# 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, Massachusetts, 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 (*Quercus ilicifolia* Wangenh.) 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. Seeds of key grassland dominants were absent from scrub oak and heathland samples but were found in grassland samples. Our results suggest that lack of seed bank of desirable grassland species 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 when no nearby seed sources of target species remain, 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 heath-

lands (hereafter abbreviated as "grass-lands" 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 com-pletely deforested. Aggressive re-growth of native woody species since that time (due to abandonment of grazing and fire suppression), combined with development or cultivation, have 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 ilici-folia* Wangenh.), native dwarf chinquapin oak (*Q. prinoides* Willd.), and re-intro-duced 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 occupy 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 Nan-tucket'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; Lezberg et al. 2006; Beattie et al. unpubl. data). In order to examine whether the soils of scrub oak areas retain a suf-ficient 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

**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 (States) | Remaining Area Estimates | State Listed Species (MA) |
|---|---|---|---|---|
| Sandplain Grassland | Global: G2<br>Massachusetts: S1 | MA, NY, RI | Regional/Global: 1619 ha (Leahy 1993)<br>Nantucket: 251 ha (TNC 1998) | 21 plants, 4 birds, 7 arthropods |
| Coastal Heathland | Global: G3<br>Massachusetts: S1 | MA, NY | Regional/Global: 1619 ha (Leahy 1993)<br>Nantucket: 1121 ha (TNC 1998) | 10 plants, 3 birds, 5 arthropods |
| Scrub Oak Shrubland | Global: Unranked<br>Massachusetts: S1 | MA, NH, NJ<br>NY, RI | Regional/Global: Unknown<br>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).

determine whether or not 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 (41°15'24"N, 70°3'35"W) (Figure 1). Nantucket comprises approximately 116 km² 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 grass (*Schizachyrium scoparium* (Michx.) Nash), bentgrass (*Agrostis hyemalis* (Walter) B.S.P.), sedges (*Carex* spp.), rushes (*Juncus* spp.) and poverty oat grass, (*Danthonia spicata* (L.) Beauv. Ex Roemer and J.A. Shultes) 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, creating varied ecological niches for a taxonomically diverse group of rare species (Sorrie and Dunwiddie 1996;
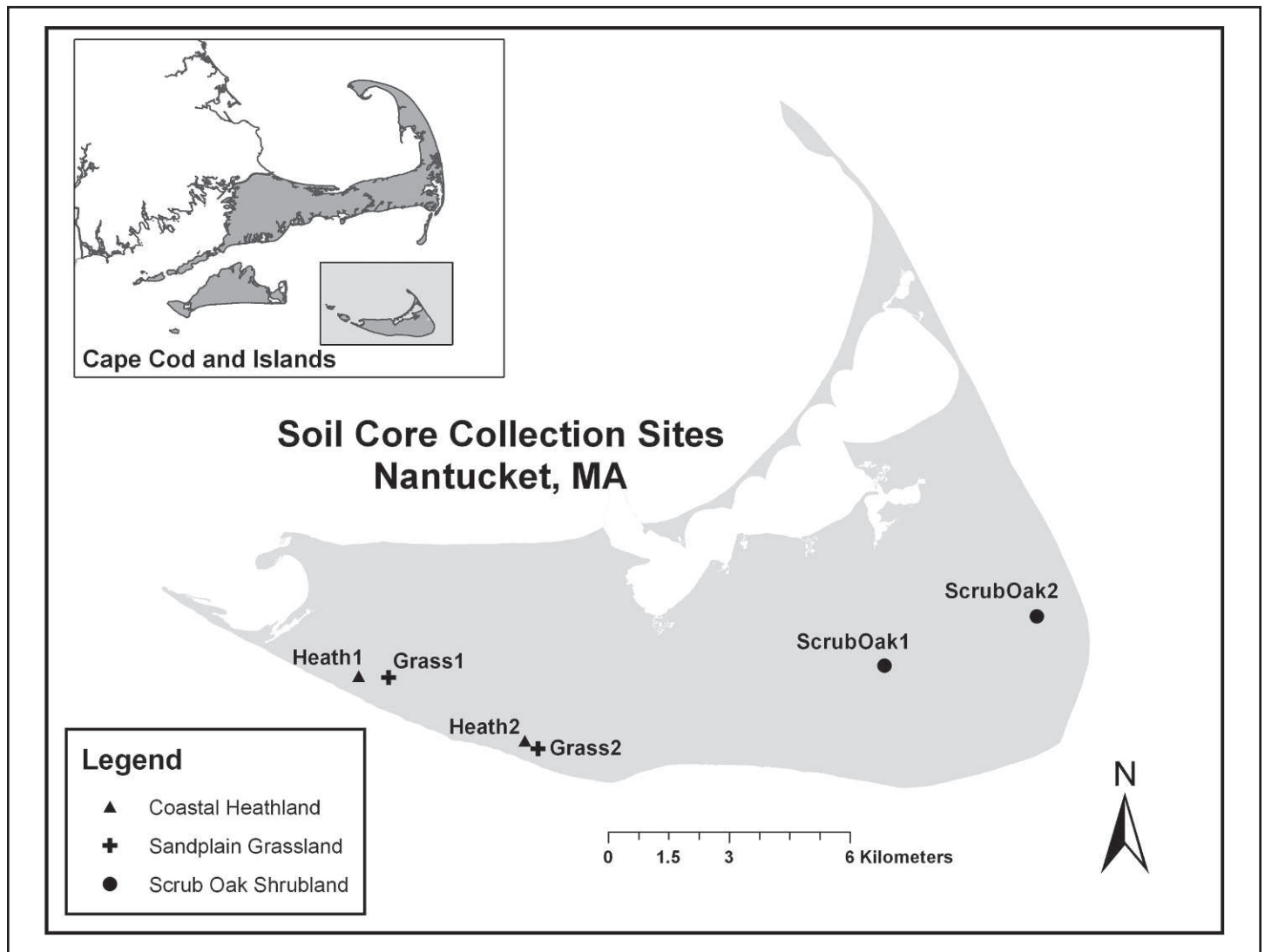


Figure 1. Map depicting soil core collection sites for seed bank comparison along a successional gradient in sandplain grassland, coastal heathland, and scrub oak shrubland, Nantucket Island, Massachusetts.

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.) K. Koch), low bush blueberries *(Vaccinium* spp.), and bearberry *(Arctostaphylos uva-ursi* (L.) Spreng.). Woody species cover in heathlands exceeds 40%, but substantial herbaceous cover and some graminoids of the species described above for grasslands are also included. 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 Middle Moors (197 ha, the Nantucket Conservation Foundation), and ScrubOak2 was located in the Sesachacha Heathlands Wildlife Preserve (349 ha, the Massachusetts Audubon Society). 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 100-m x 100-m grid, from which we randomly selected one grid square from each of 10 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. At each point, we collected one soil sample using a square metal device (designed by Dave Sampson, Manhattan, Kansas) to extract 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.

The seedling emergence method is commonly used to estimate the density and species composition of viable seeds in the soil seed bank (Warr et al. 1994; Looney and Gibson 1995; Ne'emen and Izhaki 1999; Godefroid et al. 2006; Landman et al. 2007; Lang and Halpern 2007). This study used a modified version of the seedling emergence method to determine seed bank composition. We separated soil blocks into duff and mineral subsamples when duff was present, following the U.S. Forest Service definitions of these layers (Woodall and Monleon 2007), as there is evidence suggesting that duff may inhibit seed germination (E. Steinauer, unpubl. 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
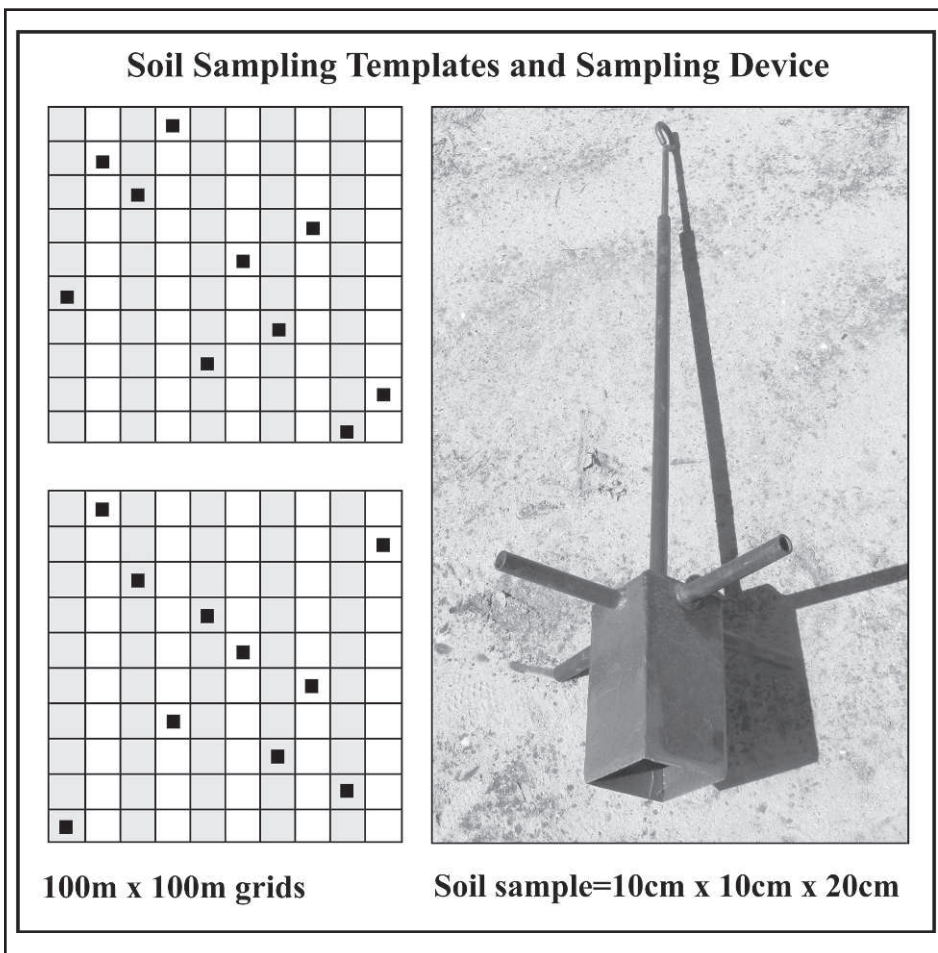


**Figure 2. Sampling templates and soil core sampling device; one template of randomly selected points was applied at each of the collection sites, enabling us to collect ten soil samples at each site distributed over a 100-m x 100-m area (n = 10 for each site), Nantucket Island, Massachusetts.**

potting mix (Metro Mix® 200) in 11" x 20" Kord® fiber trays, which allowed us to standardize soil depth to a thickness of 0.5cm – 1.5 cm (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 seedlings and recording growth form (graminoid, forb, 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).

### Data Analysis

In order to graphically evaluate similarities in species composition among our six sampling locations we conducted a non-metric Multidimensional Scaling Analysis (nMDS) based on a Bray-Curtis dissimilarity matrix 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). The nMDS indicated a difference in species composition between the two scrub oak sites leading us to continue analyzing each site separately and not pool the data by community type. To examine differences in average species composition between each site, we conducted a per MANOVA, 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 (Heath 1, Heath 2, ScrubOak 1, ScrubOak 2); 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 (Figure 3). Grass 1 and Grass 2 sites plotted with dominant graminoids including little bluestem, bentgrass (Agrostis spp.), 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.). ScrubOak 2 was more strongly associated with graminoid species than ScrubOak 1, and hence plotted closer on the ordination to the grassland and heathland sites.

The per MANOVA results indicated a significant difference in average species composition among the six sampling sites (df = 5, F = 3.4296, p < 0.000999). Mann-Whitney u-tests used to examine pairwise relationships between sites for seedling densities by growth form indicated that graminoid density in ScrubOak 1 was significantly lower than all other sampling locations (Table 2). 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 ScrubOak 2 (p = 0.002), while forb density was significantly higher in the duff layer of Heath1 (p = 0.007). ISA was unable to determine whether any of the species were significantly associated with particular sampling sites (six 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$^2$ ± SE) were highest at Grass1 (8740 m$^{-2}$ ± 3474) and Grass2 (8600 m$^{-2}$ ± 2764). Densities were intermediate at Heath 1 (6100 m$^{-2}$ ± 1737), Heath 2 (4470 m$^{-2}$ ± 973), and ScrubOak 2 (5890 m$^{-2}$ ± 2191). ScrubOak 1 seedling densities were the lowest (1680 m$^{-2}$ ± 699), amounting to less than 20% of the seedling density at Grass 2, 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 3). We did not identify any state or federally listed rare or endangered plant species. Seed bank percent composition by growth form varied between sites,
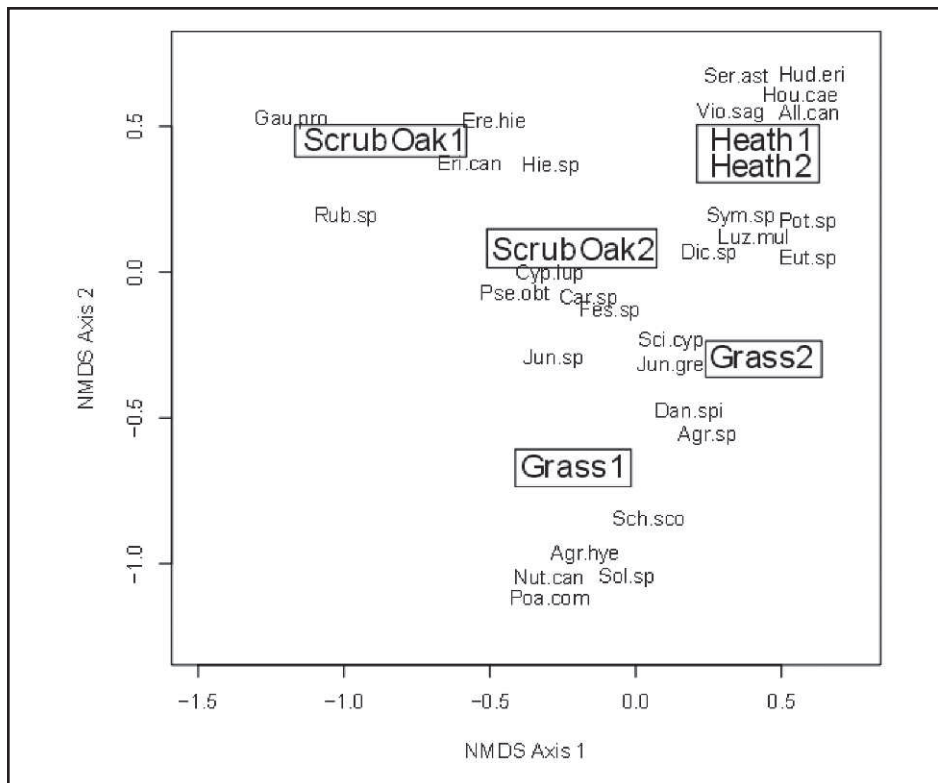
**Figure 3. The nMDS ordination of all emerged seedlings, identified to genus or species, with sampling sites (Grass 1, Grass 2, Heath 1, Heath 2, ScrubOak 1, and ScrubOak 2) grouped based on species composition. Individual taxa are represented by six letter codes: the first three letters indicate genus, and second three letters indicate species, and "sp" indicates those identified only to genus, Nantucket Island, Massachusetts.**

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 and among individual sites on Nantucket. In the nMDS ordination, the ScrubOak 1 site differed the most from all the other sites, plotting far to the left on Axis 1, and was associated with woody species and the weedy native forb, horseweed, rather than with the varied forb species characteristic of grasslands. In contrast, ScrubOak 2 plotted closer to the heathland and grassland sites along Axis 1, primarily due to a higher content of graminoids. It should be noted

that the chief graminoids at this site were *Juncus* spp., and that the dominant grass species of sandplain grasslands, such as little bluestem or bentgrass, were absent. ScrubOak 2 (near the eastern shore) and the heathland and grassland sites (near the southern shore) were all much closer to the coastline than ScrubOak 1, the most inland site. Distance to the shoreline and the degree of wind and salt spray exposure can strongly affect island vegetation development and composition, likely contributing to differences in the two scrub oak sites along with variations in historic use (Tiffney and Eveleigh 1985; Sorrie and Dunwiddie 1996).

The two heathland sites were the most similar to each other of any sites within a community type; they shared many of the forbs typical of grassland and heathland communities, but lacked little bluestem and other key dominant grass species found in the seed bank of the grassland sites. Grassland and heathland sites shared some

seed bank species in common, which is visible in the ordination, and is more clearly depicted in the table of all identified seed bank taxa (Table 3). The species composition similarities in both seed bank species and documented standing vegetation of these communities (Sorrie and Dunwiddie 1996; Swain and Kearsley 2001) support the concept that conversion of heathland to grassland over time, or conversion of scrub oak to heathland as an intermediate stage (with seed addition of key grassland species absent from a site) may facilitate gradual conversion of scrub oak to grassland.

Absence of key grassland dominants in both scrub oak sites, along with extremely low graminoid densities at ScrubOak1, imply that 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 for many species, either via wind or large mammals such as deer (*Odocoileus virginianus*). Other than hawkweeds (*Hieracium* spp.), the forb seed bank of scrub oak sites includes early colonists of disturbed areas such as horseweed or pilewort (*Erechtites hieraciifolius* (L.) Raf. Ex DC), rather than forbs common in heathlands or grasslands (Table 3). It is unclear whether these species form long-term seed banks, but both are wind dispersed. Horseweed seeds have been recorded at altitudes of 140 m and may be transported freely from nearby disturbed sites by strong winds (Weaver 2001; Shields et al. 2006; Darbyshire et

**Table 2. 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 – Grass 1 and 2, coastal heathland = Heath 1 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 Pairwise 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 |

al. 2012).

Higher density of graminoids at ScrubOak 2, 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, or proximity to disturbed areas or shoreline) may strongly influence the seed bank. The fact that little bluestem and bentgrass were absent from the seed bank of 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 grass-dominated vegetation. 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, members of this genus may play an important role in local grassland restoration projects, especially following soil disturbance, colonizing rapidly and stabilizing 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, however, that we have successfully germinated most of the common grassland species in the re-

search 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. obser.). Better climate and moisture control in the research greenhouse would likely have reduced seedling mortality, enabling us to more accurately determine species richness; 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 have been 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 would have allowed us to collect twice as many samples at each site and yet remain within the size constraints of our research greenhouse, possibly improving our ability to detect rarer species and to determine whether particular species were indicators

| Scientific Name | Seed Bank Sampling Sites | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | 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 |

*Continued*

Table 3 (Continued)

| | | | | | | |
|---|---|---|---|---|---|---|
| **Euthamia spp. +** | **0** | **0** | **90 (60)** | **30 (21)** | **130 (80)** | **0** |
| Hieracium spp. + | 440 (244) | 760 (585) | 70 (40) | 1360 (674) | 0 | 0 |
| Houstonia caerulea + | 0 | 0 | 0 | 10 (10) | 0 | 0 |
| Nuttallanthus canadensis + | 0 | 0 | 0 | 0 | 0 | 20 (13) |
| Potentilla canadensis + | 0 | 0 | 0 | 30 (30) | 10 (10) | 0 |
| **Potentilla spp. +** | **0** | **0** | **10 (10)** | **40 (40)** | **20 (20)** | **0** |
| Pseudognaphalium obtusifolium + | 0 | 10 (10) | 0 | 0 | 0 | 0 |
| Sericocarpus asteroides + | 0 | 0 | 10 (10) | 10 (10) | 0 | 0 |
| Solidago spp. + | 0 | 0 | 0 | 0 | 0 | 10 (10) |
| Symphyotrichum spp. + | 0 | 0 | 10 (10) | 10 (10) | 10 (10) | 0 |
| Viola sagittata + | 0 | 0 | 10 (10) | 0 | 0 | 0 |
| unknown forb spp. | 1030 (447) | 1680 (629) | 960 (960) | 2110 (1220) | 530 (216) | 270 (84) |
| **Woody** | | | | | | |
| Hudsonia ericoides + | 0 | 0 | 50 (34) | 110 (110) | 0 | 0 |
| Gaultheria procumbens | 10 (10) | 0 | 0 | 0 | 0 | 0 |
| Rubus flagellaris | 30 (15) | 0 | 0 | 0 | 0 | 0 |
| **Rubus spp.** | **30 (15)** | **0** | **0** | **0** | **0** | **10 (10)** |
| unknown woody spp. | 10 (10) | 0 | 20 (20) | 10 (10) | 0 | 0 |
| **Unknown** | | | | | | |
| unknown spp. | 0 | 0 | 0 | 0 | 40 (40) | 10 (10) |

of each site or community type.

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 between duff and mineral layers 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 persistent seeds of *Juncus* spp.) may also result in higher germination of grassland species from the deeper mineral layer. Differences in duff thickness between samples result in seedling densities from the duff and mineral layers being reported for different volumes of soil, which further complicates comparisons.

## CONCLUSIONS AND FURTHER RESEARCH

Our results demonstrated a scarcity of key grassland species' seeds at overgrown scrub oak sites, which may hinder grassland restoration projects. Overlap in seed bank species composition between grassland and heathland sites implies that converting shrubland to heathland as a transitional phase, combined with seed addition of key grassland dominants, may be more practical than converting shrubland directly to grassland. Heathland sites appear to retain a greater variety of native non-woody early successional species in their seed bank than do scrub oak sites. Targeting restoration to sites with the most favorable characteristics (such as proximity to intact grasslands or to shoreline, exposure to wind and salt spray, or sandy low-nutrient soils) will likely further enhance results. We have initiated additional 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.
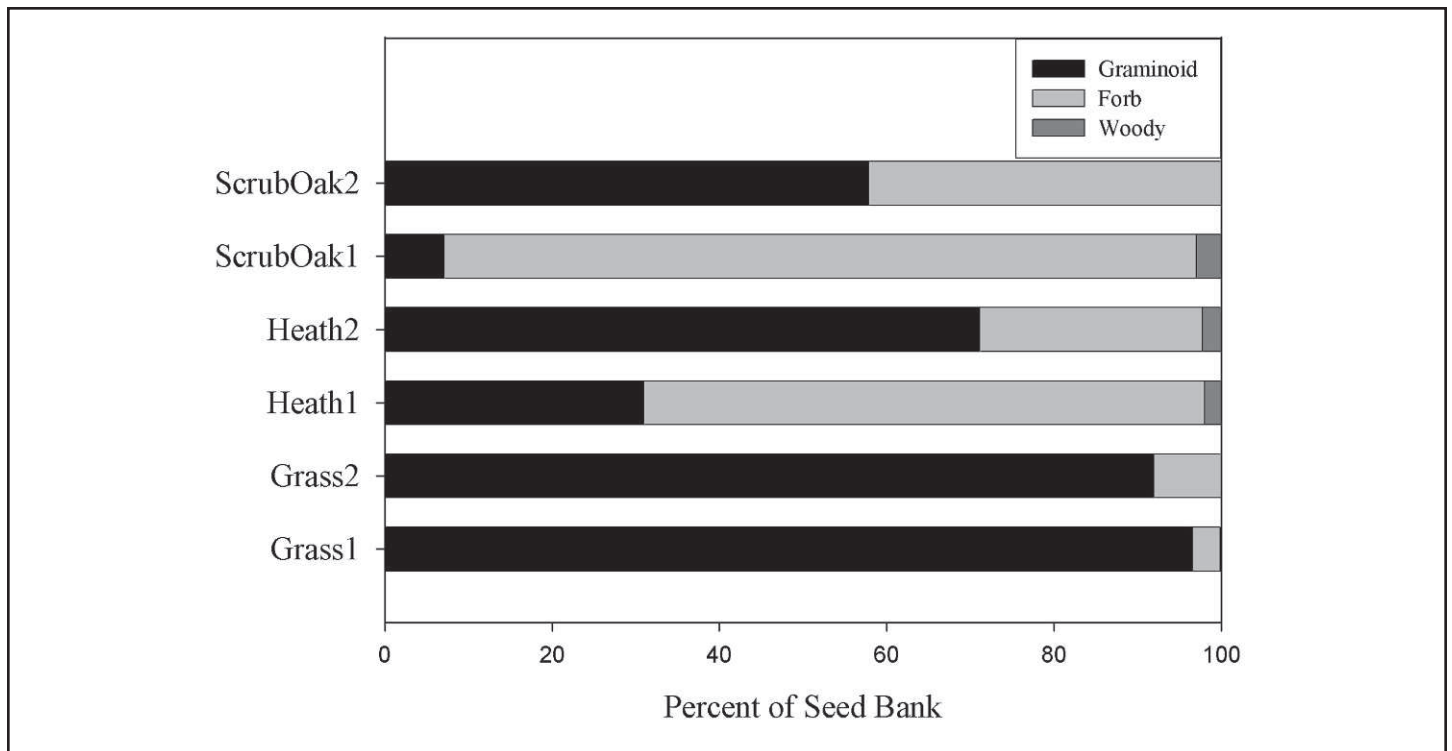
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**Figure 4. Percent composition of seed bank classified by growth form at the six seed bank collection sites along a successional gradient (sandplain grassland = Grass 1 and 2, coastal heathland = Heath 1 and 2, and scrub oak shrubland = ScrubOak 1 and 2), Nantucket Island, Massachusetts.**

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## LITERATURE CITED

Allen, E.A. and R.S. Nowak. 2008. Effect of pinyon-juniper tree cover on the soil seed bank. Rangeland Ecological Management 61:63-73.

Barbour, H., T. Simmons, P. Swain, and H. Woolsey. 1999. Our irreplaceable heritage: protecting biodiversity in Massachusetts. Natural Heritage and Endangered Species Program, Massachusetts Division of Fish and Wildlife, and the Massachusetts Chapter of the Nature Conservancy, Boston, MA.

Bossuyt, B. and M. Hermy. 2003. The potential of soil seedbanks in the ecological restoration of grassland and heathland communities. Belgian Journal of Botany 136:23-34.

Bond W.J., and J.J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution 16:45-51.

Darbyshire, S.J., A. Francis, A. DiTommaso, and D.R. Clements. 2012. The biology of Canadian weeds. 150. *Erechtites hieraciifolius* (L.) Raf. Ex DC. Canadian Journal of Plant Science 92:729-746.

Dunwiddie, P.W. 1997. Long term effects of sheep grazing on coastal sandplain vegetation. Natural Areas Journal 17:261-264.

Dunwiddie, P.W., W. A. Patterson III, J.L. Rudnicky, and R.E. Zaremba. 1997. Vegetation management in coastal grasslands on Nantucket Island, Massachusetts: effects of burning and mowing from 1982 to 1993. Pp. 85-97 *in* P.D. Vickery and P.W. Dunwiddie, eds., Grasslands of Northeastern North America: Ecology and Conservation of Native and Agricultural Landscapes. Massachusetts Audubon Society, Lincoln, MA.

Figueroa, J.A., S.Teillier, and F.M. Jaksic. 2004. Composition, size and dynamics of the seed bank in a Mediterranean shrubland of Chile. Austral Ecology 29:574-584.

Glass, S., and E. Howell. 1993. Mechanisms responsible for the re-vegetation of a former oak barrens after removal of the canopy. 1993 Proceedings of the Editors: Forest Stearns, Emeritus; Karen Holland, U.S. Environmental Protection Agency, June 1995. Proceedings of the Midwest Oak Savanna Conferences, Chicago, IL.

Godefroid, S., S.S. Phartyal, and N. Koedam. 2006. Depth distribution and composition of seed banks under different tree layers in a managed temperate forest ecosystem. Acta Oelogica 29:283-292.

Godfrey, P. J., and P. Alpert. 1985. Racing to save the coastal heaths. The Nature Conservancy News 35:11-13.

Haines, A. 2011. Flora Novae Angliae. Yale University Press, New Haven, CT.

Landman, G.B., R.K. Kolka, and R.R. Sharitz. 2007. Soil seed bank analysis of planted and naturally revegetating thermally-distributed riparian wetland forests. Wetlands 27:211-223.

Lang, N.L., and C.B. Halpern. 2007. The soil seed bank of a montane meadow: consequences of conifer encroachment and implications for restoration. Canadian Journal of Botany 85:557-569.

Langlois, Jr., K.H. 1979. Soil Survey of Nantucket County, Massachusetts. U.S. Department of Agriculture, Soil Conservation Service, in Cooperation with Massachusetts Agricultural Experiment Station [Washington D.C.].

Laughlin, D.C. 2003. Lack of native propagules in a Pennsylvania, USA, limestone prairie seed bank: futile hopes for a role in ecological restoration. Natural Areas Journal 23:158-164.

Leahy, C.W. 1993. Eden's End: The Case for Ecological Protection in Massachusetts. Massachusetts Audubon Society, Lincoln, MA.

Lezberg, A.L., K.C. Buresch, C. Neill, and T. Chase. 2006. Mechanical land clearing to promote establishment of coastal sandplain grassland and shrubland communities. Restoration Ecology 14:220-232.

Looney, P.B., and D.J. Gibson. 1995. The relationship between the soil seedbank and above-ground vegetation of a coastal barrier island. Journal of Vegetation Science 6:825-836.

Lunt, I.D. 1997. Germinable soil seed banks of anthropogenic native grasslands and grassy forest remnants in temperate south-eastern Australia. Plant Ecology 130:21-34.

Matlack, G.R. 2005. Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. Journal of Ecology 93:50-59.

McCune, B., J.B. Grace, and D.L. Urban. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR.

Motzkin, G., and D.R. Foster. 2002. Grasslands, heathlands and shrublands in coastal New England: historical interpretations and approaches to conservation. Journal of Biogeography 29:1-22.

NatureServe. 2009. NatureServe Explorer: An Online Encyclopedia of Life. Accessed 28 January 2010 from <http://www.natureserve.org/explorer>.

Ne'eman, G., and I. Izhaki. 1999. The effect of stand age and microhabitat on soil seed banks in Mediterranean Aleppo pine forests after fire. Plant Ecology 144:115-125.

Norment, C. 2002. On grassland bird conservation in the Northeast. The Auk 119:271-279.

[NTG] Nantucket Town Government Home Page. 2010. Accessed 10 March 2010 from <http://www.nantucket-ma.gov/Pages/index>.

Olano, J.M., I . Caballero, N.A. Laskurain, J. Loidi, and A. Escudero. 2002. Seed bank spatial pattern in a temperate secondary forest. Journal of Vegetation Science 13:775-784.

Oldale, R.N. 1985. Geologic Map of Nantucket and Nearby Islands, Massachusetts. Department of the Interior, U.S. Geological Survey, Arlington, VA.

Perez, C.J., S.S. Waller, L.E. Moser, J.L. Stubbendieck, and A.A. Steuter. 1998. Seed bank characteristics of a Nebraska sandhills prairie. Journal of Range Management 51:55-62.

R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available online <http://www.R-project.org/>.

Rice, E.L., W.T. Penfound, L.M. Rohrbaugh. 1960. Seed dispersal and mineral nutrition in succession in abandoned fields in central Oklahoma. Ecology 41:224-228.

Shields, E.J, J.T. Dauer, M.J. van Gessel, and G. Neumann. 2006. Horseweed (*Conyza canadensis*) seed collected in the planetary boundary layer. Weed Science 55:185.

Shriver, W.G., A.L. Jones, P.D. Vickery, A. Weik, and J.Wells. 2005. The distribution and abundance of obligate grassland birds breeding in New England and New York. General Technical Report PSW-GTR-191, U.S. Department of Agriculture, Forest Service [Albany, CA].

Sorrie, B.A., and P.W. Dunwiddie. 1996. The Vascular and Non-Vascular Flora of Nantucket, Tuckernuck, and Muskeget Islands. Massachusetts Audubon Society, MA Natural Heritage and Endangered Species Program, Nantucket Maria Mitchell Association, The Nature Conservancy. Nantucket, MA.

SPSS 16.0. 2007. Statistical Analysis Software. SPSS Inc. Chicago.

Swain, P.C., and J.B. Kearsley. 2001. Classification of the Natural Communities of Massachusetts. Natural Heritage & Endangered Species Program, Massachusetts Division of Fisheries and Wildlife, Westborough, MA.

Thompson, K. 1987. Seeds and seed banks. New Phytologist 106:23-34.

Tiffney, W.N. and D.E. Eveleigh. 1985. Nantucket's endangered maritime heaths. Pp.1093-1109 *in* O.T Magoon, H. Converse, D. Miner, D. Clark, and L. T. Tobin, eds. Coastal Zone '85. July 30-August 2, 1985. Proceedings of the Fourth Symposium on Coastal and Ocean Management, Baltimore, MD.

[TNC] The Nature Conservancy. 1998. Vegetation Community Map of Nantucket, GIS Data Layer, The Nature Conservancy [Arlington, VA].

Valko, O., P. Torok, B. Tothmeresz, and G. Matus. 2011. Restoration potential in seed banks of acidic fen and dry mesophilous meadows: can restoration be based on local seed banks? Restoration Ecology 19:9-15.

van der Valk, A.G. and R.L. Pederson. 1989. Seed banks and the management and restoration of natural vegetation. Pp. 329-346 *in* M.A. Leck, V.T. Parker, and R.L. Simpson, eds., Ecology of Soil Seed Banks. Academic Press, San Diego, CA.

von Blanckenhagen, B. and P. Poschlod. 2005. Restoration of calcareous grasslands: the role of the soil seed bank and seed dispersal for recolonisation processes. Biotechnology Agronomy Society and Environment 9:143-149.

Wagner, D.L., M.W. Nelson, and D.F. Schweitzer. 2003. Shrubland Lepidoptera of southern New England and southeastern New York: ecology, conservation, and management. Forest Ecology and Management 185:95-112.

Walck, J.L., J.M. Baskin, C.C. Baskin, and S.N. Hidayati. 2005. Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns. Seed Science Research 15:189-196.

Warr, S.J., M. Kent, and K. Thompson. 1994. Seed bank composition and variability in five woodlands in south-west England. Journal of Biogeography 21:151-168.

*Weaver*, J.E. 1958. Summary and interpretation of underground development in natural grassland communities. Ecological Monographs 28:55-78.

Weaver, S.E. 2001. The biology of Canadian weeds.115. *Conyza canadensis.* Canadian Journal of Plant Sciences 81:867-875.

Woodall, C.W. and V.J. Monleon. 2007. Sampling protocol, estimation, and analysis procedures for the Down Woody Materials Indicator of the FIA Program. General Technical Report NRS-22, U.S. Department of Agriculture, Forest Service, [Newton Square, PA].