 46). The effects of trampling disturbance on chlorophyll *a* also varied from community to community. The greatest amounts of chlorophyll *a* were found in off-trail areas of the low marsh community, where the median amount of chlorophyll *a* was 3.30 mg/m^2. The smallest amounts of chlorophyll *a* were present in off-trail areas of the *D. spicata/S. patens* community, where the medium amount of chlorophyll *a* was 0.14 mg/m^2. The amount of chlorophyll *a* present in on-trail areas was significantly higher than the amount of chlorophyll *a* found in off-trail areas in both the *J. roemerianus*, and *D. spicata/S. patens* communities. The median amount of chlorophyll *a* in the on-trail areas of the *D. spicata/S. patens* community was 2.25 mg/m^2. The median amount of chlorophyll *a* in the *J. roemerianus* community was 2.87 mg/m^2 in on-trail areas, but was only 1.37 mg/m^2 in off-trail areas. The amount of chlorophyll *a* present in on- and off-trail areas did not vary significantly in either the creek bank or low marsh communities. The average ratio of on- to off-trail chlorophyll *a* (on-trail chlorophyll *a* (mg/m^2)/off-trail chlorophyll *a* (mg/m^2)) did not differ significantly among the four communities (Table 20, Figure 47). The mean ratio of on – to off-trail chlorophyll *a* was 46.61/1 in the *D. spicata/S. patens* community and 3.99/1 in the *J. roemerianus* community.

Table 19. Means and medians for numbers of *I. obsoleta* in low marsh on-trail, 1 m off-trail, and 2 m off-trail areas. Results of one-tailed Wilcoxon Signed Ranks tests used to compare densities from the different areas. Tests were significant at α ≤ 0.05.

Area	***Mean***	***Median***
On-trail	126	16
1m Off-trail	11	0
2m Off-trail	18	0

Areas compared	Z score	Sig. (p value)
On-trail \ 1m Off-trail	6.244	0.0000
On-trail \ 2m Off-trail	5.237	0.0000
1m Off trail \ 2m Off-trail	-1.420	0.0808

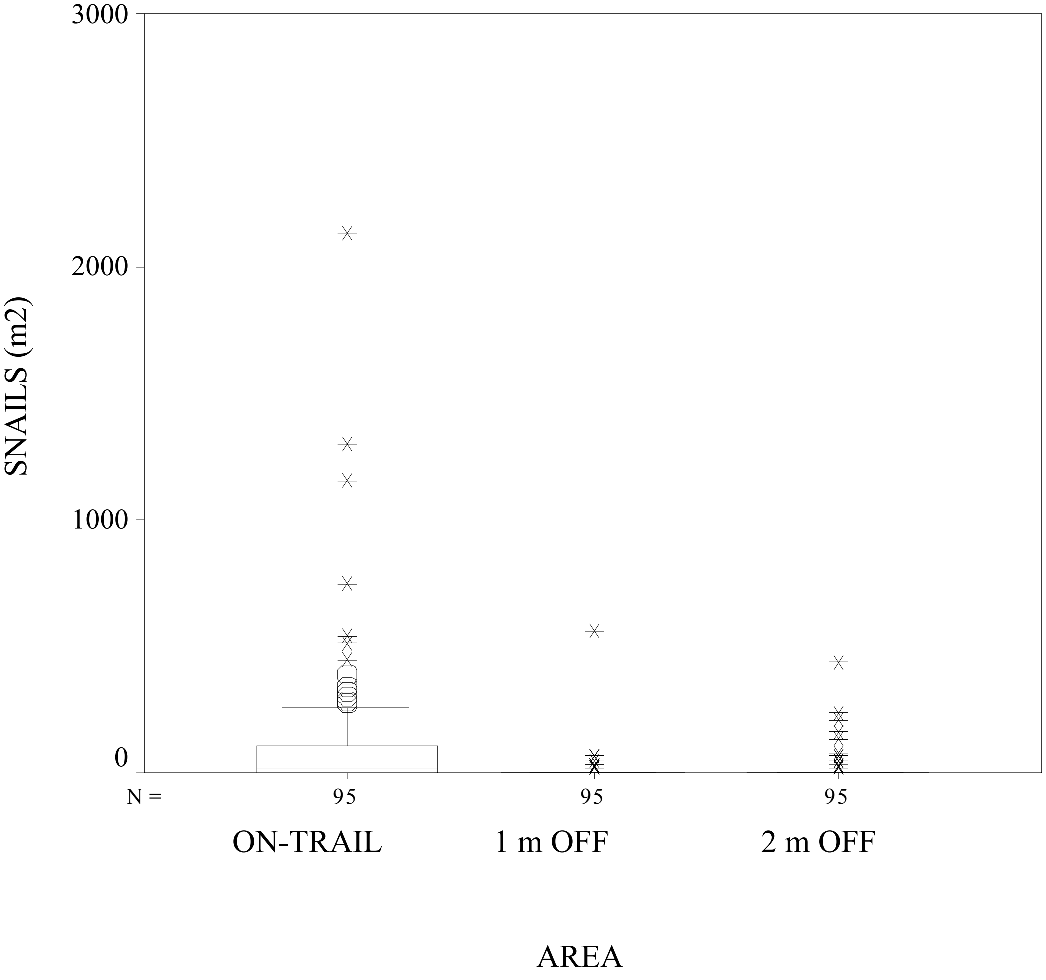

Figure 45. Number of snails m^2 on-trail, 1 m off-trail, and 2 m off-trail. See Table 3 for symbol identification.

Table 20. Amount of chlorophyll *a* present in on- and off trail areas in four marsh communities. Results of one-tailed Wilcoxon Signed Ranks test used to compare on- and off-trail chlorophyll *a*. Results of Kruskal-Wallis test used to compare ratios of on- to off-trail chlorophyll *a* in four marsh communities. Tests significant at $\alpha < 0.05$. See Table 3 for symbol identification.

Area	*Mean (mg/m^2)*	*Median (mg/m^2)*	*Z score*	*Wilcoxon Sig (p value)*	*Mean ratio*	*Median ratio*	*Chi-square score*	*Kruskall-Wallis Sig (p value)*
J+	*5.81*	*2.87*	*2.629*	*0.0036*	*3.99/1*	*1.84/1*	*4.795*	*0.187*
J-	1.87	1.37						
HM+	3.11	2.25	1.672	0.0492	46.61/1	0.96/1		
HM-	1.43	0.14						
LM+	3.87	2.81	-0.0286	0.4944	1.39/1	0.62/1		
LM-	3.88	3.30						
CB+	5.17	2.90	1.114	0.1384	9.12/1	1.22/1		
CB-	2.88	2.59						

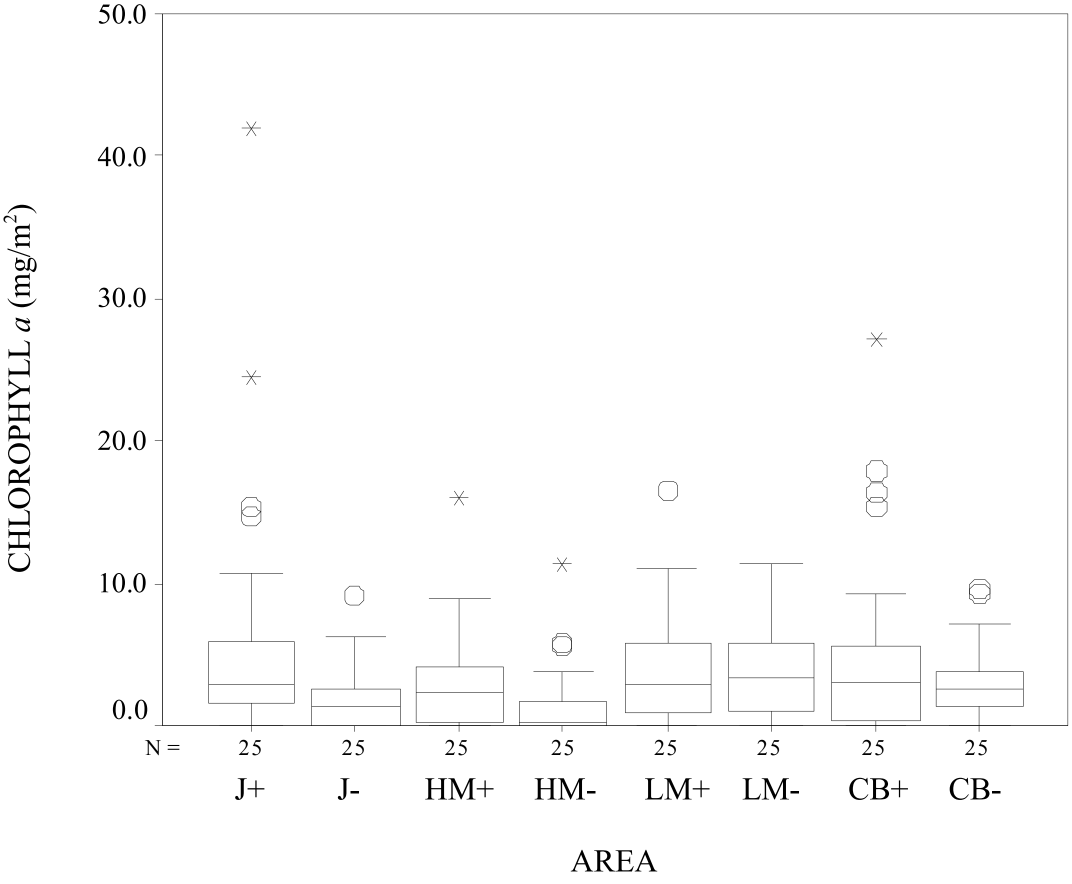

Figure 46. On- and off-trail chlorophyll *a* in four marsh communities. See Table 3 for symbol identification.

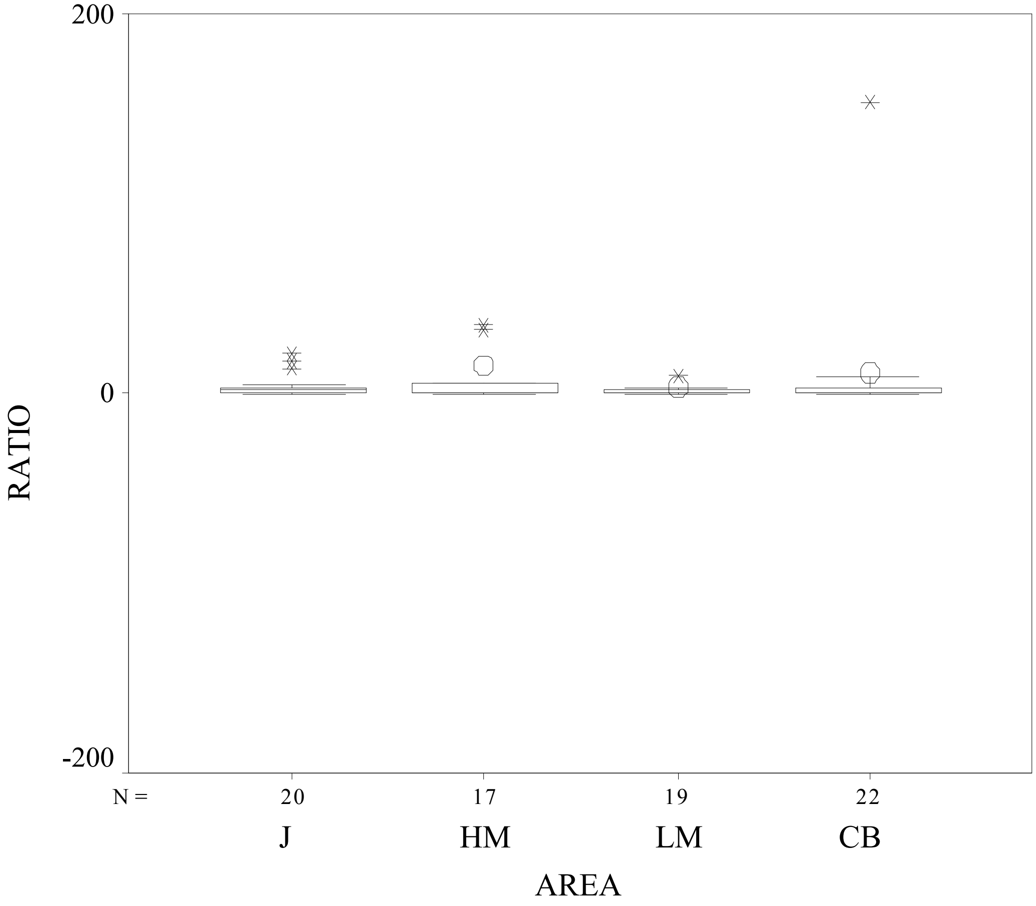

Figure 47. Ratio of on- to off-trail chlorophyll *a* in four marsh communities. See Table 3 for symbol identification.

DISCUSSION

In this section, I discuss the results of various analyses undertaken in this study as they relate to the extent of trampling in the salt marsh, and the specific effects of trampling within trails in the four marsh communities. I also address material from published literature that relates to individual analyses and hypotheses. The discussion takes place within the context of the model of the effects of trampling (Figure 1).

Trails and movement of deer

Oertel and Woo (1994) developed a system of landscape classification and terminology for salt marshes such as the Brownsville Marsh complex. According to Oertel and Woo (1994), mainland salt marshes situated along barrier lagoons, such as the Brownsville Marsh complex, may contain various types of marshes (Figure 48). The formation of these different marsh types is controlled by antecedent landscape characteristics. For instance, valley marshes arise " . . . in the valleys of streams that drain into the barrier lagoon" (Oertel and Woo 1994). These marshes are " . . . completely surrounded by the mainland" (Oertel and Woo 1994). Headland marshes, on the other hand, " . . . are located on the headlands of necks (interfluves) between the valleys that drain into the lagoon" (Oertel and Woo 1994). These marshes have mainland on one side and lagoon on the other. Finally, hammock marshes ". . . occur adjacent to hammocks commonly along the mainland sides of . . . lagoons" (Oertel and Woo 1994). Hammocks are essentially marsh-surrounded islands that are generally positioned parallel to mainland areas. Generally, valley and hammock marshes may be subject to higher levels of deer trampling than headland marshes due to their position in the landscape. This seems to be the case at the Brownsville Marsh complex, where trail density is higher in valley and hammock marshes than in headland marshes (Figure 48). Both valley and hammock marshes are positioned between upland areas where deer may be common, and as such, may be used by deer to transit between these areas. Headland marshes, however, may border upland areas on only one side - so there may be no reason for deer to venture across them.

Most trails found in the study site ran between forested areas. This is generally to be expected, as white tailed deer do not graze extensively in salt marshes (Pfeiffer and Wiegert 1981, Newsome 1984, Turner and Bratton 1987). If deer were grazing in the marsh, one might expect trail locations to be less restricted to these inter-forest areas.

It is possible that deer enter the marsh for other reasons such as to find areas to bed and to escape biting insects. Young deer were observed bedding in the low marsh and *J. romerianus* communities on two occasions in June and August. How often marsh areas may be used for this purpose is unknown. Severinghaus and Cheatum (1956) noted that ". . . in low ground or on the borders of wet areas deer lie down in dry, slightly elevated places." One would presume that such areas are not particularly common in salt marshes. Marchinton and Hirth (1984) suggested that " . . . deer try to avoid areas where temperatures are high and insects annoying", but that ". . . when temperatures are moderate beds may be in the open with little or no shelter." The bedding of deer in the salt marsh then, may be dependent on climatic factors. Also, deer may submerge themselves to escape bothersome insects (Marchinton and Hirth 1984). Biting insects are certainly ubiquitous in salt marshes during certain times of the year. Most deer observed

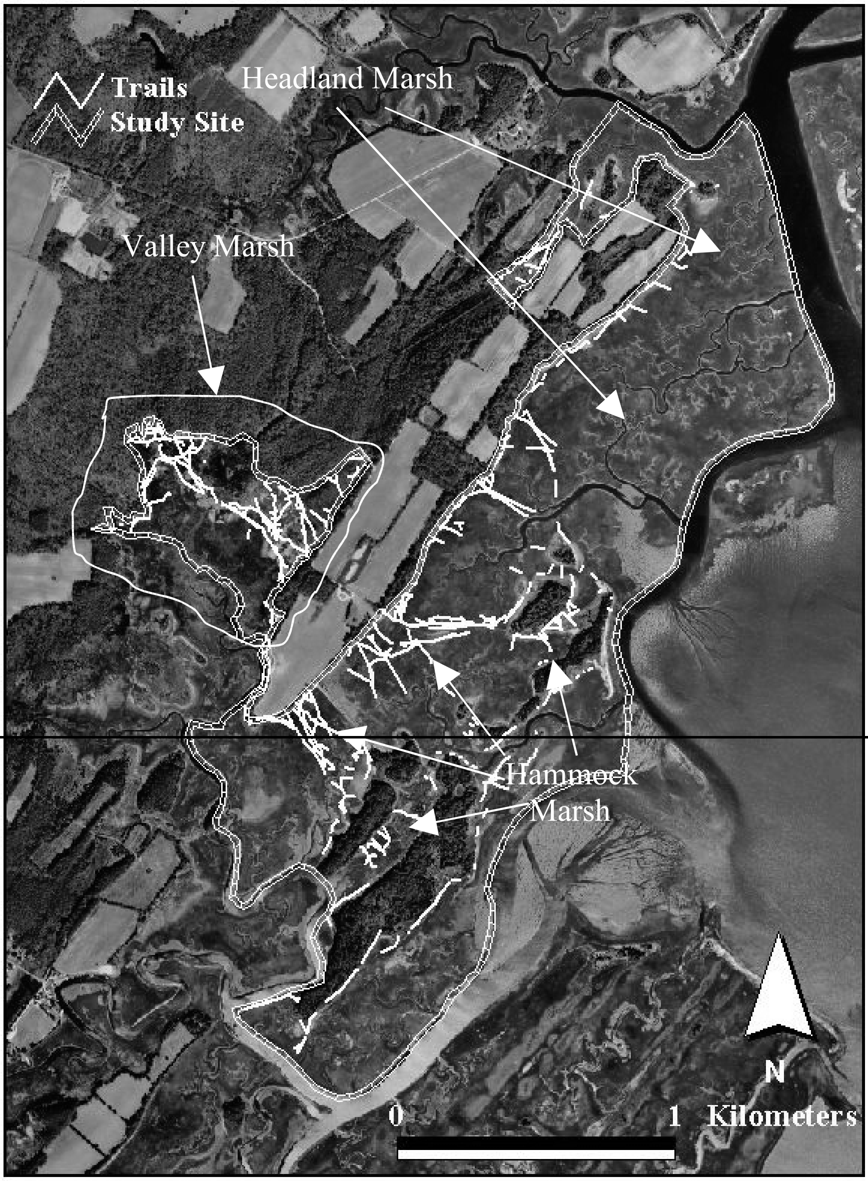

Figure 48. 1994 United States Geographical Survey aerial photo showing locations of marsh types at the VCR-LTER.

in the salt marsh during the course of this study were running towards areas where they could gain cover. However, on one occasion in June a single deer was observed crossing a creek bank at high tide and moving across flooded low marsh. The deer moved in an unhurried fashion and stopped periodically in water coming up to its belly. It may have been using the water to escape tormenting insects.

Though the tracks of both deer and raccoon were observed on many trails, deer tracks seemed to predominate - indicating that deer may be primarily responsible for the creation, or at least the maintenance, of those trails (Table 7). However, a small percentage of trails in the marsh appeared to be created and maintained primarily by the trampling of raccoon. Raccoons have been found to enter the salt marsh at low tide to feed (Kiviat 1989). They are omnivorous and may feed on *S. alterniflora* (Harman and Stains 1979), *Geukensia demissa*, and *Uca* spp. (Day et al. 1973, Teal 1958). Raccoon trails were quite narrow (8-12 cm) and tended to turn in different directions more often than trails made primarily by deer. Raccoon trails generally led from upland areas to pools or creek bank areas in the marsh, where raccoons apparently hunt for food.

Deer movements on the study trails seemed to peak in late autumn and again in early spring (Table 5). Deer activity seemed to be lowest in July - September. A variety of factors affect the seasonal movements of deer. The observed late autumn increase in movement could be associated with rutting behavior, which may be the most active period for deer (Pledger 1975, Rue 1989, Ivey and Causey 1984) (but *see* Holzenbein and Schwede 1989). Rutting behaviors occur in several phases, which generally begin in September and continue through January (Marchinton and Hirth 1984). The first phase is sparring, when males engage in aggressive interactions to establish hierarchies before breeding (Townsend 1973, Hirth 1977). The second phase is courtship (chasing), where dominant bucks chase does and subordinate bucks may follow (Marchinton and Hirth 1984). The final phase ends when does stop running from courting bucks, and tending and copulation occur (Marchinton and Hirth 1984).

Beier and McCullough (1990), however, suggested that differences in seasonal activity patterns may be explained by changes in necessary foraging time. In a study of the factors influencing the activity patterns of deer on the George Reserve, Michigan, Beier and McCullough (1990) found that deer activity peaked in autumn, declined in January - February, rose markedly in late winter to peak in May, and declined substantially in June - July. This activity pattern seems to be similar to that of deer in the VCR-LTER (Table 5). The autumn peak in activity coincided with a decline in forage quality, " . . . in the face of continued high metabolic demand as deer put on weight for winter" (Beier and McCullough 1990). The slowing of activity in winter was consistent with a decline in deer metabolic rate (Silver et al. 1969, Moen 1978, Rogers et al. 1987). Increased metabolic demand in spring caused an increase in foraging time and increased activity (Beier and McCullough 1990). Finally, even though energy demands for antler growth and lactation were at maximum levels, activity declined during June - July. On the George Reserve, Beier (1987) found that forage quality peaked during the May - July period, and forage quantity peaked during the June - August period (McCoullough, unpublished data cited in Beier and McCullough 1990). Because of these changes in available forage, Beier and McCullough (1990) suggest that deer are able to meet their metabolic needs with fewer hours spent foraging each day.

Conceptual model of effects of trampling disturbance

The following sections discuss the effects of trampling disturbance within the context of the cascade of effects arising from trampling presented in Figure 1 and Table 1. Tables 21 and 22 show those hypotheses that were consistent with the results of the present study and those that were not for each marsh community. The table results are organized into various sections including the direct effects of trampling, secondary effects of trampling, and effects on marsh communities. In sections 5.3 - 5.10.3 I discuss individual variables in Tables 21 and 22, and in section 6.0 I summarize the information related to low marsh and high marsh ecosystem states and the changes associated with sea level rise and disturbance.

Biomass

Biomass loss is a primary and direct effect of trampling in the conceptual model (Figure 1). Trampling, by killing and injuring plants, significantly reduced on-trail above-ground plant biomass relative to off-trail above-ground plant biomass in all four marsh communities. However, the degree to which this occurred varied among the different communities. In the 2000 biomass sampling period it was found that the creek bank community retained the least amount of on-trail biomass relative to off-trail biomass, followed by the *J. roemerianus* community, the low marsh community and the *D. spicata/S.* patens community. In the 2001 biomass sampling period it was found that, again, the creek bank community retained the least amount of on-trail biomass relative to

Table 21. Results of *J. roemerianus* and *D. spicata/S. patens* community analyses. Observations different from hypothesized direction are in italics.

J. roemerianus community	*D. spicata/S. patens* community
Direct trampling effects	
Biomass less on-trail	Biomass less on-trail
Bulk density no different on- trail	Bulk density higher on-trail
Secondary effects	
Light intensity higher on-trail	Light intensity higher on trail
Surface temperatures higher higher on-trail	Surface temperatures higher on-trail
Soil salt content no different on- trail	*Soil salt content no different on- trail*
Organic content no different on-trail	Organic content lower on-trail
Elevation lower on-trail	*Elevation no different on-trail*
Community effects	
More *D. spicata*/Less *J. roemerianus* on-trail	More *D. spicata*/Less *S. patens* on-trail

More chlorophyll *a*

on-trail

More chlorophyll *a*

on-trail

Table 22. Results of low marsh and creek bank community analyses. Observations different from hypothesized direction are in italics.

Low marsh community	Creek bank community
Direct trampling effects	
Biomass less on-trail	Biomass less on-trail
Bulk density higher on-trail	*Bulk density no different on-trail*
Secondary effects	
Light intensity higher on trail	Light intensity higher on-trail
Surface temperatures not higher on-trail	*Surface temperatures not higher on-trail*
Soil salt content no different on- trail	*Soil salt content no different on- trail*
Organic content no different on-trail	*Organic content no different on-trail*
Elevation lower on-trail	Elevation lower on-trail
Community effects	
Less *D. spicata* on-trail	Same on- and off-trail vascular plant community
No difference in amount	*No difference in amount*

of chlorophyll a on-trail	*of chlorophyll a on-trail*
More *I. obsoleta* on trails	More *I. obsoleta* on trails

off-trail biomass, followed by the low marsh community, the *J. roemerianus* community, and the *D. spicata/S.* patens community. Differently shaped quadrats were used to collect biomass in the two sampling periods. A square quadrat 0.25 m on a side was used in 2000, while a rectangular quadrat with dimensions of 0.5 X 0.125 m was used in 2001. The quadrat used in 2001 fit more neatly into trails and therefore included less off trail vegetation than the quadrat used in the 2000 sampling period, thereby characterizing on-trail vegetation more accurately.

One source of variation in community response to trampling may come from differences in trampling intensity - the greater the trampling intensity, the greater the loss of vegetation cover or biomass (Edmond 1964, Burden and Randerson 1972, Weaver and Dale 1978, Hylgaard and Liddle 1981, Cole 1995a, Whinam and Chilcott 1999). Although there did not seem to be any statistically significant difference in the presence or absence of prints found on the study trails, there may have been differences in trampling intensity. Trampling intensity was assessed by indexing the frequency of prints found on trails as high frequency, medium frequency, or low frequency. This semiquantitative assessment method reveals that the majority of high frequency trampling occurred in low marsh and creek bank communities. High frequency trampling was noted 7 times in the low marsh community and 6 times in the creek bank community, but only 2 times in the *J. roemerianus* community and 1 time in the *D. spicata/S. patens* community. Furthermore, while medium frequency trampling was noted 4 times in the *J. roemerianus* community, and 3 times each in the low marsh and creek bank communities, it was observed only 1 time in the *D. spicata/S. patens* community. This may be an indication that individual trails were trampled more often in low marsh and creek bank communities than in the *J. roemerianus* and, particularly, the *D. spicata/S. patens* communities. Deer trails in general may be used to greater or lesser degrees, or even abandoned temporarily or permanently, depending on ". . . change of season, change of location, abundance or distribution of food and water, change in usability, or some combination of these. . . " (Servinghaus and Cheatum 1956). Interestingly, two study trails in the *D. spicata/S. patens* communities seemed to become less well used over the course of this study. By the summer of 2002 portions of the trails had become hard to discern.

Variation in community response to trampling may also arise from differences in the resistance and resilience of individual plant species to trampling. According to Cole (1995b) resistance is " . . . the ability of a vegetation type to resist change when trampled," and resilience is " . . . . the ability of a vegetation type to recover following the cessation of trampling." Cole (1995b) conducted a study involving the experimental trampling of different vegetation types in several different mountainous regions of the United States. He found that resistance to trampling was " . . . primarily a function of vegetation stature, erectness and whether plants are graminoids, forbs, or shrubs." For graminoids and forbs, resistance to trampling was negatively correlated with plant height - the taller the plants, the less resistant they were to trampling (Cole 1995b). Others have noted that vegetation in trampled areas tends to be shorter than vegetation in untrampled areas, or that tall plants are less resistant to trampling (Jeffreys 1917, Bates 1935, Gillham 1956, Sun and Liddle 1993a, Ikeda and Okutomi 1995, Kobayashi et al. 1997, Cole and Spildie 1998, Kobayashi et al. 1999, Whinam and Chilcott 1999). Furthermore, graminoids, particularly those matted or growing in dense tufts, were found to be more resistant to trampling than forbs, especially those growing in an erect fashion (Cole 1995b). Others have also found that forbs are less resistant to trampling than graminoids (Sun and Liddle 1993a, Andersen 1995, Yorks et al. 1997, Whinam and Chilcott 1999). Cole (1995b) also found that, in a given species, the location of the perennating bud was the primary determinant of resilience to trampling. The perennating bud, or persistent bud, is the area from which growth is initiated after a period of unfavorable environmental conditions (McIntyre et al. 1995). Raunkiaer (1934) categorized plants based upon the position of the perennating bud in relation to the soil. He termed plants with perennating buds located on aerial shoots as chamaephytes, plants with perennating buds located just at the soil surface as hemicryptophytes, and plants with perennating buds located well beneath the surface as cryptophytes. Annuals were referred to as therophytes. Cole (1995b) found that "resilience was significantly greater for hemicryptophytes and geophytes than for chamaephytes." Other studies support this finding, though it is not clear whether cryptophytes or hemicryptophytes are more resilient. Bates (1935) found that plants on trails were more commonly cryptophytes, while the flora of off-trail areas were mainly hemicryptophytes. However, others found that hemicryptophytes were more prevalent on trails (Gillham 1956, Liddle and Greig-Smith 1975, Hall and Kuss 1989). Part of the difficulty may have to do with assigning plants to the cryptophyte or the hemicryptophyte camp. Both Smith (1913) and Bates (1935) note that drawing a line between the cryptophytes and the hemicryptophytes, and the hemicryptophytes and the chamaephytes, is difficult. However, " . . . there is no doubt as to which species tend to the cryptophytic habit and which to the chamaephytic" (Bates 1935).

According to Cole (1995b), tolerance is " . . . the ability of a vegetation type to tolerate a cycle of disturbance and recovery" and is " . . . a reflection of both resistance and resilience . . . ". Cole (1995b) found that tolerance to trampling disturbance was correlated more with resilience than resistance, and that therefore the plants least tolerant of trampling were chamaephytes, " . . . while the most tolerant were the non-erect hemicryptophytes and geophytes [cryptophytes]."

For the dominant plant species in the four marsh communities of the VCR-LTER, the order of trampling tolerance based upon Cole's concept of the relative tolerance of plants to trampling, from most tolerant to least, may be as follows: *S. patens* and *D. spicata* > *J. roemerianus* and short form *S. alterniflora* > tall form *S. alterniflora* > *Salicornia* spp. (Table 23). Both *S. patens* and *D. spicata* are cryptophytes (Conrad 1935), so they should quite resilient to trampling. Furthermore, both species are graminoids and tend to grow in tufts, so they should both be quite resistant. *J. roemerianus* is also a cryptophyte (Conrad

1935), and *S. alterniflora* may be either a cryptophyte (U. S. Department of Agriculture 2002) or a hemicryptophyte (Marchant and Goodman 1969), so both species should be resilient to trampling. However, both species grow in a more erect form than *S. patens* and *D. spicata*, so may be less resistant to trampling. Furthermore, *J. roemerianus* is generally taller than either *S. patens* or *D. spicata*, so again, resistance to trampling may be less. Also, though *S. alterniflora* growing in the low marsh may be no

Table 23. Hypothesized relative tolerance of individual marsh plant species to trampling. Species ranked from highest to lowest based upon Cole (1987 and 1995b).

Species	Growth form	Location of bud	Relative off-trail height	Hypothesized tolerance
D. spicata and *S. patens*	graminoid	cryptophyte	short	highest
J. roemerianus	graminoid	cryptophyte	tall	↓
S. alterniflora	graminoid	cryptophyte *or* Hemicryptophyte	short	
Tall form *S. alterniflora*	graminoid	cryptophyte *or* hemicryptophyte	tall	
Salicornia spp.	forb	therophyte cryptophyte *or* hemicryptophyte	short	lowest

taller than *S. patens* or *D. spicata*, its stems may be more brittle, or rigid. Plants that have flexible stems are generally more tolerant of trampling (Cole 1987, Sun and Liddle 1993b). Tall form *S. alterniflora* may be more susceptible to trampling than either shorter *S. alterniflora* or *J. roemerianus,* because it combines the height of *J. roemerianus* with the brittleness of *S. alterniflora*. There are three species of *Salicornia* present in the marshes of the VCR-LTER. *Salicornia europaea* and *Salicornia biglovii* are therophytes, while *Salicornia virginica* is most likely a cryptophyte or hemicryptophyte (C. Jolls, 2002, East Carolina University, *personal communication*). There seems to be little information regarding the tolerance of therophytes to trampling disturbance. However, Andersen (1995) reported that trampling reduced the number of species of therophytes on trails relative to off-trail areas. But he also noted that *Spergularia marina*, an annual salt marsh species, was recorded only on trails. Trampling may have released the species from competition and allowed it to become established (Andersen 1995). Finally, the three *Salicornia* spp. are all erect forbs, and are therefore probably less resistant to trampling than the other aforementioned marsh species.

Another factor that may interact with trampling in the reduction of biomass is slope. Weaver and Dale (1978) and Burden and Randerson (1972) reported that damage from trampling is generally greater on slopes than on level ground (but see Moles 1992). Trimble and Mendel (1995) noted that the total force of a cow hoof propelling an animal up a slope is " . . . high indeed" and, while that force directed onto level ground might simply compact the soil, on a steep slope " . . . the power to shear and move soil downslope, reshaping the surface, is greatly enhanced." The same would be true for deer moving uphill. Trails leaving tidal creeks invariably slope up to the marsh surface. It is possible that increased slope contributed to the loss of biomass on creek bank trails, which was found to be the greatest among marsh communities in both 2000 and 2001.

Light

The conceptual model (Figure 1) links the loss of biomass to light intensity at the soil surface. The finding that the amount of light reaching the marsh surface in on-trail areas was significantly greater than that of off-trail areas in all marsh communities concurs with the hypothesis that light intensity would be higher in on-trail areas of the marsh because of reductions in biomass in on-trail areas. In both on- and off-trail areas, changes in the amount of light reaching the ground in a particular marsh community are a reflection of both the amount of biomass removed by trampling, and of the height and density of plants in the community. The more biomass is removed, the greater will be the intensity of light at the marsh surface; while the taller and more dense the vegetation, the lesser will be the intensity of light reaching the marsh surface. It follows that the greatest relative differences in on- and off-trail light intensities would occur in a community if off-trail vegetation was both tall and dense and the on-trail vegetation was short and sparse. It is perhaps not surprising then, that the greatest increases in relative light intensity were recorded in the *J. roemerianus* community. *J. roemerianus* grows both tall and dense off-trail and had large decreases in biomass on-trail. Increases in on-trail relative light intensities were roughly equal in the creek bank and *D. spicata/S. patens* communities. Though tall form *S. alterniflora* grows to considerably greater heights than either *S. patens* or *D. spicata*, it also grows less densely. The creek bank community experienced the largest decrease in biomass from trampling, while the *D. spicata/S. patens* community retained the largest percentage of biomass. Relative light intensities increased the least on trails in the low marsh. Compared with other marsh communities, vegetation in this community grows neither particularly tall nor particularly dense.

Temperature

The conceptual model (Figure 1) links increases in temperatures to increases in light intensity at the soil surface brought about by reductions in biomass from trampling. In August 2001 both on-trail surface temperatures and temperatures at a depth of 5 cm were statistically significantly warmer than off-trail temperatures in the *J. roemerianus* and *D. spicata/S. patens* communities. On-trail surface temperatures in the creek bank community were not significantly warmer than off-trail surface temperatures, but temperatures at a depth of 5 cm were significantly warmer on- than off-trail. On- and off-trail temperatures in the low marsh did not differ significantly at either the surface or at a depth of 5 cm. In March 2002 the same surface temperature results were found - on-trail temperatures were significantly warmer than off-trail temperatures in the *J. roemerianus* and *D. spicata/S. patens* communities, but not in the low marsh and creek bank communities. However, at a depth of 5 cm, on-trail temperatures were significantly warmer than off-trail temperatures in all four communities.

Removal of vegetation, whether through trampling, wrack deposition, or some other disturbance, allows more light to reach the marsh surface and may consequently cause soil temperatures to increase (Bertness et al. 1992). However, the relationship between open areas and temperature may not be so straightforward. In a variety of ecosystems, temperatures in open areas have been shown to fluctuate more than temperatures in shaded areas - vegetation cover may serve to moderate temperature fluctuations (Siira 1970, Chappell et al. 1971, Liddle and Moore 1974, Meyer et al. 1995, Kobayashi et al. 1997, but see Pomeroy 1959). For instance, Chappell et al. (1971) compared grazed and ungrazed areas of a chalk grassland ecosystem and found that after a severe frost the soils in grazed areas were frozen to a depth of 3 - 4 cm, while soil temperature in an ungrazed area was above freezing. Kobayashi et al. (1997), who examined the effects of trampling on herbaceous communities, found that the daily fluctuation of temperatures in a trampled plot was greater than fluctuations in an untrampled plot. They emphasized that in the trampled plot ". . . the soil temperatures during midday in summer were much higher than those of the other plots." Liddle and Moore (1974) compared on- and off-trail microclimates in sand dunes in Wales. They suggested that vegetation moderates the range of temperature in soil by restricting the penetration of light to the soil surface, and reducing net heat loss by long-wave radiation from the soil at night. Meyer et al. (1995) found that temperature ranges, both at the soil surface and down to a depth of 5 cm, increased in grazed areas of a salt marsh in Europe. Siira (1970) found that temperature variation increased in bare areas of salt marshes in Finland. Interestingly, Pomeroy (1959), working in a Georgia salt marsh, found that, while soil temperatures in bare areas in winter were warmer than those beneath dense stands of *S. alterniflora*, in summer the opposite situation occurred - the sediment temperature beneath *S. alterniflora* was higher than in bare areas. Pomeroy (1959) credited " . . . a combination of greenhouse effect and reduced evaporation of water from the sediments" for this phenomenon.

Another factor that may affect soil temperatures in the low marsh and creek bank communities of the VCR-LTER is tidal influx. Water from high tides moderates the soil temperatures of these two communities, both of which receive regular tidal input. Tidal influx may be responsible for the varying statistical significance of increases in temperatures found in on-trail areas of low marsh and creek bank communities.

Soil salt content

The conceptual model (Figure 1) links increases in salinity to increased evaporation brought about by increases in temperature which stem from increases in light intensity. However, no significant differences between on- and off-trail levels of soil salt content were found in any marsh community.

Another measure of the salt content of marsh soils is salinity. Salinity was not measured in this study because soil samples were inadvertently allowed to dry before determining their water content. This made calculation of salinity impossible.

Salinity and salt content of marsh soils reflect a variety of different factors including " . . . the salinity of ambient tidal water, the frequency of tidal flooding and amount of precipitation which limit salt accumulation, and the intensity of solar radiation which dictates evaporation and the potential extent of salt accumulation" (Bertness and Pennings 2000). Many studies conducted in salt marshes have found that disturbances such as grazing, trampling, or wrack deposition can reduce vegetation cover and thereby cause salinity levels to increase because of increased evaporation (Siira, 1970, Bakker and Ruyter 1981, Bertness 1991b, Bertness et al. 1992, Meyer et al. 1995, Srivastava and Jefferies 1996, Miller et al. 1998) (but see Christian et al. 1978). Other studies have found little or no difference between salinities of disturbed and non-disturbed areas of salt marshes (Bakker 1985, Hartman 1988, Shumway and Bertness 1994, Kiehl et al. 1996, van Wijnen et al. 1999). Size of open patches may play a role in the level of salinity. Salinities seem to increase with patch size because of increased exposure to direct solar radiation and surface heating (Bertness 1991b). Most trails in the marsh were roughly 30 cm wide. It is possible that these trails, though "large" in a linear sense, were simply too narrow to have increased salinity. On-trail temperature increases may not have been great enough to increase evaporation significantly. Additionally it is possible that tidal activity removed salt in low marsh and creek bank communities.

Soil organic content

In the conceptual model (Figure 1) decreases in the organic content of soil are linked to both reductions in biomass brought about by trampling, and to increases in decomposition arising from increases in temperature. Indeed, a significantly lower percentage (median = 54.4%) of organic matter was present in the upper 10 cm of soil in the on-trail areas of the *D. spicata/S. patens*, than in the off-trail areas (median = 72%) of the same community. However, no significant differences were found between the percentages of organic matter in the upper 10 cm of the on- and off-trail areas of the *J roemerianus*, low marsh, and creek bank communities.

A number of studies in a variety of ecosystems have found that trampling tends to remove organic matter from the soil surface (Frissell and Duncan 1965, Manning 1979, Liddle and Chitty 1981, Cole 1987), which could lead to a loss of organic horizons below-ground. Ford and Grace (1998) hypothesized that the removal of above-ground vegetation by grazing would lead to increased soil temperatures and increased decomposition (Ford and Grace 1998). It is possible that trampling disturbance without the feeding component of grazing may have the same net effect on soil organic content. Presumably increases in decomposition could lead to decreases in soil organic content. However, in an examination of the effects of grazing on a salt marsh in Louisiana, Ford and Grace (1998) did not find that grazing changed soil organic content. They suggested the time frame of their study was too short (2 years) and that, given more time, such a change would have occurred.

Bulk density

Increased soil compaction is another primary and direct effect of trampling in the conceptual model (Figure 1). On-trail soil bulk density was hypothesized to be significantly greater than off-trail soil bulk density because of compaction brought about directly by trampling. The bulk densities of the upper 10 cm of soil in on-trail areas of the low marsh and *D. spicata/S. patens* communities were significantly greater than that of off-trail areas in the same communities. There were no significant differences between the bulk densities of the upper 10 cm of soil in on- and off-trail areas of the *J. roemerianus* and creek bank communities, however.

The measurement of bulk density is commonly undertaken to determine the degree of compaction in soil (Tanner and Mamaril 1959, Soane 1990). Soane (1990) defined compaction as " . . . a process which leads to the densification of soils as a result of the application of stresses . . ." Trampling may increase soil compaction, or bulk density (Bates 1935, Edmond 1964, Chappell et al. 1971, Liddle and Greig-Smith 1975, Weaver and Dale 1978, Cole 1987, Trimble and Mendel 1995, Kozlowski 1999). In salt marshes, increased compaction has been variously ascribed to trampling by voles (Howell 1984) and cattle (Chabreck 1968). Kozlowski (1999) said that ". . . compaction typically alters soil structure and hydrology by increasing soil bulk density, breaking down soil aggregates, decreasing soil porosity, aeration, and infiltration capacity . . ." Tanner and Mamaril further stated that ". . . soil compaction . . . results in increased mechanical impedance to root growth . . ." Trimble and Mendel (1995) said that compaction can also increase the overland flow of water, which in turn may lead to increased erosion.

According to Soane (1990), "the bulk density of organic materials is usually appreciably less than that of mineral soil." It stands to reason then, that decreases in the organic content of soil may lead to increases in bulk density. The *D. spicata/S. patens* community was the only marsh community in which both significant on-trail decreases in organic content and significant on-trail increases in bulk density were observed. However, to what degree either on-trail compaction or on-trail reductions in soil organic content were responsible for observed increases in bulk density is unknown.

According to Soane (1990) and Kozlowski (1999), soils with higher organic content are less susceptible to compaction than soils with higher mineral content, especially at high soil moisture content. It is perhaps somewhat surprising then, that the bulk-density of on-trail areas in the *D. spicata/S. patens* community was significantly higher than off-trail areas, given both the high organic content of the soil in that community and the presumed lower levels of trampling.

One source of variation in the analysis of bulk density may have come from the method used to divide soil cores. Soil cores were quartered, but without precise measuring. Therefore, it is possible that samples used to calculate bulk density varied in volume to a degree that any on-trail/off-trail differences could not be statistically determined.

Decrease in trail elevation

On-trail elevations were hypothesized to be lower than off-trail elevations because of subsidence brought about by reductions in below-ground biomass and the amount of sediment trapped, and by increases in soil compaction, erosion, and decomposition (Figure 1). Indeed, on-trail elevations were significantly lower than off-trail elevations in every marsh community except the *D. spicata/S. patens* community. However, it should be noted that two of the three *D. spicata/S. patens* study trails were located in a hummock and hollow areas of the high marsh. Given the great variation in elevation occurring in hummock and hollow marshes, it is uncertain whether or not differences in elevation between these areas could have been discerned.

Many researchers have noted that trampling may lower the elevation of soil in relation to surrounding untrampled areas in a variety of ecosystems including English heath (Jeffreys 1917) and grasslands (Bates 193), northern Rocky Mountain forests and grasslands (Dale and Weaver 1974, Weaver and Dale 1978), wetlands (Hole 1981), sand dunes (Hylgaard and Liddle 1981), and grazed fields (Trimble and Mendel 1995). Jeffreys (1917), perhaps the earliest recorder of this phenomenon, suggested that "owing to the repeated pressure, the earth tends to be pressed down . . .on the paths, which are thus lower than their surroundings." Bates (1935), another early researcher, also used the term "pressed down" to describe what was happening to the soil on paths. Hole (1981) said that trails formed by ungulates in wetlands " . . . are commonly depressed by compaction as much as 30 cm below the surface of the surrounding soil." Hylgaard and Liddle (1981), in their study of a sand dune ecosystem, also suggested that soil compaction from trampling led to the lowering of the soil surface. Trimble and Mendel (1995) noted that the lowered elevation of grazed fields relative to ungrazed fields may have resulted from erosion. Weaver and Dale (1978) said that increases in the depth of trails might be the result of both erosion and compaction.

Ford and Grace (1998) found that herbivory in salt marshes might contribute to subsidence, or the loss of elevation. They suggested that the removal of above-ground vegetation results in increased light penetration and therefore increased soil temperatures. Increased soil temperatures may result in increased decomposition rates (Godshalk and Wetzel 1978). Trampling, which results in increased light penetration and soil temperature, could also cause increased decomposition rates. Ford and Grace (1998) also found that grazing lowered below ground biomass production. They concluded that, because below ground tissues might make up a considerable portion of soil volume (Nyman et al. 1990), this reduction in biomass production could lead to subsidence (Ford and Grace 1998). Ford and Grace (1998) did not ascribe the decrease in below ground production specifically to either the trampling or cropping components of grazing, but it is possible that trampling alone may lead to a reduction below ground production.

A final point is that the lowering of trail surface relative to surrounding areas could cause increased puddling. This is a phenomenon noted by early researchers such as Jefferies (1917) and Bates (1935). Redfield (1972) suggested that increased puddling on the marsh surface could lead to the creation of pond holes, or pannes, in a New England salt marsh. He credited increased standing water in slight depressions for the ". . . death of the vegetation and the subsequent decomposition of the turf" (Redfield 1972). Increased puddling caused by trampling could have similar effects.

Community changes

Differences in on- and off-trail community composition are examined in the following sections. The cascade of effects brought about by trampling (Figure 1, Tables 21 and 22) alters the abiotic environment in which organisms live - thereby contributing to shifts in community structure.

Vascular plant community composition

The conceptual model of the cascade of effects brought about by trampling (Figure 1) links changes in the vascular plant community with increases in light, salinity, and subsidence. Based upon the examination of live above-ground plant biomass, on- and off-trail community composition differed significantly only in the *J. roemerianus* community in 2000. However, in 2001 on- and off-trail community composition was found to be significantly different in the *J. roemerianus*, *D. spicata/S. patens*, and low marsh communities. This apparent difference in community composition between the two years probably arises from the differing shapes of the quadrats used to collect biomass (See above). The wider quadrat used in 2000 for the collection of biomass on trails undoubtedly picked up more off-trail biomass than the narrower quadrat used to collect biomass in 2001.

It should be noted that trampling disturbances in any given area of the marsh may occur repeatedly over a prolonged time period, and therefore accompanying changes in community structure may also be relatively long-term. Trails described in a forested area of New York in the 1890's were still in use as recently as 1951 (Servinghaus and Cheatum 1956). Thus, the potentially great length of time that trampling by deer may influence an area stands in marked contrast to that of another common marsh disturbance - wrack deposition. Wrack deposition may affect community composition for as little as 2-4 years (Bertness and Ellison 1987).

Species composition in the *J. roemerianus* community. In both 2000 and 2001, the percentage of on-trail biomass composed of *D. spicata* was significantly higher than the percentage of off-trail biomass. Little to no differences were found for other species.

A variety of factors influence the colonization of disturbed areas in a salt marsh including competition among the different species involved and changes in abiotic characteristics brought about by the disturbance. One of the most common disturbances in a salt marsh is the deposition of floating rafts of plant matter, or wrack, on the marsh surface (Hartman et al. 1983, Bertness and Ellison 1987). Wrack creates bare areas by destroying underlying vegetation (Bertness and Ellison 1987) (but see Pennings and Richards 1998). Tolley (1996) and Tolley and Christian (1999) found that *D. spicata* dominated the colonization of wrack-disturbed patches in the *J. roemerianus* community of the VCR-LTER.

Bertness (1987) described *D. spicata* as " . . . a disturbance-dependent species whose success is a product of its ability to tolerate and recover from disturbance in marsh habitats." The plant uses adventitious rhizomes to quickly spread into bare, or even modestly thinned patches, that have been created by disturbance (Bertness 1987, Brewer et al. 1998, Allison 1995). This manner of growing may be characterized as a guerilla strategy (Lovett Doust 1981). *S. patens* and *J. gerardi* (and *J. roemerianus*) spread more slowly via dense fronts of ". . . rhizomes, roots and associated tillers" (Bertness 1987). This manner of growing may be characterized as a phalanx strategy (Lovett Doust 1981). The dense turf morphology of the phalanx growth strategy helps make *S. patens* and *J. gerardi* competitively dominant to *D. spicata* in undisturbed areas (Bertness 1991b), but not in disturbed patches (Bertness et al. 1992).

It may be the case then, that competitive interactions and tolerance to trampling determine the makeup of the on-trail *J. roemerianus* community rather than facilitation. On-trail salinity levels were not found to be any higher than off-trail salinity at the VCR-LTER. This competition among species now takes place, however, in the face of trampling disturbance in an altered environment. Also, on-trail areas in the *J. roemerianus* community were lower in elevation than off-trail areas. This difference in elevation may result in increased ponding on the trail. Increased ponding may stress plants and inhibit recolonization - particularly by *J. roemerianus* (Tolley 1996).

Though the low marsh dominant *S. alterniflora* made up a higher percentage of the on-trail biomass than of the off-trail biomass in the *J. roemerianus* community, this amount was not statistically significant. This finding does not accord with the hypothesis that low marsh species will become more prevalent in on-trail areas of the high marsh (Table 1). However, visual inspection of certain areas in the *J. roemerianus* community suggests that *S. alterniflora* may be more prevalent in certain on-trail areas - particularly those relatively near tidal creeks eroding into the *J. roemerianus* community. The distribution of S. *alterniflora* in the *J. roemerianus* seems to be quite aggregated, and any existing on- and off-trail differences involving this species may not have been discerned in my study.

Species composition in the *D. spicata*/*S. patens* community. No statistically significant differences were found between on and off-trail community structure in 2000. However, in 2001, a significantly lower percentage of *S. patens* and a significantly higher percentage of *D. spicata* biomass were found in on-trail areas. This finding accords with the hypothesis that disturbance tolerant species would become more prevalent in on-trail areas of the high marsh (Table 1). A variety of factors may be responsible for these differences in on- and off-trail community structure including soil compaction, individual species tolerance of trampling, and flooding regime. Soil compaction, indexed in this study by bulk density, may slow plant growth (Kozlowski 1999). In the *D. spicata*/*S. patens* community, on-trail bulk density was found to be significantly greater than off-trail bulk density. It is possible that this plays a role in the observed differences between on- and off-trial community composition. It may be that *D. spicata* is more tolerant of trampling than *S. patens*. Interestingly, however, no difference was found between the percentage of on- and off-trail *S. patens* biomass in the *J. roemerianus* community. This is, perhaps, an indication that *S. patens* is fairly tolerant of trampling, and that another factor must be at work in the *D. spicata/S. patens* community. *S. patens*, which has poorly developed arenchyma (Anderson 1974, Naidoo et al. 1992), is less tolerant of flooding than *D. spicata* (Bertness 1987). *D. spicata*, on the other hand, has aerenchyma in its rhizome, roots and leaf sheath which may ". . . provide sufficient gas exchange for respiration to take place in heavily inundated . . . soils" (Hansen et al. 1976). Roberts (2000) found that *S. patens* dominated *D. spicata* in more benign areas, but that *S. patens* is limited in saturated soils, and was released from competition with *S. patens* in more saturated areas of the marsh. The three *D.* s*picata/S. patens* trails examined in this study may have occupied areas in the marsh that, because of flooding, were already fairly marginal habitat for *S. patens* - as indicated by the dominance of *D. spicata* in off-trail areas. One trail began near low marsh in an area that was probably subject to more flooding than other high marsh areas. The trail continued from there into high marsh. The percentage of off-trail *S. patens* biomass along this trail seemed to increase with distance from the low marsh (*S. patens* increased from 29.4% of biomass in samples taken close to the low marsh to 56.7% of biomass farther from the low marsh), presumably as flooding stress lessened. The other two study trails were located in hummock and hollow portions of the marsh. Hummock and hollow topography develops when intact portions of the marsh degrade, forming potholes, or "hollows" (Roberts 2000). Ponding in hollows creates more stress on plants. Both Roberts (2000) and Buck (2001) found that *D. spicata* dominates the hollow and hummock areas of the high marsh. It is possible then, that trampling was another stress upon *S. patens* already existing in a marginal environment. This additional stress may have been enough to reduce the on-trail percentage of *S. patens* biomass relative to *D. spicata* biomass. Furthermore, given the difficulties associated with measuring elevation in hollow and hummock areas with its associated great variation in topography, *D. spicata/S. patens* trails, or portions thereof, may be lower in elevation than surrounding areas and therefore subject to greater inundation (see below). If this were the case, it would also serve to shift community composition toward *D. spicata*.

Species composition in the low marsh community. Contrary to the high marsh communities, *D. spicata* accounted for a significantly smaller percentage of on-trail biomass than off-trail biomass, at least in 2001. The percentages of on- and off-trail biomass composed of *S. alterniflora* and *Salicornia* spp. did not differ. Generally, the low marsh is dominated by *S. alterniflora*. *S. alterniflora* is better able to survive regular flooding than other species of salt marsh flora at least partly because it can oxygenate its rhizosphere in anoxic soils (Teal and Kanwisher 1966, Howes et al. 1981, Bertness 1991a, Naidoo et al. 1992,). Bertness and Ellison (1987) suggested that, while *S. alterniflora* has the highest tolerance to physical conditions across the marsh, *D. spicata* is the second most tolerant species, and may dominate some physically marginal habitats such as waterlogged soils. The upper edge of the low marsh may be such a marginal habitat for *D. spicata*. It may be the case then, that *D. spicata* cannot withstand the additional disturbance of trampling on trails in the low marsh.

Species composition in the creek bank community. Tall form *S. alterniflora* is the only species of vascular plant to occupy this community. It is unlikely for other species to invade disturbed creek banks.

Benthic chlorophyll *a*

I hypothesized that significantly more chlorophyll *a* would be present in on-trail areas of the marsh communities because of increases in light intensity. Indeed, significantly more benthic chlorophyll *a* was found in on-trail areas of the *J. roemerianus* and *D. spicata/S. patens* than in off-trail areas. Median concentrations of chlorophyll *a* increased in the *J. roemerianus* community from 1.37 mg/m^2 in off-trail areas to 2.87 mg/m^2 in on-trail areas, and in the *D. spicata/S. patens* community from 0.14 mg/m^2 in off-trail areas to 2.25 mg/m^2 in on-trail areas. However, no statistically significant on- and off-trail differences in the amount of chlorophyll *a* were found in the low marsh and creek bank communities where off-trail concentrations were already high. Median concentrations of chlorophyll a in the low marsh community were 2.81 mg/m^2 in on-trail areas and 3.30 mg/m^2 in off-trail areas. In the creek bank community median concentrations were 2.90 mg/m^2 in the on-trail areas and 2.90 mg/m^2 in the off-trail areas.

Light is likely to be the most important determinant of microalgae production (van Raalte et al. 1976, Williams et al. 2001). Note that the production of benthic microalgae was not measured in this study - only biomass. Given other factors are equal, I am inferring that if microalgal production is greater, then standing stocks of biomass will also be greater. Other factors, such as temperature and nutrient concentrations, may also play a role in regulating production, but they do not influence production as much as light intensity (van Raalte 1976). It might be the case that light was more limiting for microalgae in the high marsh, as off-trail areas in the two high marsh communities had the lowest standing stocks of algal biomass. Certainly, light intensities in on-trail areas relative to off-trail areas increased the most in the *J. roemerianus* community. Trampling disturbance may have simply opened up the canopy and released microalgae from that limiting factor in both the *J. roemerianus* and *D. spicata/S. patens* communities. Meanwhile, in the low marsh and creek bank communities, light may not have been limiting the growth of microalgae. Light intensities in on-trail areas relative to off-trail areas increased the least in the low marsh community. The standing crops of off-trail microalgae in these two communities were considerably higher than in either high marsh community. Apparently increased light levels, brought about by trampling, had little to no effect on total biomass in the low marsh and creek bank communities.

Grazing often plays an important role in regulating standing stocks of microalgae (Castenholz 1961, Duffy et al. 1977, Gallagher and Daiber 1974). For instance Pace et al. (1979) found that removal of the snails from an area of salt marsh mudflat resulted in a significant increase in algal standing stock. However, it seems unlikely that *I. obsoleta* grazing plays a role in reducing algal biomass on the trails examined in the low marsh and creek bank communities. I rarely observed mud snails on the three low marsh study trails and on two of the three creek bank study trails.

Distribution of *Ilyanassa obsoleta*

As hypothesized, because of increased puddling significantly more *I. obsoleta* were found on low marsh and creek bank trails than in marsh areas adjacent to trails. The snails were not, however, observed on every creek bank or low marsh trail. Mud snails were generally absent from creek bank trails crossing tidal creeks eroding into high marsh areas. Snails were also generally absent from low marsh trails that did not intersect directly with creek bank trails where mud snails were present.

I. obsoleta is a prosobranch neogastropod that occurs both intertidally and subtidally along the Atlantic coast of North America (Cranford 1988). The snail is a marine deposit feeder (Curtis and Hurd 1980, Feller 1984) and feeds primarily upon benthic algae (Wetzel 1977). The procurement of food may affect the movements of snails (Crisp 1969, Levinton et al 1995). However, given that there seems to be no more benthic microalgae in on-trail areas than off, it seems unlikely that snails are congregating in trails because of food, although this is possible.

It may be that snails congregate on trails as the tide recedes - simply because trails offer a wetter environment than surrounding areas. *I. obsoleta* are susceptible to desiccation (Levinton et al. 1985), and according to Cranford (1988) the snails migrate daily into drainage channels and other damp depressions during exposure. Crisp (1969) observed that snails ". . . were concentrated in pools or damper areas whilst firmer clean sandy areas . . . were often free of snails." Furthermore, on an incoming tide, Crisp (1969) observed that snails in channels " . . . tended to move uphill towards the waterline . . . " It is possible then, that trails act as damp places for snails to retreat to when tides are low.

CONCLUSIONS

The different responses of the four marsh communities to trampling may be influenced by the antecedent conditions present within each community. For instance, the low marsh and creek bank communities are both characterized by regular tidal flooding, mineral soils, and low vascular plant species diversity, while the two high marsh communities are characterized by irregular tidal flooding, organic soils, and relatively high vascular plant species diversity. The differences between the zones of the two former and the two latter communities were great enough that Brinson et al. (1995) classified them as separate ecosystem states.

Trampling significantly reduced biomass in the on-trail areas of all communities, and this reduction in biomass led to significant increases in light intensity at the marsh surface of all such areas in all communities. However, increases in light intensity did not lead to increases in summer surface soil temperatures in the low marsh and creek bank communities, where regular tidal flooding may have ameliorated temperatures. The organic content of soils in the on-trail areas of both the low marsh and creek bank communities were not significantly different than those of off-trail areas. This is perhaps unsurprising, given that the off-trail organic content of soils in these communities is low. Bulk density was found to be significantly greater in on-trail areas of the low marsh community, but not in on-trail areas of the creek bank communities. The soil of creek bank areas is often fairly unconsolidated, and perhaps relatively difficult to compact. The composition of on-and off-trail vascular plant species was unaffected in the creek bank community. Changes to the community brought about by trampling did not make conditions more amenable for the establishment of species other than tall form S. alterniflora.

Differences in vegetation type between the two high marsh communities may have played a role in determining response to trampling. The soil organic content of on-trail areas in the *D. spicata/S. patens* community was significantly lower than that of off-trail areas. Interestingly, however, there was no change in the soil organic content of on-trail areas in the *J. roemerianus* community. It may be the case that the roots and rhizomes of vegetation in the *J. romerianus* community are more resistant to trampling than that of vegetation in the *D. spicata/S. patens* communities. The finding that the bulk density of soils in the on-trail areas of the *D. spicata/S. patens* communities was significantly increased relative to off-trail areas, while that of on-trail areas in the *J. roemerianus* communities was not, may be indicative of the same phenomena. The apparently contradictory finding that on-trail elevation was significantly lower relative to off-trail areas in the *J. roemerianus* community, but not in the *D. spicata/ S. patens* community, may perhaps be explained by the varied microtopography of the off-trail areas of the *D. spicata/S. patens* community. The great differences in elevation between hollows and hummocks may have masked the signal of on-trail elevation change in that community.

Rising sea level essentially lowers the relative elevation of mainland surfaces, making them more vulnerable to flooding from brackish water (Brinson et al. 1995). According to Brinson et al. (1995), disturbance may weaken marsh resistance to sea level rise by altering sediment conditions and facilitating plant species replacement. Trampling, to the extent that it removes *S. alterniflora* biomass in creek bank and low marsh communities, may help facilitate ecosystem state change in those areas. The reduction in stem density arising from trampling may reduce sedimentation, thereby slowing accretion of the marsh surface. Furthermore, increased erosion on sloping creek bank trails may further help to lower the elevation of those areas. In high marsh areas, the loss of biomass from trails may slow the accumulation of peat. Also, as discussed above, trails in the *J. roemerianus* community were lower in elevation than surrounding areas, whether because of compaction, increased decomposition, erosion, reduced below ground production, or some combination of all these factor. This lowering of the marsh surface could increase ponding, which may in turn, lead to further subsidence (McKee and Mendelssohn 1989, Brinson et al. 1995). It is possible that trampling in the *D. spicata/S. patens* community may also help to lower the marsh surface, though as mentioned above, any lowering of the on- trail surface would have been difficult to discern given the great variation in the surrounding topography. Certainly, as in the other communities, shifts in species composition, and increases in light intensity and temperature were observed on trails in the *D. spicata/S. patens* community. Furthermore, the soil organic content of on-trail areas in the *D. spicata/S. patens* community was found to be lower than that of off-trail areas, perhaps indicative of either decreased below ground production or increased decomposition, either of which could lead to subsidence (sensu Ford and Grace 1998). Finally, on-trail areas of the *D. spicata/S. patens* community were also more compacted than surrounding areas, as indexed by bulk density. This compaction could lead to the relative lowering of the marsh surface as well. As previously discussed, the observed increase in the percentage of *D. spicata* relative to *S. patens* could indicate that trails were subject to greater inundation than surrounding off-trail areas. Buck (2001) concluded that increased flooding in the high marsh caused decreases in the above-ground biomass, and that this loss of biomass " . . . and continued stress to the existing plant community may be facilitating the transition from organic high marsh to mineral low marsh through the formation of a transitionary open-water environment." Given this, it seems reasonable to assume that, to the extent trails lower the marsh surface and disallow accretion, trampling disturbance facilitates ecosystem state change in high marsh areas. However, given that trails cover only a small percentage of the overall marsh surface, it seems that the effects of trampling, as they relate to facilitating state change in a salt marsh, are quite localized.

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APPENDIX A. GENERAL FORMAT FOR APPENDICES B - N: The following table and bulleted statements describe the symbols and format used in appendices B – N.

J+	J-	HM+	HM-	LM+	LM-	CB+	CB-
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

- Values in "+" columns are on-trail. Values in "-" columns are off-trail.

- Values in "J" columns are from the *J. roemerianus* community.

- Values in "HM" columns are from the *D. spicata/S. patens* community.

- Values in "LM" columns are from the low marsh community.

- Values in "CB" columns are from the creek bank community.

- Species symbols are explained in Table 3.

- The values in the first three rows are from trail "1" replicates. The values in the second three rows are from trail "2" replicates. The values in the last three rows are from trail "3" replicates. Therefore, each row represents a replicate within a trail. The three values from each trail are listed in the order in which they were collected.

- Appendices J - N display values from trails in which five replicates rather than three replicates were collected in each trail. The same general format applies for these appendices.

APPENDIX B. AUGUST 2000 - TOTAL BIOMASS (G/M^2) FROM 3 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES.

J+	J-	HM+	HM-	LM+	LM-	CB+	CB-
25.6	2979.2	1065.6	3563.2	243.2	508.8	33.6	568.0
25.6	900.8	904.0	1331.2	220.8	523.2	4.8	494.4
60.8	3008.0	152.0	1403.2	478.4	465.6	155.2	772.8
470.4	1723.2	528.0	801.6	432.0	788.8	0	1139.2
1158.4	1608.0	161.6	787.2	318.4	644.8	44.8	1024
827.2	1603.2	414.4	1099.2	523.2	779.2	0	374.4
72.0	2812.8	332.8	979.2	20.8	665.6	0	678.4
75.2	2355.2	686.4	867.2	96.0	587.2	0	1534.4
97.6	1668.8	470.4	1379.2	9.6	446.4	84.8	947.2

APPENDIX C. AUGUST 2000 - LIVE BIOMASS (G/M^2) FROM 3 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES.

J+	J-	HM+	HM-	LM+	LM-	CB+	CB-
20.8	1574.4	529.6	1641.6	192.0	380.8	32.0	473.6
14.4	444.8	488.0	712.0	174.4	366.4	3.2	406.4
40.0	1308.8	78.4	856.0	347.2	275.2	140.8	691.2
280.0	1084.8	374.4	318.4	329.6	603.2	0	886.4
569.6	779.2	132.8	280.0	243.2	496.0	36.8	854.4
496.0	816.0	313.6	470.4	411.2	640.0	0	321.6
38.4	1449.6	273.6	526.4	16.0	569.6	0	560.0
73.6	1232.0	409.6	515.2	70.4	499.2	0	675.2
81.6	875.2	179.2	1038.4	8.0	347.2	84.8	750.4

APPENDIX D. AUGUST 2000 - TOTAL BIOMASS PER SPECIES (G/M^2) FROM 3 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES.

J+ SP	J- SP	J+ DS	J- DS	J+ SA	J- SA	J+ J	J- J
8.0	0	0	216.0	0	0	17.6	2763.2
0	1.6	11.2	0	0	0	14.4	899.2
3.2	0	27.2	36.8	0	0	30.4	2971.2
0	638.4	56.0	8.0	0	0	414.4	1076.8
265.6	0	0	38.4	0	0	892.8	1569.6
86.4	88.0	32.0	17.6	0	0	708.8	1497.6
0	0	0	0	0	0	72.0	2812.8
0	0	19.2	0	0	0	56.0	2355.2
4.8	60.8	8	62.4	0	0	84.8	1545.6

HM+ SP	HM- SP	HM+ DS	HM-DS	HM+ SA	HM- SA
868.8	2366.4	196.8	1196.8	0	0
480.0	952.0	424.0	379.2	0	0
49.6	888.0	102.4	515.2	0	0
320.0	289.6	208.0	512.0	0	0
118.4	0	43.2	787.2	0	0
344.0	803.2	70.4	299.2	0	0
121.6	392.0	204.8	587.2	0	0
313.6	364.8	372.8	502.4	0	0
216.0	472.0	254.4	907.2	0	0

LM+ SA	LM- SA	LM+ SAL	LM- SAL	LM+ SP	LM- SP	LM+ DS	LM- DS
230.4	459.2	12.8	49.6	0	0	0	0
214.4	516.8	6.4	6.4	0	0	0	0
478.4	465.6	0	0	0	0	0	0
432.0	769.6	0	19.2	0	0	0	0
318.4	644.8	0	0	0	0	0	0
481.6	339.2	41.6	440.0	0	0	0	0
20.8	665.6	0	0	0	0	0	0
96.0	587.2	0	0	0	0	0	0
9.6	446.4	0	0	0	0	0	0

APPENDIX D. CONT.

CB+ SA	CB- SA
33.6	568.0
4.8	494.4
155.2	772.8
0	1139.2
44.8	1024.0
0	374.4
0	678.4
0	1534.4
84.8	947.2

APPENDIX E. AUGUST 2000 - LIVE BIOMASS PER SPECIES (G/M^2) FROM 3 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES.

J+ SP	J- SP	J+ DS	J- DS	J+ SA	J- SA	J+ J	J- J
4.8	0	0	32.0	0	0	16.0	1542.4
0	0	9.6	0	0	0	4.8	444.8
1.6	0	17.6	1.6	0	0	20.8	1307.2
0	569.6	25.6	8.0	0	0	254.4	507.2
113.6	0	0	3.2	0	0	456.0	776.0
20.8	22.4	28.8	16.0	0	0	446.4	777.6
0	0	0	0	0	0	38.4	1449.6
0	0	17.6	0	0	0	56.0	1232.0
4.8	8.0	4.8	9.6	0	0	72.0	857.6

HM+ SP	HM- SP	HM+ DS	HM- DS	HM+ SA	HM- SA
400.0	1025.6	129.6	616.0	0	0
283.2	478.4	204.8	233.6	0	0
22.4	569.6	56.0	286.4	0	0
227.2	104.0	147.2	214.4	0	0
102.4	0	30.4	280.0	0	0
259.2	315.2	54.4	155.2	0	0
97.6	156.8	176.0	369.6	0	0
206.4	216.0	203.2	299.2	0	0
104.0	363.2	75.2	675.2	0	0

LM+ SA	LM- SA	LM+ SAL	LM- SAL	LM+ SP	LM- SP	LM- DS	LM- DS
179.2	334.4	12.8	46.4	0	0	0	0
168.0	360.0	6.4	6.4	0	0	0	0
347.2	275.2	0	0	0	0	0	0
329.6	584.0	0	19.2	0	0	0	0
243.2	496.0	0	0	0	0	0	0
385.6	640.0	25.6	366.4	0	0	0	0
16.0	569.6	0	0	0	0	0	0
70.4	499.2	0	0	0	0	0	0
8.0	347.2	0	0	0	0	0	0

APPENDIX E. CONT.

CB+ SA	CB- SA
32.0	473.6
3.2	406.4
140.8	691.2
0	886.4
36.8	854.4
0	321.6
0	560.0
0	675.2
84.8	750.4

APPENDIX F. AUGUST 2001 - TOTAL BIOMASS (G/M^2) FROM 3 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES.

J+	J-	HM+	HM-	LM+	LM-	CB+	CB-
20.8	3017.6	227.2	643.2	0	788.8	36.8	964.8
19.2	3569.6	40.0	1310.4	30.4	654.4	73.6	812.8
467.2	3240	72.0	616.0	3.2	595.2	3.2	777.6
60.8	3267.2	94.4	798.4	14.4	356.8	129.6	995.2
51.2	2134.4	515.2	801.6	14.4	390.4	0	2129.6
468.8	1750.4	52.8	481.6	1.6	350.4	0	2705.6
233.6	1364.8	49.6	720.0	35.2	598.4	0	1180.8
160.0	2184.0	81.6	462.4	35.2	680.0	0	1126.4
268.8	2600.0	46.4	1713.6	94.4	307.2	0	1057.6

APPENDIX G. AUGUST 2001 - LIVE BIOMASS (G/M^2) FROM 3 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES.

J+	J-	HM+	HM-	LM+	LM-	CB+	CB-
9.6	1499.2	176.0	396.8	0	323.2	29.7	811.2
19.2	2060.8	33.6	657.6	25.6	360.0	56.0	729.6
332.8	1444.8	48.0	240.0	1.6	416.0	3.2	705.6
33.6	1878.4	84.8	486.4	0	288.0	78.4	422.4
48.0	1144.0	358.4	657.6	12.8	260.8	0	1609.6
404.8	929.6	24.0	353.6	1.6	270.4	0	2435.2
94.4	334.4	36.8	513.6	32.0	465.6	0	1060.8
73.6	736.0	60.8	225.6	32.0	385.6	0	1064.0

112.0	859.2	35.2	1305.6	60.8	190.4	0	992.0

APPENDIX H. AUGUST 2001 - TOTAL BIOMASS PER SPECIES (G/M^2) FROM 3 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES.

J+ SP	J- SP	J+ DS	J- DS	J+ SA	J- SA	J+ J	J- J
0	0	0	0	0	0	20.8	3017.6
0	0	0	0	0	0	19.2	3569.6
0	0	6.4	0	0	0	460.8	3240.0
0	400.0	25.6	281.6	0	0	35.2	2585.6
0	0	4.8	6.4	43.2	0	3.2	2128.0
6.4	83.2	16.0	0	305.6	16.0	140.8	1651.2
0	180.8	17.6	9.6	0	0	216.0	1174.4
9.6	337.6	52.8	65.6	0	0	97.6	1780.8
0	1139.2	188.8	233.6	0	0	80.0	1227.2

HM+ SP	HM- SP	HM+ DS	HM- DS	HM+ SA	HM- SA
11.2	208.0	216.0	435.2	0	0
0	400.0	40.0	908.8	0	0
17.6	457.6	54.4	158.4	0	0
0	6.4	57.6	792.0	36.8	0
1.6	3.2	513.6	798.4	0	0
12.8	412.8	40.0	68.8	0	0
4.8	105.6	44.8	614.4	0	0
3.2	179.2	78.4	283.2	0	0
1.6	896.0	44.8	817.6	0	0

LM+ SA	LM- SA	LM+ SAL	LM- SAL	LM+ SP	LM- SP	LM+ DS	LM- DS
0	0	0	0	0	96.0	0	675.2
30.4	649.6	0	0	0	0	0	4.8
3.2	595.2	0	0	0	0	0	0
14.4	172.8	0	184.0	0	0	0	0
6.4	366.4	8	24.0	0	0	0	0
1.6	220.8	0	129.6	0	0	0	0
35.2	84.8	0	312.0	0	0	0	201.6
35.2	72.0	0	315.2	0	0	0	292.8
94.4	169.6	0	0	0	0	0	137.6

APPENDIX H. CONT.

CB+ SA	CB- SA
36.16	964.8
73.6	812.8
3.2	777.6
129.6	995.2
0	2129.6
0	2705.6
0	1180.8
0	1126.4
0	1057.6

APPENDIX I. AUGUST 2001 - LIVE BIOMASS PER SPECIES (G/M^2) FROM 3 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES.

J+ SP	J- SP	J+ DS	J- DS	J+ SA	J- SA	J+ J	J- J
0	0	0	0	0	0	9.6	1499.2
0	0	0	0	0	0	19.2	2060.8
0	0	6.4	0	0	0	326.4	1444.8
0	174.4	19.2	163.2	0	0	14.4	1540.8
0	0	4.8	3.2	43.2	0	0	1140.8
6.4	54.4	11.2	0	284.8	4.8	102.4	870.4
0	14.4	6.4	9.6	0	0	88.0	310.4
9.6	68.8	33.6	20.8	0	0	30.4	646.4
0	152.0	99.2	105.6	0	0	12.8	601.6

HM+ SP	HM- SP	HM+ DS	HM- DS	HM+ SA	HM- SA
3.2	116.8	172.8	280.0	0	0
0	164.8	33.6	491.2	0	0
16.0	136.0	32.0	104.0	0	0
0	0	48.0	486.4	36.8	0
1.6	1.6	356.8	656.0	0	0
0	300.8	24.0	52.8	0	0
4.8	83.2	32.0	430.4	0	0
3.2	76.8	57.6	148.8	0	0
1.6	716.8	33.6	588.8	0	0

LM+ SA	LM- SA	LM+ SAL	LM- SAL	LM+ SP	LM- SP	LM+ DS	LM- DS
0	0	0	0	0	65.6	0	257.6
25.6	355.2	0	0	0	0	0	4.8
1.6	416.0	0	0	0	0	0	0
0	104.0	0	184.0	0	0	0	0
4.8	236.8	8	24.0	0	0	0	0
1.6	140.8	0	129.6	0	0	0	0
32.0	76.8	0	243.2	0	0	0	145.6
32.0	51.2	0	212.8	0	0	0	121.6
60.8	128.0	0	0	0	0	0	62.4

APPENDIX I. CONT.

CB+ SA	CB- SA
29.76	811.2
56.0	729.6
3.2	705.6
78.4	422.4
0	1609.6
0	2435.2
0	1060.8
0	1064.0
0	992.0

APPENDIX J. LIGHT INTENSITY (UE/(M2 X SEC)X 1000) MEASURED AT 5 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES.

J+	J-	HM+	HM-	LM+	LM-	CB-	CB+
0.35	0	0.150	0.080	0.620	0.420	0.450	0.060
0.52	0.050	0.128	0.165	0.130	0.160	0.600	0.310
0.35	0.250	0.295	0.700	0.700	0.350	0.650	0.220
0.72	0.055	0.235	0.220	0.570	0.270	0.790	0.470
0.43	0.020	0.220	0.150	0.080	0.150	0.880	0.330
0.21	0.050	0.130	0.060	0.830	0.720	0.820	0.230
0.42	0.010	0.120	0.030	0.840	0.740	0.850	0.330
0.30	0.010	0.190	0.030	0.970	0.790	0.930	0.270
0.21	0.015	0.200	0.055	0.960	0.880	0.910	0.500
0.38	0.040	0.220	0.025	0.970	0.830	0.920	0.680
0.53	0	0.420	0.130	0.370	0.200	0.460	0.290
0.52	0.040	0.300	0.130	0.220	0.080	0.460	0.150
0.675	0.025	0.190	0.025	0.400	0.120	0.460	0.130
0.61	0.020	0.280	0.150	0.430	0.230	0.460	0.130
0.61	0.050	0.115	0.105	0.360	0.270	0.460	0.130

APPENDIX K. AUGUST 2001 - SURFACE TEMPERATURES (C) MEASURED AT PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES. 5 ON- AND OFF-TRAIL SAMPLES WERE MEASURED AT EACH HM TRAIL. 3 ON- AND OFF-TRAIL SAMPLES WERE MEASURED AT EACH J, LM, AND CB TRAIL.

J+	J-	HM+	HM-	LM+	LM-	CB+	CB-
23.9	23.3	27.2	24.4	25.6	24.4	23.9	22.8
23.9	22.2	27.2	27.5	26.7	24.4	22.8	22.8
23.3	22.2	27.8	25.6	26.1	26.1	22.8	22.8
25.6	22.8	28.9	28.9	28.9	28.9	23.9	24.4
23.3	22.2	28.3	27.2	29.4	29.4	25.0	24.7
22.2	22.2	20.0	19.4	29.4	29.4	25.0	25.0
22.2	23.3	18.9	18.9	32.2	31.4	28.9	27.8
23.9	22.2	18.9	18.9	31.1	32.5	27.8	26.7
22.8	21.9	19.7	20.0	31.1	31.1	26.7	26.7
		20.6	20.0				
		20.8	20.3				
		20.0	20.3				
		20.3	20.0				
		20.0	20.0				
		20.0	20.0				

APPENDIX L. AUGUST 2001 - TEMPERATURES (C) FROM A DEPTH OF 5 CM MEASURED AT PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES. 5 ON- AND OFF-TRAIL SAMPLES WERE MEASURED AT EACH HM TRAIL. 3 ON- AND OFF-TRAIL SAMPLES WERE MEASURED AT EACH J, LM, AND CB TRAIL.

J+	J-	HM+	HM-	LM+	LM-	CB+	CB-
22.8	22.2	26.1	23.3	26.7	23.3	22.8	22.5
22.2	21.1	25.3	24.4	26.7	25.0	22.8	22.8
22.2	20.6	27.2	24.4	25.3	26.1	22.8	22.2
22.8	21.7	28.9	28.3	28.3	28.1	24.4	23.9
22.2	21.1	27.2	23.9	29.4	28.3	24.4	24.4
22.2	21.7	20.0	19.7	28.9	27.8	23.9	23.9
23.3	22.2	19.4	19.2	28.9	30.6	27.5	25.6
22.8	21.1	19.4	19.4	30.0	28.9	26.7	25.6
21.7	21.7	20.0	20.0	27.8	26.4	26.1	25.3
		20.6	20.6				
		21.1	20.6				
		16.1	20.0				
		20.0	20.6				
		20.6	20.6				
		20.0	19.4				

APPENDIX M. MARCH 2002 - SURFACE TEMPERATURES (C) MEASURED AT 5 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES.

J+	J-	HM+	HM-	LM+	LM-	CB+	CB-
15.0	13.0	13.8	13.5	14.0	14.2	13.8	13.5
13.0	12.0	13.0	12.5	14.0	13.8	14.4	15.0
12.0	11.8	13.5	12.9	14.0	14.4	14.4	15.0
12.5	12.0	13.6	13.8	13.0	13.0	14.5	15.0
13.0	13.2	13.2	13.8	13.6	13.2	14.4	14.0
17.5	14.0	15.0	14.8	20.1	21.0	14.6	15.0
15.0	15.0	17.0	14.4	19.0	19.2	15.0	14.4
14.0	14.0	15.0	14.2	17.2	19.0	14.0	14.0
14.2	14.5	16.0	14.0	18.0	18.6	13.8	14.2

15.5	13.8	15.2	14.0	18.0	19.0	14.2	14.2
14.0	13.0	14.8	14.2	18.0	19.0	18.0	16.5
12.2	12.2	14.0	14.0	18.0	17.5	19.0	16.2
12.0	12.0	14.0	12.5	17.0	17.0	18.5	16.8
14.4	12.9	12.0	13.0	20.0	18.2	18.0	16.0
11.2	10.1	12.4	13.0	19.0	19.8	17.5	16.2

APPENDIX N. MARCH 2002 - TEMPERATURES (C) FROM A DEPTH OF 5CM MEASURED AT 5 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES. SEE TABLE 3 FOR SYMBOL IDENTIFICATION.

J+	J-	HM+	HM-	LM+	LM-	CB+	CB-
14.8	12.0	13.8	12.2	14.2	14.0	13.8	12.8
12.2	9.4	13.0	12.2	13.8	13.8	15.0	14.5
12.8	10.1	12.9	11.9	15.0	13.2	15.0	14.0
11.8	11.2	13.6	13.0	13.0	11.0	14.5	13.0
13.5	11.0	14.0	11.2	13.0	12.5	14.5	14.0
14.0	12.0	14.2	13.0	21.8	18.5	15.0	12.9
14.4	11.0	15.0	12.2	19.0	17.0	14.6	12.6
12.8	10.5	14.0	10.9	18.2	18.0	13.8	12.0
14.5	9.5	15.8	12.5	18.2	17.0	13.8	13.0
12.5	10.8	14.4	13.4	18.0	16.5	14.2	13.5
14.0	13.8	14.4	11.9	18.0	17.0	18.4	16.2
12.2	12.8	14.0	12.0	16.0	14.5	18.8	16.0
12.0	10.2	11.5	9.9	16.5	17.0	18.5	16.2
14.4	12.0	12.5	13.0	17.5	17.0	17.8	14.5
11.2	8.9	11.8	11.8	19.2	17.0	17.5	16.2

APPENDIX O. RELATIVE ELEVATION MEASUREMENTS (M) TAKEN AT 5 PAIRED ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS IN 4 MARSH COMMUNITIES. 3 MEASUREMENTS WERE MADE AT EACH LOCATION: 1 IN THE CENTER OF THE TRAIL, AND 1 AT 10 CM ON EITHER SIDE OF THE MIDDLE MEASUREMENT. MEASUREMENTS IN OFF TRAIL AREAS WERE DONE AT DISTANCES OF 90CM, 100CM AND 110CM FROM ON-TRAIL AREAS. THE FIRST ROW IN EACH DATA SET IS THE CENTER MEASUREMENT, THE SECOND ROW IS +10CM AND THE THIRD ROW IS -10CM. NOTE: DUE TO DIFFICULTIES MEASURING ELEVATION IN CREEK BANK AREAS, FEWER MEASUREMENTS WERE MADE IN THAT COMMUNITY.

J+

1.541	1.546	1.544
1.632	1.642	1.645
1.670	1.606	1.616
1.589	1.593	1.603
1.629	1.607	1.621
1.525	1.503	1.515
1.599	1.601	1.587
1.552	1.546	1.547
1.520	1.525	1.521
1.547	1.530	1.532
1.572	1.560	1.581
1.560	1.562	1.568
1.556	1.552	1.562
1.610	1.608	1.609
1.596	1.593	1.590

J-

1.564	1.564	1.566
1.563	1.565	1.562
1.560	1.556	1.568
1.561	1.568	1.571
1.581	1.572	1.581
1.498	1.507	1.501
1.529	1.526	1.520
1.540	1.527	1.532
1.531	1.523	1.536
1.532	1.516	1.531
1.558	1.549	1.560
1.561	1.568	1.556
1.576	1.578	1.572
1.590	1.587	1.588
1.573	1.577	1.586

HM+

			HM-		
1.570	1.560	1.562			
1.572	1.568	1.574	1.582	1.581	1.573
1.602	1.590	1.588	1.581	1.576	1.580
1.600	1.598	1.589	1.602	1.600	1.595
1.619	1.616	1.616	1.589	1.590	1.591
1.547	1.516	1.552	1.600	1.609	1.604
1.495	1.486	1.496	1.427	1.410	1.437
1.550	1.551	1.554	1.500	1.490	1.501
1.562	1.562	1.576	1.554	1.550	1.542
1.520	1.506	1.488	1.536	1.525	1.520
1.325	1.306	1.307	1.442	1.427	1.431
			1.307	1.336	1.321

APPENDIX O. CONT.

1.341	1.321	1.320
1.330	1.323	1.325
1.275	1.268	1.256
1.347	1.335	1.342

LM+			LM-		
1.100	1.090	1.098	1.070	1.072	1.072
1.131	1.130	1.111	1.092	1.098	1.110
1.161	1.132	1.132	1.082	1.098	1.098
1.156	1.152	1.162	1.108	1.115	1.088
1.151	1.136	1.131	1.094	1.093	1.092
1.252	1.243	1.243	1.237	1.237	1.287
1.275	1.275	1.276	1.276	1.263	1.265
1.295	1.296	1.287	1.288	1.285	1.285
1.316	1.312	1.315	1.308	1.308	1.308
1.344	1.339	1.339	1.336	1.333	1.335
1.212	1.201	1.197	1.196	1.194	1.188
1.208	1.202	1.203	1.195	1.195	1.195
1.213	1.210	1.214	1.205	1.208	1.204
1.212	1.206	1.211	1.225	1.223	1.217
1.226	1.218	1.223	1.236	1.231	1.222

CB+			CB-		
1.346	1.323	1.336	1.263	1.256	1.246
1.352	1.346	1.345	1.282	1.270	1.320
1.365	1.342	1.339	1.306	1.341	1.300
1.342	1.351	1.323	1.35	1.386	1.335
1.392	1.387	1.387	1.365	1.362	1.398
1.225	1.221	1.220	1.217	1.210	1.206
1.315	1.319	1.322	1.341	1.300	1.322
1.400	1.408	1.415	1.382	1.386	1.384
1.602	1.53	1.562	1.455	1.468	1.446
1.723	.	.	1.544	.	.
1.410	1.421	1.412	1.515	1.495	1.501
1.714	1.692	1.714	1.591	1.589	1.587
2.083	2.035	.	1.711	.	.

APPENDIX P. SOIL SALT CONTENT (MG SALT/G SOIL) MEASURED AT 3 PAIRED ON- AND OFF-TRAIL LOCATIONS AT 4 DIFFERENT DEPTHS ON 3 TRAILS IN 4 MARSH COMMUNITIES. THE NUMBER IMMEDIATELY FOLLOWING THE COMMUNITY SYMBOL IS THE TRAIL NUMBER - EITHER 1, 2, OR 3. EACH OF THE 3 SAMPLE LOCATIONS ON A GIVEN TRAIL ARE DESIGNATED WITH THE LETTER A, B, OR C. THE NUMBERS 1-4 INDICATE THE DEPTH FROM WHICH THE SAMPLE WAS TAKEN. 1 = 0-1 CM. 2= 2-3 CM. 3= 4-5 CM. 4 = 5-10 CM. THE SALT CONTENT OF THE 10CM CORE WAS ARRIVED AT BY MULTIPLYING THE SALT CONTENT OF EACH INDIVIDUAL SECTION BY THE PERCENT OF THE ENTIRE CORE VOLUME OF THAT SECTION. THESE VALUES WERE THEN ADDED TOGETHER.

Sample	Salt Content	Salt content of 10cm core	Sample	Salt content	Salt content of 10cm core
j1a+1	10.0	51.0	j1a-1	60.0	46.5
j1a+2	65.0		j1a-2	40.0	
j1a+3	60.0		j1a-3	50.0	

j1a+4	50.0		j1a-4	45.0	
j1b+1	16.0	37.6	j1b-1	30.0	40.5
j1b+2	24.0		j1b-2	40.0	
j1b+3	36.0		j1b-3	35.0	
j1b+4	48.0		j1b-4	45.0	
j1c+1	30.0	42.0	j1c-1	30.0	46.0
j1c+2	30.0		j1c-2	50.0	
j1c+3	40.0		j1c-3	40.0	
j1c+4	50.0		j1c-4	50.0	
j2a+1	55.0	63.5	j2a-1	60.0	70.0
j2a+2	50.0		j2a-2	70.0	
j2a+3	90.0		j2a-3	75.0	
j2a+4	60.0		j2a-4	70.0	
j2b+1	40.0	69.0	j2b-1	40.0	42.5
j2b+2	65.0		j2b-2	40.0	
j2b+3	85.0		j2b-3	40.0	
j2b+4	70.0		j2b-4	45.0	
j2c+1	55.0	76.0	j2c-1	50.0	36.0
j2c+2	70.0		j2c-2	50.0	
j2c+3	70.0		j2c-3	50.0	
j2c+4	85.0		j2c-4	22.0	
j3a+1	40.0	39.0	j3a-1	25.0	38.5
j3a+2	40.0		j3a-2	35.0	
j3a+3	35.0		j3a-3	45.0	
j3a+4	40.0		j3a-4	40.0	

APPENDIX P. CONT.

Sample	Salt Content	Salt content of 10cm core	Sample	Salt content	Salt content of 10cm core
j3b+1	25.0	32.0	j3b-1	50.0	60.0
j3b+2	55.0		j3b-2	65.0	
j3b+3	30.0		j3b-3	60.0	
j3b+4	25.0		j3b-4	60.0	
j3c+1	60.0	35.0	j3c-1	25.0	48.0
j3c+2	55.0		j3c-2	40.0	
j3c+3	40.0		j3c-3	50.0	
j3c+4	20.0		j3c-4	55.0	
hm1a+1	60.0	22.0	hm1a-1	65.0	36.5
hm1a+2	40.0		hm1a-2	60.0	
hm1a+3	20.0		hm1a-3	50.0	
hm1a+4	8.0		hm1a-4	16.0	
hm1b+1	35.0	17.5	hm1b-1	45.0	23.5
hm1b+2	25.0		hm1b-2	30.0	
hm1b+3	20.0		hm1b-3	25.0	
hm1b+4	10.0		hm1b-4	16.0	
hm1c+1	10.0	7.4	hm1c-1	10.0	7.0
hm1c+2	12.0		hm1c-2	10.0	

hm1c+3	10.0		hm1c-3	10.0	
hm1c+4	4.0		hm1c-4	4.0	
hm2a+1	20.0	34.0	hm2a-1	10.0	21.0
hm2a+2	50.0		hm2a-2	10.0	
hm2a+3	35.0		hm2a-3	15.0	
hm2a+4	30.0		hm2a-4	30.0	
hm2b+1	10.0	21.0	hm2b-1	20.0	37.0
hm2b+2	25.0		hm2b-2	35.0	
hm2b+3	25.0		hm2b-3	40.0	
hm2b+4	20.0		hm2b-4	40.0	
hm2c+1	25.0	26.0	hm2c-1	25.0	29.0
hm2c+2	40.0		hm2c-2	35.0	
hm2c+3	40.0		hm2c-3	35.0	
hm2c+4	15.0		hm2c-4	25.0	
hm3a+1	25.0	59.0	hm3a-1	32.5	54.75
hm3a+2	25.0		hm3a-2	40.0	
hm3a+3	70.0		hm3a-3	55.0	
hm3a+4	75.0		hm3a-4	65.0	
hm3b+1	70.0	62.0	hm3b-1	45.0	73.0
hm3b+2	70.0		hm3b-2	65.0	
hm3b+3	55.0		hm3b-3	90.0	
hm3b+4	60.0		hm3b-4	75.0	
hm3c+1	75.0	76.5	hm3c-1	20.0	51.5
hm3c+2	70.0		hm3c-2	60.0	
hm3c+3	75.0		hm3c-3	50.0	
Hm3c+4	80.0		hm3c-4	55.0	
lm1a+1	15.0	36.5	lm1a-1	120.0	110
lm1a+2	10.0		lm1a-2	120.0	

APPENDIX P. CONT.

Sample	Salt Content	Salt content of 10cm core	Sample	Salt content	Salt content of 10cm core
lm1a+3	25.0		lm1a-3	70.0	
lm1a+4	56.0		lm1a-4	120.0	
lm1b+1	167.3	116.2	lm1b-1	70.0	131
lm1b+2	110.0		lm1b-2	120.0	
lm1b+3	125.0		lm1b-3	150.0	
lm1b+4	105.0		lm1b-4	140.0	
lm1c+1	80.0	54.0	lm1c-1	120.0	92.0
lm1c+2	100.0		lm1c-2	115.0	
lm1c+3	55.0		lm1c-3	110.0	
lm1c+4	30.0		lm1c-4	70.0	
lm2a+1	25.0	15.9	lm2a-1	10.0	11.0
lm2a+2	24.0		lm2a-2	8.0	
lm2a+3	8.0		lm2a-3	12.0	
lm2a+4	14.0		lm2a-4	12.0	
lm2b+1	20.0	15.8	lm2b-1	15.0	19.1
lm2b+2	16.0		lm2b-2	18.0	
lm2b+3	18.0		lm2b-3	20.0	
lm2b+4	14.0		lm2b-4	20.0	

lm2c+1	50.0	21.6	lm2c-1	50.0	30.5
lm2c+2	28.0		lm2c-2	40.0	
lm2c+3	30.0		lm2c-3	25.0	
lm2c+4	10.0		lm2c-4	25.0	
lm3a+1	70.0	97.0	lm3a-1	60.0	121.0
lm3a+2	90.0		lm3a-2	50.0	
lm3a+3	100.0		lm3a-3	100.0	
lm3a+4	104.0		lm3a-4	170.0	
lm3b+1	85.0	113.5	lm3b-1	70.0	93.0
lm3b+2	100.0		lm3b-2	80.0	
lm3b+3	100.0		lm3b-3	100.0	
lm3b+4	130.0		lm3b-4	100.0	
lm3c+1	75.0	87.5	lm3c-1	65.0	78.5
lm3c+2	75.0		lm3c-2	80.0	
lm3c+3	75.0		lm3c-3	70.0	
lm3c+4	100.0		lm3c-4	84.0	
cb1a+1	30.0	44.0	cb1a-1	30.0	32.0
cb1a+2	70.0		cb1a-2	40.0	
cb1a+3	45.0		cb1a-3	35.0	
cb1a+4	36.0		cb1a-4	28.0	
cb1b+1	50.0	37.0	cb1b-1	45.0	45.5
cb1b+2	45.0		cb1b-2	60.0	
cb1b+3	40.0		cb1b-3	45.0	
cb1b+4	30.0		cb1b-4	40.0	
cb1c+1	25.0	15.5	cb1c-1	35.0	43.5
cb1c+2	30.0		cb1c-2	40.0	
cb1c+3	25.0		cb1c-3	35.0	
cb1c+4	4.0		cb1c-4	50.0	

APPENDIX P. CONT.

Sample	Salt Content	Salt content of 10cm core	Sample	Salt content	Salt content of 10cm core
cb2a+1	60.0	59.0	cb2a-1	30.0	72.0
cb2a+2	70.0		cb2a-2	70.0	
cb2a+3	75.0		cb2a-3	75.0	
cb2a+4	48.0		cb2a-4	80.0	
cb2b+1	75.0	56.0	cb2b-1	50.0	54.0
cb2b+2	80.0		cb2b-2	60.0	
cb2b+3	50.0		cb2b-3	60.0	
cb2b+4	45.0		cb2b-4	50.0	
cb2c+1	45.0	37.5	cb2c-1	40.0	39.3
cb2c+2	35.0		cb2c-2	35.0	
cb2c+3	40.0		cb2c-3	60.0	
cb2c+4	36.0		cb2c-4	32.5	
cb3a+1	25.0	32.5	cb3a-1	30.0	31.0
cb3a+2	20.0		cb3a-2	15.0	
cb3a+3	25.0		cb3a-3	25.0	
cb3a+4	42.0		cb3a-4	40.0	
cb3b+1	25.0	25.0	cb3b-1	25.0	23.5
cb3b+2	30.0		cb3b-2	25.0	

cb3b+3	20.0		cb3b-3	20.0	
cb3b+4	25.0		cb3b-4	24.0	
cb3c+1	25.0	23.0	cb3c-1	25.0	34.5
cb3c+2	30.0		cb3c-2	30.0	
cb3c+3	10.0		cb3c-3	30.0	
cb3c+4	25.0		cb3c-4	40.0	

APPENDIX Q. PERCENT ORGANIC CONTENT MEASURED AT 3 PAIRED ON- AND OFF-TRAIL LOCATIONS AT 4 DIFFERENT DEPTHS ON 3 TRAILS IN 4 MARSH COMMUNITIES. THE NUMBER IMMEDIATELY FOLLOWING THE COMMUNITY SYMBOL IS THE TRAIL NUMBER - EITHER 1, 2, OR 3. EACH OF THE 3 SAMPLE LOCATIONS ON A GIVEN TRAIL ARE DESIGNATED WITH THE LETTER A, B, OR C. THE NUMBERS 1-4 INDICATE THE DEPTH FROM WHICH THE SAMPLE WAS TAKEN. 1 = 0-1 CM. 2= 2-3 CM. 3= 4-5 CM. 4 = 5-10 CM. THE PERCENT ORGANIC CONTENT OF THE 10CM CORE WAS ARRIVED AT BY MULTIPLYING THE ORGANIC CONTENT OF EACH INDIVIDUAL SECTION BY THE PERCENT OF THE ENTIRE CORE VOLUME OF THAT SECTION. THESE VALUES WERE THEN ADDED TOGETHER.

	%	% organic		%	% organic

Sample	organic	10cm core	Sample	organic	10cm core
j1a+1	67.1	58.0	j1a-1	26.4	26.6
j1a+2	56.8		j1a-2	43.3	
j1a+3	54.8		j1a-3	24.3	
j1a+4	58.0		j1a-4	20.9	
j1b+1	67.0	58.0	j1b-1	78.7	55.4
j1b+2	56.8		j1b-2	82.7	
j1b+3	54.8		j1b-3	76.9	
j1b+4	58.0		j1b-4	31.3	
j1c+1	68.2	58.2	j1c-1	56.3	62.9
j1c+2	66.3		j1c-2	57.6	
j1c+3	66.2		j1c-3	52.9	
j1c+4	49.8		j1c-4	70.4	
j2a+1	60.1	58.5	j2a-1	33.3	33.2
j2a+2	66.4		j2a-2	32.4	
j2a+3	65.2		j2a-3	30.6	
j2a+4	52.3		j2a-4	34.5	
J2b+1	55.0	48.6	j2b-1	74.0	66.0
j2b+2	55.6		j2b-2	71.9	
J2b+3	50.0		j2b-3	66.3	
J2b+4	44.0		j2b-4	62.0	
j2c+1	50.5	49.0	j2c-1	28.1	28.1
j2c+2	50.4		j2c-2	30.2	
j2c+3	57.6		j2c-3	30.3	
j2c+4	44.7		j2c-4	26.3	
j3a+1	78.6	74.2	j3a-1	71.7	71.8
j3a+2	82.5		j3a-2	76.6	
j3a+3	76.0		j3a-3	77.0	
j3a+4	69.2		j3a-4	67.9	
j3b+1	80.2	57.5	j3b-1	36.9	35.5
j3b+2	77.1		j3b-2	35.8	
j3b+3	66.5		j3b-3	41.4	
j3b+4	41.4		j3b-4	32.7	

APPENDIX Q. CONT.

Sample	% organic	% organic 10cm core	Sample	% organic	% organic 10cm core
j3c+1	80.1	54.3	j3c-1	69.0	64.0
j3c+2	75.5		j3c-2	72.5	
j3c+3	72.6		j3c-3	70.1	
j3c+4	33.4		j3c-4	57.1	
hm1a+1	53.6	21.7	hm1a-1	37.8	26.2
hm1a+2	37.4		hm1a-2	39.9	
hm1a+3	21.6		hm1a-3	34.2	
hm1a+4	9.1		hm1a-4	15.3	
hm1b+1	17.8	11.4	hm1b-1	18.8	15.9
hm1b+2	19.7		hm1b-2	21.2	
hm1b+3	13.1		hm1b-3	18.2	
hm1b+4	6.1		hm1b-4	12.3	
hm1c+1	6.6	3.2	hm1c-1	7.4	8.7
hm1c+2	3.9		hm1c-2	12.0	

hm1c+3	2.8		hm1c-3	12.9	
hm1c+4	2.4		hm1c-4	5.9	
hm2a+1	78.4	60.4	hm2a-1	86.9	76.4
hm2a+2	77.4		hm2a-2	86.4	
hm2a+3	77.8		hm2a-3	86.8	
hm2a+4	43.0		hm2a-4	66.2	
hm2b+1	79.9	57.4	hm2b-1	86.5	77.3
hm2b+2	72.3		hm2b-2	86.6	
hm2b+3	74.4		hm2b-3	84.7	
hm2b+4	40.2		hm2b-4	68.7	
hm2c+1	88.2	50.3	hm2c-1	78.7	55.4
hm2c+2	74.1		hm2c-2	82.7	
hm2c+3	69.8		hm2c-3	76.9	
hm2c+4	25.4		hm2c-4	31.3	
hm3a+1	78.2	67.2	hm3a-1	82.2	72.0
hm3a+2	82.1		hm3a-2	81.1	
hm3a+3	69.9		hm3a-3	80.4	
hm3a+4	57.9		hm3a-4	63.0	
hm3b+1	75.3	61.7	hm3b-1	78.2	76.5
hm3b+2	72.6		hm3b-2	84.0	
hm3b+3	70.5		hm3b-3	78.0	
hm3b+4	51.1		hm3b-4	72.5	
hm3c+1	74.9	63.1	hm3c-1	81.5	80.9
hm3c+2	66.2		hm3c-2	85.8	
hm3c+3	60.5		hm3c-3	86.2	
hm3c+4	60.5		hm3c-4	76.6	
lm1a+1	4.1	14.4	lm1a-1	60.8	58.4
lm1a+2	7.2		lm1a-2	57.4	
lm1a+3	11.6		lm1a-3	61.8	
lm1a+4	20.5		lm1a-4	57.1	
lm1b+1	56.4	46.1	lm1b-1	51.8	52.8
lm1b+2	58.0		lm1b-2	48.0	
lm1b+3	56.4		lm1b-3	54.0	
lm1b+4	35.2		lm1b-4	54.5	
lm1c+1	42.5	21.7	lm1c-1	58.4	42.0

APPENDIX Q. CONT.

Sample	% organic	% organic 10cm core	Sample	% organic	% organic 10cm core
lm1c+2	49.1		lm1c-2	50.9	
lm1c+3	24.0		lm1c-3	24.3	
lm1c+4	5.7		lm1c-4	42.2	
lm2a+1	3.4	3.2	lm2a-1	2.1	2.7
lm2a+2	3.8		lm2a-2	2.6	
lm2a+3	2.6		lm2a-3	3.0	
lm2a+4	3.1		lm2a-4	2.7	
lm2b+1	4.8	3.7	lm2b-1	5.1	4.0
lm2b+2	4.6		lm2b-2	5.1	
lm2b+3	3.6		lm2b-3	4.9	
lm2b+4	3.2		lm2b-4	3.0	
lm2c+1	8.3	6.5	lm2c-1	6.8	5.3
lm2c+2	7.5		lm2c-2	7.6	
lm2c+3	7.2		lm2c-3	4.9	
lm2c+4	5.5		lm2c-4	4.3	

lm3a+1	13.9	18.4	lm3a-1	15.5	19.7
lm3a+2	22.6		lm3a-2	12.0	
lm3a+3	17.4		lm3a-3	17.6	
lm3a+4	18.1		lm3a-4	24.4	
lm3b+1	21.8	23.5	lm3b-1	39.5	32.4
lm3b+2	18.3		lm3b-2	40.6	
lm3b+3	16.7		lm3b-3	30.3	
lm3b+4	28.6		lm3b-4	28.6	
lm3c+1	26.8	26.7	lm3c-1	17.9	25.4
lm3c+2	27.3		lm3c-2	27.1	
lm3c+3	29.2		lm3c-3	27.0	
lm3c+4	25.4		lm3c-4	25.6	
cb1a+1	32.4	30.1	cb1a-1	27.3	29.7
cb1a+2	31.9		cb1a-2	22.8	
cb1a+3	39.2		cb1a-3	34.9	
cb1a+4	25.3		cb1a-4	30.9	
cb1b+1	35.2	40.4	cb1b-1	26.4	26.6
cb1b+2	46.7		cb1b-2	43.3	
cb1b+3	53.6		cb1b-3	24.3	
cb1b+4	33.8		cb1b-4	20.9	
cb1c+1	12.3	8.3	cb1c-1	24.5	19.8
cb1c+2	13.3		cb1c-2	21.7	
cb1c+3	10.3		cb1c-3	20.5	
cb1c+4	4.8		cb1c-4	17.8	
cb2a+1	16.5	22.1	cb2a-1	14.6	17.8
cb2a+2	28.6		cb2a-2	19.0	
cb2a+3	31.0		cb2a-3	14.6	
cb2a+4	17.0		cb2a-4	19.2	
cb2b+1	22.2	16.8	cb2b-1	16.4	18.4
cb2b+2	17.9		cb2b-2	17.9	
cb2b+3	14.7		cb2b-3	20.5	
cb2b+4	16.2		cb2b-4	18.1	
cb2c+1	13.0	11.8	cb2c-1	13.0	16.9
cb2c+2	12.1		cb2c-2	12.6	

APPENDIX Q. CONT.

Sample	% organic	% organic 10cm core	Sample	% organic	% organic 10cm core
cb2c+3	13.4		cb2c-3	13.1	
cb2c+4	10.7		cb2c-4	20.8	
cb3a+1	5.8	7.8	cb3a-1	5.7	7.6
cb3a+2	5.4		cb3a-2	6.5	
cb3a+3	6.4		cb3a-3	5.4	
cb3a+4	9.8		cb3a-4	9.2	
cb3b+1	5.5	6.3	cb3b-1	6.3	5.7
cb3b+2	6.1		cb3b-2	5.8	
cb3b+3	6.1		cb3b-3	5.8	
cb3b+4	6.7		cb3b-4	5.5	
cb3c+1	5.8	5.9	cb3c-1	6.0	7.5
cb3c+2	5.7		cb3c-2	6.5	
cb3c+3	6.0		cb3c-3	8.8	
cb3c+4	5.9		cb3c-4	7.8	

APPENDIX R. SOIL BULK DENSITY (G/M^3) MEASURED AT 3 PAIRED ON- AND OFF-TRAIL LOCATIONS AT 4 DIFFERENT DEPTHS ON 3 TRAILS IN 4 MARSH COMMUNITIES. THE NUMBER IMMEDIATELY FOLLOWING THE COMMUNITY SYMBOL IS THE TRAIL NUMBER - EITHER 1, 2, OR 3. EACH OF THE 3 SAMPLE LOCATIONS ON A GIVEN TRAIL ARE DESIGNATED

WITH THE LETTER A, B, OR C. THE NUMBERS 1-4 INDICATE THE DEPTH FROM WHICH THE SAMPLE WAS TAKEN. 1 = 0-1 CM. 2= 2-3 CM. 3= 4-5 CM. 4 = 5-10 CM. THE PERCENT ORGANIC CONTENT OF THE 10CM CORE WAS ARRIVED AT BY MULTIPLYING THE BULK DENSITY OF EACH INDIVIDUAL SECTION BY THE PERCENT OF THE ENTIRE CORE VOLUME

Sample	Density (g/cm^3)	10 cm Core Density (g/cm^2)	Sample	Density (g/cm^3)	10 cm Core Density (g/cm^3)
j1a+1	0.13671	0.15913	j1a-1	0.14880	0.15262
j1a+2	0.20321		j1a-2	0.13857	
j1a+3	0.14973		j1a-3	0.17438	
j1a+4	0.14973		j1a-4	0.15029	
j1b+1	0.08556	0.17075	j1b-1	0.11625	0.14973
j1b+2	0.13811		j1b-2	0.13532	
j1b+3	0.19902		j1b-3	0.14648	
j1b+4	0.18954		j1b-4	0.16350	
j1c+1	0.15066	0.14731	j1c-1	0.12276	0.16136
j1c+2	0.09068		j1c-2	0.14508	
j1c+3	0.09812		j1c-3	0.15206	
j1c+4	0.18898		j1c-4	0.17931	
j2a+1	0.12741	0.16294	j2a-1	0.19158	0.20405
j2a+2	0.07301		j2a-2	0.16694	
j2a+3	0.13160		j2a-3	0.21902	
j2a+4	0.21855		j2a-4	0.21539	
j2b+1	0.23064	0.21716	j2b-1	0.15066	0.13346
j2b+2	0.23994		j2b-2	0.11207	
j2b+3	0.25622		j2b-3	0.11393	
j2b+4	0.18972		j2b-4	0.14638	
j2c+1	0.19251	0.13457	j2c-1	0.34597	0.28356
j2c+2	0.11951		j2c-2	0.23018	
j2c+3	0.11997		j2c-3	0.23157	

APPENDIX R. CONT.

	Density	10 cm Core Density		Density	10 cm Core Density

Sample	(g/cm^3)	(g/cm^3)	Sample	(g/cm^3)	(g/cm^3)
j2c+4	0.13485		j2c-4	0.31323	
j3a+1	0.09579	0.12871	j3a-1	0.11253	0.10732
j3a+2	0.09719		j3a-2	0.07952	
j3a+3	0.12741		j3a-3	0.11160	
j3a+4	0.14843		j3a-4	0.11569	
j3b+1	0.10788	0.24869	j3b-1	0.24180	0.22162
j3b+2	0.14555		j3b-2	0.19670	
j3b+3	0.19391		j3b-3	0.19856	
j3b+4	0.34001		j3b-4	0.23678	
j3c+1	0.10230	0.24422	j3c-1	0.11625	0.14787
j3c+2	0.12555		j3c-2	0.08277	
j3c+3	0.19205		j3c-3	0.11114	
j3c+4	0.34094		j3c-4	0.19493	
hm1a+1	0.19065	0.55661	hm1a-1	0.13206	0.42809
hm1a+2	0.19809		hm1a-2	0.10602	
hm1a+3	0.48872		hm1a-3	0.19949	
hm1a+4	0.80037		hm1a-4	0.70756	
hm1b+1	0.57010	0.87980	hm1b-1	0.30040	0.70709
hm1b+2	0.32644		hm1b-2	0.52360	
hm1b+3	0.81748		hm1b-3	0.51104	
hm1b+4	1.18800		hm1b-4	0.94025	
hm1c+1	0.71053	1.63218	hm1c-1	0.85934	0.95671
hm1c+2	1.63404		hm1c-2	0.62544	
hm1c+3	1.71495		hm1c-3	0.59568	
hm1c+4	1.78266		hm1c-4	1.25310	
hm2a+1	0.06696	0.15550	hm2a-1	0.10044	0.10165
hm2a+2	0.06882		hm2a-2	0.06092	
hm2a+3	0.09672		hm2a-3	0.08835	
hm2a+4	0.23139		hm2a-4	0.12351	
hm2b+1	0.08742	0.15401	hm2b-1	0.10602	0.13597
hm2b+2	0.09021		hm2b-2	0.12881	
hm2b+3	0.11346		hm2b-3	0.14973	
hm2b+4	0.20907		hm2b-4	0.13932	
hm2c+1	0.06975	0.25947	hm2c-1	0.09114	0.15317
hm2c+2	0.11439		hm2c-2	0.08510	
hm2c+3	0.11904		hm2c-3	0.10742	
hm2c+4	0.41163		hm2c-4	0.21111	
hm3a+1	0.09579	0.14266	hm3a-1	0.07626	0.11709
hm3a+2	0.08882		hm3a-2	0.08045	

APPENDIX R. CONT.

	10 cm Density	Core Density		10 cm Density	Core Density

Sample	(g/cm^3)	(g/cm^3)	Sample	(g/cm^3)	(g/cm^3)
hm3a+3	0.15206		hm3a-3	0.09254	
hm3a+4	0.16982		hm3a-4	0.14973	
hm3b+1	0.13113	0.17168	hm3b-1	0.13485	0.11002
hm3b+2	0.14508		hm3b-2	0.08789	
hm3b+3	0.18926		hm3b-3	0.10044	
hm3b+4	0.18340		hm3b-4	0.11774	
hm3c+1	0.11346	0.15485	hm3c-1	0.04929	0.10704
hm3c+2	0.12788		hm3c-2	0.14276	
hm3c+3	0.15159		hm3c-3	0.12509	
hm3c+4	0.17522		hm3c-4	0.09709	
lm1a+1	1.11881	0.62953	lm1a-1	0.17949	0.12444
lm1a+2	0.92909		lm1a-2	0.10137	
lm1a+3	0.61149		lm1a-3	0.12648	
lm1a+4	0.41907		lm1a-4	0.12183	
lm1b+1	0.16182	0.18061	lm1b-1	0.07440	0.14583
lm1b+2	0.11579		lm1b-2	0.09068	
lm1b+3	0.12602		lm1b-3	0.11486	
lm1b+4	0.23213		lm1b-4	0.19456	
lm1c+1	0.19065	0.50658	lm1c-1	0.14787	0.20749
lm1c+2	0.15438		lm1c-2	0.11160	
lm1c+3	0.14694		lm1c-3	0.16089	
lm1c+4	0.85450		lm1c-4	0.27640	
lm2a+1	1.02860	1.33150	lm2a-1	2.14648	1.37903
lm2a+2	1.12904		lm2a-2	1.33318	
lm2a+3	1.72983		lm2a-3	1.37642	
lm2a+4	1.31374		lm2a-4	1.24492	
lm2b+1	1.27319	1.27821	lm2b-1	0.79516	1.20233
lm2b+2	1.31365		lm2b-2	1.14485	
lm2b+3	1.12439		lm2b-3	1.01558	
lm2b+4	1.32658		lm2b-4	1.38145	
lm2c+1	0.79981	1.07854	lm2c-1	0.70681	1.13211
lm2c+2	0.84027		lm2c-2	0.89561	
lm2c+3	0.81004		lm2c-3	0.95792	
lm2c+4	1.33699		lm2c-4	1.38145	
lm3a+1	0.54592	0.36968	lm3a-1	0.40549	0.37126
lm3a+2	0.35713		lm3a-2	0.74355	
lm3a+3	0.47756		lm3a-3	0.34922	
lm3a+4	0.29630		lm3a-4	0.22432	
lm3b+1	0.47059	0.37145	lm3b-1	0.51430	0.30728

APPENDIX R. CONT.

	10 cm Density	Core Density		10 cm Density	Core Density

Sample	(g/cm^3)	(g/cm^3)	Sample	(g/cm^3)	(g/cm^3)
lm3b+2	0.58591		lm3b-2	0.34271	
lm3b+3	0.43385		lm3b-3	0.27854	
lm3b+4	0.24087		lm3b-4	0.26319	
lm3c+1	0.44362	0.40781	lm3c-1	0.43711	0.38596
lm3c+2	0.39619		lm3c-2	0.51197	
lm3c+3	0.38642		lm3c-3	0.45617	
lm3c+4	0.41386		lm3c-4	0.29723	
cb1a+1	0.12090	0.20860	cb1a-1	0.50035	0.34020
cb1a+2	0.14136		cb1a-2	0.36736	
cb1a+3	0.18182		cb1a-3	0.20367	
cb1a+4	0.26375		cb1a-4	0.35192	
cb1b+1	0.16275	0.17150	cb1b-1	0.33295	0.34048
cb1b+2	0.08975		cb1b-2	0.35573	
cb1b+3	0.11997		cb1b-3	0.23715	
cb1b+4	0.22655		cb1b-4	0.37721	
cb1c+1	0.52267	0.83506	cb1c-1	0.28365	0.30960
cb1c+2	0.56731		cb1c-2	0.25110	
cb1c+3	0.69612		cb1c-3	0.28505	
cb1c+4	1.06022		cb1c-4	0.34801	
cb2a+1	0.41851	0.33685	cb2a-1	0.60358	0.30877
cb2a+2	0.21530		cb2a-2	0.34876	
cb2a+3	0.20507		cb2a-3	0.26366	
cb2a+4	0.42186		cb2a-4	0.25185	
cb2b+1	0.38968	0.32569	cb2b-1	0.39805	0.33741
cb2b+2	0.30691		cb2b-2	0.26273	
cb2b+3	0.34178		cb2b-3	0.40363	
cb2b+4	0.31397		cb2b-4	0.32867	
cb2c+1	0.52174	0.41451	cb2c-1	0.65938	0.42297
cb2c+2	0.28645		cb2c-2	0.42130	
cb2c+3	0.41944		cb2c-3	0.38038	
cb2c+4	0.44232		cb2c-4	0.39340	
cb3a+1	0.82120	0.71063	cb3a-1	0.58684	0.63130
cb3a+2	0.90909		cb3a-2	0.70728	
cb3a+3	0.73750		cb3a-3	0.58684	
cb3a+4	0.59837		cb3a-4	0.62757	
cb3b+1	0.93467	0.71779	cb3b-1	0.74959	0.69444
cb3b+2	0.90305		cb3b-2	0.68310	
cb3b+3	0.72402		cb3b-3	0.70216	
cb3b+4	0.59781		cb3b-4	0.68486	

APPENDIX R. CONT.

		10 cm			10 cm
	Density	Core Density		Density	Core Density

Sample	(g/cm^3)	(g/cm^3)	Sample	(g/cm^3)	(g/cm^3)
cb3c+1	0.80167	0.86017	cb3c-1	1.06115	0.58070
cb3c+2	0.90723		cb3c-2	0.51848	
cb3c+3	0.82539		cb3c-3	0.39665	
cb3c+4	0.86696		cb3c-4	0.58312	

APPENDIX S. *ILLYANASSA OBSOLETA* ABUNDANCE. NUMBER OF SNAILS SAMPLED IN FIVE 0.0625 M^2 QUADRATS PER TRAIL ON 19 TRAILS IN CREEK BANK AND LOW MARSH COMMUNITIES. SNAILS WERE SAMPLED ON TRAILS, AND AT DISTANCES OF 1 AND 2 M PERPENDICULAR TO ON-TRAIL SAMPLED SITES. THE FIRST NUMBER LISTED FOR EACH TRAIL IS THE NUMBER OF SNAILS FOUND AT THE FURTHEST DISTANCE FROM A CREEK BANK. THE LAST NUMBER LISTED FOR EACH TRAIL IS THE NUMBER OF SNAILS FOUND AT THE CREEK BANK. THE MIDDLE THREE NUMBERS ARE THE NUMBERS OF SNAILS FOUND AT 3 RANDOMLY SELECTED LOCATIONS BETWEEN THE FURTHEST SNAILS AND THE CREEK BANK.

Trail#	# Snails ontrail	# Snails 1m off-trail	#Snails 2m off-trail
1	5	0	0
	0	1	0
	0	1	2
	0	0	0
	0	0	0
2	1	0	0
	1	0	0
	0	0	0
	0	0	1
	0	0	0
3	2	0	0
	3	0	0
	8	2	1
	34	35	15
	19	4	27
4	8	0	0
	0	0	0
	4	3	8
	2	1	4
	4	4	2
5	1	0	0

	0	0	0
	2	0	0
	10	0	0
	20	0	0
6	2	0	0
	0	0	0
	1	4	4
	0	0	0
	0	0	0
7	1	0	0
	0	0	0
	0	0	0

APPENDIX S. CONT.

Trail#	# Snails ontrail	# Snails 1m off-trail	#Snails 2m off-trail
	0	0	0
	0	0	0
8	4	0	0
	11	0	0
	81	0	0
	133	0	0
	47	0	0
9	2	0	0
	9	0	0
	32	0	0
	17	0	10
	72	0	5
10	2	0	0
	0	0	0
	5	2	0
	7	0	1
	6	1	13
11	1	1	1
	0	0	0
	0	0	3
	28	1	1
	0	2	0
12	1	0	0
	1	0	0
	2	0	0
	3	2	0
	11	0	0
13	4	0	0
	0	0	0
	0	0	0
	0	0	0
	0	0	0
14	2	0	0
	1	0	0
	0	0	0
	16	0	0

	18	0	1
15	5	0	0
	13	2	0
	8	0	0
	5	0	0
	0	0	0
16	1	0	0
	0	0	0
	0	0	0
	0	0	0
	0	0	0

APPENDIX S. CONT.

Trail#	# Snails ontrail	# Snails 1m off-trail	#Snails 2m off-trail
17	1	0	0
	0	0	3
	0	0	0
	2	0	0
	24	1	0
18	1	0	0
	3	0	0
	0	0	0
	5	0	0
	1	0	0
19	21	0	0
	0	0	0
	0	0	0
	10	0	3
	2	0	0

APPENDIX T. CHLOROPHYLL *A* CONCENTRATION (MG/M^2)SAMPLED AT 9 ON- AND OFF-TRAIL LOCATIONS ON 3 STUDY TRAILS (DISIGNATED BY THE LETTERS A - I) IN 4 MARSH COMMUNITIES.

Sample	Concentration	Sample	Concentration
J1A+	2.0314	J1A-	1.1216
J1B+	1.4872	J1B-	2.2329
J1C+	3.3691	J1C-	1.7967
J1D+	1.5869	j1d-	1.1341
J1E+	0.2285	J1E-	2.0397
J1F+	3.9050	J1F-	0.1932
J1G+	2.9059	J1G-	0.9949
J1H+	1.8673	J1H-	1.2878
J1I+	2.8706	J1I-	1.3688
J2A+	3.3673	J2A-	3.8466
J2B+	10.5562	J2B-	3.9076
J2C+	41.9473	J2C-	3.1105
J2D+	4.5460	J2D-	6.3024
J2E+	5.8788	J2E-	1.8729
J2F+	24.3410	J2F-	0.0000
J2G+	2.2185	J2G-	0.0000
J2H+	15.3795	J2H-	3.5187
J2I+	0.0000	J2I-	9.0920
J3A+	6.3606	J3A-	2.5394
J3B+	0.0000	J3B-	0.0000
J3C+	0.2268	J3C-	0.0000
J3D+	0.0000	J3D-	0.0000

J3E+	3.6176	J3E-	0.0000
J3F+	0.0000	J3F-	0.0000
J3G+	14.7223	J3G-	0.8536
J3H+	0.8472	J3H-	1.8308
J3I+	2.7158	J3I-	1.5553
HM1A+	2.2050	HM1A-	2.3014
HM1B+	0.0000	HM1B-	0.0967
HM1C-	2.5939	HM1C+	5.5955
HM1E+	0.0946	HM1E-	5.7447
HM1F+	0.0000	HM1F-	0.0652
HM1G+	4.0068	HM1G-	1.1162
HM1H+	8.6969	HM1H-	0.0126
HM1i+	3.9601	HM1I-	0.1177
HM2A+	3.0946	HM2A-	0.2084
HM2B+	0.0000	HM2B-	0.0000
HM3C+	1.1209	HM2C-	2.8776
HM2D+	0.7253	HM2D-	0.0000
HM2E+	5.7085	HM2E-	1.0656
HM2F+	2.2949	HM2F-	0.0000
HM2G+	5.0981	HM2G-	11.2447

APPENDIX T. CONT.

Sample	Concentration	Sample	Concentration
HM2H+	1.7206	HM2H-	0.0000
HM2I+	0.0000	HM2I-	0.1595
HM3A+	6.5890	HM3A-	0.0000
HM3B+	3.4689	HM3B-	0.7593
HM3C+	0.0000	HM3C-	0.0000
HM3D+	2.6246	HM3D-	3.6454
HM3E+	8.8520	HM3E-	0.0000
HM3F+	1.9801	HM3F-	1.6377
HM3G+	16.0047	HM3G-	0.4381
HM3H+	0.0000	HM3H-	0.0000
HM3I+	0.0000	HM3I-	0.0000
LM1A+	3.6427	LM1A-	3.4262
LM1B+	2.8083	LM1B-	4.5655
LM1C+	1.4336	LM1C-	3.3043
LM1D+	4.2902	LM1D-	3.7310
LM1E+	5.5934	LM1E-	8.9734
LM1F+	0.0000	LM1F-	0.0000
LM1G+	5.9297	LM1G-	8.0422
LM1H+	0.1450	LM1H-	9.8289
LM1i+	16.5077	LM1I-	9.5725
LM2A+	0.0000	LM2A-	6.7923
LM2B+	6.6404	LM2B-	2.2185
LM2C+	1.3413	LM2C-	5.4360
LM2D+	0.8771	LM2D-	2.9736
LM2E+	1.4055	LM2E-	0.0000

LM2F+	0.0000	LM2F-	2.9800
LM2G+	3.9919	LM2G-	0.0000
LM2H+	0.6033	LM2H-	0.0000
LM2I+	2.4046	LM2I-	0.9777
LM3A+	10.8619	LM3A-	1.1740
LM3B+	4.6855	LM3B-	4.4728
LM3C+	2.5586	LM3C-	5.6724
LM3D+	9.6411	LM3D-	0.0000
LM3F+	5.6915	LM3F-	0.0000
LM3G+	5.6575	LM3G-	1.6909
LM3I+	0.0000	LM3I-	11.2384
CB1A+	16.2526	CB1A-	2.6255
CB1B+	5.5577	CB1B-	3.1780
CB1C+	2.0397	CB1C-	0.0000
CB1D+	9.2025	CB1D-	2.6753
CB1E+	27.1012	CB1E-	0.1766
CB1F+	0.0000	CB1F-	7.0291
CB1G+	2.7729	CB1G-	3.6682
CB1H+	0.2929	CB1H-	9.2025
CB1i+	15.3740	CB1i-	1.4945
CB2A+	17.9048	CB2A-	2.3326
CB2B+	3.0248	CB2B-	2.5569

APPENDIX T. CONT.

Sample	Concentration	Sample	Concentration
CB2C+	3.9307	CB2D-	1.5994
CB2E+	0.1973	CB2E-	0.1576
CB2F+	5.4421	CB2F-	0.0000
CB2G+	1.6056	CB2G-	3.3884
CB2H+	0.0000	CB2H-	9.6755
CB2I+	3.2175	CB2I-	1.7946
CB3A+	0.0000	CB3A-	0.0000
CB3C+	0.0000	CB3C-	4.6265
CB3D+	8.6497	CB3D-	1.5723
CB3E-	3.4473	CB3E+	3.7436
CB3F+	0.3048	CB3F-	3.6743
CB3G+	3.5986	CB3C-	5.3916
CB3H+	0.0000	CB3H-	0.0000
CB3I+	1.9338	CB3I-	2.8734