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Species Distributions in Interdunal Swale Communities: The Effects of Soil Waterlogging

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ABSTRACT.—The influence of soil waterlogging in determining plant species distributions among interdunal swales and between dunes and swales on Cape Cod was investigated employing field and greenhouse experiments. Most species exhibited significant responses to experimental treatments that closely matched their distributions in the field. In general dune species such as *Ammophila breviligulata* and *Solidago sempervirens* grew poorly under waterlogged conditions. When transplanted to the dry sand dune all species grew poorly or died. Swale species exhibited a range of responses to waterlogging conditions. Growth of *Juncus canadensis, Scirpus pungens* and *Vaccinium macrocarpon* increased with waterlogging. *Cyperus dentatus, Juncus pelocarpus* and *Solidago tenuifolia* grew equally well across all waterlogging conditions and are present in most swales. *Juncus greenei* and *Myrica pensylvanica* grew best in drier swales and their distributions appear to be restricted to the perimeters of swales.

Soil waterlogging is an important determinant of species distributions among swales and between swales and dunes. However, the effect of biotic factors such as competition, seed dispersal, soil seed banks and seedling recruitment needs to be examined as well to show how swale communities change over time.

INTRODUCTION

Coastal sand dune communities are characterized by plant species adapted to tolerate dry, unstable and nutrient poor soil conditions (Ranwell, 1972; Maun and Baye, 1989; Ehrenfeld, 1990; Maun, 1998). Extensive dune systems may include interdunal swales which are low elevation areas located between dunes. Swales are also known as dune slacks (Ranwell, 1959, 1960) and interdunal wetlands (McAvoy and Clancy, 1994). Swale soils are subject to seasonal changes in the level of the water table, but are not tidally influenced (Odum and Harvey, 1988; McAvoy and Clancy, 1994). Swales may receive occasional salt input from spray and storm washovers. However, swale soil waters are usually not saline (McAvoy and Clancy, 1994). Swales typically support densely populated wetland plant communities that form a striking contrast to the surrounding xeric dune vegetation.

A preliminary vegetation inventory of twenty swales on a Cape Cod barrier beach revealed that swales differ from one another in species composition and can be classified into three distinct types which will be referred to as barren, rush and cranberry swales (Shumway, 1996). Swales on Cape Cod span a range in soil moisture content influenced by their proximity to the water table and plants inhabiting swales are exposed to a wide range of soil waterlogging conditions. During winter and early spring swales may function as vernal pools with plants submerged under as much as 50 cm of water. For the remainder of the year swales are not flooded, yet soils remain damp as the water table is generally within 50 cm of the surface. Several studies comparing distributions of Dutch dune and swale species have identified soil waterlogging and the availability of minerals as important determinants of growth and distribution of swale species (Jones and Etherington, 1971; Jones, 1972; Schat, 1984). Grasses found in dunes and at the edges of swales were not tolerant of experimentally waterlogged soils while growth of sedges commonly found in swales was stim-

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ulated under waterlogged conditions (Jones and Etherington, 1971). Jones (1972) has also suggested that uptake of toxic levels of iron from waterlogged soils may contribute to the exclusion of certain species from swales. Schat (1984) observed differences in growth and nutrient acquisition in four swale species in response to experimental waterlogging. The responses were associated with differences in root porosity (aerenchyma development) and reflected the distributions of these species across waterlogging gradients within swales. Schat (1984) further suggested that *Juncus maritimus,* which has extensive aerenchyma tissue in its roots, may enhance the ability of neighboring species to withstand waterlogging stress through oxygenation of the soil.

We hypothesized that variation in soil waterlogging among swales combined with interspecific differences in the ability of plants to tolerate waterlogging are responsible for the observed differences in species composition among swale types on Cape Cod. In this study we compared waterlogging tolerance of ten species found growing in swales and dunes in an effort to understand the importance of waterlogging in determining swale species distributions and in generating differences in plant community composition among swales. This is addressed by combining experimental manipulations of waterlogging in the greenhouse with transplant experiments in the field.

METHODS

Study site.—All field work was conducted at Sandy Neck, a 10 km long by 0.5–1 km wide barrier beach located in Barnstable, Massachusetts on the north side of Cape Cod (41°43′ N, 70°22′ W), bordered by Cape Cod Bay to the north and the Great Marsh and Barnstable Harbor to the south. The geologic history of the development of the barrier beach and salt marsh has been described in detail by Redfield (1972). The landscape is dominated by parabolic sand dunes interspersed with maritime forest. Interdunal swales are common in the low elevation areas between dunes. The sand dunes are inhabited by *Ammophila breviligulata* (American beachgrass), *Hudsonia tomentosa* (beach heath), *Myrica pensylvanica* (Northern bayberry) and *Solidago sempervirens* (seaside goldenrod). The most common species inhabiting the interdunal swales are *Agrostis hyemalis* (hairgrass), *Carex silicea* (sand sedge), *Cyperus dentatus* (nut sedge), *Drosera intermedia* (spatulate sundew), *Juncus canadensis* (Canada rush), *Juncus greenei* (Greene's rush), *Juncus pelocarpus* (mud rush), *Lycopodium inundatum* (bog club moss), *Myrica pensylvanica, Phragmites australis* (reed grass), *Scirpus pungens* (three square), *Solidago tenuifolia* (narrow-leaved goldenrod), *Vaccinium macrocarpon* (large cranberry) and *Xyris torta* (slender yellow-eyed grass).

Greenhouse waterlogging experiment.—Tolerance to waterlogging of five common swale species was compared by growing them in a greenhouse under a range of experimental conditions designed to mimic the range of waterlogging that exists in sand dunes and swales. In June 1996 *Ammophila breviligulata* (recently emerged seedlings 8 cm tall with at least 2 leaves), *Cyperus dentatus* (established single ramets 3 cm tall with at least 3 leaves), *Juncus pelocarpus* (single ramets 10 cm tall with at least 3 shoots), *Myrica pensylvanica* (seedlings 0.5 cm tall with at least 2 leaves) and *Solidago tenuifolia* (single ramets 4 cm tall with at least 10 leaves) were collected from Sandy Neck and brought to the Wheaton College greenhouse. Forty individuals of each species were planted in 10-cm-square pots in dune sand. Pots were placed in 60 cm × 34 cm × 19 cm plastic bins and assigned to one of four different treatments (N = 10 replicates/treatment for each species) designed to mimic conditions along the waterlogging gradient in swales in late spring: 0% (no standing water in bin), 50% (water level half-way up the soil level), 100% (water level up to the soil surface) and 110% (water level 3 cm above the soil surface). The bins were placed in the greenhouse from 11 June to 11 September 1996 and plants were exposed to natural sunlight. Plants in

TABLE 1.—Relative abundance of the most common plant species in dune and swale transplant areas determined from 3 y of monthly surveys of relative species abundance based on visual estimation of species density. D (dominant) > A (abundant) > F (frequent) > O (occasional) > R (rare) > — (absent)

Species	Dune	Barren swale	Rush swale	Cranberry swale
Agrostis hyemalis	—	—	A	O
Ammophila breviligulata	D	R	R	—
Cyperus dentatus	—	D	A	O
Drosera intermedia	—	—	—	A
Juncus canadensis	—	—	F	F
Juncus greenei	—	—	A	F
Juncus pelocarpus	—	—	D	A
Myrica pensylvanica	—	—	F	A
Scirpus pungens	—	—	O	F
Solidago tenuifolia	—	—	A	A
Solidago sempervirens	A	—	R	R
Vaccinium macrocarpon	—	—	R	D
Xyris torta	—	—	—	O
Number of species present	3	7	15	20

the 0% treatment were watered every other day which allowed the soil to dry out between watering. The standing water in the waterlogged treatments was maintained at a constant level throughout the experiment. Every 2 wk the water in the bins was changed and all plants were randomized within treatments by rearranging the location of pots within the bins and by rearranging the location of the bins on the greenhouse bench.

After 3 mo plant height, leaf number and flower number (if present) was measured for each replicate. Plants were then removed from the sand, separated into above- and below-ground parts, dried in a 70 C oven and weighed to determine dry biomass.

Swale transplant experiment.—The ability of swale species to grow in different swale types was compared by transplanting 10 common dune and swale species to a dune and to three swales with distinctly different types of vegetation and water availability (Table 1). The first transplant area is a sand dune dominated by *Ammophila breviligulata.* The soil is extremely dry and never flooded. Transplants to the dune were watered several times over the first week of the experiment to increase the chances of survival. Barren Swale is little more than a seasonally wet area in the sand with very sparse vegetative cover, primarily *Cyperus dentatus.* Most of the swale consists of unvegetated bare ground. Throughout most of the summer the soil surface looks and feels indistinguishable from the surrounding dry dunes. Rush Swale is moderately vegetated with small areas of unvegetated bare ground. The vegetation is dominated by monocotyledonous plants including the rushes *Juncus canadensis, J. greenei* and *J. pelocarpus* and the sedges *Cyperus dentatus* and *Scirpus pungens. Solidago tenuifolia* occurs throughout the swale and *Myrica pensylvanica* grows along one edge. Cranberry Swale has nearly complete vegetative cover, the highest species richness and is dominated by *Vaccinium macrocarpon.* All of the species found in the other swale types are also found here. Dense growth of 1–2 m-tall *Myrica pensylvanica* rings the perimeter of Cranberry Swale. All three swales are flooded by up to 50 cm of water for several weeks during the spring. Parts of Cranberry Swale still had several centimeters of water over the surface at the start of the experiment. During the summer months (June–September) the swales are not flooded, but, due to their close proximity to the water table, the soil surfaces are always damp in Rush and Cranberry swales.

To compare waterlogging among transplant locations the depth to the water table was measured in each location by coring with a soil auger until the water table was reached. The distance between the soil surface and the water table was then measured by lowering a ruler into the excavated hole. This was repeated five times at locations within 1–2 m of each transplant area. Measurements were repeated at weekly intervals from 28 May–13 August 1997.

On 28 and 29 May 1997 *Ammophila breviligulata* (seedlings 5–8 cm tall with 2 leaves), *Cyperus dentatus* (single ramets 5 cm tall with 4 leaves), *Juncus canadensis* (single ramets 16–24 cm tall with 3 leaves), *Juncus greenei* (single ramets 10–15 cm tall with 3 leaves), *Juncus pelocarpus* (single ramets 7–11 cm tall with 4 leaves), *Myrica pensylvanica* (seedlings 1 cm tall with 1–2 true leaves plus cotyledons), *Scirpus pungens* (ramets 6–10 cm tall with 1–3 leaves), *Solidago sempervirens* (seedlings 1–2 cm tall with 1–2 true leaves), *Solidago tenuifolia* (single ramets 7–11 cm tall with 10–14 leaves) and *Vaccinium macrocarpon* (vine segments consisting of 3 uprights and connecting rooted horizontal stem) were excavated from the field. All plants were collected from nearby swale and dune areas that were not being used as transplant sites. For each species twelve individuals were transplanted to each treatment area. Aboveground vegetation was removed from within 10 cm of the transplants to ammeliorate possible species interactions.

Plants were monitored weekly throughout the summer for survival. Transplants were harvested at the end of August. Growth was assessed by measuring plant height, leaf number, flower number (if appropriate), ramet number and dry biomass. Flower number was determined by counting flower heads for *Juncus canadensis,* seed capsules for *J. greenei* and *J. pelocarpus,* spikelets for *Carex dentatus* and flower spikes for *Scirpus pungens.* Biomass was determined by isolating aboveground plant parts, drying them in a 70 C oven and weighing them. Measuring belowground biomass was not attempted due to the difficulty of excising complete root systems in the field.

Analyses.—Overall treatment effects were determined using MANOVA followed by one way ANOVA for each trait for each species in the waterlogging and transplant experiments. If a significant treatment effect was detected, then Student-Newman-Keuls post hoc tests were performed to determine significance among treatments.

RESULTS

Greenhouse waterlogging experiment.—All species had significant overall responses to waterlogging treatments (MANOVA $P < 0.05$). *Ammophila, Myrica* and *Solidago tenuifolia* exhibited the greatest responses to waterlogging whereas *Cyperus* and *Juncus pelocarpus* exhibited the least response (Table 2). In general *Ammophila* and *Solidago tenuifolia* grew best under the less waterlogged conditions. *Myrica* grew best in the 0% treatment with significant reductions in growth in waterlogged treatments. All *Myrica* in the 110% treatment died before completion of the experiment. *Cyperus* grew equally well in all treatments, but produced more leaves under less waterlogged conditions. *Juncus pelocarpus* also grew well across all waterlogged conditions with a trend toward an increase in shoot mass with increased levels of waterlogging.

Swale transplant experiment.—Depth to the water table differed among the transplant locations with Cranberry > Rush > Barren > dune (Fig. 1). Data from the dune site are incomplete because on most dates the depth was too great for the coring technique (the auger was not long enough and the test hole collapsed).

All species displayed significant overall responses to transplant treatments (MANOVA P

TABLE 2.—Results of the greenhouse waterlogging experiment showing growth ($\bar{x} \pm$ SE) under four different waterlogging treatments. * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$ in ANOVAs. Means with different superscripts are significantly different from one another at the 0.05 level in post-hoc tests

	Waterloging treatment			
Species	0%	50%	100%	110%
Ammophila breviligulata				
Height (cm)***	38.0 ± 1.6^{a}	17.6 ± 1.4^{b}	19.4 ± 1.7^{b}	25.8 ± 2.0^{c}
Leaf number***	5.1 ± 0.1^{a}	5.7 ± 0.1^{b}	5.7 ± 0.2^{b}	4.3 ± 0.1^{c}
Shoot mass (g)***	0.17 ± 0.02^{a}	0.05 ± 0.006^{b}	0.05 ± 0.006^{b}	0.06 ± 0.01^{b}
Root mass (g)***	0.21 ± 0.04^{a}	0.06 ± 0.01^{b}	0.04 ± 0.008^{b}	0.10 ± 0.01^{b}
Cyperus dentatus				
Height (cm)	24.1 ± 0.6	21.9 ± 0.9	26.4 ± 1.9	24.2 ± 0.8
Leaf number***	8.8 ± 0.2^{a}	6.2 ± 0.3^{b}	6.1 ± 0.3^{b}	4.7 ± 0.3^{c}
Shoot mass (g)	0.12 ± 0.005	0.09 ± 0.007	0.12 ± 0.01	0.14 ± 0.06
Root mass (g)	0.95 ± 0.44	1.20 ± 0.39	1.29 ± 0.55	0.34 ± 0.08
Juncus pelocarpus				
Height (cm)	29.6 ± 1.8	33.9 ± 2.1	33.5 ± 1.0	35.4 ± 1.5
Leaf number	8.4 ± 1.2	9.3 ± 1.1	8.5 ± 0.9	6.8 ± 0.6
Flower number	63.2 ± 14.7	79.1 ± 10.3	80.6 ± 7.6	74.9 ± 9.7
Shoot mass (g)*	0.19 ± 0.022^{a}	0.27 ± 0.023^{b}	0.24 ± 0.02^{ab}	0.29 ± 0.01^{b}
Root mass (g)	1.26 ± 0.18	1.74 ± 0.37	1.44 ± 0.22	1.89 ± 0.17
Myrica pensylvanica				
Height (cm)***	6.4 ± 0.3^{a}	2.8 ± 0.2^{b}	2.7 ± 0.34^{b}	—
Leaf number***	17.1 ± 0.6^{a}	6.9 ± 0.6^{b}	6.4 ± 0.8^{b}	—
Shoot mass (g)**	0.20 ± 0.07^{a}	0.02 ± 0.005^{b}	0.02 ± 0.005^{b}	—
Root mass (g)	0.24 ± 0.03	0.18 ± 0.05	0.14 ± 0.03	—
Solidago tenuifolia				
Height (cm)***	21.1 ± 1.3^{a}	18.5 ± 0.8^{a}	12.8 ± 0.9^{b}	17.3 ± 1.2^{a}
Leaf number***	31.9 ± 2.2^{a}	21.5 ± 1.1^{b}	18.3 ± 2.2^{b}	18.2 ± 2.6^{b}
Shoot mass (g)***	0.11 ± 0.008^{a}	0.07 ± 0.007^{b}	0.05 ± 0.007^{b}	0.07 ± 0.008^{b}
Root mass (g)**	0.79 ± 0.09^{a}	0.82 ± 0.10^{a}	0.38 ± 0.05^{b}	0.52 ± 0.07^{b}

< 0.01, Table 3). Growth in the dune was significantly lower in the dune compared to the swales for all species. *Ammophila, Myrica* and *Solidago sempervirens* did not survive in the dune. *Ammophila, Juncus canadensis* and *Scirpus* grew best in the Cranberry Swale. *Vaccinium* grew best in the Rush and Cranberry Swales. *Juncus greenei* and *J. pelocarpus* grew best in the Barren Swale. *Myrica* also grew best in Barren Swale, but biomass remained low and did not differ significantly among swales. *Cyperus* grew well in all swales with no differences in biomass among swales, but grew tallest in Cranberry Swale and produced more flowers in the drier swales. *Solidago tenuifolia* and *S. sempervirens* grew equally well in all three swale types. However, *S. sempervirens* biomass was low across all treatments.

DISCUSSION

Experimental flooding and transplanting had significant effects on the growth of most swale species. Species with the most restricted distributions in the field exhibited the greatest differences in response to experimental treatments and species with the widest distribution ranges among swale types responded the least to experimental manipulations.

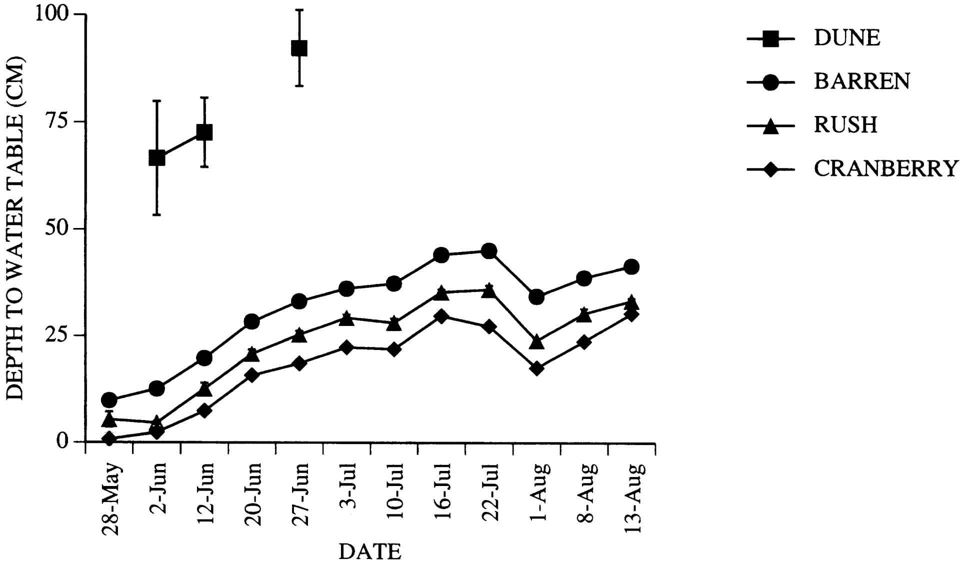

FIG. 1.—Depth to the water table ($\bar{x}$ ± SE) in the transplant areas from May–August. Error bars are smaller than the symbols in most cases

All species grew poorest in the dune where water availability is extremely low. *Ammophila, Myrica* and *Solidago sempervirens* did not survive transplantation to the dune despite being restricted to the dune, or, in the case of *Myrica,* common in both dunes and swales. This discrepancy may be due to the fact that they were transplanted as seedlings with little to no substrate remaining attached to their roots while all other species were transplanted with a small amount of substrate from their collection site. *Ammophila* and *Myrica* were highly intolerant of experimental flooding. However they were able to survive and, in the case of *Ammophila,* grow well when transplanted to waterlogged swales although their growth in swales was considerably less than in the greenhouse. The sharp delineation between dune and swale vegetation is most likely the result of poor growth of swale species in the dry soils of the dunes and the inability of dune species to grow well under waterlogged conditions found in swales.

Juncus canadensis, Scirpus and *Vaccinium* show a clear preference for growth in more waterlogged conditions. *Vaccinium* is restricted to highly waterlogged swales while *J. canadensis* and *Scirpus* have a wider distribution but appear to grow best in wetter regions within swales. *Juncus pelocarpus* and *Cyperus* are the only species to grow equally well across all swales and *J. pelocarpus* is the only species to grow equally well across all experimental flooding regimes. Similarly, *Solidago tenuifolia* grew equally well among all swales, but grew best in the non-waterlogged treatment in the greenhouse. These highly tolerant species are found in virtually all of the swales on Sandy Neck (Shumway, pers. obs.). *Cyperus* is the first species to invade newly formed swales and may be the only species to survive well in the driest swales.

The *Juncus* species and the sedges *Cyperus* and *Scirpus* are all capable of expanding their distribution in swales through a combination of clonal growth and sexual recruitment. By examining production of ramets and flowers it is possible to predict the colonizing abilities of these species. All of these species produced the lowest number of ramets and flowers when transplanted to the dune, indicating that even if they were able to recruit to this area, further spread would be unlikely. The *Juncus* species are capable of producing large numbers of seeds in each seed capsule and *Juncus* seedlings are abundant in most swales (S. Shumway, pers. obs.). Ramet and flower production did not differ among swales for *J. canadensis* suggesting that it is equally capable of spreading in swales spanning a wide range of waterlogging. *Juncus greenei,* however, grew best and produced the greatest numbers of flowers and ramets in the Barren Swale suggesting that it is best able to spread throughout drier swales. Although found in most swales, its distribution, like that of *Myrica,* is restricted to the drier perimeters of swales. *Juncus pelocarpus* produced the most flowers in Barren Swale and an equal number of ramets in all swales. Therefore, it has the potential to spread more quickly in drier swales, providing seedling recruitment is also more successful in these areas.

The results from this study indicate that differences in species composition among interdunal swales may be due to interspecific differences in the ability to tolerate waterlogging. However, the experimental waterlogging regimes are an underestimation of the magnitude and duration of flooding that swale species must endure. Natural winter and spring flooding covers plants with tens of centimeters of water compared to the approximately 3 cm used in the 110% treatment in the greenhouse. The survival of the dune species *Ammophila* in the 110% treatment may be due to its ability to extend leaves above the water level and to transport sufficient oxygen to the rest of the plant (Armstrong *et al.,* 1994). Natural flooding lasts for several months and is likely to influence when perennial plants break dormancy and resume growth, as well as the breaking of seed dormancy and timing of seedling emergence (Baskin *et al.,* 1996). Elevation differences and microtopography within swales may influence plant waterlogging and may be responsible for some of the within swale distribution patterns such as the restriction of *Juncus greenei* and *Myrica* to the drier outer perimeters of swales. Species restricted to swales are well adapted to soil waterlogging and their inability to tolerate drought conditions found in drier swales and dunes may be equally important for determining their distributions. The 0% treatment in the greenhouse provided a realistic simulation of nonwaterlogged soils, yet, because it was watered every other day, fails to adequately simulate the severe water stress imposed by the dunes.

Other factors in addition to waterlogging may contribute to the observed species distribution patterns among swales. In the transplant experiment, interspecific competition was ameliorated, but not eliminated, by weeding aboveground vegetation out of the transplant areas. Interspecific competition has been shown to interact with flood tolerance to generate species distribution patterns in other wetlands communities (Grace and Wetzel, 1981; Bertness, 1991a, b) and its role in interdunal swales remains to be investigated.

Seed dispersal, soil seed banks, seed dormancy requirements, seedling water demands and seedling flood tolerance may also be important determinants of swale species distributions. The ability of most species to survive when transplanted to Barren Swale, despite their absence from the existing vegetation, strongly suggests that seed dispersal and seedling recruitment are important in determining swale species compositions. Seed and seedling ecology have been studied for some North American dune plants (reviewed by Ehrenfeld, 1990; and Maun, 1994). However, virtually nothing is known about these factors for swale species and will be addressed in a future study.

Barren, Rush and Cranberry swales used in the transplant experiment characterize the three most common swale vegetation types on Cape Cod. Distinct vegetation differences among swales is not unique to Cape Cod dunes and has been reported for swales in the Mid-Atlantic US (McAvoy and Clancy, 1994) and the UK (Ranwell, 1960). The three swale types on Cape Cod are likely to represent different successional seres, however, this has not

TABLE 3.—Results ($\bar{x} \pm$ SE) of the transplant experiment showing the growth of ten species planted in the dune and three swales. * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$ in ANOVAs. Means with different superscripts are significantly different from one another at the 0.05 level in post-hoc tests

	Transplant location			
Species	Dune	Barren	Rush	Cranberry
Ammophila breviligulata				
Height (cm)***	—	10.8 ± 0.7^{a}	12.1 ± 0.5^{a}	22.1 ± 1.6^{b}
Leaf number***	—	1.7 ± 0.1^{a}	3.4 ± 0.2^{b}	5.1 ± 0.2^{c}
Biomass (g)***	—	0.009 ± 0.001^{a}	0.02 ± 0.002^{a}	0.07 ± 0.01^{b}
Cyperus dentatus				
Height (cm)***	5.7 ± 0.9^{a}	15.8 ± 0.4^{b}	14.7 ± 0.8^{b}	19.9 ± 0.7^{c}
Leaf number	10.3 ± 1.3	12.0 ± 1.9	10.7 ± 0.7	8.5 ± 0.3
Flower number***	0^{a}	108.3 ± 20.9^{b}	67.6 ± 5.7^{c}	25.2 ± 2.6^{a}
Ramet number*	1.1 ± 0.1^{a}	1.8 ± 0.2^{b}	1.5 ± 0.2^{ab}	1.0 ± 0.0^{a}
Biomass (g)***	0.05 ± 0.01^{a}	0.52 ± 0.11^{b}	0.45 ± 0.03^{b}	0.32 ± 0.01^{b}
Juncus canadensis				
Height (cm)***	17.5 ± 1.0^{a}	33.6 ± 1.3^{b}	35.3 ± 1.3^{b}	45.5 ± 1.2^{c}
Leaf number***	4.2 ± 0.5^{a}	7.7 ± 0.5^{b}	6.6 ± 0.5^{b}	7.6 ± 0.4^{b}
Flower number***	0^{a}	11.0 ± 0.8^{b}	9.0 ± 1.7^{b}	21.9 ± 4.1^{c}
Ramet number***	1.7 ± 0.3^{a}	3.5 ± 0.4^{b}	2.9 ± 0.3^{b}	3.4 ± 0.2^{b}
Biomass (g)***	0.11 ± 0.01^{a}	0.74 ± 0.06^{b}	0.65 ± 0.07^{b}	1.13 ± 0.11^{c}
Juncus greenei				
Height (cm)***	11.8 ± 1.2^{a}	29.7 ± 0.8^{b}	30.6 ± 2.6^{b}	34.2 ± 1.8^{b}
Leaf number***	3.3 ± 0.3^{a}	9.1 ± 1.0^{b}	4.5 ± 0.4^{a}	3.2 ± 0.1^{a}
Flower number***	2.0 ± 1.3^{a}	15.7 ± 2.2^{b}	13.4 ± 2.1^{b}	10.2 ± 2.4^{b}
Ramet number***	1.4 ± 0.2^{a}	5.8 ± 0.6^{b}	3.0 ± 0.3^{c}	3.1 ± 0.3^{c}
Biomass (g)***	0.03 ± 0.009^{a}	0.31 ± 0.02^{b}	0.21 ± 0.02^{c}	0.24 ± 0.02^{c}
Juncus pelocarpus				
Height (cm)***	7.3 ± 1.2^{a}	25.6 ± 0.8^{b}	26.5 ± 1.1^{b}	29.0 ± 1.9^{b}
Leaf number*	2.5 ± 1.1^{a}	8.5 ± 0.9^{b}	8.2 ± 1.0^{b}	7.7 ± 0.7^{b}
Ramet number**	1.0 ± 0.0^{a}	4.3 ± 0.5^{b}	4.5 ± 0.5^{b}	4.9 ± 0.6^{b}
Flower number***	0^{a}	338.9 ± 43.1^{b}	144.1 ± 17.6^{c}	159.4 ± 25.3^{c}
Biomass (g)***	0.02 ± 0.009^{a}	0.59 ± 0.06^{b}	0.36 ± 0.03^{c}	0.39 ± 0.04^{c}
Myrica pensylvanica				
Height (cm)***	—	4.0 ± 0.2^{a}	3.1 ± 0.1^{b}	2.9 ± 0.1^{b}
Leaf number***	—	11.0 ± 0.4^{a}	8.2 ± 0.6^{b}	7.4 ± 0.4^{b}
Biomass (g)	—	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.002
Scirpus pungens				
Height (cm)	15.3 ± 1.2	18.0 ± 1.0	17.9 ± 1.0	20.1 ± 1.4
Leaf number	1.3 ± 0.1	2.1 ± 0.2	1.1 ± 0.2	3.2 ± 0.7
Flower number**	0.1 ± 0.1^{a}	0.5 ± 0.1^{ab}	0.7 ± 0.1^{ab}	1.4 ± 0.2^{b}
Ramet number***	1.0 ± 0.0^{a}	1.7 ± 0.1^{a}	1.5 ± 0.2^{a}	2.8 ± 0.2^{b}
Biomass (g)***	0.02 ± 0.005^{a}	0.04 ± 0.006^{a}	0.05 ± 0.01^{a}	0.13 ± 0.01^{b}
Solidago sempervirens				
Height (cm)	—	3.9 ± 0.4	5.0 ± 0.3	4.7 ± 0.4
Leaf number*	—	3.8 ± 0.3^{a}	5.0 ± 0.2^{b}	3.5 ± 0.3^{a}
Biomass (g)	—	0.01 ± 0.005	0.02 ± 0.005	0.03 ± 0.006

TABLE 3.—Continued

Species	Transplant location			
	Dune	Barren	Rush	Cranberry
Solidago tenuifolia				
Height (cm)***	15.5 ± 0.9^{a}	20.2 ± 1.4^{b}	23.0 ± 0.9^{b}	22.6 ± 1.3^{b}
Leaf number***	40.8 ± 4.6^{a}	91.0 ± 11.5^{b}	89.7 ± 12.2^{b}	118.0 ± 18.0^{b}
Biomass (g)***	0.13 ± 0.01^{a}	0.26 ± 0.04^{b}	0.28 ± 0.01^{b}	0.31 ± 0.03^{b}
Vaccinium macrocarpon				
Height (cm)*	7.4 ± 0.4^{a}	8.6 ± 0.8^{ab}	9.1 ± 0.5^{ab}	9.8 ± 0.3^{b}
Leaf number***	42.6 ± 7.4^{a}	55.9 ± 10.8^{a}	209.4 ± 26.5^{b}	211.5 ± 19.9^{b}
Biomass (g)***	0.23 ± 0.01^{a}	0.17 ± 0.02^{a}	0.38 ± 0.04^{b}	0.45 ± 0.04^{b}

been documented and we remain largely ignorant of how these communities change over time.

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