

SALT SPRAY DIFFERENTIALLY AFFECTS WATER STATUS, NECROSIS, AND GROWTH IN COASTAL SANDPLAIN HEATHLAND SPECIES¹

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Sandplain heathlands are disturbance-dependent plant communities that occur infrequently in coastal areas of the northeastern United States. We hypothesize that salt spray plays a role in maintaining the composition of the heathland community by excluding salt-intolerant species close to the ocean. We examined the distributions of *Solidago nemoralis*, *Myrica pensylvanica*, *Pinus rigida*, and *Quercus* spp. in heathlands and conducted greenhouse studies to determine whether different levels of salt spray tolerance explain patterns found in the field. We found that common heathland forb and shrub species grow closer to the ocean than successional woody species. In greenhouse experiments, these species differ in their water status, necrosis, and growth responses to salt spray. The tree species *P. rigida* and *Q. rubra* are more susceptible to salt spray than the common heathland species *M. pensylvanica*. Our results suggest that salt spray may prevent tree species in heathlands from growing close to the ocean and therefore might be an important factor in maintaining the characteristic community composition of these dwarf shrublands in coastal habitats.

Key words: coastal sandplain heathlands; *Myrica pensylvanica*; *Pinus rigida*; *Quercus ilicifolia*; *Quercus rubra*; salt spray; *Solidago nemoralis*.

Critical questions in plant ecology are how communities assemble and how community composition affects ecosystem function and vulnerability to invasion (Sait et al., 2000; Symstad, 2000). These questions are of particular interest in disturbance-dependent systems, in which abiotic and biotic processes influence plant community structure. By understanding the underlying physiological and morphological mechanisms affecting community composition, we may be able to predict how disturbances might modify the community in the future. These mechanisms are important not only from a theoretical perspective, but also from a management perspective for rare disturbance-dependent plant communities.

The coastal sandplain heathland is an endangered ecosystem in northeastern North America that is maintained by disturbances. Without disturbance processes, these dwarf shrub communities are succeeded by native woody species, such as *Pinus rigida* and *Quercus* spp., that outcompete shorter heathland plants (Dunwiddie, 1989). Disturbances in heathland communities historically included fire set by Native Americans and domestic livestock grazing by European settlers (Patterson and Sassman, 1988; Dunwiddie, 1990). The large-scale increase in heathland acreage following European settlement is attributed to anthropogenic processes (Dunwiddie, 1989), as is the production of the heathland communities in North America

(Litvaitis et al., 1999). To date, the possible influence of natural processes on coastal heathlands has largely been ignored.

Studies in coastal plant communities have found that salt spray is an important natural selective abiotic factor. Salt-sensitive species like *P. taeda* can be eliminated entirely from areas with high salt spray (Wells and Shunk, 1938). Different levels of salt spray tolerance among species can result in vegetation zonation; plants adapted to salt spray grow close to the ocean and are replaced by less salt-resistant plants farther inland (Oosting and Billings, 1942; Oosting, 1945; Buschbom, 1968; van der Valk, 1974a; Barbour, 1978; Parsons, 1981; Yura, 1997). In New England coastal sandplain heathland plant communities, we found that natural salt spray accumulation on plants in the field is correlated with lowered predawn xylem pressure potential, increased necrosis, and short stature (M. E. Griffiths and C. M. Orians, unpublished data). We also have evidence that oceanic salt spray may limit the growth of the invasive tree species *P. rigida* from heathlands near the Atlantic coast (M. E. Griffiths and C. M. Orians, unpublished data).

Based on these observations, we hypothesize that heathland community composition and zonation are structured by the effects of salt spray. Furthermore, we hypothesize that plants typical of coastal heathlands are more salt tolerant than successional trees. To test these hypotheses, we surveyed the distribution of species in heathland communities and experimentally manipulated salt spray in the greenhouse to determine whether interspecific differences in salt spray tolerance might be driving the field distribution of species. Our field sampling and greenhouse research involved four species: *Solidago nemoralis* and *Myrica pensylvanica*, representatives of typical heathland species, and *Pinus rigida* and *Quercus rubra*, native successional tree species in these communities. Using these species, we determined the effect of salt spray on water status, necrosis, and growth. Based on the timing and intensity of these responses, we infer that interspecific differences in salt spray tolerance may alter the composition of the heathland plant community.

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MATERIALS AND METHODS

Field distributions—Field surveys were carried out on Martha's Vineyard, Massachusetts, USA (41°22' N, 70°40' W) during the summer of 1999. Study sites included three conservation areas along the southern shore of the island in close proximity to the ocean: Priscilla Hancock Meadow, Quansoo Beach, and Long Point Wildlife Refuge. We found that salt spray accumulates on plants growing in these areas and that it accumulates in a predictable spatial pattern. Mean salt spray accumulation on *M. pensylvanica* plants was high at 25 m from the dune crest ($4.5 \text{ mg NaCl} \cdot \text{dm}^{-2} \cdot \text{d}^{-1}$) and decreased steadily along a gradient of increasing distance (data not shown). At all field sites, we measured plant species canopy coverage in six randomly placed 1-m² plots at each of eight distances from the dune crest: 25, 50, 75, 100, 125, 150, 175, and 200 m. Canopy coverage was estimated using a 20 × 20 cm grid on a 1-m² frame. We found *S. nemoralis*, *M. pensylvanica*, and *Q. ilicifolia* in our sampling plots. *Pinus rigida* and *Q. rubra*, although present in the inland forests nearby, were not captured in our census.

Greenhouse experiment—Four focal species were used in this study: *Solidago nemoralis* Aiton, *Myrica pensylvanica* Mirbel, *Pinus rigida* Miller, and *Quercus rubra* L. *Quercus ilicifolia* is the most common successional oak species in coastal heathlands, but the seed for this species was unavailable. *Quercus rubra*, another successional oak species in the same subgenus as *Q. ilicifolia*, was used in its place.

Seeds of *S. nemoralis* from Prairie Moon Nursery (Winona, Minnesota, USA) were cold stratified for 2 mo at 5°C and then germinated in sand. Plants were then transplanted into pots and grown for 2 mo before the start of the experiment. One-year-old plants of *M. pensylvanica* from New England Wetland Plants (Amherst, Massachusetts, USA) were transplanted into pots and grown for 4 mo. Seeds of *Pinus rigida* were collected in Barnstable, Massachusetts, USA, and germinated in peat; the seedlings were transplanted into pots and grown for 6 mo. One-year-old *Q. rubra* liners from Forest Keeling Nursery (Elsberry, Missouri, USA) were grown in individual pots for 2 mo. All species were planted in 25.5 × 6.5 cm pots filled with sterilized sand because coastal heathlands grow in very sandy soil that tends to be nutrient deficient. Furthermore, because the soil is porous, leaching rate is high and salt does not accumulate in the root zone (M. E. Griffiths, personal observation).

Sixty plants of each species were randomly assigned a position on the greenhouse bench. On 1 July 2001, plants were randomly assigned to one of two spray treatments: control or salt spray. Both treatments were applied by removing plants from the watering system, taking them outside, and spraying each individual plant with solution using a hand-held plant mist bottle. The control treatment, in which plants were sprayed with deionized water, was designed to control for any mechanical or physical effects of the misting process. Salt solutions were prepared with Instant Ocean artificial sea salt (Aquarium Systems, Mentor, Ohio, USA) to concentrations of 31 ppt, with sodium and chloride accounting for approximately 86% of the ions present, similar to the natural composition of salt water (Millero, 1974).

Spray treatments began on 3 July 2001 and continued until 10 October 2001. Plants were sprayed two times weekly, and all parts of plants were equally exposed. Spray was allowed to accumulate throughout the experiment so that we could identify the level of salt spray at which water status, necrosis, and growth measurements began to be affected and how this response time differed among species. This condition is realistic in the field because in years with infrequent rain salt spray is not washed off during the summer growing season (M. E. Griffiths, personal observation). The salt loads that accumulated on plants were checked by spraying test plants, sampling leaves from those plants, eluting the salt from the leaves with deionized water, and measuring the fluid conductivity. Plants were sprayed at a level at which their accumulated salt spray by the middle of the experimental period was equivalent to that under normal conditions at 25 m from the dune crest ($4.5 \text{ mg NaCl} \cdot \text{dm}^{-2} \cdot \text{d}^{-1}$). By the last sampling, the salt load on leaves was equivalent to the amount of salt that would be on a plant under dry tropical storm conditions at 25 m from the dune crest ($8 \text{ mg NaCl} \cdot \text{dm}^{-2} \cdot \text{d}^{-1}$; M. E. Griffiths, unpublished data).

Plants were watered with tap water using an automatic system that fed directly into the pots to ensure that any salt accumulation on the leaves and aboveground tissue was not washed off. Plants were watered once daily at 0600. Plants were not fertilized because previous research had indicated that nutrient solutions containing nitrogen can reduce the tolerance of plants to salt spray (Boyce, 1954) and because heathlands are typically low in nutrients.

We used physiological, morphological, and growth measurements to quantify the effects of salt spray on plant performance. Measurements of plant water status, necrosis, and growth were taken on 2 July, 24 July, 15 August, 14 September, and 11 October. On each sampling date, six plants per species per spray treatment were destructively harvested, so the plants were never sampled more than one time. Water status indices included xylem pressure potential and leaf water content. Predawn xylem pressure potential was measured at 0400 using a pressure chamber (PMS Instrument, Corvallis, Oregon, USA). Leaf water content was measured on the first fully expanded leaf or needle at the top of each plant. Leaf water content was calculated using the following equation: $\text{water content} = (\text{leaf wet mass} - \text{leaf dry mass}) / \text{leaf dry mass}$. Leaf necrosis, often used as an index for salt spray damage because it results directly from a buildup of chloride ions (Boyce, 1954; Morris, 1992), was assessed on the same leaf used for water content measurements. Leaf necrosis was measured as a proportion of the total leaf area.

Several growth measurements were made on each plant. Total leaf area and leaf number were measured. For *P. rigida*, needle length was used to approximate leaf area. The total number of needles on each *P. rigida* plant was not counted. On *M. pensylvanica* plants, leaf number was estimated based on a subsample; the number of leaves along a 5-cm length of shoot was multiplied by height. Plant height was measured for each plant on the sampling date only. Aboveground biomass was harvested, oven-dried at 60°C for 48 h, and massed.

All statistical analyses were run using SAS (SAS Institute, 1990). Three-way analyses of variance using the main effects of species, spray treatment, and day of exposure were run on all data. Additional two-way analyses of variance using the main effects of spray treatment and day of exposure were run for each individual species because of significant interaction effects involving species.

RESULTS

Field distributions—Field surveys of the plant community revealed that different species have different distributions (Fig. 1). *Solidago nemoralis* occurred at low levels close to the ocean, had highest coverage at 125 m from the dune crest, and then had decreasing cover as distance from the dune crest increased. *Myrica pensylvanica* had moderate cover close to the ocean, a slight decrease in cover at 50 and 75 m from the ocean, and then increasing cover as distance from the dune crest increased. We did observe this species growing abundantly between 25 and 50 m, but most of these plants were not captured by our sampling technique. *Quercus ilicifolia* did not appear in the community until 175 m from the dune crest and then increased in cover farther inland. *Quercus rubra* and *P. rigida* were observed in inland forests adjacent to the study sites, but they were not found anywhere within the areas of heathland surveyed and therefore are not included in any analyses for field distributions.

Greenhouse experiment—Water status—Throughout 14 wk of salt spray treatment, all the species tested showed a significant difference in predawn xylem pressure potential with salt spray treatment (Table 1; Fig. 2). Overall, plants treated with salt spray had more negative xylem pressure potentials than plants growing in control treatments. One exception to this trend is that salt-spray-treated plants of *M. pensylvanica* had higher predawn xylem pressure potential on the last sampling date (Fig. 2b). We also found an interaction between salt

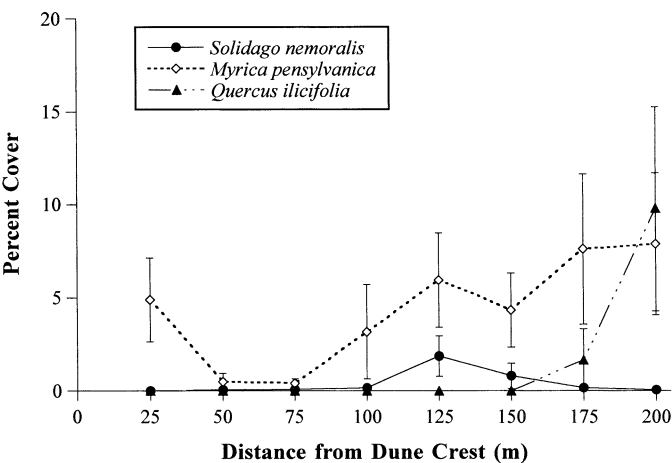


Fig. 1. Field distributions of common heathland plants and a successional oak species. The percent canopy coverages of *Solidago nemoralis*, *Myrica pensylvanica*, and *Quercus ilicifolia* in protected heathlands at Priscilla Hancock Meadow, Quansoo Beach, and Long Point Wildlife Refuge on Martha's Vineyard, Massachusetts, USA, are given (means $\pm$ 1 SE). Canopy cover was estimated in six 1-m² plots at each distance for each of the field sites. *Quercus rubra* and *Pinus rigida* were not present in the study areas within 200 m of the ocean.

spray treatment and length of exposure to salt spray. In *S. nemoralis* and *Q. rubra*, the xylem pressure potential decreased over time in the salt-spray-treated plants, but this trend was not observed in the control plants in the same species. Leaf or needle water content decreased with exposure time in all species, but were significant only in *Q. rubra* (Table 1; Fig. 3). *Quercus rubra* plants treated with salt spray had lower leaf water content than plants grown in the control treatment.

Necrosis—Necrosis levels were significantly higher in *S. nemoralis*, *P. rigida*, and *Q. rubra*, treated with salt spray, but *M. pensylvanica* was unaffected (Table 1; Fig. 4). In *S. nemoralis* and *P. rigida*, necrosis increased as exposure time to salt spray increased. This trend was also observed in *Q. rubra* until day 78, but then leaf necrosis decreased on the last sampling point because of leaf senescence and regrowth of new leaves. Species differed in their degree of necrosis; *Q. rubra* had the highest necrosis, with levels approaching 100% of the entire leaf area at day 78.

Growth—In all species, plants grown in salt spray had less leaf area than plants in control treatments (Table 2; Fig. 5). Leaf number was also affected by salt spray (Table 2; Fig. 6). *Solidago nemoralis* and *Q. rubra* plants in the salt spray treatment

had fewer leaves than did controls. *Myrica pensylvanica* showed a similar trend, but the salt-spray-treated plants had a higher estimated leaf number on the last sample date as compared to the control. Aboveground biomass increased during the experimental period in all species except *Q. rubra*, and the biomass increase was most pronounced in *M. pensylvanica* (Table 2; data not shown). Biomass was affected by salt spray in *S. nemoralis* and *Q. rubra*, but not in the other two species tested. *Solidago nemoralis* bolted during the experiment, but mean height did not differ between treatments (control = 36.52 ± 4.91 cm, salt spray = 33.33 ± 5.23 cm; data not shown).

DISCUSSION

Plants growing in coastal areas are frequently exposed to high levels of salt spray. Some species are able to maintain homeostasis in environments with high salt spray stress (Zhu, 2001), and many coastal plants are resistant to salt spray. However, the selective effect of salt spray on species with different levels of tolerance could have an effect on community composition. We found that the distribution of species in heathlands correlates with distance from the ocean; some species grow in close proximity to the ocean, and others grow farther inland. Furthermore, our greenhouse research demonstrates that the effects of salt spray differ among species, with some species unable to tolerate salt spray and others more resistant. Taken together, these results suggest that coastal sandplain heathland communities could be structured, in part, through the selective effects of salt spray, which limits the growth of salt-intolerant species. In particular, we think salt spray might exclude or slow the succession of woody species that have low salt spray tolerance from heathlands that are growing close to the ocean. In this manner, salt spray could be an important natural abiotic factor that maintains the unique species composition found in heathlands.

Field distribution—*Solidago nemoralis* occurs in a narrow band from 100 m to 175 m from the dune crest, suggesting that growth is limited close to the ocean and also farther inland, perhaps by competition. *Myrica pensylvanica* is the only plant species used in the greenhouse experiment that grows 25 m from the dune crest, suggesting that it is not limited. *Quercus ilicifolia* does not occur in the community until 175 m from the dune crest. *Pinus rigida* and *Q. rubra* are not found within 200 m of the dune crest, even though they are present in the forest community farther inland. Overall, these distribution patterns suggest that an abiotic factor such as salt spray could prevent the growth of *S. nemoralis*, *P. rigida*, *Q. ilicifolia*, and *Q. rubra* close to the ocean, while *M. pensylvanica*,

TABLE 1. ANOVA table of water status (xylem pressure potential and leaf water content) and necrosis responses of *Solidago nemoralis*, *Myrica pensylvanica*, *Pinus rigida*, and *Quercus rubra* grown in a greenhouse with salt spray or deionized water for 102 d.

Source of variation	df	Xylem potential		Leaf water content		Necrosis	
		F	P	F	P	F	P
Day	4	12.24	<0.001	18.20	<0.001	3.24	0.014
Treatment	1	89.38	<0.001	2.62	0.107	297.45	<0.001
Species	3	64.93	<0.001	55.61	<0.001	40.44	<0.001
Day $\times$ treatment	3	8.05	<0.001	2.09	0.104	4.32	0.006
Day $\times$ species	12	27.30	<0.001	2.21	0.013	1.48	0.136
Treatment $\times$ species	3	22.16	<0.001	4.55	0.004	36.54	<0.001
Day $\times$ treatment $\times$ species	9	28.31	<0.001	0.67	0.733	2.11	0.031
Error	180						

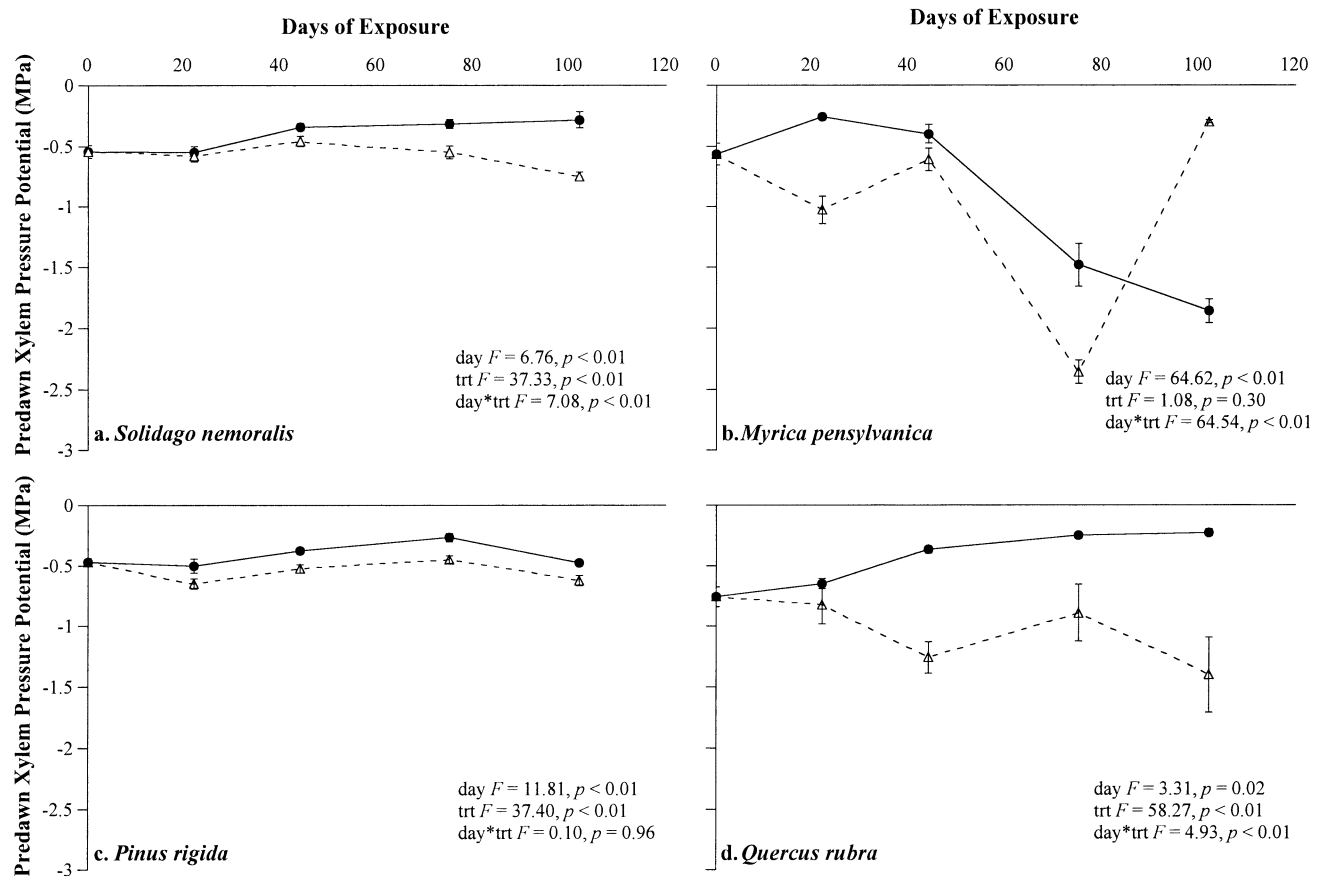


Fig. 2. Mean predawn xylem pressure potential of *Solidago nemoralis*, *Myrica pensylvanica*, *Pinus rigida*, and *Quercus rubra* plants after control spray with water (filled circles) or salt spray (open triangles) (means ± 1 SE). Predawn xylem pressure potential was measured at 0400 h.

with a higher degree of resistance, is not excluded from coastal areas.

Greenhouse experiment—The water status, necrosis, and growth responses of the plants used in this study are consistent with a biphasic model of plant growth in conditions with salt stress (Munns, 1993). This model predicts that plants exposed to salt grow less in response to the water stress and inhibited leaf expansion caused by a decrease in xylem pressure potential. Simultaneously, leaves develop necrosis as sodium and chloride ions accumulate, leading to a loss of photosynthetic tissue and inhibition of growth. Together, leaf loss through necrosis and inhibited leaf production inhibit growth independently of the water status effects. In our study, the degree of plant response to salt spray varied among species, but this model helps to describe the sequence of events that occur in response to salt spray.

Water status—Predawn xylem pressure potential is one measure of plant water status; individuals with lower xylem pressure potentials are generally under a higher degree of water stress. The four species in our greenhouse experiments had lower xylem pressure potentials after salt spray treatment, and species differed in their degree of response to salt spray. *Quercus rubra* consistently had the lowest xylem pressure potential. This species also demonstrated the largest difference between the salt spray and control treatments on day 44, when salt spray was equivalent to levels found at 25 m from the dune

crest. This indicates that *Q. rubra*—and perhaps other *Quercus* species—might be excluded by salt spray in heathlands very close to the ocean. *Myrica pensylvanica* had extremely low xylem pressure potentials at 78 d. Like other species in this study, *M. pensylvanica* plants in the salt spray treatment generally had lower predawn xylem pressure potentials than plants in the control treatment. At the last sampling date, however, *M. pensylvanica* had a trend reversal in which the plants treated with salt spray had higher xylem pressure potentials than control plants at the last sampling point.

While leaf water content decreased in all species during the study, *S. nemoralis* and *Q. rubra* had lower leaf water content after salt as compared to the control on the last sampling date. This decrease was related to the fact that *S. nemoralis* and *Q. rubra* had high levels of necrosis, which had virtually no water. These two species also had the most difference between salt and control treatments on day 44, when salt spray accumulation is equivalent to that found at 25 m from the dune crest, indicating that they might be limited in areas close to the ocean. Unlike *S. nemoralis* and *Q. rubra*, however, *P. rigida* leaf water content did not differ among treatments despite substantial necrosis. We hypothesize that this could be due to differences in the quality of necrotic tissue between deciduous and evergreen plants. Leaf water content did not increase in any plants, thus these four species did not increase leaf succulence to maintain osmotic balance (Boyce, 1951; Rozema et al., 1982).

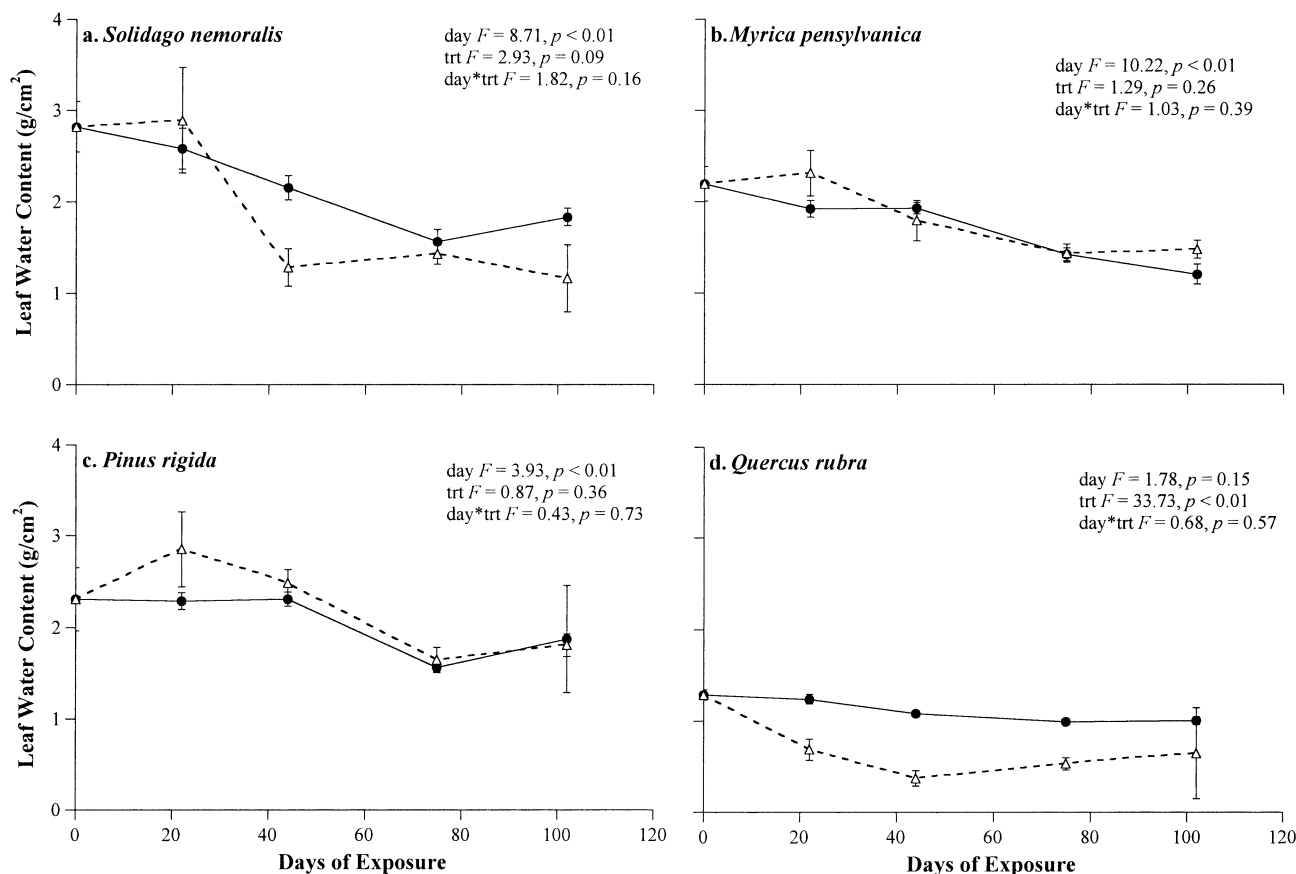


Fig. 3. Mean water content of the first fully expanded leaf of *Solidago nemoralis*, *Myrica pensylvanica*, *Pinus rigida*, and *Quercus rubra* plants after control spray with water (filled circles) or salt spray (open triangles) (means $\pm$ 1 SE).

Necrosis—For the sodium and chloride ions in salt spray to damage leaves, they must enter the leaf and be translocated to the leaf tip where necrosis occurs. All the species in our greenhouse study developed necrosis when exposed to salt spray, demonstrating that salt spray entered the leaves through cuticular penetration (Leyton and Juniper, 1963; Bukovac, 1973), through breaks in the cuticle (Boyce, 1954; Krause, 1982), or through the stomata (Cassidy, 1968; Grieve and Pitman, 1978; Zobel and Nighswander, 1990). Although all species had necrosis after treatment with salt spray, the degree of necrotic response varied among species. *Quercus rubra* had severe necrosis by 22 d, while *S. nemoralis* and *P. rigida* had only moderate damage at that sampling. All three species had high levels of necrosis after 102 d of exposure to salt spray. We observed a decrease in *Q. rubra* at the last sampling, which reflects the fact that leaf necrosis was so extensive that the leaves had abscised, and the plants put out a second flush of leaves. The overall necrotic response of *S. nemoralis*, *P. rigida*, and *Q. rubra* indicates that these species are highly susceptible to damage by salt spray. Previous research has shown severe consequences from mid-season defoliation (Parker and Patton, 1975). When leaf area is lost to necrosis, total photosynthesis and carbohydrate stores in the root decrease, leading to decreased growth in subsequent years. These results suggest that all three of these species might be limited with high salt spray. Our field data support this supposition: the two tree species did not grow in close proximity to the ocean, and *S. nemoralis* did not occur until 100 m from the dune crest.

Necrosis of *M. pensylvanica* did not increase with salt spray or over time, suggesting that this species would not be excluded from high salt spray heathlands. Our field observations support this; *M. pensylvanica* grows close to the ocean in the high salt spray zone. Interestingly, necrosis in *M. pensylvanica* is higher in the field, particularly after acute doses of salt spray during tropical storm events (M. E. Griffiths, unpublished data). This suggests that the observed necrosis was low because these plants were grown in the protective environment of the greenhouse and, as a result, the leaves had few traumata or breaks in the cuticle to serve as entry points to salt spray.

Growth—Plant growth can be inhibited by salt, and this inhibition is often expressed as a decrease in leaf area (Munns, 1993; Goldstein et al., 1996; Neves-Piestun and Bernstein, 2001). As a result of reduced leaf size, plants have less photosynthetic area and, consequently, lower survivability. In our greenhouse study, plants of all four tested species had less leaf area when they were treated with salt spray, although this trend was less pronounced in *M. pensylvanica*. *Solidago nemoralis*, *P. rigida*, and *Q. rubra* had the greatest response and the strongest effect with increasing exposure days, although *Q. rubra* had the largest separation between treatments at 22 and 44 d. Thus, this tree species might be limited from growing in areas with extremely high salt spray because of reduced leaf area and reduced photosynthesis.

Leaf production is also inhibited in plants grown in saline conditions (Alpha et al., 1996). As with leaf area, reduced leaf

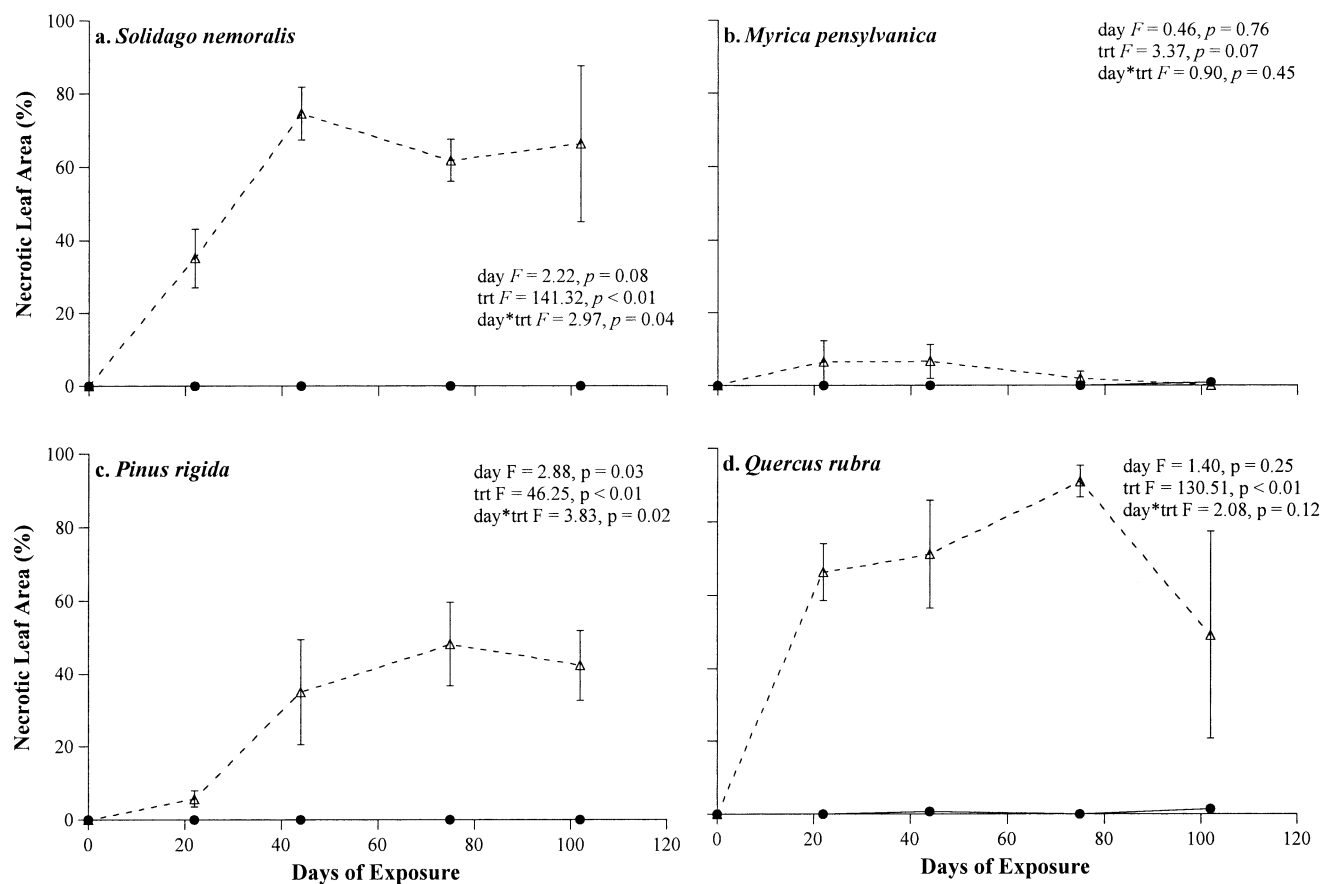


Fig. 4. Proportion of the first fully expanded leaf with necrosis of plants of *Solidago nemoralis*, *Myrica pensylvanica*, *Pinus rigida*, and *Quercus rubra* after control spray with water (filled circles) or salt spray (open triangles) (means $\pm$ 1 SE).

number could result in lower photosynthetic capacity for a plant and ultimately limit growth. We found that *M. pensylvanica* had significant treatment effects for leaf number; plants exposed to salt spray had fewer leaves than control except on the last sampling day. We also found that *S. nemoralis* and *Q. rubra* had fewer leaves when grown in salt spray, although this reduction did not occur in *S. nemoralis* until 44 d, when salt spray was equivalent to levels found 25 m from the dune crest. In an experiment using *Solidago*, defoliation reduced the plants' ability to grow new leaves (Meyer, 1998). Our study showed that leaves of *S. nemoralis* and *Q. rubra* developed high levels of necrosis, effectively removing photosynthetic tissue and perhaps accounting for the observed decrease in leaf

production. Growth could also have been inhibited by damage to photosynthetic machinery or by inhibition of cell expansion (Zhu, 2001). If salt spray, through necrosis or other physiological effects, inhibits growth of leaves and subsequent photosynthesis, these two species may be excluded from areas with high salt spray.

Solidago nemoralis was the only species tested that had a significant treatment effect on aboveground biomass. On two sampling dates, the salt-spray-treated plants had lower biomass. *Myrica pensylvanica* was the only tested species in which biomass dramatically increased. None of the plants were fertilized during the experiment, but *M. pensylvanica* has nitrogen-fixing nodules, which may have enhanced the growth

TABLE 2. ANOVA table of growth responses of *Solidago nemoralis*, *Myrica pensylvanica*, *Pinus rigida*, and *Quercus rubra* grown in a greenhouse with salt spray or deionized water for 102 d.

Source of variation	df	Leaf area		Number of leaves		Aboveground biomass	
		F	P	F	P	F	P
Day	4	4.96	<0.001	4.63	0.001	19.42	<0.001
Treatment	1	30.41	<0.001	7.69	0.006	0.26	0.611
Species	3	48.13	<0.001	346.33	<0.001	433.52	<0.001
Day $\times$ treatment	3	0.22	0.885	5.35	0.002	0.84	0.475
Day $\times$ species	12	2.74	0.002	4.78	<0.001	10.67	<0.001
Treatment $\times$ species	3	2.96	0.001	5.36	0.002	0.50	0.684
Day $\times$ treatment $\times$ species	9	1.03	0.027	5.85	<0.001	1.53	0.142
Error	180						

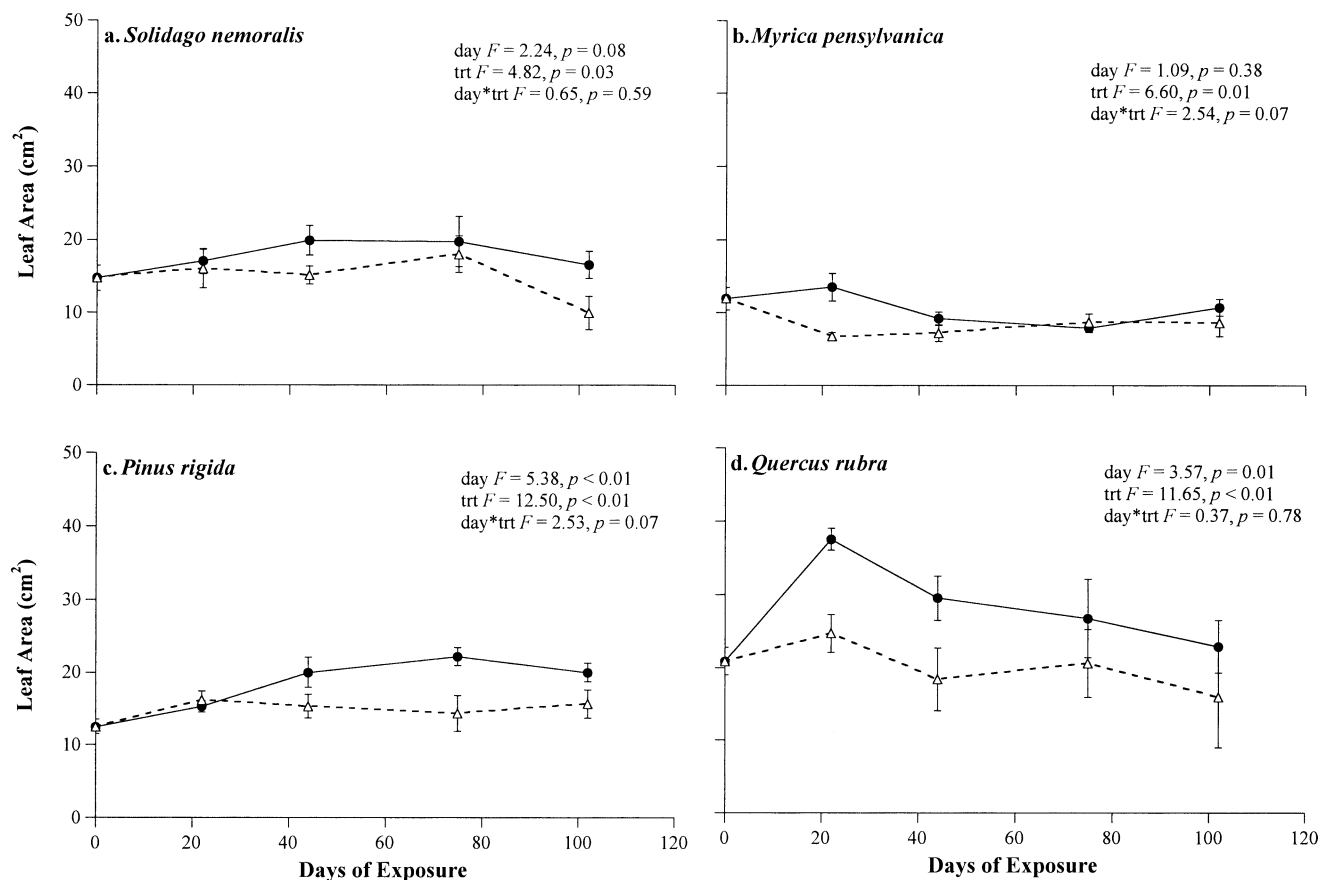


Fig. 5. Total leaf area of the first fully expanded leaf, including necrotic area (means ± 1 SE). Growth responses of plants of *Solidago nemoralis*, *Myrica pensylvanica*, *Pinus rigida*, and *Quercus rubra* after control spray with water (filled circles) or salt spray (open triangles).

of this species. *Solidago nemoralis* grew slightly, but this growth did not vary between treatments.

It is interesting to note that, although *M. pensylvanica* and *S. nemoralis* were selected to represent typical heathland species, the two differed in their responses to salt spray. This result indicates that, within the heathland community, plant species have a range of salt spray tolerances. In the greenhouse experiment, we also observed that *M. pensylvanica* response changed substantially on the last sampling date. Compared with the control, plants grown in salt spray showed a decrease in water stress and increases in leaf water content, leaf number, and biomass. We hypothesize that *M. pensylvanica* may have been able to use mineral cations in the salt spray as nutrients. Salt spray has been shown to be an important source of potassium, calcium, and magnesium in coastal plant communities (Etherington, 1967; Clayton, 1972; Art et al., 1974; van der Valk, 1974b), and the apparent trend reversal observed in the greenhouse experiment is consistent with these findings.

Conclusions—The observational and experimental evidence presented here suggests that salt spray effects may be sufficient to maintain some stability in the composition of coastal sandplain heathlands. Field surveys revealed that *S. nemoralis*, *P. rigida*, and *Q. rubra* did not grow close to the ocean, while *M. pensylvanica* was present in these areas. In greenhouse experiments, we found that common and successional heathland species differed in their water status, necrosis, and growth responses to salt spray. *Solidago nemoralis*, *P.*

rigida, and *Q. rubra* were identified as being more susceptible to salt spray damage than the common heathland species *M. pensylvanica*.

There are several factors that could influence the compositional patterns observed in heathland communities. First, species could be absent from coastal areas because there is no local seed source or there is a barrier to seed dispersal. No studies have examined the seed bank and seed rain conditions in coastal heathlands, and this possibility deserves further study. Modern heathland communities could also be structured by the land use history of particular sites. Research has demonstrated that differences in the timing of agricultural use and cessation (Foster and Motzkin, 1999; Eberhardt, 2000), as well as the fire history (Dunwiddie, 1989; Stevens, 1996), create heathland heterogeneity on a landscape scale. While we do not discount the importance of these factors in structuring heathland plant communities, we think it is unlikely that they are causing the small-scale patterns in species distribution within individual field sites.

We propose that salt spray is the most likely explanation for the observed field distribution patterns. Our research demonstrates that species differ in their tolerance to salt spray and that the photosynthetic potential and growth of species can be compromised under high salt spray conditions. The species we found to be intolerant of salt spray in the greenhouse were not found growing near the ocean in the field. These field distribution patterns suggest that *S. nemoralis* establishment and *P.*

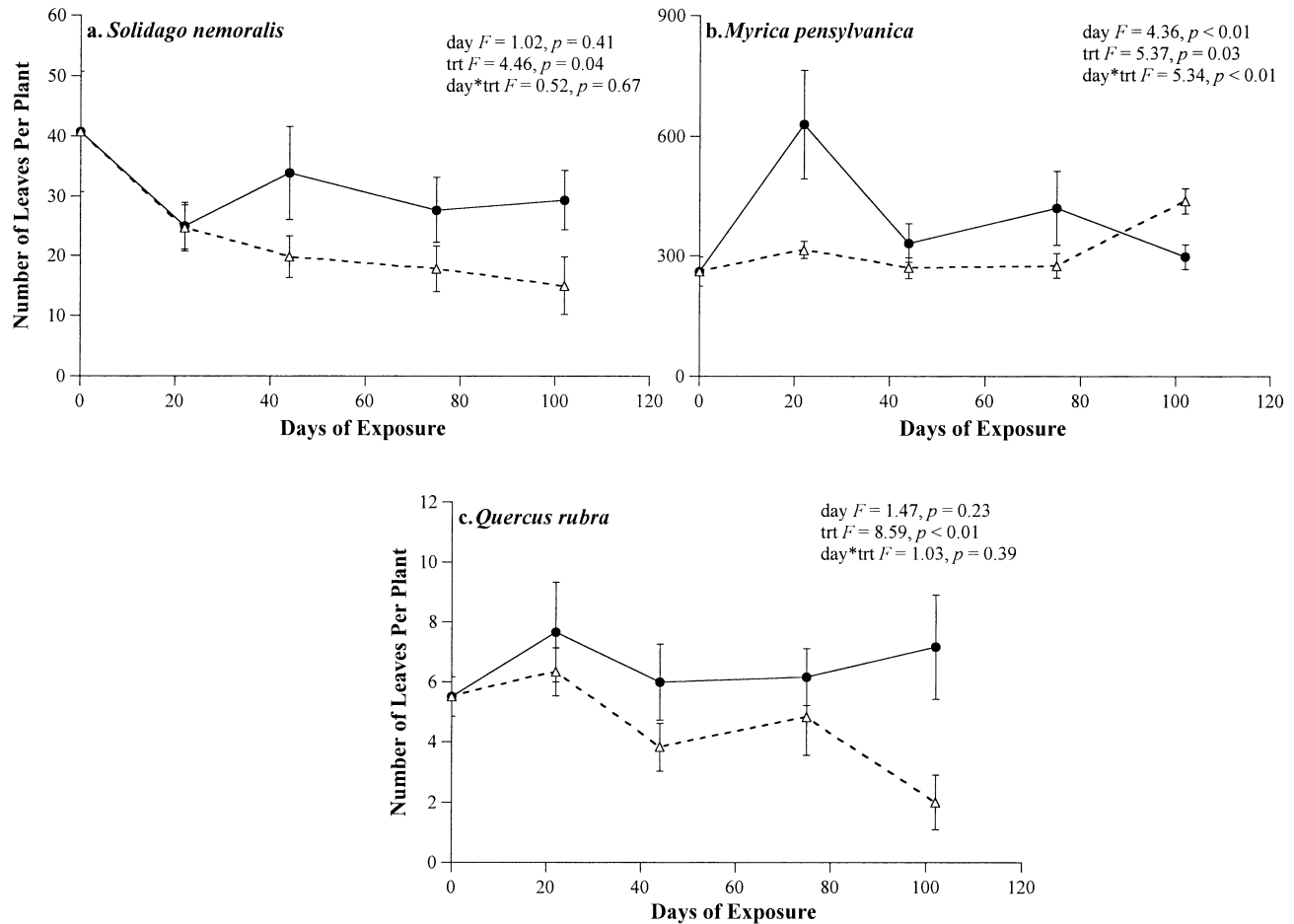


Fig. 6. Growth responses of plants of *Solidago nemoralis*, *Myrica pensylvanica*, and *Quercus rubra* after control spray with water (filled circles) or salt spray (open triangles). Total number of leaves per plant (means ± 1 SE). *Pinus rigida* plants were not included.

rigida and *Quercus* spp. succession may be slowed or prevented by salt spray near the coast. As a result, salt spray may act as a selective factor that excludes certain species from the plant community and that this mechanism could help to maintain the unique composition that is characteristic of heathlands.

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