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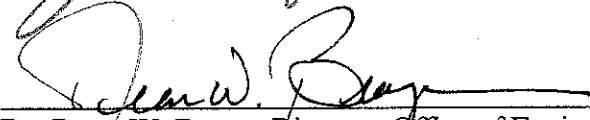
This is to certify that the thesis prepared by Michael T. Elliott entitled "Influences of Tidal Litter (Wrack) and Microtopography on Strand Species and on Community Composition" has been approved by his committee as satisfactory completion of the thesis requirement for the degree of Master of Science.


  
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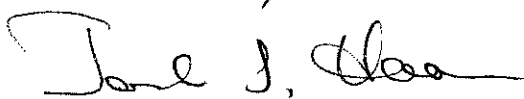
  
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INFLUENCES OF TIDAL LITTER (WRACK) AND MICROTOPOGRAPHY ON STRAND  
SPECIES AND ON COMMUNITY COMPOSITION

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Virginia Commonwealth University

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December, 1997

## ACKNOWLEDGMENTS

The staff of the Nature Conservancy and the LTER, particularly Mr. Randy Carlson and James Spitler, minimized the logistical problems related to conducting field work within the Virginia Coast Reserve. The comments of Drs. G. R. Peters, L. A. Smock, J. F. Pagels and D. W. Broga on an earlier version of the manuscript were greatly appreciated. Ms. Dot Field provided invaluable assistance during the planning and preparation of the experimental gardens on Hog Island. Ms. Ann Wijnholds provided extensive laboratory and field assistance throughout the project. Additional field assistance was provided by Ms. Katherine Tolliver, Mr. Edward Crawford, Ms. Michele Elliott and Mr. Raymond Elliott.

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## ABSTRACT

The relationship of strand plant distribution patterns and the occurrence of tidal wrack was examined on a Virginia barrier island to determine if tidal wrack facilitates the establishment and survival of strand species. Test gardens composed of transplants of five native strand species were prepared in adjacent, exposed and tidal wrack-covered areas to quantify interspecific differences in tissue nutrient concentrations, survivability, and total/flowering structure biomass. Soil samples were also collected from exposed and wrack-covered areas to compare nitrogen and phosphorus content. Variations in species composition as influenced by wrack cover and microtopography were quantified by utilizing fifty transects which included 350 1 m<sup>2</sup> plots. Interspecific differences in frequency, density, total and flowering structure biomass, and biomass partitioning were observed between wrack-covered areas and adjacent exposed areas. The annual forb, *Cakile edentula*, occurred with significantly greater frequency and in greater density within wrack-covered strand areas. Annual forbs, grown in the experimental gardens, produced significantly greater flowering structure biomass (*Pluchea odorata*, *Salsola kali*), and greater total biomass (*Salsola kali*) in wrack-covered soils than in adjacent exposed soils. The responses of two perennial grasses to wrack cover varied interspecifically. *Ammophila breviligulata* produced significantly less total biomass and flowering structure biomass with wrack treatment. *Spartina patens* exhibited significant increases in flowering structure biomass, but no changes in total biomass with wrack treatment. Frequency of occurrence and density of perennial grass species (*Ammophila breviligulata*, *Panicum amarum* and *Spartina Patens*) did not differ significantly between exposed and wrack-covered soils. Increased concentrations of nitrogen were detected in wrack-covered soils; plant tissue nitrogen concentrations, however, did not differ significantly

between exposed and wrack-covered soils. Soils beneath wrack cover tended to be more acidic than adjacent exposed soils. Differences relating to species growth form were observed in regard to performance in varying strand microtopography. Frequency of occurrence of perennial grass species was positively associated with stable dune slope and crest areas, while the annual forb, *Cakile edentula*, conversely, occurred more frequently in less stable overwash and overwash fan areas. Unstable overwash and overwash fan areas with wrack cover provide microsites which facilitate the establishment of annual fugitive species such as *Cakile edentula*, offering increased concentrations of soil nitrogen and reduced competition from perennial species such as *Ammophila breviligulata*. Tidal wrack and microtopography are, thus, key factors influencing small-scale distribution patterns and species composition of strand communities.

## Introduction

Coastal plant species inhabit highly dynamic ecosystems characterized by frequent stress from an array of physical factors (Hayden et al. 1991). These stressors may include: elevated soil salinity, nutrient poor soils, temperature extremes, poor water retention of soils, sand scouring, erosion and inundation (Carter 1988; Eherenfeld 1990; Levy 1990). Local topography and degree of soil exposure are major factors affecting establishment of pioneer plant communities in sandy soils (Crawford 1988 ; Pakeman and Lee 1991a). Dune and swale areas with increased cover may provide enhanced nutrient availability and increased protection from drought and other climatic extremes (Crawford 1988; Pakeman and Lee 1991a). Recruitment and sustainment of species in strand areas may be influenced greatly by availability of cover, such as tidal wrack, and by the ability to exploit a limited number of cover-providing microsites (Barbour et al. 1985; Pakeman and Lee 1991a). Such microsites may provide ameliorated microclimatic and edaphic conditions that allow retainment of seeds and protection of seed banks over winter, greater percentages of successfully germinating seeds, and increased growth and seed production.

Tidal wrack, is a common allochthonous deposit along oceanic beaches (Holton 1980; Polis and Hurd 1996). Wrack is comprised of materials with terrestrial and marine origins, including: dead plant parts, living plant propagules, macro algal fronds, animal detritus, and man-made refuse (Garcia-Novo 1976; Pakeman and Lee 1991a). Significant amounts of wrack of terrestrial origin are deposited on strand areas as a result of disturbance of salt marshes and other coastal areas during extratropical and tropical storms (Young et al. 1995). Wrack materials of marine origin, such as algal debris and carrion, are regularly deposited on the strand as a result of shore drift and tidal action (Barbour et al. 1985; Polis and Hurd 1996). Marine allochthonous



deposition may provide significant nutrient input to strand communities (Pakeman and Lee 1991a, 1991b; Polis and Hurd 1996). Success of annual fugitive species in strand communities has been correlated to the proximity of nutrient-rich allochthonous deposits (Pakeman and Lee 1991a, 1991b; Polis and Hurd 1996). The extent of wrack deposition in strand ecosystems, thus, may influence the distribution patterns of some annual species.

Documentation of physiological and biotic factors which influence distribution and zonation of species in strand communities has been a major theme of strand research throughout the twentieth century (Barbour et al. 1985). The distinct zonation patterns and patchy distribution of species characteristic of strand communities has been attributed to a number of factors including: frequent disturbance, climatic stress and limited availability of microsites providing sufficient nitrogen supplies (Johnson and York 1915; Veldkamp 1971). Past research has suggested that primary productivity and reproductive success of annual forbs may be linked to microtopographic position and proximity to wrack lines (Garcia-Novo 1976; Barbour et al. 1985; Pakeman and Lee 1991a, 1991b). Thus, the distinct zonation and patchy distribution of species evident in strand communities may be related to a positive association of some species with wrack-covered microsites. Positive plant-wrack associations may, thus, be a factor in determining composition and small-scale distribution patterns within strand communities.

Field observations along a Virginia barrier island strand have indicated that the distribution of several native strand species may be influenced positively by the incidence of wrack cover (M. T. Elliott, unpublished data). I hypothesize that tidal wrack influences small-scale distribution patterns and composition of strand communities. The specific objectives of this study were to: 1) determine whether presence of wrack cover increases recruitment, survivability, growth and

reproductive effort, 2) determine whether wrack cover affects nutrient availability and other edaphic parameters, and 3) identify potential plant-wrack associations in a strand ecosystem.

### METHODS:

*Study site* - Field work was conducted on Hog Island (37° 40' N, 75° 40' W), a barrier island located on the Eastern Shore of Virginia, USA. A field site was selected on the north end of Hog Island on an accreting oceanside strand approximately 0.5 km in length. The study site displayed widely varying microtopographic features. Southern areas were relatively stable, with a nearly continuous developing foredune providing protection of interior swale and dunelet areas. Breaches in the developing foredune became apparent near the center of the study site, increasing in frequency and intensity toward the northern margin of the site. Broad strand areas along the northern third of the study site were totally exposed or protected only by low embryonic dunes, allowing frequent overwashing of terrain up to 40 m inland of the mean high tide line. Stable dune areas were dominated by *Ammophila breviligulata*, a perennial grass, while less stable overwash and overwash fan areas supported a more diverse community consisting of annual forbs (e.g. *Cakile edentula*, *Salsola kali*) and perennial grasses (e.g. *Ammophila breviligulata*, *Panicum amarum*, *Spartina patens*).

*Wrackline vegetation survey* - From May through September, 1995 wrack lines and adjacent bare soil areas along the study site were examined biweekly to record temporal and spatial variation in species composition. Strand areas from the tide line to approximately 50 m inland were included in the survey. Species richness, approximate densities and possible plant-

wrack associations were examined qualitatively. Species were classified as common, occasional, rare or absent according to distribution in exposed and wrack-covered areas of the study site.

*Experimental gardens* - Five experimental gardens were established along wrack lines to compare differences in total and flowering structure biomass, belowground to aboveground biomass ratios and plant tissue nutrient concentrations (nitrogen and phosphorus) between wrack-covered and exposed strand soils. The experimental gardens included equal areas (25 m<sup>2</sup>) of wrack-covered and exposed soils oriented so that microtopography and distance to the tide line were similar. Test plants included transplants of five native species which were abundant (as determined in the survey described above) in the strand community. These species included: *Ammophila breviligulata*, a C3 perennial grass; *Spartina patens*, a C4 perennial grass; *Cakile edentula*, an annual C3 herb; *Salsola kali*, a C4 annual herb; and *Pluchea odorata*, an annual C3 herb. Seventy-five plants of each species were planted in wrack covered soils with equal numbers of each species also planted in adjacent exposed soils. The test gardens were weeded prior to planting. Transplants were collected from sites of similar microtopography and edaphic conditions, and were of similar size and age class. All plants were transplanted into the experimental gardens in May, 1996. Harvesting occurred during late August, 1996, when evidence of flowering was visible in the majority of plants within each species. For each test species, surviving plants were tallied in bare and adjacent wrack-covered gardens. A paired t-test was utilized to determine survivability differences between bare and wrack-covered soils. Following harvest, the plants were oven-dried at 80° C and weighed to determine: total mass, aboveground mass, belowground mass, flowering structure mass (included seeds, flowers and supporting structures) and belowground to aboveground biomass ratio. For the above-listed

parameters, t-tests determined significant differences between exposed and wrack treatments for each species. The plants were then ground through a fine mesh with a Wiley mill and composited by species and origin, i.e. wrack or exposed. Composite samples were analyzed at the Cornell University Nutrient Analysis Laboratories of Ithaca, New York, for total nitrogen and phosphorus. The analytical method involved extraction via the 2 M KCL method (Allen et al. 1986). Sample analysis was conducted via colormetric testing methods to determine total nitrogen and phosphorus (Allen et al. 1986). For the above mentioned parameters, paired t-tests (Zar 1984) identified significant differences between wrack and exposed treatments for each species.

*Transects* -In order to identify potential plant-wrack associations in the strand community, 50 transects were established at 10 m intervals and running perpendicular to the mean high tide line. Each transect was initiated at the high tide line and proceeded inland 30 m. Along each transect wrack distribution and microtopographical characteristics were recorded at 1 m increments. At 5 m increments, a 1 m<sup>2</sup> quadrat was placed parallel to the transect line. Within each quadrat (n = 350), species were identified and counted to determine frequency and density. For each species, chi-squared analyses (Zar 1984) determined significant associations between species occurrence, microtopographical position and wrack occurrence.

*Edaphic characteristics* - To determine whether nitrogen and phosphorus concentrations differ between wrack covered and exposed soils, ten soil collection sites were selected along wrack lines within the study area. Two of the collection sites were located in frequently overwashed areas located within 10 m of the mean high tide line. Four of the soil collection sites were positioned in less frequently overwashed swale areas located approximately 10 to 30 m

inland of the high tide line. The remaining four soil collection sites were positioned in broad swale areas which were located approximately 30 to 50-m inland of the high tide line. At approximately biweekly intervals, soil samples were gathered at each of the collection sites from April through August, 1996. Sample collection at each site included the extraction of a pair of composite samples (each consisting of five pooled random subsamples), one sample collected from wrack-covered soil, the other collected from adjacent exposed soil. The soils were analyzed at Cornell Nutrient Analysis Laboratories of Ithaca, New York. Sample analysis involved determination of total nitrogen and phosphorus via colorimetric methods following extraction with 2M KCL (Allen et al. 1986).

Total chlorides and pH were also determined at each of the above listed soil collection sites to further examine edaphic differences between wrack-covered and exposed soils. A 40 g portion of each of the soil samples ( $n = 180$ ) was oven dried at  $105^{\circ}\text{C}$  for 72 h. To each 40 g sample distilled water was added until a 1:5 ratio (soil to water volume:volume) was created. The pH of each sample was measured with a pH electrode (Orion 1994). Following pH testing 5 M  $\text{NaNO}_3$  was added as an ion equalizer and samples were tested with a chloride electrode (Orion 1994) to determine total chlorides (Young et al. 1994). For the edaphic parameters listed above, paired t-tests identified mean and temporal differences between wrack and exposed treatments.

## RESULTS

*Wrack line vegetation survey* - Mere observation revealed the presence of forty-six different species within the study site (Table 1). The effect of wrack cover on relative abundance varied interspecifically. Species more common in wrack soils than in exposed soils included:

*Teucrium canadensis*, *Atriplex patula*, *Cakile edentula*, *Cyperus strigosus* and *Myrica cerifera*. Species more common in exposed soils than in wrack soils included: *Salicornia virginica*, *Suaeda maritima*, *Conyza canadensis* and *Gnaphalium chilense*. No difference in abundance relating to wrack versus exposed soils was observed in a number of common species including: *Ammophila breviligulata*, *Panicum amarum*, *Pluchea odorata*, *Spartina patens* and *Salsola kali*. Species richness was slightly greater in exposed areas (41) than in wrack-covered areas (39) (Table 2). The qualitative survey indicated the presence of interspecific variation regarding habitat preference. For the annuals, individual species were limited to either wrack or exposed areas, while perennial species were more generally distributed between wrack-covered and exposed areas.

*Experimental gardens* - Paired t-test results indicated that survivability of all test species was significantly reduced with wrack treatment ( $0.01 < P < 0.025$ ) (Table 2). The detrimental effects of wrack cover on survivability were more pronounced on the perennial species (*Ammophila breviligulata* and *Spartina patens*) than on the annual species (*Salsola kali* and *Pluchea odorata*). Results of the t-test revealed interspecific variation in biomass partitioning in response to wrack cover (Table 3). The perennial grass *Ammophila breviligulata* produced significantly less total and flowering structure biomass in wrack-covered gardens ( $P < 0.01$  and  $P < 0.05$ , respectively). The perennial grass, *Spartina patens*, did not differ significantly in total biomass ( $P > 0.05$ ), but flowering structure biomass was greater in wrack-covered gardens ( $P < 0.05$ ). Significant increases of total and flowering structure biomass were observed in the annual forb *Salsola kali* with wrack treatment ( $P < 0.01$  and  $P < 0.01$ , respectively) (Table 3). Differences in the total biomass of *Pluchea odorata* were not significant between wrack-covered

and exposed gardens, flowering structure biomass, however, increased significantly in wrack-covered gardens ( $P < 0.05$ ). The garden holding *Cakile edentula* were destroyed prior to harvesting by flooding related to Hurricane Bertha (July, 1997).

Interspecific differences were also observed in belowground-to-aboveground biomass ratios (Table 3). The perennial grasses, *Ammophila breviligulata* and *Spartina patens*, had greater belowground-to-aboveground biomass ratios in wrack-covered versus exposed gardens, while the annual forbs, *Salsola kali* and *Pluchea odorata*, had lower belowground-to-aboveground biomass ratios in wrack-covered versus exposed gardens. Although greater concentrations of nitrogen were present in the tissue of wrack-treated plants of three out of four selected species, a paired t-test did not reveal a significant difference ( $0.05 < P < 0.10$ ) in comparison to exposed garden cultivars (Table 4). Tissue nitrogen concentrations of *Spartina patens* and *Pluchea odorata* were approximately 30% greater in wrack gardens. *Salsola kali* exhibited a slight decrease in tissue nitrogen levels with wrack treatment. Significant differences in plant tissue total phosphorus concentrations were not observed between wrack treatment and exposed gardens (Table 4). Tissue concentrations of total phosphorus were quite limited (near detection limits) in all test plants regardless of wrack incidence.

*Transects* - Wrack materials were present within 160 of the 350 1m<sup>2</sup> plots (45.7%). Surface area coverage provided by wrack varied greatly among the plots ranging to 0% to 100% coverage. Depth of wrack materials ranged from 1 cm to approximately 30 cm, with an average depth of approximately 12 cm. Interspecific differences in frequencies were observed in relation to the incidence of wrack (Table 5). Thirteen species were identified within the 1 m<sup>2</sup> plots along the fifty 30 m transects established at the study site (Table 5). Six of the thirteen species were

recorded with frequencies exceeding 1.0% in all 1 m<sup>2</sup> plots: the perennial grasses *Ammophila breviligulata*, *Spartina patens*, *Panicum amarum* and *Eragrostis spectabilis*; and, the annual forbs *Cakile edentula* and *Conyza canadensis*. *Ammophila breviligulata* was the dominant species at the study site with a frequency of nearly 50% in wrack-covered plots and frequency of over 80% in exposed plots (Table 5). Relative densities of *Ammophila breviligulata* were also greater than any other species in wrack-covered and exposed plots (Table 5). The frequency of occurrence and density of all grass species tended to be greater in exposed plots than in wrack-covered plots. *Spartina patens* and *Panicum amarum* were well distributed throughout the transect plots, occurring with slightly higher frequencies in exposed plots than in wrack-covered plots. The annual forb, *Cakile edentula*, was common in wrack covered plots but occurred infrequently and at a lower density within exposed plots, while the annual forb, *Conyza canadensis*, occurred with greater frequency and at higher densities in exposed plots than in wrack-covered plots.

Four distinctive microtopographical classifications were recorded along the transects: 1) dune crest areas: relatively stable regions perched on the tops of dune formations, 2) dune slope areas (relatively stable dunelets, basal dune and other sloping areas subjected to minimal or infrequent overwash); 3) overwash areas (immediate beachhead flats, flattened dune areas or embryonic dunes subject to frequent overwash); 4) overwash fan areas (interior swale areas affected by deposition of materials from overwashed areas). A chi-squared analysis determined the association of the distribution of four common species to topographical position (Table 6). Interspecific differences in distribution were related to topographical position. Frequency of occurrence of the perennial grass, *Ammophila breviligulata*, was associated positively with stable



dune crest and dune slope regions ( $P < 0.01$ ). Frequency of occurrence of the perennial grasses, *Spartina patens* and *Panicum amarum*, was associated positively with dune slope areas ( $P < 0.01$ ). The annual forb, *Cakile edentula*, occurred with greater frequency within overwash and overwash fan areas ( $P < 0.01$ ).

In order to remove bias related to interspecific topographical association and the less frequent incidence of wrack in dune slope and dune crest plots, wrack versus nonwrack frequencies were calculated through a chi-squared analysis which was limited to combined data from overwash and overwash fan plots (Table 7). Four strand species appeared with sufficient frequencies in overwash and overwash fan plots for the calculation of wrack-related distributional differences (the frequencies of both *Conyza canadensis* and *Eragrostis spectabilis*, at well below 1% in combined overwash and overwash fan plots, were considered too low). The results of the topography independent chi-squared analysis indicated that distribution of *Cakile edentula* was significantly higher in wrack-covered plots as compared to exposed plots ( $P < 0.01$ ). The distribution of *Ammophila breviligulata*, *Spartina patens* and *Panicum amarum* was not influenced significantly by incidence of wrack within the overwash and overwash fan plots ( $P > 0.05$ ).

*Edaphic characteristics* - A paired t-test indicated that significantly greater concentrations of nitrogen were present in soil samples collected from wrack-covered sites as compared to those collected from adjacent exposed sites ( $0.025 < P < 0.05$ ). A general trend toward greater nitrogen concentration in wrack-covered sites was observed from the tide line inland. Soil nitrogen concentrations within exposed sites were uniformly low throughout the study site regardless of microtopography and distance to tide line. Soil phosphorus

concentrations were below laboratory detection limits ( $< 100$  ppm) at all wrack and exposed soil sites sampled throughout the study area. A paired t-test did not reveal significant salinity differences between soil samples collected from wrack-covered sites and adjacent exposed areas (Table 7). A paired t-test indicated significant pH differences between soils collected from wrack covered sites and soils collected from adjacent exposed areas (Table 8). Soil pH was significantly lower in wrack-covered soils than in exposed soils ( $0.01 < P < 0.025$ ).

## DISCUSSION

Total nitrogen and phosphorus concentrations were quite low throughout the study site. The low concentrations are comparable to those reported by Young et al. (1992) at a similar strand site. Concentrations of total nitrogen were greater in soils lying beneath wrack cover than in adjacent exposed soils. The higher concentration of total nitrogen within wrack soils may be attributable to leachate from the decomposing organic components of the wrack deposits (Art et al 1974). Concentrations of total phosphorus were extremely low regardless of the incidence of wrack cover, microtopographical position or distance to tide line. The limited availability of phosphorus observed at the study site is consistent with the findings of other strand studies (Lee 1985; Young et al. 1992). Thus, presence of wrack cover led to significant increases in nitrogen concentrations, but had no significant effect on phosphorus concentrations within underlying soils.

The low concentrations of phosphorus recorded during this study and by Young et al. (1992) at a similar site suggest that phosphorus may act as the primary limiting nutrient. Previous studies have produced conflicting results regarding whether phosphorus may act as the primary limiting nutrient in strand ecosystems. Lee (1985) concluded that phosphorus may frequently be

the primary limiting nutrient, while Pakeman and Lee (1991b) identified nitrogen as the primary limiting nutrient. The low concentrations of nitrogen observed in exposed soil areas, in conjunction with previous research (Art et. al. 1984; Conn and Day 1995, 1997) indicate that nitrogen prevails as the primary limiting nutrient on Atlantic Coast barrier islands. It is possible, however, that phosphorus may act as the primary limiting nutrient within limited areas where wrack cover enhances nitrogen availability.

While significant differences in the soil salinity of wrack-covered and exposed soils were not observed, the abnormally wet conditions experienced during the field work should be considered. During the summer of 1996, on Hog Island precipitation was 200% above normal (Krovetz and Porter 1996). The regular input of precipitation and prevalent moist conditions may have prevented normal salinity trends from developing along the strand. During dry periods wrack cover may provide a barrier which retards evaporation and blocks solar radiation, resulting in greater moisture retention and reduced salinity within underlying soils in comparison to exposed soils (Bertness et al. 1992).

While presence of wrack cover did not effect soil salinity, a significant reduction in the pH of underlying soils was observed in the presence of wrack cover. Previous research conducted by Art et. al. (1984) attributed similar soil pH reduction trends to the leaching of acidic chemical compounds from overlying decomposing wrack materials. The more acidic wrack soils may be more favorable to some strand species, while adjacent exposed soils may support species which prefer, or are more tolerant of alkaline conditions. *Ammophila breviligulata* may exhibit greater productivity in alkaline strand soils (Eldred and Maun 1982). The differing edaphic nutrient and chemical characteristics revealed between exposed and wrack-covered soils appear to have

influenced the performance and resource allocation of annual and perennial species within the experimental gardens.

The annual forb species within the experimental gardens had reduced belowground-to-aboveground biomass ratios in response to wrack cover. The reduction of belowground biomass ratio may reflect a positive response to the greater availability of nitrogen which was evident in wrack-covered soils. The greater availability of nitrogen would reduce root allocation requirements and allow increased aboveground development (Orians and Solbrig 1977; Chapin 1980). The reduced belowground-to-aboveground biomass ratios support the hypothesis that wrack-covered soils provide more favorable growing conditions than adjacent exposed soils. Perennial grasses displayed higher belowground-to-aboveground biomass ratios in wrack-covered soils. Increased root allocation within perennial species may be a response to stress related to limited nutrient availability (Grime 1977; Chapin 1980; Waring 1983) or may indicate allocation of resources toward dispersal via rhizomes, or storage of surplus resources, and, thus, not an adverse response to wrack cover (Harper 1977, Krajnyk and Maun 1981). The testing of tissue nutrient concentrations indicated that both annual and perennial species are under stress in relation to limited nutrient availability.

Tissue nitrogen concentrations of plants harvested from all experimental garden plants were low. The tissue nitrogen concentrations of the test plants ranged from 0.4 % to near 1.0%, well below the 1% to 3% range reported in previous studies of strand vegetation (Dubois 1977; Barbour et al. 1985; Pakeman and Lee 1991b). The tissue nitrogen levels recorded in the experimental gardens were comparable with tissue nitrogen concentrations (0.47 - 0.81%) reported by Conn and Day (1997) in their Hog Island strand study. Tissue nitrogen levels for

plants from exposed and wrack-treated gardens were well below levels required for optimal plant growth (Epstein 1972, Shaver and Melillo 1984).

Tissue phosphorus concentrations were also limited regardless of wrack treatment or growth form. The limited concentrations of phosphorus within plant tissue of the annual forb *Salsola kali* were similar to those reported by Pakeman and Lee (1991a). Conn and Day (1997) recorded low plant tissue levels of phosphorus in the perennial grass, *Spartina patens*, comparable to those observed during this study. The low tissue levels of nitrogen and phosphorus are probably attributable to the low concentrations of both nutrients in the sandy island soils.

Despite the presence of greater concentrations of nitrogen within wrack-covered soils, survivability of all test species was higher in bare soil gardens than in wrack-covered gardens. Survivability rates of both annual species (*Salsola kali* and *Pluchea odorata*) were only slightly lower in wrack-covered gardens, while both perennial species (*Ammophila breviligulata* and *Spartina patens*) displayed drastic reductions in survivability with wrack treatment. The results of this study indicate that perennial strand species may suffer significantly increased mortality rates in the presence of wrack cover, while the presence of wrack cover is a lesser detriment to annual strand species survivability.

Total biomass and biomass partitioning comparisons conducted utilizing surviving test plants revealed further differences between annual and perennial species in response to wrack cover. The significant differences in total biomass and flowering structure biomass evident between exposed and wrack-treated gardens were growth form and species specific. Annual forbs responded positively to wrack treatment. The significant increases in total biomass and flowering structure biomass of *Salsola kali* observed in wrack-treated gardens corresponded with

similar trends reported by Pakeman and Lee (1991a, 1991b) indicating a positive influence of wrack cover. Total biomass of *Pluchea odorata* was not altered significantly with wrack treatment, flowering structure biomass, however, was increased significantly with wrack treatment, indicating a positive association between this annual species and wrack cover. Several studies have documented greater total biomass and flowering structure biomass in *Cakile edentula* plants growing in or immediately adjacent to wrack lines when compared to plants growing in exposed sites (Keddy 1982; Pakeman and Lee 1991a, 1991b), indicating a positive association between this species and wrack cover.

The two perennial grasses responded quite differently to wrack treatment. *Ammophila breviligulata* produced less total and flowering structure biomass in wrack-covered gardens, indicating a negative association with wrack cover. In contrast, evidence of a possible positive relationship between flowering structure biomass and wrack cover was observed in *Spartina patens*. The lower total and flowering structure biomass for *Ammophila breviligulata* may relate to an adverse response to the more acidic soil conditions (Eldred and Maun 1982) and/or to alteration of sand accretion patterns produced by the presence of wrack cover (Olson 1958; Barbour et al. 1985; Carter 1988). The significant increases in flowering structure biomass observed in wrack-treated *Spartina patens*, but lack of significant differences in total biomass between wrack and exposed gardens may indicate that this species is utilizing different growth strategies in response to presence of wrack. The greater nutrient availability in wrack-treated soils may allow *Spartina patens* to accelerate seed production (Harper 1977; Oriens and Solbrig 1977; Chapin 1980), while optimal reproductive success in nutrient poor, exposed soils may be

contingent on the development of more extensive belowground reserves and the delaying of reproductive effort (Grime 1977; Chapin 1980; Waring 1983).

In addition to the wrack-related changes in total and flowering structure biomass discussed above, interspecific differences in frequency of occurrence in relation to wrack presence were also observed. The annual forb, *Cakile edentula*, exhibited a strong positive association between occurrence and the incidence of wrack cover within overwash and overwash fan areas of the study site. The other annual species (i.e. *Salsola kali*, *Pluchea odorata*) occurred too infrequently to provide relevant data, but Pakeman and Lee (1991a, 1991b) reported a positive relationship between wrack lines and occurrence of the annual forb, *Salsola kali*. The incidence of wrack in overwash and overwash fan areas did not have a significant effect on frequency of occurrence of perennial grass species. *Ammophila breviligulata*, *Spartina patens* and *Panicum amarum* all were dispersed evenly between wrack-covered and exposed sites within overwash and overwash fan areas. Dispersal of the perennial grass species exhibited a stronger relationship to microtopography than to incidence of wrack cover.

The frequency of occurrence and densities of all strand species were strongly influenced by microtopographic position. The perennial grass species, *Ammophila breviligulata*, *Spartina patens* and *Panicum amarum*, occurred more frequently and at greater densities within relatively stable dune slope and dune crest areas. Occurrence of the annual forb, *Cakile edentula*, conversely, was positively associated with unstable overwash and overwash fan areas. Many of the microtopographical trends displayed by strand species in the study area can be attributed to seed dispersal methods, growth form and habitat requirements. Seeds of *Cakile edentula* which utilizes a dual dispersion method involving seeds specialized for short and long distance dispersal

(Keddy 1980, 1981), are more likely to be deposited in overwash and overwash fan areas than in more elevated dune areas (Keddy 1982). Seeds of *Cakile edentula* which are specialized for long distance dispersal via marine transport are deposited in greater concentrations in overwash and overwash fan areas than in more protected dune slope and crest areas (Keddy 1980, 1981, 1982). Seeds of *Cakile edentula* which are specialized for short distance dispersal form clusters in the immediate vicinity of parent plants (Keddy 1980, 1981, 1982).

Through clustering of locally dispersed seeds and marine deposition of long distance dispersed seeds, *Cakile edentula* seed density and plant abundance is greater in overwash and overwash fan areas than in dune areas (Barbour 1970b, 1972; Keddy 1982; Pakeman and Lee 1991a). Pemadosa and Lovell (1975) concluded that fugitive annual species such as *Cakile edentula*, are poor competitors which are inhibited by the presence of the perennial grass *Ammophila breviligulata*. The high frequency of occurrence and density of *Ammophila breviligulata* and other competitive perennial species within stable dune slope and crest areas may limit the distribution of *Cakile edentula* in these areas. More frequent and intense disturbance within overwash and overwash fan areas, however, may result in the removal of perennial species, reducing competition and creating exploitable sites for annual fugitive species such as *Cakile edentula* (Carter 1988; Fahrig et al. 1993). The more frequent deposition of seeds in overwash/fan areas (Keddy 1982), habitat preference for low-lying areas providing tidal wrack cover and possible related enhancement of soil nutrient/moisture availability (Pakeman and Lee 1991a), and the poor competitive capabilities characteristic of annual fugitive species (Pemadosa and Lovell 1975), are primary factors influencing the greater distribution and density of annual forb, *Cakile edentula*, in wrack-covered overwash and overwash fan areas.



Habitat preferences and reproductive strategies of the common perennial species differ from those exhibited by the annual *Cakile edentula*. The dominant perennial species, *Ammophila breviligulata*, is a clonal dune building grass, that requires constant sand accretion and alkaline soils for optimal growth (Olson 1958; Martin 1959; Eldred and Maun 1982; Barbour et al. 1985). The sand capturing strategy and ability to thrive despite continual burial allows *Ammophila breviligulata* to overwhelm competing species in actively growing dune areas (Eldred and Maun 1982; Carter 1988). The dune building strategy of *Ammophila breviligulata*, preference of the edaphic conditions provided in accreting dune areas, and expansion of coverage via rhizomes, leads to a greater density in stable dune areas with active sand deposition (Eldred and Maun 1982, Carter 1988). In addition to providing less favorable soil conditions, broad, unstable overwash and overwash fan areas may be too distant from dune strongholds and subjected to disturbance too frequently to allow swift establishment and domination by perennial species such as *Ammophila breviligulata*.

The distribution and density of annuals versus perennials may fluctuate highly from year to year, in response to the frequency and severity of disturbance, and related wrack deposition patterns. The processes associated with the deposition of tidal wrack, and actual wrack deposition are related to disturbances which create favorable microsites for opportunistic annual fugitive species. Overwashing tides may uproot and or inundate perennial species or create temporary hypersaline conditions (Young et al. 1995). Overwash deposition and the deposition of wrack material results in the burial and smothering of existing perennial vegetation (Bertness et al. 1992; Fahrig et al. 1993). Overwashing also flattens dunes removing existing vegetation and creating lower relief, which in turn increases vulnerability to subsequent disturbance (Carter

1988). These denuded, unstable strand areas provide highly favorable microsites to fugitive species such as the annual forbs, *Cakile edentula* and *Salsola kali*, offering elimination of competition, relatively low relief and a steady supply of nutrients from decomposing wrack materials (Keddy 1982; Platt 1985; Brokaw 1985; Carter 1988). Without recurrent disturbance and wrack deposition, more competitive perennial species, such as *Ammophila breviligulata* and *Spartina patens*, would be expected to recover, leading to the eventual displacement of annual forbs (Barbour 1970b, 1972; Pemadosa and Lovell 1975). Wrack deposition may be critical in maintaining diversity in strand communities: with the microsites created during the initial deposition of wrack benefitting fugitive annual species and residual nutrient sources benefitting more competitive perennial and annual species following post disturbance recovery. Deposition of tidal wrack and microtopography are, thus, key factors which influence strand species distribution and community composition.

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Table 1. Strand line species occurrence in exposed versus wrack-covered soils along the strand of north Hog Island. Species were classified as common (C), occasional (O), rare (R) or absent (-).

Species	Growth Form	Exposed Soil	Wrack-Covered Soil
<i>Agalinis fasciculata</i>	annual forb	C	O
<i>Ammophila breviligulata</i>	perennial grass	C	C
<i>Atriplex patula</i>	annual forb	O	C
<i>Baccharis halimifolia</i>	shrub	O	O
<i>Batis maritima</i>	perennial herb	R	-
<i>Borrchia frutescens</i>	shrub	-	O
<i>Cakile edentula</i>	annual forb	O	C
<i>Calystegia sepium</i>	perennial vine	-	R
<i>Cenchrus incertus</i>	annual grass	O	C
<i>Chamaesyce polygonifolia</i>	annual forb	O	R
<i>Chenopodium album</i>	annual forb	R	O
<i>Cirsium horridulum</i>	biennial herb	R	O
<i>Conyza candensis</i>	annual forb	C	C
<i>Cyperus filicinus</i>	perennial sedge	-	R
<i>Cyperus strigosus</i>	perennial sedge	O	C
<i>Distichlis spicata</i>	perennial grass	R	-
<i>Eragrostis spectabilis</i>	perennial grass	O	O
<i>Erechtites hieracifolia</i>	annual forb	O	O
<i>Eupatorium capillifolium</i>	perennial herb	R	R
<i>Eupatorium hyssopifolium</i>	perennial herb	O	C
<i>Euthamia tenuifolia</i>	perennial herb	O	O
<i>Fimbristylis castanea</i>	perennial sedge	R	-
<i>Gnaphalium chilense</i>	annual/biennial herb	C	O

Species	Growth Form	Exposed Soil	Wrack-Covered Soil
<i>Gnaphalium purpureum</i>	annual/biennial herb	C	O
<i>Iva frutescens</i>	shrub	-	O
<i>Juncus gerardi</i>	perennial rush	O	O
<i>Juncus roemerianus</i>	perennial rush	O	O
<i>Linaria canadensis</i>	annual forb	C	O
<i>Limonium carolinianum</i>	annual forb	R	-
<i>Linum medium</i>	annual forb	C	R
<i>Myrica cerifera</i>	shrub	O	C
<i>Panicum amarum</i>	perennial grass	C	C
<i>Pluchea odorata</i>	annual forb	C	C
<i>Sabatia stellaris</i>	annual forb	C	O
<i>Sagina decumbens</i>	perennial herb	O	C
<i>Salicornia europaea</i>	annual forb	O	-
<i>Salsola kali</i>	annual forb	C	C
<i>Scirpus americanus</i>	perennial sedge	R	-
<i>Sesuvium portulacastrum</i>	perennial herb	O	-
<i>Spartina alterniflora</i>	perennial grass	R	-
<i>Spartina patens</i>	perennial grass	C	C
<i>Strophistyles helvola</i>	annual vine	O	O
<i>Suaeda linearis</i>	annual forb	O	-
<i>Teucrium canadense</i>	annual forb	O	C
<i>Triplasis purpurea</i>	annual grass	O	O
<i>Xanthium strumarium</i>	annual forb	-	O
Species Richness		41	37

Table 2. Comparison of survivorship of four strand species: surviving transplants in bare (n = 75) versus wrack-covered (n = 75) experimental gardens. There was a significant negative relationship ( $\alpha < 0.025$ ) between survivorship and presence of wrack cover.

Species	<i>Ammophila breviligulata</i>		<i>Spartina patens</i>		<i>Salsola kali</i>		<i>Pluchea odorata</i>	
	Bare	Wrack	Bare	Wrack	Bare	Wrack	Bare	Wrack
# Survivors	59	48	49	27	30	29	75	70
% Survivorship	78.7	64.0	65.3	36.0	40.0	38.7	100.0	93.3

Table 3. Comparison of biomass partitioning for four native strand species: wrack treatment versus bare soil. \* denotes significant ( $\alpha < 0.05$ ) relationship between parameter and presence of wrack cover.

	<i>A. breviligulata</i>		<i>S. patens</i>		<i>P. odorata</i>		<i>S. kali</i>	
	Bare	Wrack	Bare	Wrack	Bare	Wrack	Bare	Wrack
Shoot Mass (g)	2.97 $\pm$ 0.03	2.04 $\pm$ 0.03	1.45 $\pm$ 0.02	1.38 $\pm$ 0.03	1.80 $\pm$ 0.01	1.91 $\pm$ 0.03	0.90 $\pm$ 0.03	2.93 $\pm$ 0.08
Root Mass (g)	0.68 $\pm$ 0.01	0.49 $\pm$ 0.01	0.46 $\pm$ 0.01	0.64 $\pm$ 0.02	0.79 $\pm$ 0.01	0.74 $\pm$ 0.03	0.09 $\pm$ 0.01	0.23 $\pm$ 0.01
Total Mass (g)	3.65 $\pm$ 0.02	2.53 $\pm$ 0.03*	1.91 $\pm$ 0.03	2.02 $\pm$ 0.05	2.59 $\pm$ 0.02	2.65 $\pm$ 0.04	0.99 $\pm$ 0.03	3.16 $\pm$ 0.09*
Root/Shoot Mass (%)	0.23	0.24	0.32	0.47	0.44	0.39	0.10	0.08
Reproductive Mass (g)	0.15 $\pm$ 0.01	0.07 $\pm$ 0.01*	0.01 $\pm$ 0.01	0.02 $\pm$ 0.01*	0.18 $\pm$ 0.01	0.23 $\pm$ 0.01*	0.02 $\pm$ 0.01	0.48 $\pm$ 0.02*

Table 4. Comparison of tissue nitrogen and phosphorus concentrations ( $\mu\text{g g-dry wt}^{-1}$ ) of four strand species, wrack treatment versus bare soil experimental gardens. \* denotes near significant ( $0.05 < P < 0.10$ ) association between wrack cover and parameter.

Nutrient	<i>A. breviligulata</i>		<i>S. patens</i>		<i>P. odorata</i>		<i>S. kali</i>	
	Bare	Wrack	Bare	Wrack	Bare	Wrack	Bare	Wrack
Nitrogen	4900 $\pm$ 100	5300 $\pm$ 100*	4100 $\pm$ 100	5900 $\pm$ 100*	7100 $\pm$ 100	9900 $\pm$ 100*	6300 $\pm$ 100	6200 $\pm$ 100*
Phosphorus	100	100	100	100	200 $\pm$ 100	200 $\pm$ 100	200 $\pm$ 100	300 $\pm$ 100

Table 5. Frequency (% occurrence in plots) and density ( $\# \text{ m}^{-2}$ ) for thirteen species along the strand line of north Hog Island.

Species	Growth Form	Bare soil		Wrack-covered soil	
		Frequency (%)	Density ( $\#/\text{m}^2$ )	Frequency (%)	Density ( $\#/\text{m}^2$ )
<i>Ammophila breviligulata</i>	perennial grass	81.0	6.68	47.5	2.63
<i>Adropogon glomeratus</i>	perennial grass	0.0	0.00	0.3	0.01
<i>Cakile edentula</i>	annual forb	2.1	0.02	33.1	0.85
<i>Cenchrus incertus</i>	annual grass	3.7	0.11	1.9	0.03
<i>Chamaesyce polygonifolia</i>	annual forb	0.6	0.03	0.0	0.00
<i>Conyza canadensis</i>	annual forb	9.5	0.56	0.6	0.03
<i>Cyperus strigosus</i>	perennial sedge	1.1	0.02	3.8	0.13
<i>Eragrostis spectabilis</i>	perennial grass	8.4	0.47	4.4	0.14
<i>Myrica cerifera</i>	shrub	0	0	0.3	0.01
<i>Panicum amarum</i>	perennial grass	60.5	3.95	46.9	1.58
<i>Salsola kali</i>	annual forb	2.1	0.04	1.9	0.02
<i>Spartina patens</i>	perennial grass	33.2	1.91	44.4	0.87
<i>Triplasis purpurea</i>	annual grass	3.2	0.15	0.0	0.00

Table 6. Association of four common strand species to microtopographical position on north Hog Island. For all four species the association was significant ( $P < 0.001$ ).

	<i>A. breviligulata</i>		<i>S. patens</i>		<i>C. edentula</i>		<i>P. amarum</i>	
	Present	Absent	Present	Absent	Present	Absent	Present	Absent
<b>Dune Slope</b>								
Expected value	85	39	36	88	20	104	70	54
Observed value	114	10	50	74	4	120	87	37
Chi-squared	9.9	21.5	5.3	2.2	13	2.5	4.0	5.3
<b>Dune Crest</b>								
Expected value	27	13	12	28	7	33	23	17
Observed value	35	5	15	25	0	40	31	9
Chi-squared	2.1	4.6	1.0	0.4	6.5	1.3	3.1	5.3
<b>Overwash</b>								
Expected value	82	37	35	84	19	100	82	37
Observed value	50	69	18	101	27	92	50	69
Chi-squared	12.2	26.7	8.0	3.3	3.0	6.0	12.2	26.7
<b>Overwash Fan</b>								
Expected value	46	21	20	47	11	56	38	29
Observed value	41	26	19	48	26	41	30	37
Chi-squared	0.5	1.2	0.0	0.0	20.1	4.1	1.6	2.1
<b>Total Chi-Squared</b>	78.7		20.2		51.1		60.3	

Table 7. Chi-Squared analysis of frequency of four species in wrack versus exposed soil 1 m<sup>2</sup> plots within overwash and overwash fan catagorized microtopographical areas, at the study site on Hog Island, Virginia. \*denotes significant association ( $P < 0.01$ ) between frequency and incidence of wrack.

Species	Bare Soil		Wrack Soil		Chi-Squared
	Observed	Expected	Observed	Expected	
<i>Ammophila breviligulata</i>	18	17	63	64	0.07
<i>Spartina patens</i>	4	8	33	29	2.55
<i>Panicum amarum</i>	10	16	69	63	2.88
<i>Cakile edentula</i>	1	12	55	44	11.92*



Table 8. A comparison of total nitrogen and phosphorus concentrations (ppm), total chlorides (ppm) and pH values of bare versus wrack covered strand soil, study site north Hog Island, Virginia. \*denotes significant ( $P < 0.05$ ) difference between wrack-covered soil and exposed soil for edaphic parameter.

Soil collection site	Total Nitrogen		Total Phosphorus		Salinity		pH value	
	Bare	Wrack	Bare	Wrack	Bare	Wrack	Bare	Wrack
U1 (n = 8)	100	100*	<100	<100	94.8	115.0	7.8	7.6*
U2 (n = 8)	100	200*	<100	<100	91.8	114.3	8.1	7.3*
U3 (n = 8)	<100	500*	<100	<100	115.5	123.4	7.0	6.9*
U4 (n = 8)	100	300*	<100	<100	109.6	106.3	7.2	7.2*
M1 (n = 8)	<100	100*	<100	<100	125.1	121.9	7.4	7.4*
M2 (n = 8)	100	200*	<100	<100	106.8	119.4	7.6	6.9*
M3 (n = 8)	100	100*	<100	<100	109.5	113.8	7.6	7.0*
M4 (n = 8)	<100	<100*	<100	<100	119.0	112.4	7.0	6.8*
L1 (n = 8)	<100	<100*	<100	<100	79.3	74.4	6.7	6.8*
L2 (n = 8)	100	<100*	<100	<100	80.3	85.8	6.9	6.8*

U sites: Located approximately 30 to 50 m inland of tide line  
M sites: Located approximately 10 to 30 m inland of tide line  
L sites: Located from tide line to approximately 10 m inland.

## APPENDIX

*Seed bank experiment* - Seed bank composition of wrack-covered soils was determined from samples ( $n = 10$ ) of wrack materials and underlying soil gathered along deposition lines throughout the subject site. Samples (800 ml) were composed of pooled wrack material and underlying soils (extracted to 2 cm in depth) subsamples (5) collected randomly within wrack-covered regions in April, 1995. The wrack and soil materials were cold stratified at 4° C for 3 weeks, then mixed with sterilized sand and placed in a greenhouse (Gross 1990) with a 30/20° C temperature regime and natural photoperiod. The soils were monitored weekly for the emergence of seedlings for a period of six months. Species were identified and relative abundance was determined.

Glasshouse germination of wrack seed bank revealed a limited number of species; some were common, while others were rare or absent at the study site (Table 1A). *Acer rubrum*, which was not documented in past vegetative surveys of Hog Island (McCaffrey 1991), appeared twice in the seed bank. Many species which are common along wrack lines, such as *Ammophila breviligulata*, *Cakile edentula*, *Salsola kali* and *Panicum amarum*, were either absent or poorly represented in the seed bank (Table 1). Common species within the study site which appeared frequently in the seed bank study included *Spartina patens*, *Pluchea odorata* and *Conyza canadensis*. A nearly even number of perennial and annual species were observed in the seed bank. An equal number of individual perennial and annual seedlings were tallied (Table 1).

The species composition of wrack soil seed banks did not closely resemble the community structure observed at the field site. Several perennial (e.g. *Ammophila breviligulata*) and annual species (e.g. *Cakile edentula*) which were widely dispersed at the study site were either absent or

present in disproportionately low numbers in the seed bank. The absence of *Ammophila breviligulata* seedlings within the seed bank may be attributed to annual variations in seed production and/or an increased allocation of resources toward reproduction via rhizomes (Harper 1977). The relatively low density of *Cakile edentula* in the seedbank, however, is more difficult to explain, considering its abundance along wracklines at the study site. The unique seed dispersal strategy of *Cakile edentula*, which involves the production of seeds specialized for long distance dispersal via water transport, and seeds specialized for local dispersal in the immediate area of the parent plant, would seem to be well-suited for capture and deposition within wrack lines (Barbour 1970a, 1970b; Keddy 1982). It is possible that the April collection date of wrack and soil samples was too late in the season to accurately represent the component of early germinating species such as *Cakile edentula* (Keddy 1982; Joy 1997). Many seeds may have germinated prior to sample collection, contributing to the disproportionately low representation of affected species within the seed bank.

The appearance of *Acer rubrum* within the wrack soil seed bank was also unexpected. Because no mature *Acer rubrum* were observed on Hog Island during the study, the seeds originated either on the mainland or on other barrier islands. The position of the seeds (beneath wrack piles on the ocean side of the island) strongly suggests that the seeds were directly deposited on the strand via marine transport. These results indicate that viable seeds from distant sources are transported to the study site via wind and/or marine transport prior to wrack deposition. The seeds present in the wrack seed bank are thus a mixture of seeds from a wide range of local and distant origins, and of widely differing habitats. Many wrack deposited seeds may not be suited to the harsh environment present in strand areas, and thus under natural

conditions would fail to germinate or die off in early seedling stages (Looney and Gibson 1995). Such nonnative seeds would be more likely to germinate and continue growth under ideal glass house conditions, and thus may lead to unexpected seed bank results such as those observed during this study (Looney and Gibson 1995).

Table A-1. Wrack seed bank experiment: identification and abundance of species which germinated under glass house conditions over 6 month period.

<i>Species/(common name):</i>	<i>Number of Seedlings:</i>	<i>Growth Form:</i>
<i>Acer rubrum</i>	2	tree
<i>Cakile edentula</i>	1	annual forb
<i>Cenchrus incertus</i>	1	annual grass
<i>Conyza canadensis</i>	9	annual forb
<i>Cyperus strigosus</i>	3	perennial sedge
<i>Distichlis spicata</i>	2	perennial grass
<i>Erechtites hieracifolia</i>	1	annual forb
<i>Pluchea odorata</i>	3	annual forb
<i>Sagina decumbens</i>	1	annual forb
<i>Scirpus americanus</i>	2	perennial sedge
<i>Spartina patens</i>	8	perennial grass

## VITA

Michael T. Elliott was born February 19, 1961 in the District of Columbia. He lived in northern Kentucky until the beginning of his senior year in high school, at which time he was relocated to central Virginia, graduating from Randolph-Henry High School in Charlotte County Virginia in 1979. His Bachelor of Science degree was earned from Longwood College of Farmville, Virginia, in 1983. Following completion of the undergraduate program, Elliott began a career as an environmental consultant. He currently serves as a Senior Safety Engineer with the Virginia Commonwealth University Office of Environmental Health and Safety, and resides with his wife and two cats in Ashland, Virginia. When not on the job or working on completion of his Masters Degree, he can usually be found fishing in one of the many fine streams of central Virginia.