Soil Seed Bank in Nantucket's Early Successional Communities: Implications for Management

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Abstract

Globally rare sandplain grassland and coastal heathland plant communities of Nantucket Island, MA, merit high conservation priority because they support many rare and endangered species. Management (brush-cutting, grazing, and prescribed fire) has been effective in maintaining these communities, but less successful in transforming overgrown native scrub oak shrubland to diverse grassland. These scrub oak communities may lack a seed bank of grassland species in their soil. To examine this on Nantucket, we used the seedling emergence method to compare the soil seed bank of grassland, heathland, and scrub oak sites. We classified seedlings by growth form (graminoid, forb, or woody) and identified them to genus and species when possible. We observed that seedling density declined along a successional gradient, with the highest total density and highest graminoid density at grassland sites and the lowest at one of the scrub oak sites. A nMDS ordination grouped grassland sites with dominant graminoids, and heathland sites with dominant woody species and forbs. The scrub oak samples contained fewer graminoid species. Our results suggest that seed bank of desirable grassland species is low in later successional scrub oak communities, and may be a limiting factor in restoration projects intended to convert scrub oak shrubland to sandplain grassland. Scarcity of grassland species in the scrub oak seed bank highlights the importance of maintaining existing grassland communities, rather than attempting to restore them once they are gone.

Index terms: grassland, heathland, Nantucket, sandplain, seed bank

INTRODUCTION

Seed banks have long been considered an important factor in ecological restoration (Thompson 1987; van der Valk and Pederson 1989). Ecologists recognize that stored seeds may strongly influence vegetation development at a site following disturbance, and that the seed bank may be valuable for restoring degraded sites or fostering desired vegetation development after management. This is particularly true

where there are no nearby seed sources of target species, or for species not suited to long distance dispersal (Glass and Howell 1993; Matlack 2005).

Researchers have demonstrated that the soil seed bank often reflects a past seral stage rather than the standing vegetation (Glass and Howell 1993; Looney and Gibson 1995; Lunt 1997; Perez et al. 1998; Godefroid et al. 2006; Lang and Halpern 2007; Allen and Nowak 2008), which may give stored seeds an important role in early successional restoration. Effectiveness of the seed bank in a particular restoration project depends on both species composition and seed density (van der Valk and Pederson 1989). Low seed longevity of desired grassland species has been cited as a key reason why restoration programs cannot rely solely on the seed bank (Bossuyt and Hermy 2003). von Blanckenhagen and Poschlod (2005) found that only 25-33% of calcareous grassland species accumulate a long-term persistent soil seed bank. Many studies report a sharp decline in soil seed densities over time along a successional gradient (Bossuyt and Hermy 2003; Laughlin 2003; Figueroa et al. 2004; Landman et al. 2007; Lang and Halpern 2007), although Ne'emen and Izhaki (1999) found that microhabitat had a stronger influence than stand age. Consequently, seed addition has been recommended to offset a lack of desired grassland species in the seed bank (Lunt 1997; Laughlin 2003; von Blanckenhagen and Poschlod 2005; Lezberg et al. 2006; Lang and Halpern 2007; Valko 2010).

Early Successional Communities on Nantucket

Nantucket, an island with a maritime climate and well-drained glacially derived soils, has a long history of intensive human use; this combination of environment and human history has resulted in larger expanses of early successional plant communities than remain elsewhere along the Eastern Seaboard. Early successional habitat decline has been highlighted in recent years as a major conservation concern for many rare species (Norment 2002; Wagner et al. 2003; Shriver et al. 2005). Nantucket offers exceptional opportunities to protect these vulnerable communities and associated rare species; more than

40% of the island is protected conservation land, which includes large tracts of high-quality early successional vegetation (NTG 2010).

Sandplain grasslands and coastal heathlands (hereafter abbreviated as "grasslands" and "heathlands") are limited to the sandy soils of the coastal Northeast, where they provide critical habitat for unusually high numbers of declining wildlife and regionally rare plants (Leahy 1993; Sorrie and Dunwiddie 1996; Swain and Kearsley 2001). Considered limited to small patches prior to colonial times, these communities were likely maintained by long-term Native American land use and frequent fires; land clearing and sheep grazing introduced by European colonists further expanded open grasslands (Motzkin and Foster 2002). By the mid-1800s, Nantucket was almost completely deforested. Aggressive re-growth of native woody species since that time (due to abandonment of grazing, fire suppression, development, and cultivation) has resulted in a > 90% global decline in grasslands and heathlands, including those on Nantucket (Godfrey and Alpert 1985; Barbour et al.1999). Most unmanaged areas have become overgrown with dense native scrub oak (*Quercus ilicifolia* Wangenh.), native dwarf chinquapin oak (*Q. prinoides* Willd.), and re-introduced pitch pine *(Pinus rigida* P. Mill). While scrub oak shrublands also support rare species (chiefly Lepidoptera) they are continually expanding on Nantucket due to succession, and encompass a greater regional range than the more vulnerable grasslands and heathlands (Table 1). For this reason, increasing the extent of grassland and heathland by reducing scrub oak area has been a major conservation goal.

To date, brush-cutting and prescribed fire have been instrumental in maintaining Nantucket's existing grassland and heathland, but have been less effective in converting overgrown scrub oak areas back to open grasslands (Dunwiddie 1997, Dunwiddie et al.1997; Beattie et al. 2006; Lezberg et al. 2006). In order to examine whether the soils of scrub oak areas retain a sufficient seed bank of grassland species to effect spontaneous grassland development following management or disturbance, we used the seedling emergence method to compare seed bank composition and seed density at sites along a successional

gradient on Nantucket. Evaluating the seed bank available in Nantucket's grassland, heathland, and scrub oak communities will help us determine if seed additions should play a more prominent role in our grassland restoration programs.

METHODS

Location of Study

This study was conducted on Nantucket Island, Massachusetts, approximately 42 km south of Cape Cod (lat 41˚15'24"N, long 70˚3'35"W) (Figure 1). Nantucket comprises approximately 116 km^2 of land area, ranging in elevation from sea level to 33 m. Surficial geology consists of a Pleistocene glacial end moraine in the northern half of the island, with an outwash plain extending southward (Oldale 1985). Scrub oak shrubland predominates on the glacial moraine; heathland and grassland are more common on the outwash plain. Soils in the sampling areas are deep, well- or excessively- drained loamy sands of the Evesboro and Riverhead series (Langlois 1979). Average winter and summer temperatures are 1˚C and 22˚C, respectively; mean annual precipitation is 1070 mm (45% occurring during the April-September growing season) (Langlois 1979). Windy conditions predominate year-round, intensifying in winter and spring; salt spray, wind, and sand scouring strongly influence island vegetation composition and structure (Tiffney and Eveleigh 1985).

Community Descriptions

Grasslands are dominated by graminoids (grasses, sedges, and rushes) and forbs (broadleaf non-woody plants). Little bluestem (*Schizachyrium scoparium* Michx.), bentgrass (*Agrostis hyemalis* (Walt. BSP)), sedges (*Carex* spp.), rushes (J*uncus* spp.) and poverty oat grass, (*Danthonia spicata* L.) are common. Along with these graminoids and a variety of forbs, grasslands may contain up to 40% cover of the low-growing shrubs which dominate heathlands, offering varied niches for a taxonomically diverse group of rare species (Sorrie and Dunwiddie 1996; Swain and Kearsley 2001) (Table 1).

Heathlands consist of a mosaic of low-growing, diverse vegetation dominated by patches of clonal ericaceous shrubs such as huckleberry *(Gaylussacia baccata* (Wangenh.) Koch), low bush blueberries *(Vaccinium* spp.), and bearberry *(Arctostaphylos uva-ursi* (L.) Spreng.). Woody species cover in heathlands exceeds 40%, but they also include substantial herbaceous cover and some graminoids of the species described above for grasslands. Patchiness and species diversity in heathlands provide critical habitat for a number of rare taxa (Sorrie and Dunwiddie 1996; Swain and Kearsley 2001) (Table 1).

Scrub oak shrublands are monocultures dominated by dense native scrub oak and native dwarf chinquapin oak, up to 3-6 m tall. Canopy shading results in sparse groundcover of grasses and forbs (Sorrie and Dunwiddie 1996). Less diverse than grasslands and heathlands, scrub oak shrublands nevertheless host several rare and endangered arthropods (Swain and Kearsley 2001; Wagner et al. 2003) (Table 1).

Sampling Design

We selected two representative areas within each of the grassland, heathland, and scrub oak communities (TNC 1998), for a total of six collection sites (Figure 1). Grass1 and Heath1 sites were located in the Head of the Plains Conservation Area (176 ha, owned by the Nantucket Conservation Foundation). Grass2 and Heath2 sites were located in the Smooth Hummocks Coastal Preserve (354 ha, the Nantucket Islands Land Bank Commission). ScrubOak1 was located in the Sesachacha Heathlands Wildlife Preserve (349 ha, the Massachusetts Audubon Society). ScrubOak2 was located in the Middle Moors (197 ha, the Nantucket Conservation Foundation). We chose sampling sites that shared a similar management history within each community type.

To guide the random collection of soil cores from each of the six collection sites, we created sampling templates using a 100m x 100m grid, from which we randomly selected one grid square from each of ten columns (n=10 sampling points for each collection site). At each collection site we overlaid the sampling template using ArcGIS 9.1 to create sampling coordinates (ESRI 2005) (Figure 2). We exported the coordinates to a Trimble® Geo XT™ handheld GPS unit and navigated to the 10 sampling points at each

site, collecting one soil sample at each point using a square metal device that extracted 10 cm x 10 cm blocks to a depth of 20 cm (Figure 2). Soil cores were collected in September 2007 and cold stratified in a refrigerator from September 2007-April 2008.

We separated soil blocks into duff and mineral subsamples when duff was present, following the USFS definitions of these layers (Woodall and Monleon 2007), as there is evidence suggesting that duff may inhibit seed germination (E. Steinauer, unpub. data). Between 1 April 2008 and 10 April 2008, we hand mixed each subsample and used a 5 mm mesh screen to remove large debris. Large fruit or seeds such as rose hips or acorns that did not pass through the mesh were returned to the sample, but large leaves and roots were discarded. Each mineral and duff subsample was divided as evenly as possible by mass and spread in a thin layer over a base of moistened sterile potting mix (Metro Mix® 200) in 11 x 20" Kord® fiber trays, which allowed us to standardize soil depth to a thickness of 0.5-1.5cm (intended to minimize the effect of seed burial while providing a moisture-retaining base). Each tray contained exclusively either duff or mineral material from one soil sample, and the number of duff and mineral trays for each sample varied depending on the proportion of duff to mineral in the soil block, for a total of 5-6 trays per soil sample. Some samples did not contain any duff, so all trays were mineral. We placed the trays in an unheated plastic hoop house ventilated with a thermostat-controlled fan. Control trays of sterile potting mix were placed among the experimental trays to detect potential seed contamination.

Trays were surface-watered daily and rotated weekly to minimize biases in environmental conditions. We monitored seedling emergence weekly, labeling individual seedling and recording growth form (forb, graminoid or woody). Once seedlings were large enough, we removed them to reduce crowding and transplanted representative specimens for later identification. We recorded seedling emergence until 30 September 2008, an end date selected because germination had dwindled by that point, and because a six to seven month germination time frame was common in other studies (Warr 1994; Looney and Gibson 1995; Ne'emen and Izhaki 1999; Godefroid et al. 2006; Landman et al. 2007; Lang and Halpern 2007).

Representative seedling specimens were overwintered in cold frames. We identified individuals to genus and species when possible, based on leaf morphology or floral characteristics. Botanical nomenclature follows Haines (2011).

Analysis

In order to graphically evaluate similarities in species composition among our six sampling locations we conducted a non-metric Multidimensional Scaling Analysis (nMDS) using R (R Development Core Team 2012). We utilized this ordination technique because of its lack of assumptions of normality in multivariate data and its ability to robustly handle datasets with large zero counts (McCune et al. 2002). To examine differences in average species composition between each site, we conducted a perMANOVA, a multivariate analysis of variation based on permutations, which does not require normality in multivariate data (R Development Core Team 2012). We used pairwise Mann-Whitney u tests to compare seedling densities by growth form between the six sampling sites; using a Bonferroni correction to account for multiple comparisons (15 comparisons with a significant value of $p<0.0033$) (SPSS 2007). We also used pairwise Mann-Whitney u tests to compare seedling densities in duff and mineral layers at the four sites where duff was present (Heath1, Heath2, ScrubOak1, ScrubOak2); a Bonferroni correction was used to account for multiple comparisons (6 comparisons with a significant value of $p < 0.00833$) (SPSS 2007). We performed an Indicator Species Analysis (ISA) to examine the significant association of individual species with particular sampling locations (R Development Core Team 2012). We present mean (± SE) seedling densities in seeds m^{-2}, to enable generalized comparisons with other seed bank studies (Looney and Gibson 1995; Ne'eman and Izhaki 1999; Lang and Halpern 2007).

RESULTS

The nMDS ordination separated out sampling sites based on species composition with a stress value of 0.0000670298 (Fig 3). Grass1 and Grass2 sites plotted with dominant graminoids including little bluestem, bentgrass, and Greene's rush (*Juncus greenei* Oakes and Tuckerman). Heath1 and Heath2

plotted very close together, grouping with forbs such as goldenrods (*Euthamia* spp.), cinquefoil (*Potentilla* spp.) and the low growing sub-shrub, golden heather (*Hudsonia ericoides* L). Scrub oak sites grouped with dominant woody species wintergreen (*Gaultheria procumbens* L.) and dewberry (*Rubus flagellaris* Willd.), and a ruderal forb species, horseweed (*Erigeron canadensis* L.). ScrubOak2 was more strongly associated with graminoid species than ScrubOak1, and hence plotted closer on the ordination to the grassland and heathland sites.

The perMANOVA results indicated a significant difference in average species composition among the six sampling sites ($F = 3.4296$, $p < 0.000999$) (Table 2). Mann-Whitney u tests used to examine pairwise relationships between sites for seedling densities by growth form indicated that graminoid density in ScrubOak1 was significantly lower than all other sampling locations (Table 3). Mann-Whitney u tests comparing total seedling densities in duff and mineral components indicated that there was no significant difference in total germination between the duff and mineral layers at any of the sites where both layers were present. However, graminoid density was significantly higher in the mineral component of ScrubOak2 ($p=0.002$), while forb density was significantly higher in the duff layer of Heath1 ($p=0.007$). Indicator Species Analysis (ISA) was unable to determine whether any of the species were significantly associated with particular sampling sites (6 comparisons, with a Bonferroni correction of $p < 0.00833$).

Total seedling emergence during the growing season (from 1 April through 30 September 2008) comprised 3548 individuals. Zero seedlings emerged in control trays. Seedling densities (seeds per $m^2 \pm$ SE) were highest at Grass1 (8740 $m^{-2} \pm 3474$) and Grass2 (8600 $m^{-2} \pm 2764$). Densities were intermediate at Heath1 (6100 $m^{-2} \pm 1737$), Heath2 (4470 $m^{-2} \pm 973$), and ScrubOak2 (5890 $m^{-2} \pm 2191$). ScrubOak1 seedling densities were the lowest (1680 $m^{-2} \pm 699$), amounting to less than 20% of the seedling density at Grass2, the less dense grassland site. Plants from 10 families were identified in the seed bank (Asteraceae, Cistaceae, Cyperaceae, Ericaceae, Juncaceae, Liliaceae, Poaceae, Rubiaceae, Scrophulareaceae, and Violaceae). We identified 27 genera and 28 species (Table 4). We did not identify any state or federally

listed rare or endangered plant species. Seed bank percent composition by growth form varied between sites, with the highest percentage of graminoid seedlings in grassland samples (Figure 4). Just under 50% of all seedlings identified to genus in this experiment were *Juncus* spp. Approximately 31% of seedlings were classified by growth form but did not survive the early growth stage or overwintering to be identified either to genus or species.

DISCUSSION

This study showed variations in soil seed bank composition and density along a successional gradient at grassland, heathland, and scrub oak sites on Nantucket. The nMDS ordination illustrates that ScrubOak1 differed the most from all the other sites, plotting far to the left on Axis 1, associated with woody species and horseweed, a species which typically germinate after soil disturbance. In contrast, ScrubOak2 plotted closer to the heathland and grassland sites along Axis 1, due to a higher content of graminoids. The two heathland sites were the most similar to each other of any sites within a community type. Grassland and heathland sites shared some species in common, which is visible in the ordination, and is more clearly depicted in the table of all identified seed bank taxa (Table 4). These compositional similarities support the concept that conversion of heathland to grassland over time, or conversion of scrub oak to heathland as an intermediate stage, may be more efficient than attempting to convert scrub oak directly to grassland.

Absence of key grassland dominants in both scrub oak sites, along with extremely low graminoid densities at the ScrubOak1, imply that spontaneous grassland development subsequent to management at scrub oak sites is strongly dependent on seed rain from adjacent populations, and not on stored seed bank. A recent mechanical clearing study on Martha's Vineyard corroborates our results; in that study, 12 of the 14 most common sandplain herbs appeared at cleared sites only after seed addition (Lezberg et al. 2006). Seed rain sources must be very close for colonization to occur; Glass and Howell (1993) reported that even when grassland species were present in nearby prairie remnants, seeds of these species generally remained absent from the seed rain at an adjacent restoration site. Seeds of little bluestem, for example,

often travel only a short distance (< 2 m) from the mother plant even in windy conditions (up to 32 kph) (Weaver 1958; Rice et. al. 1960). Nantucket's dense scrub oak stands present a substantial barrier to seed dispersal, either via wind or large mammals such as deer.

Higher density of graminoids at ScrubOak2, along with that site's similarity to the heathland and grassland sites in the ordination, suggest that subtle variations in scrub oak sites (such as past land use history, exposure to wind and salt spray, or proximity to disturbed areas) may influence the seed bank of target grassland species at scrub oak sites. The fact that little bluestem and bentgrass were absent from both scrub oak sites may help explain why management regimes of frequent brush-cutting or prescribed fire have not resulted in a strong shift toward grassland. Low density of woody species in the seed bank is likely due to the fact that these shrubs typically rely more heavily on re-sprouting and clonal growth rather than on seed dispersal for reproduction (Bond and Midgley, 2001).

Rushes were found in substantial densities at all six sites. High rush densities have been reported in many seed bank studies, and have been attributed to the wetland lineage of *Juncus*, which has led to adaptations such as small, long-lived seeds with very specific germination triggers (Warr et al. 1994; Looney and Gibson 1995; Lunt 1997; Olano et al. 2002). Since rushes are present in high densities in the Nantucket seed bank, this group of plants may play an important role in local grassland restoration projects, especially following soil disturbance, where they may colonize readily and stabilize soil without creating dense vegetative cover.

Some limitations of our study are inherent in the seedling emergence method. Evaluation of seedling emergence for a single growing season may have biased against species with long-term dormancy, or the individual germination requirements of some species might not have been met in our research greenhouse (Walck et al. 2005). It should be noted that we have been successfully germinating most of the common grassland species in the research greenhouse for a number of years. Our collection time (September) may not have captured some species whose seeds are retained on plants long into the winter (pers. obs.). Better

climate control and a heated greenhouse would have enabled us to more accurately determine species richness by reducing mortality of seedlings; however, we were still able to obtain percent composition of seed bank broken down by growth form. The inability of Indicator Species Analysis to determine whether any of the species were significantly associated with particular sampling sites may be due to the large numbers of zeroes in our data set and the relatively small number of samples per site. Reducing the soil sampling depth to 10 cm could have allowed us to collect twice as many samples at each site and work within the size of our research greenhouse, which may have improved our ability to detect rarer species and to determine which species were associated with each site.

Our ability to assess the role of duff or mineral substrates on seed germination was complicated by the fact that duff always forms as a surface soil layer from accumulating organic material. As a result, differences in seedling density may simply be due to depth (Perez et al. 1998; Olano et al. 2002; Godefroid et al. 2006). Burial of graminoid seeds from an earlier successional stage (such as the long-lived rushes) may also result in higher germination of grassland species with small persistent seeds (i.e. rushes) from the deeper mineral layer. Variation in duff thickness among samples also means that seedling densities from our samples are reported for different volumes of soil.

Conclusions and Future Research

Our results demonstrated a scarcity of grassland species seeds at overgrown scrub oak sites, which may hinder grassland restoration projects. Overlap in species composition between grassland and heathland sites implies that the goal of converting shrubland to heathland as a transitional phase may be more practical than converting shrubland directly to grassland. Targeting restoration to sites with the most favorable characteristics (i.e. proximity to intact grasslands, exposure to wind and salt spray, sandy low-nutrient soils) will likely further enhance results. We have initiated further research to test whether seed addition combined with existing management practices will facilitate grassland development. A controlled study of the effect of duff and mineral substrates in the germination of key grassland species

may be initiated to explore whether duff removal or mixing of these layers (via disc harrowing) should be another aspect of sandplain grassland establishment efforts.

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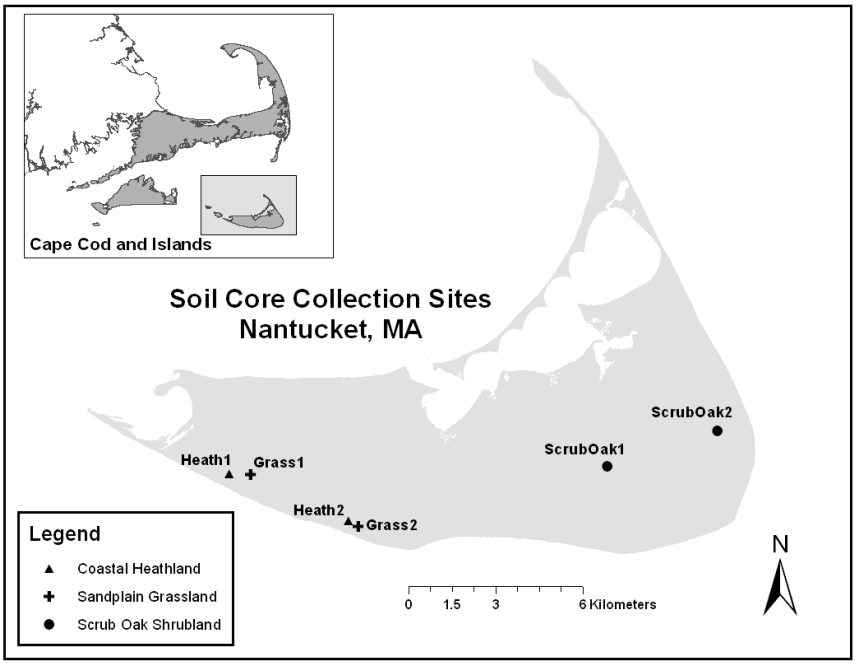

Figure 1. Map depicting soil core collection sites for seed bank comparison along a successional gradient in sandplain grassland, coastal heathland, and scrub oak shrubland, Nantucket Island, MA.

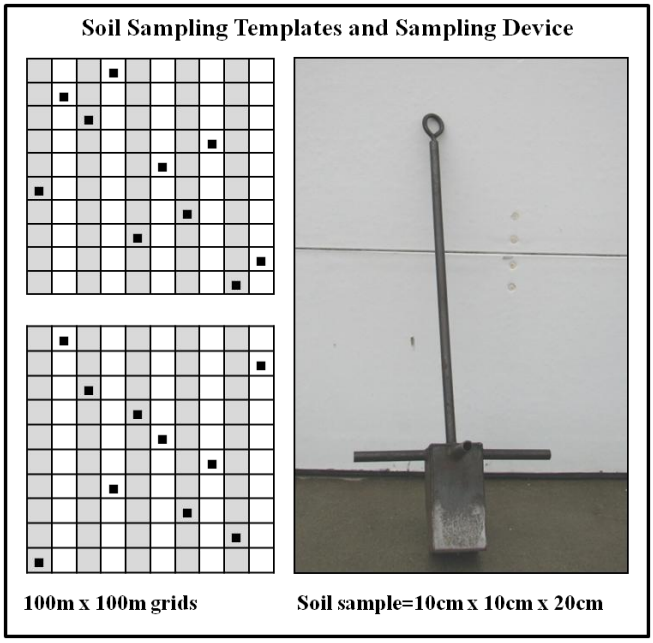

Figure 2. Sampling templates and soil core sampling device; one template of randomly selected points was applied at each of the collection sites, enabling us to collect ten soil samples at each location distributed over a 100 x100m area (n=10 for each site), Nantucket Island, MA.

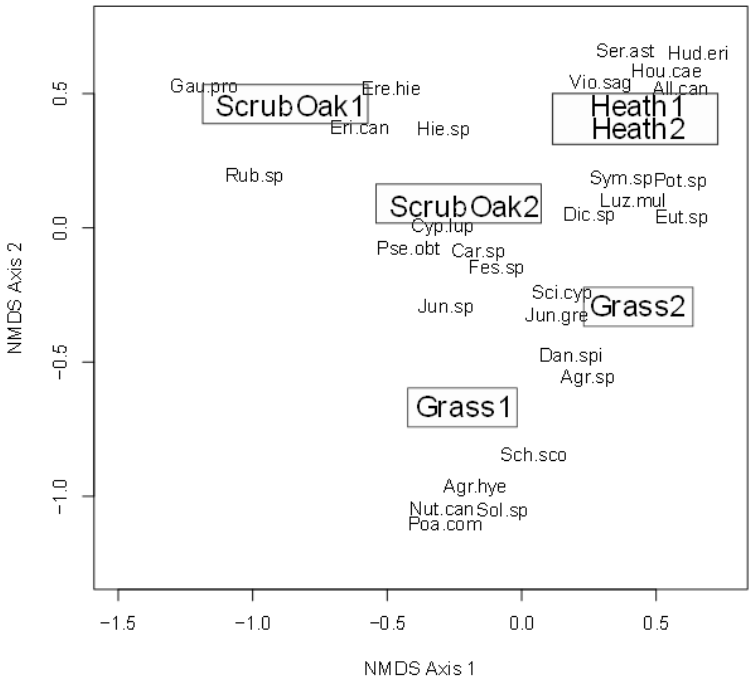

Figure 3. The nMDS ordination of all emerged seedlings, identified to genus or species, with sampling sites (Grass1, Grass2, Heath1, Heath2, ScrubOak1, and ScrubOak2) grouped based on species composition with a stress value of 0.0000670298, Nantucket Island, MA.

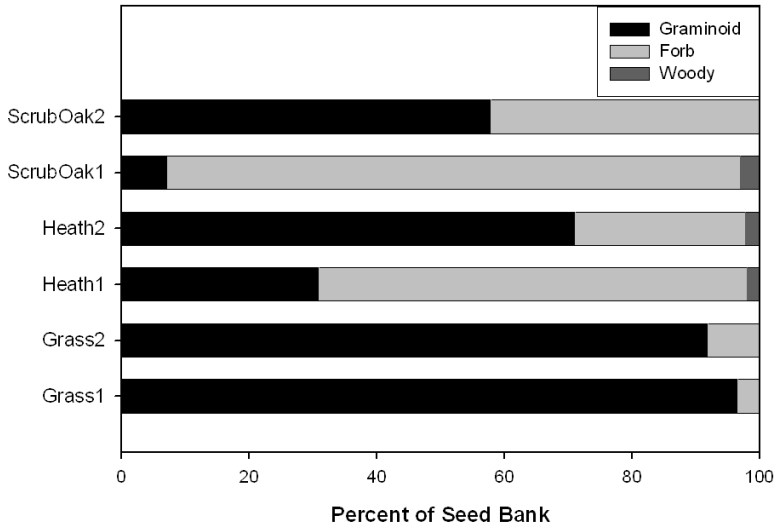

Figure 4. Percent composition of seed bank classified by growth form at the six seed bank collection sites along a successional gradient (sandplain grassland = Grass1 and 2, coastal heathland = Heath1 and 2, and scrub oak shrubland = ScrubOak1 and 2), Nantucket Island, MA.

Table 1. Conservation status and current estimated extent of native early successional sandplain grassland, coastal heathland, and scrub oak shrubland plant communities in the Northeastern United States.

Community	Rankings	Range	Remaining Area Estimates	State Listed Species (MA)
Sandplain Grassland	Global: G2 Massachusetts: S1	MA, NY, RI	Regional/Global: 1619 ha (Leahy 1993) Nantucket: 251 ha (TNC 1998)	21 plants, 4 birds, 7 arthropods
Coastal Heathland	Global: G3 Massachusetts: S1	MA, NY	Regional/Global: 1619 ha (Leahy 1993) Nantucket: 1121 ha (TNC 1998)	10 plants, 3 birds, 5 arthropods
Scrub Oak Shrubland	Global: Unranked Massachusetts: S1	MA, NH, NJ, NY, RI	Regional/Global: Unknown Nantucket: 2642 ha (TNC 1998)	15 arthropods

Global Rankings: NatureServe Rankings on a scale of 1-5, with G1 the most rare and endangered. G2=Imperiled, At high risk of extinction; G3=Vulnerable, at moderate risk of extinction (NatureServe Explorer, 2009).
Massachusetts State Ranking: Also a scale of 1-5, with S1=most rare and endangered (MA Natural Heritage and Endangered Species Program, 2010).
State Listed Species include: Watch Listed, Threatened, Special Concern, and Endangered species (MA Natural Heritage and Endangered Species Program).

Table 2. Results of perMANOVA indicated a significant difference among the six soil core sampling sites (Grass1 and 2, Heath1 and 2, ScrubOak1 and 2).

	DF	Sum of Squares	Mean Squares	F. Model	R^2	Pf(<F)
Site	5	4.2587	0.85175	3.4296	0.24102	0.000999
Seedlings (species)	54	13.411	0.24835		0.75898	
Total	59	17.6697			1	

Table 3. Results of Mann-Whitney u test pairwise comparisons of seedling emergence by growth form at all sites, including comparisons between sites within the same community type. Sandplain grassland=Grass1 and 2, coastal heathland=Heath1 and 2, and scrub oak shrubland=ScrubOak 1 and 2. Significant differences are presented in bold font.

	Seedling Emergence by Growth Form					
	Forb		**Graminoid**		**Woody**	
Overall Pair-wise Comparisons	**Z**	**p**	**Z**	**p**	**Z**	**p**
ScrubOak1 vs. Grass1	-1.942	0.052	-3.162	**0.002**	-1.902	0.057
ScrubOak1 vs. Heath1	-1.291	0.197	-3.804	**<0.001**	-1.129	0.259
ScrubOak1 vs. Grass2	-1.219	0.223	-3.729	**<0.001**	-2.517	0.012
ScrubOak1 vs. Heath2	-0.607	0.544	-3.803	**<0.001**	-0.210	0.834
ScrubOak2 vs. Grass1	-2.470	0.014	-1.022	0.307	-1.000	0.317
ScrubOak2 vs. Heath1	-3.410	0.733	-1.280	0.197	-1.451	0.147
ScrubOak2 vs. Grass2	-1.782	0.075	-1.287	0.198	0.000	1.000
ScrubOak2 vs. Heath2	-0.341	0.733	0.000	1.000	-2.163	0.031
Grass1 vs. Heath1	-2.387	0.017	-1.967	0.049	-0.669	0.503
Grass1 vs. Heath2	-2.464	0.014	-0.983	0.326	-1.640	0.101
Grass2 vs. Heath1	-1.897	0.058	-1.817	0.069	-1.451	0.147
Grass2 vs. Heath2	-1.749	0.080	-1.173	0.241	-2.163	0.031
Within Community Comparisons						
ScrubOak1 vs. ScrubOak2	-0.873	0.383	-3.618	**<0.001**	-2.517	0.012
Grass1 vs. Grass2	-0.916	0.360	-0.265	0.791	-1.000	0.317
Heath1 vs. Heath2	-6.440	0.520	-1.476	0.140	-0.866	0.376

Table 4. Taxa identified at each site, classified by growth form (graminoid, forb, woody). Values are seeds m^{-2} (SE). Sandplain Grassland=Grass1 and 2; coastal heathland=Heath1 and 2; scrub oak shrubland=ScrubOak1 and 2. Genera in bold font include all seedlings identified to the species level plus those identified only to the genus level (sum of all seedlings identified to that genus). *=Non-native species; += sandplain grassland and/or coastal heathland species; ~=wetland species (Habitat classifications from Sorrie and Dunwiddie 1996). Botanical nomenclature follows Haines (2011).

	Seed Bank Sampling Sites					
Scientific Name	**Grass1**	**Grass2**	**Heath1**	**Heath2**	**ScrubOak1**	**ScrubOak2**
Graminoid						
Agrostis hyemalis +	1330 (1170)	30 (15)	0	0	0	0
***Agrostis* spp. +**	**1390 (1230)**	**100 (49)**	**10 (10)**	**0**	**0**	**0**
Carex spp. +	120 (81)	40 (22)	30 (21)	20 (13)	90 (41)	20 (13)
Cyperus lupulinus +	0	0	0	0	10 (10)	0
Danthonia spicata +	170 (148)	50 (50)	60 (60)	0	0	0
Dichanthelium acuminatum +	10 (10)	0	60 (50)	50 (34)	60 (34)	0
***Dichanthelium* spp. +**	**30 (21)**	**30 (15)**	**130 (109)**	**100 (47)**	**70 (42)**	**0**
Festuca filiformis *	0	70 (70)	0	0	0	0
Festuca ovina *	0	10 (10)	0	0	0	10 (10)
***Festuca* spp. ***	**0**	**100 (89)**	**0**	**0**	**0**	**10 (10)**
Juncus bufonius ~	0	0	0	0	10 (10)	0
Juncus effusus ~	10 (10)	0	0	0	0	0
Juncus greenei +	1380 (641)	1010 (423)	150 (62)	310 (145)	280 (98)	0
Juncus tenuis	0	20 (13)	0	0	0	0
***Juncus* spp.**	**266370 (154583)**	**6040 (2346)**	**1170 (331)**	**2360 (625)**	**260580 (97817)**	**4040 (1649)**
Luzula multiflora +	0	40 (22)	30 (30)	30 (21)	10 (10)	0
Poa compressa *	10 (10)	0	0	0	0	0
Schizachyrium scoparium +	30 (21)	10 (10)	0	0	0	0
Scirpus cyperinus ~	0	20 (13)	0	0	0	10 (10)
unknown graminoid spp.	1310 (768)	1490 (551)	370 (99)	640 (210)	640 (138)	50 (22)
Forb						
Allium canadense	0	0	0	30 (21)	0	0
Erigeron canadensis	0	0	0	20 (20)	10 (10)	30 (21)
Erechtites hieraciifolius	0	0	20 (20)	0	0	10 (10)
Euthamia graminifolia +	0	70 (50)	30 (21)	50 (34)	0	0
Euthamia caroliniana +	0	60 (34)	0	40 (31)	0	0
***Euthamia* spp. +**	**0**	**130 (80)**	**30 (21)**	**90 (60)**	**0**	**0**
Hieracium spp. +	0	0	1360 (674)	70 (40)	760 (585)	440 (244)
Houstonia caerulea +	0	0	10 (10)	0	0	0
Nuttallanthus canadensis +	20 (13)	0	0	0	0	0
Potentilla canadensis +	0	10 (10)	30 (30)	0	0	0
***Potentilla* spp. +**	**0**	**20 (20)**	**40 (40)**	**10 (10)**	**0**	**0**
Pseudognaphalium obtusifolium +	0	0	0	0	10 (10)	0
Sericocarpus asteroides +	0	0	10 (10)	10 (10)	0	0
Solidago spp. +	10 (10)	0	0	0	0	0
Symphyotrichum spp. +	0	10 (10)	10 (10)	10 (10)	0	0
Viola sagittata +	0	0	0	10 (10)	0	0
unknown forb spp.	270 (84)	530 (216)	2110 (1220)	960 (960)	1680 (629)	1030 (447)
Woody						
Hudsonia ericoides +	0	0	110 (110)	50 (34)	0	0
Gaultheria procumbens	0	0	0	0	0	10 (10)
Rubus flagellaris	0	0	0	0	0	30 (15)
***Rubus* spp.**	**10 (10)**	**0**	**0**	**0**	**0**	**30 (15)**
unknown woody spp.	0	0	10 (10)	20 (20)	0	10 (10)
Unknown						
unknown spp.	10 (10)	40 (40)	0	0	0	0