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# Salt spray and edaphic factors maintain dwarf stature and community composition in coastal sandplain heathlands

Megan E. Griffiths[1,2,*]
*[1]Department of Biology, Tufts University, Medford, MA, 02144, USA; [2]School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209, South Africa; *Author for correspondence (e-mail: Griffithsme@ukzn.ac.za; phone: +27-332605110; fax: +27-332605105)*

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## Abstract

North American coastal sandplain heathlands are unique in species composition and vegetation, but the extent to which edaphic factors influence the structure of these communities is currently debated. It was hypothesized that salt spray and edaphic factors maintain the dwarf stature and community composition of heathlands by limiting plant growth and excluding competitively dominant woody species close to the ocean. Field surveys were carried out to investigate the spatial patterns of salt spray accumulation, soil salt and soil moisture. High salt spray correlated significantly with increased leaf necrosis and water stress in *Myrica pensylvanica* and with decreased plant height. Plant community composition changed across a salt spray and soil gradient, as well. Distinctive sub-communities were identified that separated according to soil salt and soil moisture but salt spray was the main factor affecting sites occupied only by heathland vegetation. Results from this study suggest that salt spray suppresses the growth of heathland plants in close proximity to the ocean, and therefore maintains the low stature in these dwarf shrublands. This research also demonstrates that the physical environment influences the community structure in heathlands, particularly by limiting tree species from growing in high salt spray, low water availability sites.

## Introduction

Coastal sandplain heathlands are early successional, dwarf-shrub communities with a maritime distribution in the northeastern United States and southeastern Canada (Dunwiddie et al. 1996). These communities are influenced by disturbance and land use, which limit the establishment and growth of competitively dominant species such as *Pinus rigida* and *Quercus ilicifolia* (Dunwiddie 1989; Dunwiddie and Caljouw 1990; Foster and Motzkin 1999; Eberhardt 2000). The effects of burning and domestic livestock grazing have been studied extensively in coastal sandplain heathlands and these factors are recognized as maintaining heterogeneity on a landscape scale (Patterson and Sassman 1988; Dunwiddie 1990; Stevens 1996). However, very little attention has been given to the role that natural abiotic factors may play in maintaining these communities within sites that have the same disturbance and land use history.

Due to their situation near the ocean, sandplain heathlands potentially encounter high levels of salt spray, which could suppress plant growth and consequently be important in determining the characteristic dwarf stature of heathlands (Griffiths and Orians 2003b). Salt spray and edaphic conditions, particularly soil salt and soil moisture, may also control community composition (Anderson et al. 1998). Salt spray often causes vegetation zonation (Boyce 1954; Saito et al. 1965; Randall 1970, 1974) and eliminates intolerant species from areas with high salt spray regimes (van der Valk 1974). Similarly, high soil salinity (Barbour and DeJong 1977; Young et al. 1994; Houle 1997) and low soil moisture (De Jong 1979; Sykes and Wilson 1991; Maun 1994; Smith and Steenkamp 2001) limit the survival and establishment of plants in coastal areas. Although salt spray and edaphic effects have been widely studied in other coastal communities, it is unclear whether they influence heathland community stature and structure in the field.

Manipulative studies in the greenhouse (Griffiths and Orians 2003b) and field (Griffiths and Orians 2003a, 2004) have shown that salt spray limits heathland plant growth and that species vary in their response to salt spray. In particular, tree species are particularly susceptible to damage by salt spray, which may result in their exclusion from high salt spray areas. Furthermore, it has been demonstrated that high soil water availability can ameliorate the negative effects of salt spray, allowing species with less salt resistance to grow in high salt spray, high water availability conditions (Griffiths and Orians 2003a).

The goal of this study was to augment manipulative experiments with quantitative analysis of field data. Given the results of previous investigations (Griffiths and Orians 2003a, b, 2004), it was hypothesized that: (1) salt spray limits heathland plant community stature through its physiological effects on individual plants and (2) heathland community composition is determined by the salt spray and edaphic conditions of a site. It was predicted that there would be higher levels of necrosis and water stress and lower plant height in areas with high salt spray. It was further predicted that high salt spray areas with high soil water availability would support more salt-intolerant species, such as trees, than areas with the same salt spray levels and low water availability.

## Methods

### *Study sites*

Coastal sandplain heathlands have a narrow distribution along the Atlantic Ocean from New Jersey, USA to Newfoundland, Canada (Godfrey and Alpert 1985; Noss et al. 1995). The most extensive areas of these heathlands are found on Martha's Vineyard, Nantucket, and Tuckernuck Island in Massachusetts (Dunwiddie et al. 1996; Mehrhoff 1997; Barbour et al. 1998). Grass, forb, and shrub species adapted to the dry and nutrient-poor soils of glacial outwash sandplains dominate the heathland plant community (Dunwiddie et al. 1996).

Field surveys were conducted on the island of Martha's Vineyard, Massachusetts, USA (41°22′ N 70°40′ W) during June–August 1998 and 1999. Study sites included conservation areas at Priscilla Hancock Meadow (PH), Quansoo Beach (QB), and the Scrubby Neck area of Long Point Wildlife Refuge (LP), which are located adjacent to the Atlantic Ocean along the southern shore of the island. The soils are well-drained sand and loam that were formed by glacial outwash (Fletcher and Roffinoli 1986). Winds are predominantly from the south and southwest during the summer and from the northeast in the winter. As a result, sustained strong winds generally blow inland from the ocean during the growing season (Griffiths 2003).

These three sites were chosen because they have similar location relative to the ocean, and therefore have similar potential exposure to salt spray, but they differ in land use history, topography, and elevation. Coastal areas of PH and QB have been actively managed with mowing in the last 20 years, while LP has not been managed for at least 50 years. In terms of topography, PH and QB each have a very high single dune with a slope that extends approximately 75 m inland from the dune crest, while the dune at LP is low and the slope extends 15 m inland from the dune crest. Differences in topography are reflected in elevation differences among the sites. PH and QB are located at 0–3.5 m above sea level, while LP is between 3.4 and 6.1 m above sea level. The differences in topography and elevation result in differences in the soil water availability in these sites. The choice of these sites with similar salt spray exposure but different edaphic conditions allowed the testing of the hypothesis that salt spray and soil moisture interact to control plant community composition.

In each field site, sampling of environmental variables, plant condition and stature, and plant community composition was carried out at eight distances from the dune crest: 25, 50, 75, 100, 125, 150, 175, and 200 m.

### *Environmental variables*

Salt spray accumulation was measured on leaves of *Myrica pensylvanica* (Mirbel.), a prevalent native heathland plant species. Six randomly selected plants were measured at each sampling distance in each field site. Twenty leaves were collected from every plant, 10 from the windward side and ten from the leeward side. These leaves were randomly selected from the terminal branches, marked with indelible marker, rinsed with deionized water, and collected after 24 h of exposure. Salt spray accumulation was determined according to methods described in Griffiths (2003) and leaf area was determined using a dot grid so that salt accumulation could be expressed per unit leaf area (mg NaCl $dm^{-2}$ $d^{-1}$). No salt spray measurements were taken for 50 m at PH and 25 and 75 m at QB because *M. pensylvanica* plants were infrequent, had too few leaves, or were completely absent from those sampling points.

Soils were sampled using a 2.5 cm-diameter auger. Two replicate soil cores were taken at each sampling distance in each of the three field sites, with the exception of 75 m at QB, where there was a brackish water channel. Samples were taken from the top 15 cm of the soil, excluding the litter layer. This core depth was chosen because most heathland plant roots, including shrubs and low trees, fall within this zone. Each soil sample was mixed and a 10 g soil sub-sample was dried at 110 °C for 24 h. Soil salt concentration (De Jong 1979) and gravimetric water content (Brower et al. 1997) were then determined using standard methods.

### *Plant condition and heathland community stature*

Plant measures were taken on randomly selected *M. pensylvanica* individuals. The *Myrica* genus is known to be salt-tolerant (Wells and Shunk 1938), so these measurements give a conservative estimate of the effects of salt spray on heathland species. Predawn xylem pressure potential (MegaPascals [MPa]) was measured at 0400 using a pressure chamber (PMS Instrument Company, Corvallis, Oregon). The xylem pressure potential was determined for randomly selected branches of *M. pensylvanica* from three plants sampled at each distance at one site (LP) only. Necrosis, an index for salt spray damage (Boyce 1954), was measured on all leaves used for salt spray quantification. The area of leaf tissue with necrotic damage was measured using a dot grid and expressed as the percentage of total leaf area showing necrosis. Windward and leeward heights of *M. pensylvanica* were measured on fifteen randomly selected plants at each distance in the three field sites. There were no measurements of *M. pensylvanica* height at 50 m at PH and 75 m at QB, given the absence of this species at those locations. Vegetation height was also measured on 15 randomly selected plants of any species at each distance in the three field sites, excluding 75 m at QB.

### *Heathland community structure*

Plant community composition was assessed at each distance in the three field sites. Species composition was surveyed at two scales: 1×50 m transects and 1 $m^2$ plots. For transect-level analyses, the optimal size was determined using species–area curves (Rice and Keltin 1955). A 1× 50 m transect captured the most species per sampling effort and this dimension was used for coarse-scale community composition measurements. Two transects were sampled at each distance, with transects oriented parallel to the shoreline so that all points were approximately the same distance from the dune crest. Species names were recorded according to the nomenclature of Gleason and Cronquist (1991). Plot-level analyses were used for fine-scale community composition measurements. Six 1 $m^2$ plots were placed randomly at each distance and the density, frequency and coverage were recorded for each species within each plot.

### *Statistical analyses*

Statistical analyses of environmental variables, necrosis, xylem pressure potential, and height were performed using generalized linear models procedures in SAS (SAS Institute 1990). A one-way ANOVA was used to test for the effect of distance from the dune crest on xylem pressure potential, while two-way ANOVAs were used to test for the independent and combined effects of site and distance on soil salt, soil moisture, and vegetation height. Salt spray, leaf necrosis, and *M. pensylvanica* height were analyzed using three-way ANOVAs with site, distance, and wind exposure as the main effects. If interaction terms were not significant, the models were reduced to include only significant interactions.

General trends in community composition at the transect level were examined by calculating the percentage of species from different physiognomic groups at each site and distance. The percentage of transects occupied by each individual species was also calculated for each site and distance. Using data from plot-level surveys, Hill's diversity numbers were calculated for each distance in the three field sites (Magurran 1988). These included N0, the total number of species per unit area; N1, the exponent Shannon's diversity index (H′); and N2, the reciprocal of Simpson's diversity index ( $\lambda$). N1 and N2 indicate the number of abundant and very abundant species, respectively, so as the values decrease, rare species are more important in the community. The Hill's diversity numbers were analyzed using a two-way MANOVA in SPSS (SPSS 2002) that tested for site, distance, and site×distance interactions.

Multivariate analyses were performed using PC-ORD (McCune and Mefford 1999). Non-metric multidimensional scaling (NMS) was used to detect differences in species composition between quadrats at different distances in the three sites. A randomization test on Euclidean distance values was performed using Resampling Statistics in Excel. Because this analysis revealed significant differences in community composition between sites, all further multivariate analyses were performed on a per-site basis. Additional NMS analyses were performed using data from the 1 $m^2$ plots and the scatterplots were overlaid with envelopes encircling species groups identified using two-way indicator species analysis (TWINSPAN). The influence of environmental factors on species distributions was examined using canonical correspondence analysis (CCA) for each site. Monte Carlo permutation tests were run to determine the significance of the relationship between species distributions and environmental variables.

## Results

### *Environmental variables and plant condition*

There were site, distance, and wind exposure effects on *M. pensylvanica* salt spray accumulation (Table 1; Figure 1). At LP, where the topography is higher and flatter, salt spray decreased 4-fold between sampling points at 25 and 200 m from the dune crest, but this relationship was not found at the other two sites. At all sites and distances, leaves on the windward side of plants accumulated two times the amount of salt spray found on leaves from the leeward side. There was a significant interaction between distance and wind exposure;

*Table 1.* Type III Sums of Squares results for a three-way analysis of variance for *M. pensylvanica* leaf salt spray accumulation (mg $dm^{-2}$ $d^{-1}$) and two-way analyses of variance for soil conductivity (μS) and soil moisture (%).

| Source of variation | Salt spray | | | Soil conductivity | | | Soil moisture | | |
|---|---|---|---|---|---|---|---|---|---|
| | df | *F* | *p* | df | *F* | *p* | df | *F* | *p* |
| Site | 2 | 6.41 | 0.002 | 2 | 7.32 | 0.004 | 2 | 5.21 | 0.014 |
| Distance | 7 | 26.01 | < 0.001 | 7 | 9.27 | < 0.001 | 7 | 6.04 | < 0.001 |
| Wind exposure | 1 | 419.71 | < 0.001 | | | | | | |
| Site×distance | 11 | 5.28 | < 0.001 | 13 | 5.71 | < 0.001 | 13 | 4.53 | < 0.001 |
| Distance×wind exposure | 7 | 7.10 | < 0.001 | | | | | | |
| Site×distance×wind exposure | 13 | 1.99 | 0.019 | | | | | | |
| Error | 870 | | | 23 | | | 23 | | |

Measurements were taken at three sites (PH, QB, and LP) and eight distances from the dune crest (25, 50, 75, 100, 125, 150, 175, and 200 m). For salt spray accumulation, measurements were also taken at two different wind exposures (windward and leeward sides) on the same plant.

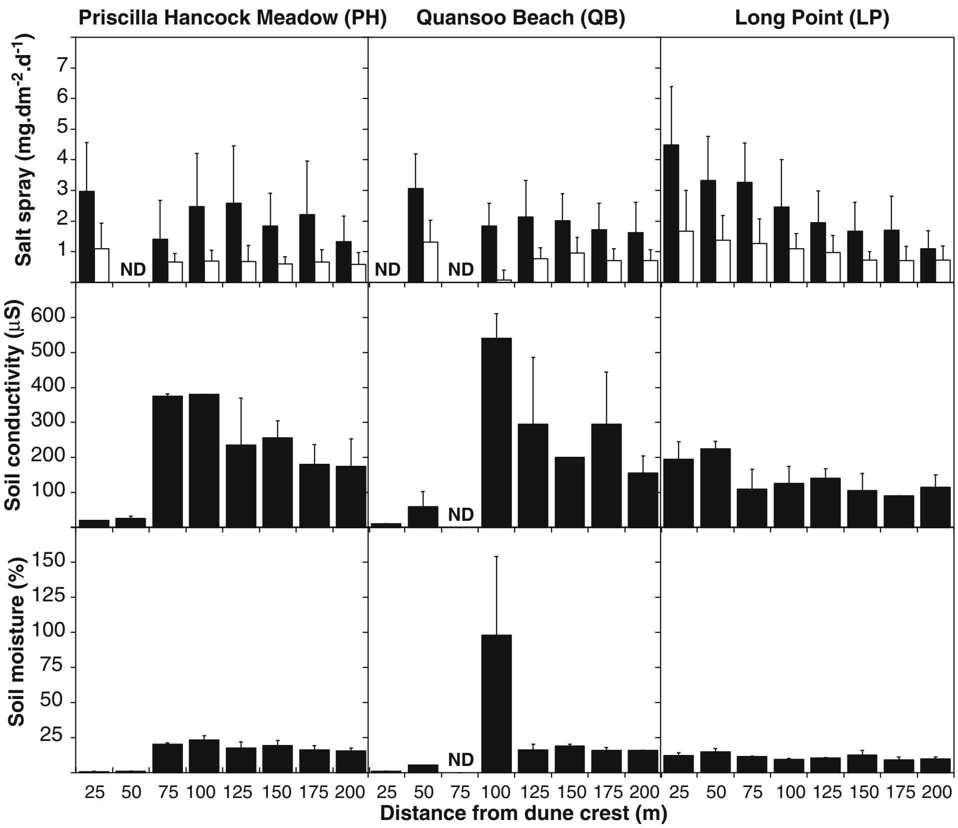


*Figure 1.* Salt spray accumulation, soil conductivity, and soil moisture as a function of distance at PH, QB, and LP. Salt spray accumulation was measured on leaves from the windward (filled bars) and leeward (open bars) side of the same *M. pensylvanica* plant. Data are mean values ± 1SD.

salt spray accumulation on the leeward side of plants decreased more gradually across the distance gradient than for the windward side.

Soil salt concentration, as measured by conductivity, varied among sites and distances, and there were site by distance interactive effects (Table 1; Figure 1). Soil salt was highly variable across the distance gradient at PH and QB, but relatively constant at a mean level of 150 µS at LP. For PH and QB, soil salt was less than 50 µS close to the dune crest, where sampling points fell on the sandy dune, increased to as much as 400 µS at intermediate distances where sampling points were on the coastal plain, and then fell to about 150 µS at 200 m from the dune crest. At QB there was a peak in soil salt to a value of 500 µS in an area of salt marsh with saline, waterlogged soils at 100 m from the dune crest.

There were significant differences for soil moisture among sites and distances, and an interactive effect between site and distance (Table 1; Figure 1). Soil moisture was highest at PH, with a mean value of 24% water content and lowest at LP, where the mean soil water content was 11%. Although significant distance effects were observed, soil moisture did not show predictable patterns across the distance gradient. For PH and QB, soil moisture was less than 1% at 25 m from the dune crest, where sampling points fell on the sandy dune. Soil moisture increased to 25% farther away from the dune crest where sampling points were on the coastal plain. At QB, soil moisture peaked to close to 100% in the salt marsh area at 100 m.

The percentage of *M. pensylvanica* leaf area showing necrosis decreased from as much as 25% at 25 m from the dune crest to less than 5% at 200 m from the dune crest (Table 2; Figure 2). Necrosis did not differ significantly between the three sites, but there was a significant difference in

*Table 2.* Type III Sums of Squares results for three-way analyses of variance for *M. pensylvanica* leaf necrosis and height, a two-way analysis of variance on the height of the entire plant community.

| Source of variation | Leaf necrosis | | | *M. pensylvanica* height | | | Community height | | |
|---|---|---|---|---|---|---|---|---|---|
| | df | *F* | *p* | df | *F* | *p* | df | *F* | *p* |
| Site | 2 | 2.07 | 0.127 | 2 | 18.08 | < 0.001 | 2 | 16.74 | < 0.001 |
| Distance | 7 | 10.31 | < 0.001 | 7 | 104.34 | < 0.001 | 7 | 21.72 | < 0.001 |
| Wind exposure | 1 | 327.85 | < 0.001 | 1 | 56.78 | < 0.001 | | | |
| Site×distance | 11 | 8.80 | < 0.001 | 12 | 6.05 | < 0.001 | 13 | 4.26 | < 0.001 |
| Error | 891 | | | 637 | | | 607 | | |

Measurements were taken at three sites (PH, QB, and LP) and eight distances from the dune crest (25, 50, 75, 100, 125, 150, 175, and 200 m). For leaf necrosis and *M. pensylvanica* height, measurements were also taken at two different wind exposures (windward and leeward sides) on the same plant.

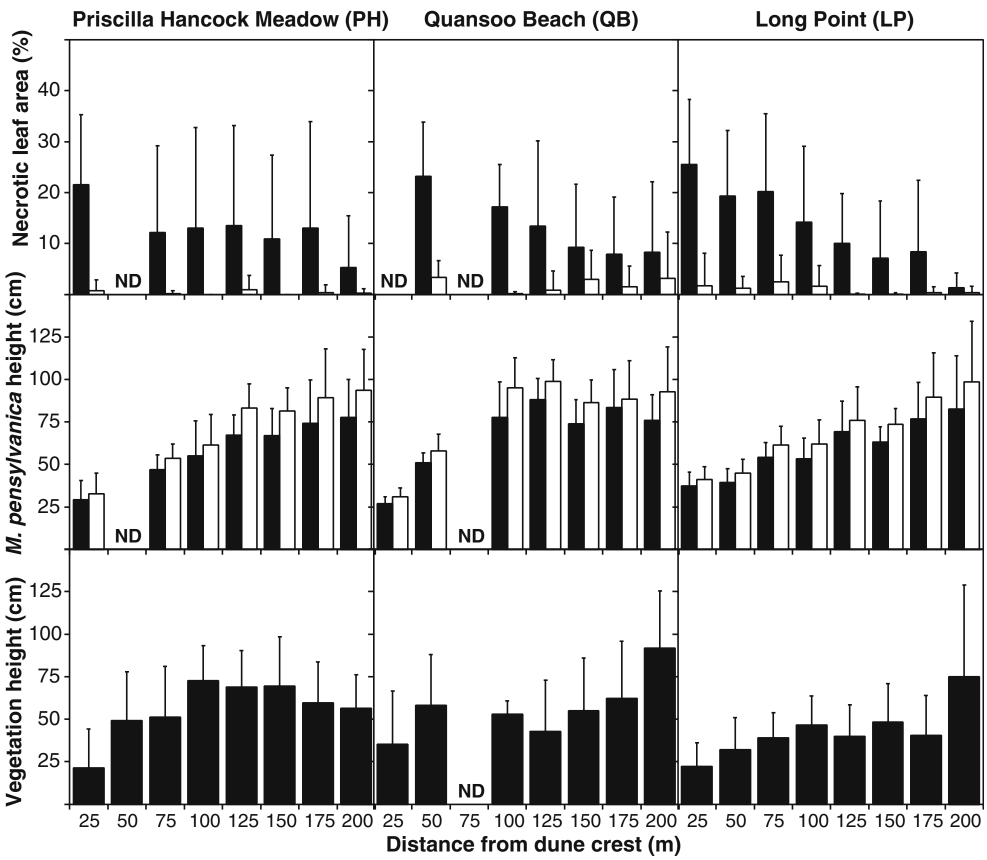


*Figure 2. Myrica pensylvanica* leaf necrosis, plant height, and surrounding vegetation height as a function of distance and orientation at PH, QB, and LP. Leaves sampled on *M. pensylvanica* plants were taken from the windward (filled bars) and leeward (open bars) side of the same plant. *Myrica pensylvanica* height was measured on the windward and leeward side of the same plant. Vegetation was measured by sampling 15 randomly chosen plants of any species surrounding each *M. pensylvanica* plant. Data are mean values ± 1SD.

necrosis levels between leaves from the windward and leeward side of the same plants, and there was a significant interaction between site and distance. Necrosis was at least four times higher on leaves from the windward side of plants as compared with leaves taken from the leaves side of the same plant. Necrosis levels changed more across the distance gradient at LP and QB than they did at PH.

Individuals of *M pensylvanica* growing close to the dune crest at LP had significantly lower predawn xylem pressure potential measurements than did plants growing farther away from the dune crest ($F_{7,16} = 10.84$, $p < 0.001$; Figure 3). All sampled plants growing within 125 m of the dune crest had predawn xylem pressure potentials below −2 MPa, indicating that water stress might be inhibiting physiological processes in the plants. Beyond 150 m, the predawn xylem pressure potentials increased to −1.5 MPa.

### *Heathland plant community stature*

Height of *M. pensylvanica* varied with site, distance and wind exposure (Table 2; Figure 2). On average, *M. pensylvanica* plants were taller at PH and QB than at LP. At all sites, there was a significant increase in the height of *M. pensylvanica* plants from approximately 30 cm at 25 m from the dune crest to over 90 cm at 200 m from the dune crest. Within individual *M. pensylvanica* plants, the windward side of the plant was up to 20 cm shorter than on the leeward side. There were significant site by distance interactions for *M. pensylvanica* height, with a relatively constant height between 100 and 200 m from the dune crest at QB and a constant increase in plant height across the distance gradient at PH and LP.

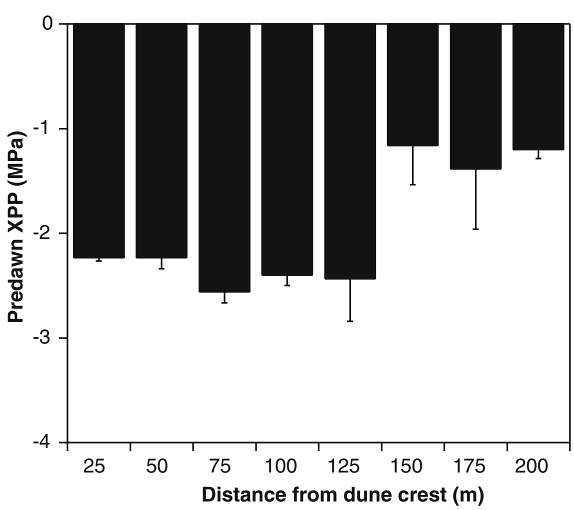


*Figure 3*. Predawn xylem pressure potential measurements taken on *M. pensylvanica* plants at LP. Data are mean values ± 1SD.

The vegetation canopy differed significantly among sites and distances and there was a site by distance interaction (Table 2; Figure 2). Overall, the vegetation was tallest at PH and lowest at LP. The vegetation was on average 25 cm tall at 25 m from the dune crest and 75 cm tall at 200 m from the dune crest. For both QB and LP, vegetation height increased as distance from the dune crest increased, while at PH maximum height occurred at intermediate distances.

### *Heathland community structure*

A total of 95 species were identified in the three sites, of which seven were introduced, accounting for less than 8% of all species (Appendix 1). The physiognomic composition of the community varied among sites and within sites by distance from the dune crest (Table 3). The plant communities had the highest percentage of graminoid, forb, vine and shrub species. Bryophyte and pteridiphyte species were not common at the three sites; a single bryophyte species was found at 50 m at QB and pteridiphyte species only appeared far from the dune crest at QB and LP. Based on physiognomic composition, PH and QB were more similar to one another than to LP, although there was a conspicuous absence of vines and shrubs in the salt marsh area at 100 m at QB. Lichens were present only at 25 and 50 m from the dune crest at PH and QB, whereas LP had lichen across the entire distance gradient measured. PH had a higher percentage of graminoid species than the other two field sites. At QB and LP, the percentage of species that were forbs peaked at intermediate distances but there were no consistent patterns for vines and shrubs. All field sites differed in the contribution of tree species to the community composition. Only one tree species, *Juniperus virginiana*, was present in transects at PH, while *J. virginiana*, *Q. ilicifolia*, *Q. velutina*, and *Prunus serotina* were present at QB beyond 125 m from the dune crest. *Acer rubra*, *Q. alba*, *Q. prinoides*, *Q. stellata*, and *P. serotina* were found in transects throughout the distance gradient at LP, even at distances closest to the ocean.

Floristic differences among sites and distances were also detected based on the presence or absence of species in transects (Appendix 1). The species that occurred in the most transects were the

*Table 3*. Percentage of species in the plant communities that are classified in different physiognomic groups at three sites (PH = Priscilla Hancock Meadow, QB = Quansoo Beach, and LP = Long Point) and eight distances from the dune crest (m).

| | Physiognomic composition of communities (%) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Lichens | Bryophytes | Pteridiphytes | Graminoids | Forbs | Vines | Shrubs | Trees |
| *PH* | | | | | | | | |
| 25 | 12.5 | 0 | 0 | 25 | 25 | 25 | 12.5 | 0 |
| 50 | 10 | 0 | 0 | 30 | 40 | 20 | 0 | 0 |
| 75 | 0 | 0 | 0 | 28 | 28.5 | 14.5 | 28.5 | 0 |
| 100 | 0 | 0 | 0 | 38.5 | 23 | 15.5 | 23 | 0 |
| 125 | 0 | 0 | 0 | 40 | 27 | 13 | 20 | 0 |
| 150 | 0 | 0 | 0 | 26 | 32 | 21 | 21 | 0 |
| 175 | 0 | 0 | 0 | 33 | 33 | 19 | 15 | 0 |
| 200 | 0 | 0 | 0 | 41 | 27 | 18 | 14 | 0 |
| *QB* | | | | | | | | |
| 25 | 17 | 0 | 0 | 17 | 33 | 33 | 0 | 0 |
| 50 | 0 | 9 | 0 | 18 | 37 | 9 | 27 | 0 |
| 100 | 0 | 0 | 0 | 44 | 56 | 0 | 0 | 0 |
| 125 | 0 | 0 | 0 | 13 | 34 | 13 | 34 | 6 |
| 150 | 0 | 0 | 0 | 17 | 43 | 17 | 20 | 3 |
| 175 | 0 | 0 | 4 | 15 | 27 | 23 | 31 | 0 |
| 200 | 0 | 0 | 4 | 14 | 32 | 11 | 28 | 11 |
| *LP* | | | | | | | | |
| 25 | 3 | 0 | 0 | 23 | 27 | 17 | 23 | 7 |
| 50 | 3 | 0 | 0 | 18 | 25 | 8 | 35 | 11 |
| 75 | 4 | 0 | 0 | 12 | 36 | 9 | 27 | 12 |
| 100 | 3 | 0 | 0 | 9 | 25 | 10 | 44 | 9 |
| 125 | 3 | 0 | 0 | 10 | 37 | 10 | 33 | 7 |
| 150 | 3 | 0 | 3 | 6 | 33 | 10 | 35 | 10 |
| 175 | 2 | 0 | 6 | 8 | 27 | 15 | 32 | 10 |
| 200 | 3 | 0 | 3 | 7 | 26 | 10 | 38 | 13 |

The presence or absence of each species was measured in 1 × 50 m transects.

graminoids *Festuca rubra* and *Schizachrium scoparium*, the vines *Rubus hispidus* and *Toxicodendron radicans*, and the shrubs *Gaylussacia baccata* and *M. pensylvanica*. All of these species were found relatively constantly throughout the distance gradient. Species characteristic of dune habitats, such as *Ammophila breviligulata*, *Lathyrus maritimus*, and *Solidago sempervirens*, were found close to the dune crest but did not occur farther inland. Ericaceous shrub species entered the plant communities at distances beyond 75 m from the dune crest. The percent of transects that contained tree species was higher farther from the dune crest.

Species diversity also showed distinctive patterns across the distance gradient in the three sites (Table 4; Figure 4). For Hill's N0 (species number), N1 ($e^{H'}$), and N2 ($1/\lambda$) there were significant site (MANOVA; Wilks' Lambda = 0.83, $F_{6,202} = 3.39$, $p = 0.003$), distance (Wilks' Lambda = 0.70, $F_{21,290} = 1.82$, $p = 0.017$, and site by distance interactions (Wilks' Lambda = 0.51, $F_{39,300} = 1.96$, $p = 0.001$). Overall, PH was less species-rich than QB and LP. LP had three times as many species at 25 m from the dune crest compared to PH and QB, most likely due to the fact that PH and QB have a sandy dune substrate at this distance. N1 and N2 for plots at 25 m from the dune crest at PH and QB were half the values for the same distance at LP, which is consistent with the interpretation that the community in these areas at PH and QB was primarily composed of a few very abundant species adapted to dunes. N1 and N2 also indicate that the community was more uniform across the distance gradient at LP than at PH and QB.

NMS showed that the community composition of quadrats at PH and QB was more similar than

*Table 4*. Type III Sums of Squares results from two-way analyses of variance for between-subjects effects in a MANOVA.

| Source of variation | Species number | | | Shannon diversity (H′) | | | Simpson diversity (λ) | | |
|---|---|---|---|---|---|---|---|---|---|
| | df | *F* | *P* | df | *F* | *P* | df | *F* | *P* |
| Site | 2 | 9.61 | < 0.001 | 2 | 5.48 | 0.005 | 2 | 2.75 | 0.069 |
| Distance | 7 | 3.23 | 0.004 | 7 | 5.37 | < 0.001 | 7 | 2.98 | 0.007 |
| Site×distance | 13 | 18.45 | 3.55 | 13 | 3.92 | < 0.001 | 13 | 2.53 | 0.005 |
| Error | 103 | | | 103 | | | 103 | | |

Measurements were taken at three sites (PH, QB, and LP) and eight distances from the dune crest (25, 50, 75, 100, 125, 150, 175, and 200 m).

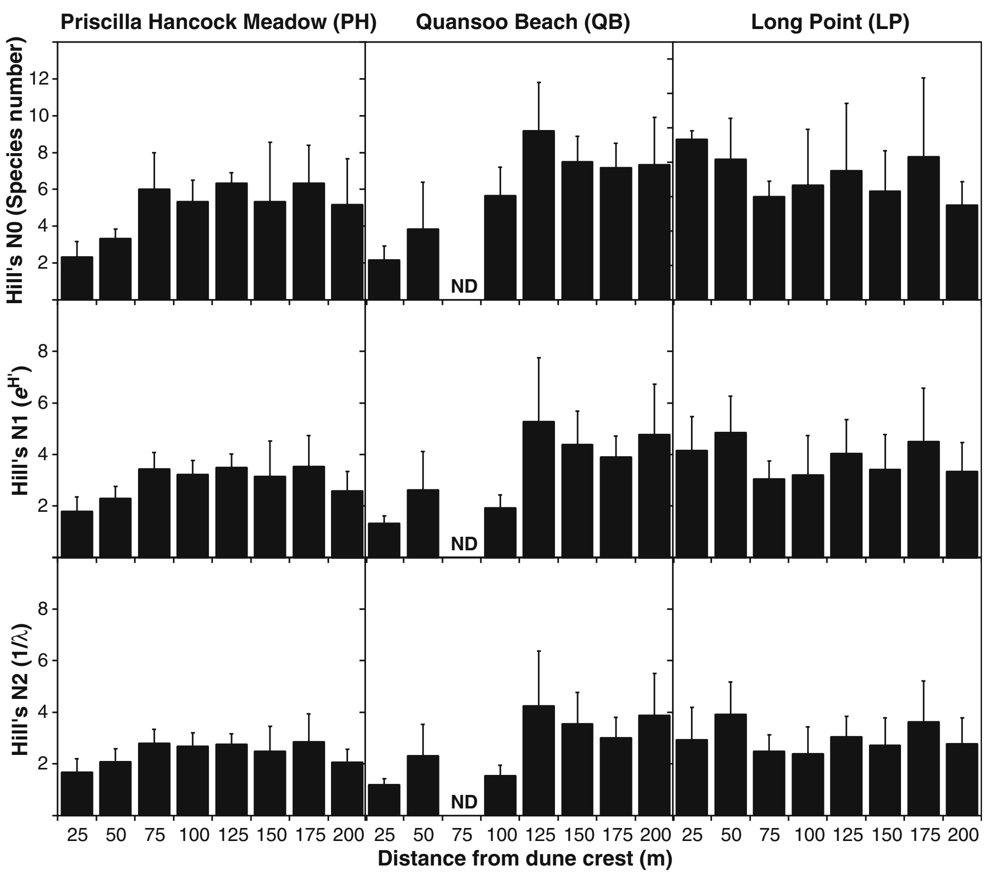


*Figure 4*. Hill's N0 (species number), N1 ($e^{H'}$), and N2 ($1/\lambda$) of the plant community at PH, QB, and LP. Data are mean values ± 1SD calculated from six 1 $m^2$ sample plots located at each distance from the dune crest.

compared to LP (Figure 5). The first NMS axis separated PH from QB and LP, and the second axis separated PH and QB from LP. The mean distance scores for each site show a wide spread for QB, whereas they are more tightly grouped for PH and LP, suggesting that community composition changes less across the distance gradient at these sites. Randomization tests confirmed that sites differed significantly from one another ($p < 0.001$ for all between-site comparisons), so all further analyses were conducted on a per-site basis.

NMS and TWINSPAN analyses of the individual sites identified dune and salt marsh species assemblages that were distinct from heathland species assemblages (Figure 6). For PH, TWINSPAN analysis identified a dune subcommunity containing *A. breviligulata*, *Conyza canadensis*, *Gnaphalium obtusifolium*, *L. maritimus*, and *S. sempervirens*, whereas all other species were characteristic of coastal heathlands. For QB, one TWINSPAN group, composed of the salt marsh species *Agrostis gigantea*, *Atriplex hastata*, *Juncus gerardii*, *Pluchea odorata*, and *Spartina patens*, was found in a single sampling quadrat located at 100 m from the dune crest in the area of salt marsh. Two additional subcommunities were detected at QB, representing dune and heathland groups similar to those found at PH. For LP, the community at was much more uniform and there were no identifiable dune subcommunities. TWINSPAN identified two species assemblages that clustered within the heathland community. One group was composed of *Cladonia* sp., *G. baccata*, *Parthenocissus quinquifolia*, and *R. hispidus*. A second group contained *Epigaea repens*, *Kalmia angustifolia*, *Melampyrum lineare*, and *Q. ilicifolia*.

CCA demonstrated that community structure is related to salt spray, soil salt, and soil moisture (Figure 6). For PH and QB, the first two axes explained 23% of the variance, while for Long Point the first two axes only explained 16%. Positive correlations were found between soil salt and moisture at PH ($r^2 = 0.90$) and QB

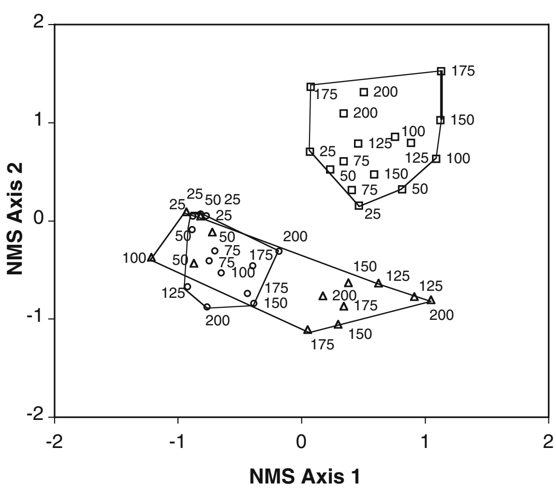


*Figure 5*. Ordination along the first two axes using NMS showing the mean quadrat scores for plant communities at different distances from the ocean at three sites on Martha's Vineyard. The code for sample scores denotes the distance from the dune crest (m). The NMS plot is overlaid with outlines of the ranges for each site and each site is represented by a different symbol: PH (circles), Quansoo Beach (triangles), and LP (squares).

($r^2 = 0.81$). At LP, positivecorrelations were found between salt spray and soil salt ($r^2 = 0.76$), between salt spray and soil moisture ($r^2 = 0.55$), and between soil salt and soil moisture ($r^2 = 0.79$). Monte Carlo permutation tests showed that the observed relationships between species distribution and environmental variables were significantly different from a null hypothesis of no linear relationship (PH, $F = 4.11$, $p = 0.002$; QB, $F = 3.61$, $p = 0.002$; LP, $F = 2.93$, $p = 0.002$). The distributions of species at PH and QB were best explained by soil moisture and soil salt. Salt spray was closely correlated with the second axis for PH and QB, and was the variable that best explained the distribution of species along that axis. Conversely, at LP salt spray was the environmental variable that best explained the species distribution and it was closely correlated with the first axis, which explains the most variance in the dataset.

## Discussion

Salt spray accumulates on coastal plants as a result of interception by aboveground vegetation and dry fallout (Gustafsson and Franzén 1996). It has been proposed that salt spray might play an important role in the vegetation dynamics of coastal sandplain heathlands (Dunwiddie 1989). At the same time, anthropogenic disturbances such as fire and livestock grazing have been shown to arrest succession in heathlands, which would suggest that the existing communities are relicts of human land use (Dunwiddie 1989; Litvaitis et al. 1999). This study is novel because until now, no studies have addressed the question of whether heathland stature and composition could historically have been maintained by natural abiotic conditions. The results of this research support the hypotheses that salt spray influences heathland stature by suppressing plant growth close to the ocean and that salt spray and edaphic factors structure the plant community composition.

### *Environmental variables and plant condition*

The finding that salt spray accumulation decreases as distance from the dune crest increases is consistent with previous investigations in other

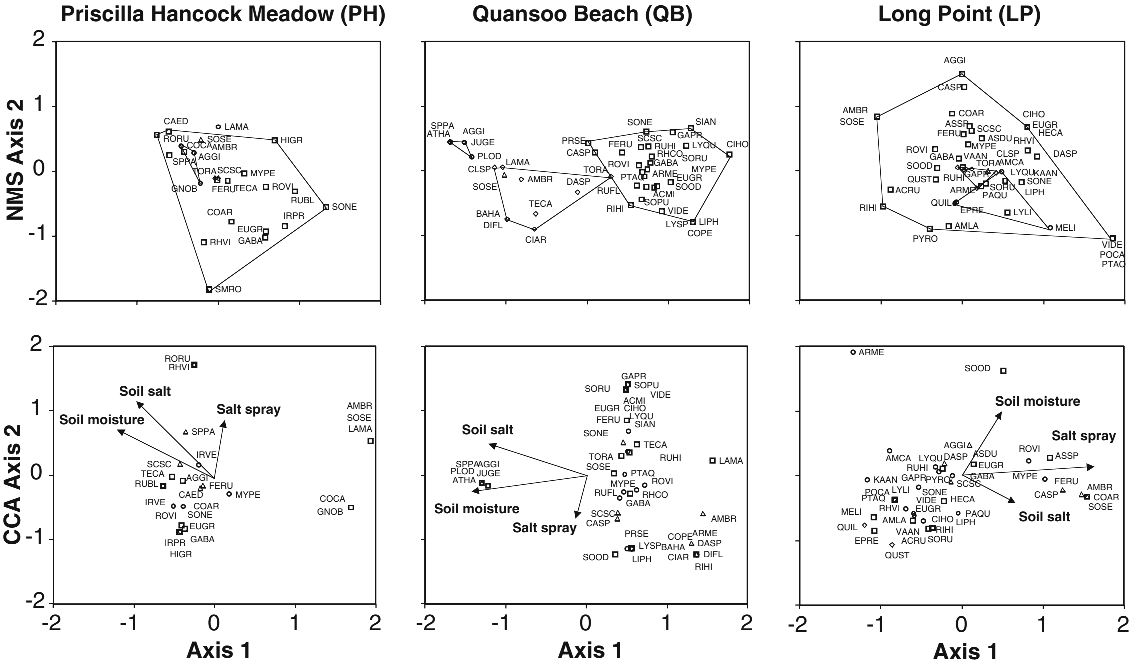


*Figure 6*. NMS and CCA for PH, QB, and LP. The points on each NMS plot represent species, which are identified by a code made up of the first two letters of the genus and the first two letters of the species name (see Appendix 1). Species groups identified by TWINSPAN are each represented by a different symbol and indicated by envelopes. For CCA, salt spray, soil salt, and soil moisture were included as environmental variables. On the CCA plots, each species is classified as graminoid (triangles), forb (squares), shrub (circles), or tree (diamonds).

coastal plant communities (Edwards and Claxton 1964; Randall 1970; Malloch 1972; Barbour 1978; Cartica and Quinn 1980; Maze and Whalley 1992), as is the result that windward leaves accumulate more salt spray than leeward leaves from the same plant (Oosting and Billings 1942; Alpha et al. 1996). Leaves and branches on the windward side of plants intercept salt spray and prevent its accumulation on the leeward side (Wells and Shunk 1938). On the leeward side, however, the main source of salt spray accumulation is from fallout. Salt accumulation from dry fallout is typically low and remains relatively constant over long distances (Toba 1965), which explains the relatively constant accumulation observed on the leeward side of plants.

Like leeward salt spray accumulation, the source of soil salt is from fallout. The amount of salt that ultimately accumulates in the soil is a function of vegetation structure (because dense plant cover will intercept much of the fallout) and the cation exchange capacity of the soil. Soil salt was variable across the distance gradient at PH and QB, where vegetation structure and soil quality were both highly variable, whereas soil salt, vegetation structure and soil quality were all relatively constant across the distance gradient at LP.

Differences among sites in terms of soil moisture can best be explained by differences in topography. The site with the lowest soil moisture, LP, also had the highest elevation and was therefore most removed from the belowground water table. Soil water availability was consistently lowest in sampling points that fell on the dune crest, where soils were very sandy. Soil type clearly influences both how much salt accumulates in the soil and how much moisture can be held in the soil.

Necrosis, predawn xylem pressure potential, and plant height showed strong patterns related to distance from the dune crest. Since soil salt concentration and water content do not show consistent spatial patterns, salt spray accumulation on plants is the most likely explanation for differences in plant performance. This study found that necrosis on *M. pensylvanica* leaves decreased as distance from the dune crest increased. Necrosis levels were also higher on leaves from the windward side of plants than on those from the leeward side. These findings are consistent with previous studies demonstrating damage to plants as a result of salt spray accumulation (Wells and Shunk 1938; Edlin 1943; Morris 1992).

Furthermore, Pammenter and Smith (1983) demonstrated that plants with increasing salt spray accumulation show a rapid decrease in xylem pressure potential. This study similarly found that predawn xylem pressure potential was lowest in plants growing close to the dune crest and higher inland, but this relationship was a threshold response rather than a gradient with increasing distance from the ocean. Since water availability was not lower at these distances, this indicates that plants receiving the highest amount of salt spray were under the most water stress, which can lead to reduced photosynthesis and growth (Cheplick and Demetri 1999).

*Heathland plant community stature*

Reduced growth due to a disruption in water balance can lead to lower vegetation stature. There were differences in the height of *M. pensylvanica* plants and the surrounding canopy vegetation across the distance gradient; plant height increased as distance from the dune crest increased. Again, these results are consistent with a salt spray effect. Interestingly, at all three sites *M. pensylvanica* is as tall as, or taller than, the surrounding vegetation. Since this genus is one of the more salt-tolerant among dune and heathland plants (Wells and Shunk 1938), this provides strong evidence that salt spray can maintain the low stature of heathlands on wind-exposed shores. The significance of windward or leeward exposure also emphasizes the importance of salt spray. At each site, the windward sides of *M. pensylvanica* plants were shorter than the leeward side of the same plant. Because salt spray kills meristems and leaf tissue, growing shoots on the windward side of a plant would be damaged by salt spray, inhibiting growth (Wells and Shunk 1937; Boyce 1954), while leeward shoots survive better because they are protected (Wells and Shunk 1938). The asymmetry in growth form that was observed is not likely due exclusively to the effects of wind, since manipulative experiments in the field (Griffiths and Orians 2003a) and greenhouse (Griffiths and Orians 2003b) have demonstrated that salt spray alone inhibits growth in *M. pensylvanica* plants.

*Heathland plant community structure*

Many mechanisms have been hypothesized to control the composition of plant communities (Palmer 1994). Previous research has shown that coastal sandplain heathlands are maintained by disturbances such as fire and grazing that slow the invasion of competitively dominant woody species (Dunwiddie and Caljouw 1990). The results presented here demonstrate that the community composition of heathlands is also strongly associated with spatial patterns in abiotic environmental conditions. These findings are consistent with other studies that have found that salt spray, soil moisture, and soil salt can cause distinctive zonation in other coastal plant communities (Oosting 1945; Parsons and Gill 1968; Barbour 1978; Sykes and Wilson 1991; Anderson et al. 1998; Hoare et al. 2000).

Species distributions at the three field sites were significantly different from one another and appeared strongly determined by topography and soil texture. The variation between sites appears to be driven by the presence of well-developed dunes at PH and QB. There were distinctive dune, salt marsh, and heathland groups at PH and QB, but the community at LP was much more uniform heathland, with no identifiable dune subcommunities. The dune communities at PH and QB were dominated by a few very abundant species that extended to 75 m from the dune crest, after which they were replaced by heathland species. Ericaceous shrubs, which are characteristic of coastal heathlands, were limited close to the ocean at PH and QB, but increased in frequency at distances beyond 75 m from the dune crest. On the other hand, the communities at LP contained more shrub and tree species, and fewer grass species, than in matched distances at PH and QB. At LP, ericaceous shrubs were found as close as 25 m from the dune crest.

One striking difference among field sites was the pattern in tree distribution. Trees were completely absent at PH, except for *J. virginiana*, but were present inland of 150 m at QB and were found throughout the distance gradient at LP. One woody species that succeeds in undisturbed heathlands, *Q. ilicifolia*, was found only at LP. Salt spray causes selective mortality in tall plants because they are more exposed to wind and intercept more salt spray (Boyce 1954); therefore, it is likely to be an important factor in limiting the occurrence of tree species in coastal habitats. Manipulative studies have demonstrated that the negative effects of salt spray can be ameliorated by high water availability (Griffiths and Orians 2003a). Surveys at PH and QB found that there was high salt spray and low water availability 25 m from the dune crest, while at LP there was high salt spray and high water availability. The high soil water close to the dune crest at LP offers an explanation for why heathlands occur closer to the ocean and why trees, although stunted, are found growing in the high salt spray zone within 25 m of the dune crest.

Within sites, community complexity and species diversity generally increased with increasing distance from the dune crest, but the patterns in community composition varied by site. The observed pattern is consistent with research in New England maritime forests that has described an increase in species diversity at increasing distances from the coast (Milne and Forman 1986). As was demonstrated in these field surveys, abiotic conditions become more extreme as proximity to the ocean increases. Species richness is expected to decrease as environmental harshness increases, but may also decrease where abiotic stresses are not as prevalent and species sorting due to competition begins to occur (Wilson and Keddy 1986).

The distributions of species at PH and QB were best explained by soil moisture and soil salt, while salt spray best explained patterns in species distribution at LP. The results for PH and QB appear to be driven by the presence of a distinctive dune community. Since dunes are recognized as having low soil salt and low water availability (Oosting and Billings 1942), it is not surprising that these two factors drove species distributions at PH and QB. At LP, where soil salt and soil moisture were uniform across the distance gradient, salt spray was the most important environmental variable explaining species distributions. Salt-tolerant species (*M. pensylvanica* and *A. breviligulata*) were separated from species with lower salt spray tolerance (*Q. ilicifolia* and *Q. stellata*), suggesting that salt spray is important in structuring the heathland community at LP. These data also suggest that salt spray might limit tree distribution at all sites because there were no trees growing close to the ocean.

## Conclusions

Collectively, these results demonstrate that belowground water availability is the most limiting environmental factor on sand dunes but heathland communities are more influenced by salt spray. From this study, a model of filters could be proposed. Where soil quality and topography lead to low soil moisture, belowground water may be the most limiting factor in these coastal communities. However, when moderate levels of water are available, salt spray controls the species composition of heathlands.

The research presented here addresses gaps in our knowledge about the ecology of an ecosystem with high conservation value. It has been demonstrated that anthropogenic disturbances such as fire and livestock grazing are necessary to maintain heathlands these factors may control the large scale patterning of heathlands. The outer boundaries of this community type are likely maintained by anthropogenic disturbances of this type. The field studies presented here find that salt spray, soil moisture, and soil salt also influence the stature and composition of coastal heathland plant communities. These results suggest that salt spray may control the fine scale distribution of species in the most coastal areas of heathlands and that, even in the absence of fire and grazing, tree growth may be limited by salt spray close to the ocean. Particularly in areas with uniform soil moisture, salt spray is likely to be the most important environmental factor determining the distribution of species because it can limit the growth of tree species.

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*Appendix 1.* Species occurrences in transects along a distance gradient (– indicates absent in all transects, + indicates present in less that 50% of the transects, + + indicates present in greater that 50% of the transects) at three sites: Priscilla Hancock Meadow (PH), Quansoo Beach (QB), Long Point (LP).

| | Distance from dune crest (m) | | | | | | | | Sites | Status |
|---|---|---|---|---|---|---|---|---|---|---|
| | 25 | 50 | 75 | 100 | 125 | 150 | 175 | 200 | | |
| **Lichens** | | | | | | | | | | |
| Cladoniaceae | | | | | | | | | | |
| *Cladonia* sp. | + + | + + | + + | + + | + | + | + | + | PH, QB, LP | N |
| **Bryophytes** | | | | | | | | | | |
| Dicranaceae | | | | | | | | | | |
| *Dicranumscoparium* | – | + | – | – | – | – | – | – | LP | N |
| **Pteridiphytes** | | | | | | | | | | |
| Aspleniaceae | | | | | | | | | | |
| *Thelypteris palustris* | – | – | – | – | – | – | + | – | LP | N |
| Dennstaedtiaceae | | | | | | | | | | |
| *Pteridium aquilinum* | – | – | – | – | – | + | + + | + + | QB, LP | N |
| **Graminoids** | | | | | | | | | | |
| Juncaceae | | | | | | | | | | |
| *Juncus gerardii* | – | – | – | + | – | – | – | – | QB | N |
| Poaceae | | | | | | | | | | |
| *Agrostis gigantea* | – | + | – | + | + | + | + | + | PH, QB, LP | I[a] |
| *Ammophila breviligulata* | + + | + + | + + | + + | – | + | + | – | PH, QB, LP | N |
| *Carex* sp. | + | + | – | – | + | + | + + | + | PH, QB, LP | – |
| *Danthonia spicata* | + | + + | – | + | + + | – | + | + | PH, QB, LP | N |
| *Festuca rubra* | + | + + | + + | + + | + + | + + | + + | + + | PH, QB, LP | N |
| *Holcus lanatus* | + | – | – | + | + | – | + | + | PH, LP | I[b] |
| *Panicum* sp. | + | – | + | – | – | – | + | – | PH, LP | – |
| *Panicum virgatum* | – | – | – | – | – | + | + | + | PH, QB | N |
| *Schizachyrium scoparium* | + | + | + + | + + | + + | + + | + + | + + | PH, QB, LP | N |
| *Spartina patens* | – | – | + + | + + | + | + | – | + | PH, QB | N |
| **Forbs** | | | | | | | | | | |
| Asteraceae | | | | | | | | | | |
| *Achillea millefolium* | – | – | – | – | + + | + | – | + | PH, QB | I[b] |
| *Anaphalis margaritacea* | – | – | + | – | – | – | – | – | LP | N |
| *Antennaria neglecta* | – | + | – | – | – | – | – | – | PH | N |
| *Aster dumosus* | + | + | + + | + + | + + | + | + | + | QB, LP | N |
| *Aster linariifolius* | – | – | – | – | – | + | – | – | QB | N |
| *Aster paternus* | – | + | – | – | – | – | – | – | LP | N |
| *Aster spectabilis* | + | + | + + | + | + | + | – | + | LP | N |
| *Aster subulatus* | – | + | – | – | – | – | – | – | PH | N |
| *Cirsium arvense* | + | + | – | – | – | – | – | – | QB, LP | I[b] |
| *Cirsium horridulum* | + | + | + | – | + + | + + | – | – | PH, QB, LP | N |
| *Conyza canadensis* | – | + | – | – | – | – | – | – | PH | N |
| *Euthamia graminifolia* | – | + | + | + + | + | + + | + + | + + | PH, QB, LP | N |
| *Euthamia tenuifolia* | – | – | – | – | – | – | + | – | LP | N |
| *Gnaphalium obtusifolium* | – | + | – | – | – | – | – | – | PH | N |
| *Hieracium gronovii* | – | – | – | – | – | – | + | + | PH | N |
| *Pluchea odorata* | – | – | – | + | + | + | – | + | QB | N |
| *Prenanthes trifoliolata* | – | – | – | – | + | – | – | – | LP | N |
| *Solidago nemoralis* | – | + | + | + + | + + | + + | + + | + + | PH, QB, LP | N |

*Appendix 1*. Continued.

| | Distance from dune crest (m) | | | | | | | | Sites | Status |
|---|---|---|---|---|---|---|---|---|---|---|
| | 25 | 50 | 75 | 100 | 125 | 150 | 175 | 200 | | |
| *Solidago odora* | – | – | + | – | – | + | + | + | QB, LP | N |
| *Solidago puberula* | – | – | – | – | – | – | + | – | QB | N |
| *Solidago rugosa* | + | + | + + | + + | + + | + + | + + | + + | PH, QB, LP | N |
| *Solidago sempervirens* | + + | + + | + + | + + | + | + | + | + | PH, QB, LP | N |
| Brassicaceae | | | | | | | | | | |
| *Cakile edentula* | – | – | + | – | – | – | – | – | PH | N |
| Caryophyllaceae | | | | | | | | | | |
| *Silene antirrhina* | – | – | – | – | + | + | – | – | QB | N |
| Chenopodiaceae | | | | | | | | | | |
| *Atriplex hastata* | + | – | + | + | – | – | – | – | PH, QB | I[a] |
| Cistaceae | | | | | | | | | | |
| *Helianthemum canadense* | – | – | – | + | + | – | + | + | LP | N |
| Fabiaceae | | | | | | | | | | |
| *Tephrosia virginiana* | – | – | – | – | – | + | + | – | LP | N |
| Iridaceae | | | | | | | | | | |
| *Iris prismatica* | – | – | – | – | – | – | + | – | PH | N |
| *Iris versicolor* | – | – | – | – | – | + | + | – | PH, QB | N |
| Lamiaceae | | | | | | | | | | |
| *Lycopus* sp. | – | – | – | – | – | – | – | + | QB | – |
| *Mentha arvensis* | – | – | – | – | – | – | – | + | PH | N |
| *Teucrium canadense* | – | + | + + | + + | + + | + | + + | + + | PH, QB | N |
| Liliaceae | | | | | | | | | | |
| *Lilium philadelphicum* | – | – | – | + + | + | + | + | + | QB, LP | N |
| Primulaceae | | | | | | | | | | |
| *Lysimachia quadrifolia* | + | + | + + | + + | + + | + + | + | + | QB, LP | N |
| *Trientalis borealis* | – | – | – | – | – | – | + | + | LP | N |
| Pyrolaceae | | | | | | | | | | |
| *Pyrola rotundifolia* | – | – | – | – | + | + | – | – | LP | N |
| Scrophulariaceae | | | | | | | | | | |
| *Melampyrum lineare* | + | – | – | – | – | – | + | + | LP | N |
| **Vines** | | | | | | | | | | |
| Anacardiaceae | | | | | | | | | | |
| *Toxicodendron radicans* | + + | + + | + + | + + | + + | + + | + + | + + | PH, QB, LP | N |
| Convolvulaceae | | | | | | | | | | |
| *Convolvulus arvensis* | + | – | – | + | + | + | + + | + | PH, QB, LP | I[a] |
| Cuscutaceae | | | | | | | | | | |
| *Cuscuta gronovii* | – | – | + | – | – | – | – | – | PH | N |
| Fabiaceae | | | | | | | | | | |
| *Lathyrus maritimus* | + + | + | – | – | – | – | – | – | PH, QB | N |
| Rosaceae | | | | | | | | | | |
| *Potentilla canadensis* | – | – | – | – | – | – | + | – | LP | N |
| *Rubus flagllaris* | – | – | – | – | + | + | + | – | QB, LP | N |
| *Rubus hispidus* | + | + | + + | + + | + + | + + | + + | + + | PH, QB, LP | N |
| *Rubus* sp. *blackberry* | + | – | – | – | – | + + | + + | + | PH, QB | – |
| Smilacaceae | | | | | | | | | | |
| *Smilax rotundifolia* | – | – | – | – | + | + | – | – | PH, QB | N |
| Vitaceae | | | | | | | | | | |
| *Parthenocissus quinquefolia* | + | – | – | + | + | + | + | + | LP | N |
| *Vitis labrusca* | – | – | – | – | – | + | + | – | QB, LP | N |
| **Shrubs** | | | | | | | | | | |
| Anacardiaceae | | | | | | | | | | |
| *Rhus copallinum* | – | – | – | – | + | + | + | + | QB | N |
| Asteraceae | | | | | | | | | | |
| *Baccharis halimifolia* | – | + | + | – | – | – | – | – | PH, QB | N |
| *Corylus americana* | – | – | – | – | + | – | – | – | QB | N |

*Appendix 1*. Continued.

| | Distance from dune crest (m) | | | | | | | | Sites | Status |
|---|---|---|---|---|---|---|---|---|---|---|
| | 25 | 50 | 75 | 100 | 125 | 150 | 175 | 200 | | |
| Caprifoliaceae | | | | | | | | | | |
| *Sambucus canadensis* | – | – | – | + | – | – | – | – | LP | N |
| *Viburnum dentatum* | – | + | – | – | + | – | + + | + | QB,LP | N |
| Ericaceae | | | | | | | | | | |
| *Epigaea repens* | – | – | – | + | + | + | + | + | LP | N |
| *Gautheria procumbens* | + | + | + | + + | + | + | + | + | QB, LP | N |
| *Gaylussacia baccata* | + | + | + + | + + | + + | + + | + + | + + | PH, QB, LP | N |
| *Kalmia angustifolia* | – | – | – | + | – | + | + | + | LP | N |
| *Lyonia ligustrina* | – | – | – | + + | + | + | + | + | LP | N |
| *Rhododendron viscosum* | – | – | – | – | – | – | + | + | LP | N |
| *Vaccinium angustifolium* | + | + | + + | + | + | – | + | + | LP | N |
| *Vaccinium pallidum* | – | + | – | + | – | – | – | – | LP | N |
| *Vaccinum corymbosum* | – | – | – | – | + | – | – | – | QB | N |
| Grossulariaceae | | | | | | | | | | |
| *Ribes hirtellum* | – | – | – | + | + | + + | + | + | QB, LP | N |
| Myricaceae | | | | | | | | | | |
| *Comptonia peregrina* | – | + | + + | + + | + | + | + | + | QB, LP | N |
| *Myrica pensylvanica* | + + | + + | + + | + + | + + | + + | + + | + + | PH, QB, LP | N |
| Rosaceae | | | | | | | | | | |
| *Amelanchier canadensis* | + | + | + + | + + | + + | + + | + | + | PH, QB, LP | N |
| *Amelanchier laevis* | + | – | – | + | + | – | + | – | LP | N |
| *Aronia melanocarpa* | – | + | – | + + | + + | + + | + | + + | QB, LP | N |
| *Prunus maritima* | – | – | – | – | – | – | + | – | QB | N |
| *Rosa rugosa* | – | – | – | + | + | + | – | – | PH | I[c] |
| *Rosa virginiana* | + | + | + + | + | + + | + + | + + | + + | PH, QB, LP | N |
| **Trees** | | | | | | | | | | |
| Aceraceae | | | | | | | | | | |
| *Acer rubrum* | – | – | – | – | – | – | + | – | LP | N |
| Cupressaceae | | | | | | | | | | |
| *Juniperus virginiana* | – | + | – | – | + | – | – | + | PH, QB | N |
| Fagaceae | | | | | | | | | | |
| *Quercus alba* | – | + | + + | – | – | + | + | + | LP | N |
| *Quercus ilicifolia* | + | + | + | + | + + | + + | + | + + | QB, LP | N |
| *Quercus prinoides* | – | – | – | + | – | – | – | – | LP | N |
| *Quercus stellata* | + | + | + | + + | + | + | + | + | LP | N |
| *Quercus velutina* | – | – | – | – | – | – | – | + | QB | N |
| Rosaceae | | | | | | | | | | |
| *Prunus serotina* | – | – | – | – | – | – | – | + + | QB, LP | N |

Species are organized according to physiognomic group and family. The status for each species is listed as native (N) or introduced (I), and the origin of introduced species is denoted by the superscript letter. (I[a] = introduced from Eurasia, I[b] = introduced from Europe, I[c] = introduced from East Asia) (Magee and Ahles 1999).

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