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Historical influences on the vegetation and soils of the Martha's Vineyard, Massachusetts coastal sandplain: Implications for conservation and restoration

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ABSTRACT

Both disturbance history and previous land use influence present-day vegetation and soils. These influences can have important implications for conservation of plant communities if former disturbance and land use change species abundances, increase colonization of non-native plant species or if they alter soil characteristics in ways that make them less suitable for species of conservation interest. We compared the plant species composition, the proportion of native and nonnative plant species, and soil biogeochemical characteristics across seven dominant land use and vegetation cover types on the outwash sandplain of Martha's Vineyard that differed in previous soil tillage, dominant overstory vegetation and history of recent prescribed fire. The outwash sandplain supports many native plant species adapted to dry, low nutrient conditions and maintenance of native species is a management concern. There was broad overlap in the plant species composition among pine (*Pinus resinosa*, *P. strobus*) plantations on untilled soils, pine plantations on formerly tilled soils, scrub oak (*Quercus ilicifolia*) shrublands, tree oak (*Q. velutina*, *Q. alba*) woodlands, burned tree oak woodlands, and sandplain grasslands. All of these land cover categories contained few nonnative species. In contrast, agricultural grasslands had high richness and cover of nonnative plants. Soil characteristics were also similar among all of the woodland, shrubland and grassland land cover categories, but soils in agricultural grasslands had higher pH, extractable Ca²⁺ and Mg²⁺ in mineral soils and higher rates of net nitrification. The similarity of soils and significant overlap in vegetation across pine plantations, scrub oak shrublands, oak woodlands and sandplain grasslands suggests that the history of land use, current vegetation and soil characteristics do not pose a major barrier to management strategies that would involve conversion among any of these vegetation types. The current presence of high cover of nonnative species and nutrient-enriched soils in agricultural grasslands, however, may pose a barrier to expansion of sandplain grasslands or shrublands on these former agricultural lands if native species are not able to outcompete nonnative species in these anthropogenically-enriched sites.

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1. Introduction

Natural and anthropogenic disturbances strongly influence the composition of plant communities and the chemical properties of soils. For example, the recurrence and severity of fires can shape forest species distribution and abundance for centuries (Grimm, 1984; Romme and Despain, 1989). Forest clearing can cause long-lasting changes to vegetation structure, such as increasing the abundance of weedy or disturbance-adapted tree species and reducing the abundance of woodland shrubs and forbs that have limited ability to recolonize second-growth forests (Motzkin et al., 1996; Bellemere et al., 2002; Dupouey et al., 2002; Eberhardt et al., 2003). Previous land use can also have long-lasting effects on soil characteristics, which include the development of persistent plow (Ap) soil horizons (Motzkin et al., 1996; Foster and Motzkin, 2003) and altered stocks and turnover rates of soil organic matter (Glatzel, 1991; Cambardella and Elliot, 1994; Compton et al., 1998; Compton and Boone, 2000; Jassy et al., 2002). There is also evidence that previous land use can affect soil biogeochemical functions by changing species composition because patterns of nutrient cycling can develop in response to the presence of dominant canopy trees (Finzi et al., 1998; Lovett and Reuth, 1999) or understory plants (Ehrenfeld et al., 2001; Gilliam et al., 2001).

A change in the susceptibility of land to colonization by nonnative plant species may be another important legacy of previous land use. Former land clearing for agriculture has been associated with increases in weedy, disturbance-dependent anthropophilous species (Dupouey et al., 2002) and recently abandoned agricultural lands are frequently dominated by nonnative species (Pickett, 1982; Rejmánek, 1989). One mechanism for this pattern appears to be an increase in the availability of limiting resources, such as nutrients, that shift competitive balance toward faster growing nonnative species (Tilman, 1993; Vitousek et al., 1996).

Understanding how previous land use, disturbances, current vegetation and soils are related has important implications for conservation and restoration of plant communities that are valued for their contributions to regional biological diversity. This information could be used, for example, when selecting sites for the restoration or intensive management of rare or geographically-restricted plant communities, to choose locations where soils are most similar to target communities, or where the probability of invasion by nonnative plants will be low.

The area of disturbance-dependent or early successional habitats in the Northeastern US is declining and these habitats have been identified as a regional conservation concern (Askins, 2001; Litvaitis, 2003). The grasslands, shrublands and heathlands that occupy the coastal sandplain of the northeastern United States are a priority for conservation. Sandplain grasslands are conservation priorities because they contain a large number of regionally rare plants (Barbour et al., 1998; MNHESP, 2001). Shrublands, particularly scrub oak (*Quercus ilicifolia*) shrublands are conservation priorities because they support a large number of rare Lepidoptera (Goldstein, 1997; Wagner et al., 2003). Although the pre-colonial configuration of communities that supported most of the sandplain plants of concern for conservation today are

not known precisely, the abundance of many of these plants apparently expanded during the period of land clearing, agricultural expansion and grazing that followed colonial settlement (Marks, 1983; Foster et al., 2002; Foster and Motzkin, 2003). After the abandonment of tilled and pasture lands that began across the sandplain region beginning as early as the 1830s and continuing into the 20th century, the area of grasslands and shrublands began a prolonged decline that continues to the present, leading to a reduction in habitat suitable for many sandplain herbaceous plant species (Motzkin and Foster, 2002; Clarke and Patterson, 2006). Today, the last remaining grassland and shrubland habitats are threatened by increases in residential development and the regrowth of woody vegetation caused in large part by improved fire detection and fire suppression since the middle of the 20th century (Patterson et al., 1983; Dunwiddie, 1994; Dunwiddie and Adams, 1995; Motzkin and Foster, 2002). Similar trends of loss of grasslands and heathlands caused by woodland expansion are occurring in many locations around the world (Sutherland and Hill, 1995; Brown and Archer, 1999; Briggs et al., 2002).

In the coastal Northeastern US, the continued presence of sandplain grasslands and shrublands will likely depend on: (1) management of the disturbances of mowing, fire and grazing to maintain existing grasslands and shrublands, and (2) restoration or expansion of these habitats from land now in other land covers. In most locations, existing woodlands or current agricultural grasslands are the most feasible starting points for restoration or expansion of grasslands or shrublands. The desirability of each of these options may be influenced by characteristics of soils, vegetation history and presence of non-native species. Improving methods for expanding or restoring disturbance-dependent sandplain plant communities based on an improved understanding of these factors is a priority for many land conservation organizations, particularly because some options to manage or restore land are increasingly constrained by the rapid suburbanization in the coastal plain region (Barbour et al., 1998; TTOR, 1999).

The Northeastern US coastal sandplain is characterized by a common geological and glacial history that resulted in relatively uniform, coarse-textured soils that have low water-holding capacity and low nutrient status (Fletcher and Roffolini, 1986). Most sandplain plant species that are targets for conservation reach their greatest abundance in sites with nutrient-poor soils that were disturbed by historic fire, grazing or clearing (Tiffney, 1997; Dunwiddie et al., 1997; Dunwiddie and Sferra, 1991; Foster and Motzkin, 1999; Motzkin and Foster, 2002). Soil fertility may be an important, but still relatively poorly-understood factor that influences the persistence and quality of remaining early-successional habitat on the sandplain. This role for soil fertility is recognized in the current management of culturally-valued European heathlands, for example, which emphasizes fire, grazing, harvesting and litter removal to perpetuate low nutrient conditions that favor native species and to inhibit colonization by introduced species and faster-growing native species (Gimingham, 1972; Sutherland and Hill, 1995; Mitchell et al., 2000).

In this paper, we evaluate how previous land use and soils are related to the current vegetation of the Martha's Vineyard

coastal sandplain. We asked the following questions: (1) how do the proportions of nonnative species and key soil characteristics differ across sites that vary in dominant overstory vegetation, previous land use and recent prescribed fire? and (2) how can these differences be used to guide efforts to conserve, manage or restore sandplain disturbance-dependent, early successional habitats?

2. Methods

2.1. Site selection

We selected 35 sites on Martha’s Vineyard, MA that included five replicate sites in seven land cover categories. These categories represented the most widespread land covers, those that are most important for plant species conservation, as well as those that encompassed historically-relevant differences in overstory vegetation, past human use and recent fire. The categories were: (1) red pine (*Pinus resinosa*) and white pine (*Pinus strobus*) plantations on untilled soils, (2) similar pine plantations on formerly tilled agricultural fields, (3) scrub oak (*Q. ilicifolia*) shrublands on untilled soils, (4) tree oak (black

oak, *Q. velutina*, white oak, *Q. alba*) woodlands on untilled soils, (5) burned tree oak woodlands on untilled soils where prescribed fire was applied during the previous five years, (6) species-rich sandplain grasslands on untilled soils, and (7) agricultural grasslands on tilled soils now managed as hay-fields (Table 1). All sites were located on the glacial outwash plain on the southern part of the island (Fig. 1) and were placed in representative areas of vegetation away from paths and other obvious recent disturbances. All sites were on coarsely textured well-drained, mesic soils with 0–2% slopes of the Carver, Riverhead and Katama series (Fletcher and Roffolini, 1986). Restricting sites to the outwash plain on similar soils permitted interpretation of the effects of dominant overstory vegetation, land use history and fire on overall plant species composition and soil biogeochemistry while minimizing the effects of the heterogeneity of underlying soils.

Pine plantations on untilled soils were planted between 1929 and 1934 and were typical of plantation forests in the Manuel F. Correllus State Forest (MFCSF) (Foster and Motzkin, 1999). Red pine and white pine are not native to Martha’s Vineyard (Sorrie and Somers, 1999). Pine plantations on formerly tilled soils were planted between 1929 and 1961 and

Table 1 – Description of land cover categories on the coastal sandplain of Martha’s Vineyard

Number	Current vegetation	Land use history	Abbreviation
1	Pine plantation	Not tilled, planted to pine 1929–1934	PP
2	Pine plantation	Tilled before 1934, planted to pine 1935–1961	TP
2	Scrub oak shrubland	Not tilled	SO
4	Tree oak woodland	Not tilled	TO
5	Burned tree oak woodland	Not tilled	BO
6	Sandplain grassland	Not tilled ^a , grasslands maintained by mowing	SG
7	Agricultural grassland	Strong evidence of tillage in last 10 years, currently maintained as hay fields	AG

a One current sandplain grassland site (Katama) showed evidence of historic tillage.

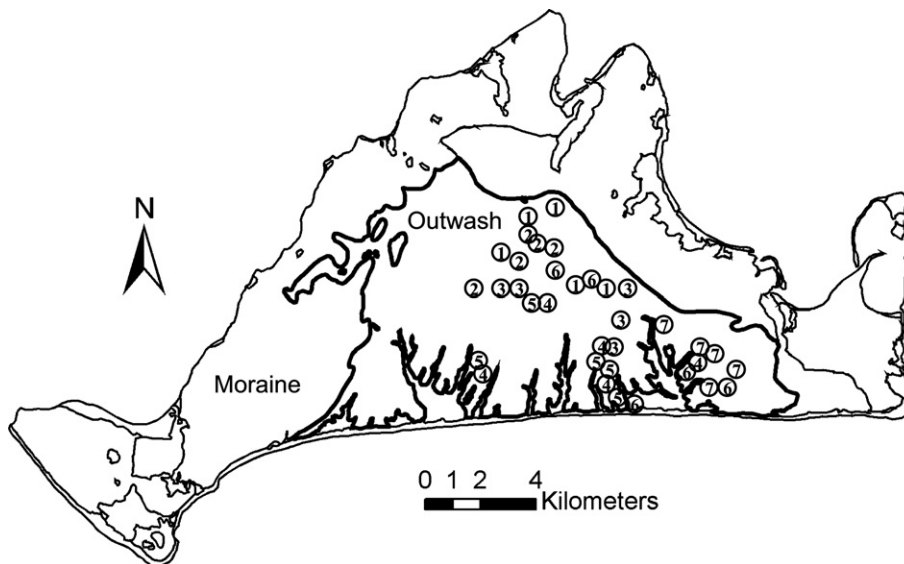


Fig. 1 – Location of sampling sites on the coastal outwash sandplain of central Martha’s Vineyard. Land cover categories are: (1) pine plantations, not tilled, (2) pine plantations, tilled, (3) scrub oak shrubland, (4) tree oak woodland, (5) burned tree oak woodland, (6) sandplain grassland and (7) agricultural grassland.

had Ap horizons. We presume that these areas were part of the approximately 29–36 ha planted to corn, clover, buckwheat, millet and sunflowers with the aim of sustaining heath hens (Gross, 1928; Foster and Motzkin, 1999). The locations of these sites were identified previously by Foster and Motzkin (1999), but there is no record of the crops planted in each location. Scrub oak shrublands occupied shallow, linear depressions that represent the shrublands that have a high and relatively stable composition of *Q. ilicifolia* over time. This dominance of scrub oak shrublands in shallow depressions in other sand plains has been attributed to low or extreme temperatures that restrict growth of tree oaks (Motzkin et al., 2002). Tree oak woodlands were second growth stands approximately 80–170 years old that had roughly equal proportions of *Q. velutina* and *Q. alba*. These tree oak woodlands were mapped as “wooded” in 1848 (US Coast and Geodetic Survey, 1848) and have likely been woodlands subjected to wood repeated wood harvest since European settlement (Foster and Motzkin, 1999). Burned tree oak woodlands of similar age and history were identified from fire management records of The Nature Conservancy and The Trustees of Reservations, both of which conduct prescribed burning on their lands. Neither the scrub oak shrublands, tree oak woodlands nor burned oak woodlands were previously tilled based on the absence of Ap horizons. Sandplain grasslands were areas that contained early-successional native grass and forb species typical of sandplain grasslands characterized as high quality by Dunwiddie et al. (1996). The sandplain grassland sites were maintained by mowing or a combination of mowing and burning. One sandplain grassland (Katama) had an apparent old but diffuse Ap horizon, indicating likely past tillage, although use of this area in recent decades has been for conservation. Agricultural grasslands were areas where land use records and the presence of a well-defined Ap horizon indicated recent tillage within the previous 10 years. Agricultural grasslands were seeded to pasture grasses, are currently maintained by cutting for hay, and have received light or occasional grazing from sheep and cattle during the last 10 years. Details of the location and history of individual plots are provided in Table S1.

2.2. Vegetation sampling and analysis

Prior to sampling, each site was checked to determine the extent of current anthropogenic disturbance. Percentage cover of all vascular plant species was estimated in eight cover-abundance classes: (<1%, 1–3%, 3–5%, 6–15%, 16–25%, 26–50%, 51–75%, >75%) in one 20 m-diameter plot in each site. For analyses, these cover classes were converted to the midpoint of the range of each cover class for each species. Tree density and basal area were determined from diameter at breast height (dbh) of all living (>2.5 cm dbh) and dead (>10 cm dbh) trees within the plot. We estimated stand age by taking increment cores from one to three of the largest sound trees (>5 cm dbh) per stand. Nomenclature followed Sorrie and Somers (1999). All species were classified as native or non native. A species was considered nonnative if its historical origin was outside of Martha’s Vineyard (Dukes County), as determined by the flora of Massachusetts (Sorrie and Somers, 1999). To reduce human-influenced bias, we re-

moved white and red pine that had been planted in two of our site types (pine plantations, and pine plantations on formerly tilled agricultural fields) from tests of differences of native and nonnative richness and cover with soil parameters and site types.

We performed Kruskal–Wallis tests for differences in the native and nonnative richness and plant cover among land cover categories. All percentage data were arc-sin square root transformed and count data were square root transformed for normality (Zar, 1999). If a categorical variable was found to be statistically significant in the full model, a posteriori tests were conducted to determine differences between categories. We conducted *G*-tests of independence (Zar, 1999), or the likelihood ratio of χ^2 analysis, for each species that occurred in four or more study plots of the sandplain grasslands and the agricultural grasslands to determine association of individual species with these two habitat types, using sequential Bonferonni adjustments.

Multivariate analyses were conducted to understand the influence of land use history, prescribed burning and dominant overstory vegetation on plant species composition. Non-metric multiple dimensional scaling (NMDS) was performed on the surveyed species abundance values for each plot. Because model instability occurred with low abundance values, only those plots that had greater than 1% cover of nonnative species were included. Each analysis was initiated with six axes, 40 runs of real data and 50 runs of randomized data, with an instability criterion of 0.00001 using PC-ORD, version 4 (McCune and Mefford, 1999). Because of the large differences between agricultural grasslands and other land cover categories, we performed one additional NMDS analysis with agricultural grasslands removed.

We conducted stepwise backwards regression analyses to understand the influence of soil characteristics on native and nonnative species richness. We wanted to understand which soil characteristics were associated with maximum native species diversity and minimum nonnative species diversity. We used Akaike’s criterion (Burnham and Anderson, 2002) to select a priori those variables predicted to have the greatest impact on species richness. We chose the following soil characteristics as independent variables: density (dry soil cm^{-3}), pH, percent carbon (C) and nitrogen (N), soil respiration (mg C g^{-1} dry soil d^{-1}), extractable NH_4^+ ($\mu\text{g N g}^{-1}$ dry soil), extractable NO_3^- ($\mu\text{g N g}^{-1}$ dry soil), net N-mineralization and net nitrification rates ($\mu\text{g N g}^{-1}$ dry soil d^{-1}), and extractable Ca, K, Mg and Na ($\text{cmol (+) } 100 \text{ g}^{-1}$ dry soil).

2.3. Soil sample collection and analyses

Soil characteristics were determined by collecting five cores to a depth of approximately 15 cm using a 5 cm-diameter stainless steel corer. Samples were collected at 5 m distances along a transect placed randomly in a representative area within each site. The soil organic (Oea) horizon was separated, and the top 10 cm of the mineral horizon were measured and collected. Soil samples were homogenized and roots and gravel were removed by hand (Oea horizon) or by passing through a 2 mm sieve (mineral horizon). Replicate cores were combined into one composite soil sample per site. Separate volumetric cores of the Oea and mineral horizons were collected

to measure soil bulk density. The depth of the Oea horizon was recorded from intact soil adjacent to each core hole and averaged for the site. At sites without an organic layer, the top 2 cm of the soil was collected and used to characterize the surface soil horizon. Samples were refrigerated until analysis.

Bulk density of dry soil was calculated after drying samples of known soil volume for 48 h at 60 °C. Soil pH was measured in water (1:1 soil to water for surface soil, 2:1 for mineral soil). Base extractable cation concentrations were measured after extraction with 1 M NH₄Cl followed by analysis of the extracts by atomic absorption spectrophotometry (Robarge and Fernandez, 1986). Soil C and N concentrations were measured on a Perkin-Elmer 2400 elemental analyzer after grinding with a mortar and pestle. Soil NH₄⁺ and NO₃⁻ concentrations were measured by extraction with 1 N KCl and analysis of the extracts by colorimetry for NH₄⁺ (alkaline phenol hypochlorite method) and NO₃⁻ (Cd reduction on Lachat autoanalyzer). We incubated soils in the laboratory for 14 d at 30 °C and reextracted them with KCl to obtain an index of net N mineralization and net nitrification. Potential nitrification was measured on soils from a subset of sites using a modification of the method of Schmidt and Belser (1982). We combined wet soil equivalent to 5 g of dry weight with 30 mL of ammonium phosphate solution in 60 mL centrifuge tubes. We shook the tubes at 150 rpm at room temperature and analyzed NO₃⁻ concentrations at 2, 6, 12, and 24 h. We

measured an index of soil respiration by incubating approximately 30 g of surface soil or 50 g of mineral soil at room temperature in sealed containers outfitted with a recirculating loop that allowed measurement of changes in CO₂ concentrations on a LICOR 6262 infrared gas analyzer. Incubations of 3 min provided sufficient changes to calculate respiration rates from the linear portion of the CO₂ concentration curve.

We used analysis of variance in SAS (GLM procedure) to test for differences in soil characteristics using land cover categories as the independent variable. Data were log transformed where necessary to meet the assumptions of a normal distribution.

3. Results

3.1. Vegetation

Agricultural grasslands had significantly higher nonnative species richness and cover than all other site types (Fig. 2a–b). Native species richness and cover did not differ significantly among site types. However, agricultural grasslands had lower native species richness than sandplain grasslands and lower native species cover than all of the other site types (Fig. 2c–d). Tree oak woodlands, burned tree oak woodlands, pine plantations, burned oak woodlands and scrub oak shrublands had low richness and very low occurrence of non-native species. Previously tilled pine plantations had slightly

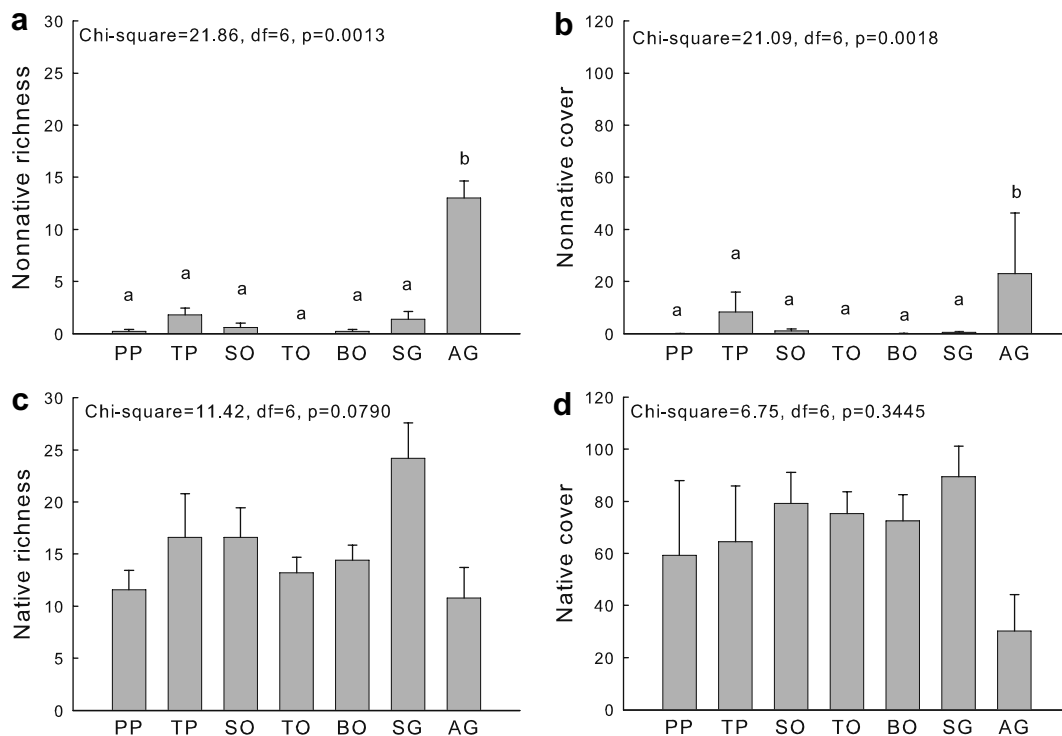


Fig. 2 – Nonnative plant species richness (a), nonnative plant cover (b), native plant species richness (c), and native plant species cover (d) among the land cover categories on the sandplain of Martha’s Vineyard. Categories are: PP, pine plantation; TP, previously plowed pine plantation; SO, scrub oak shrubland; TO, tree oak woodland; BO, burned tree oak woodland; SG, sandplain grassland; AG, agricultural grassland. For non-native species, lower-case letters indicate statistically significant differences (Kruskal–Wallis tests, P < 0.05). There were no significant differences in native species richness or cover among the land cover categories.

<i>Ilex verticillata</i>	1	0.1	1	0.1							1	0.1		
<i>Juncus greenei</i>											1	0.1		
<i>Juncus tenuis</i>													2	0.2
<i>Juniperus virginiana</i>			1	0.1									1	0.1
<i>Kalmia angustifolia</i>							1	0.4						
<i>Lespedeza hirta</i>											1	0.1		
<i>Luzula multiflora</i>													1	0.1
<i>Lysimachia quadrifolia</i>					1	0.1					1	0.1		
<i>Maianthemum canadense</i>			1	0.1	1	0.1	1	0.1	1	0.1				
<i>Melampyrum lineare</i>	1	0.1	4	0.4	2	0.2	3	0.3	3	0.3	1	0.1		
<i>Myrica pensylvanica</i>	1	0.1	2	0.5	1	0.1	2	0.2	2	0.5	3	1.0	1	0.4
<i>Oxalis stricta</i>													4	0.4
<i>Panicum spp.</i>			2	0.2							2	0.2	3	1.0
<i>Panicum verrucosum</i>													1	0.1
<i>Parthenocissus quinquefolia</i>	1	0.1	2	0.2					1	0.1	1	0.1		
<i>Phytolacca americana</i>									1	0.1				
<i>Pinus rigida</i>	3	2.0	2	0.9	4	0.7	2	7.9			3	0.3	2	0.2
<i>Polygala polygama</i>					1	0.1					1	0.1		
<i>Potentilla canadensis</i>					2	0.2	1	0.1	3	0.3	2	0.5	1	0.1
<i>Prunus pumula</i>											1	0.1		
<i>Prunus serotina</i>	3	0.3	2	0.8	1	0.4	1	0.1	1	0.1	4	0.4	2	0.5
<i>Pteridium aquilinum</i>	1	0.1	1	0.1	2	0.2	1	0.1	1	0.8	2	0.2		
<i>Quercus alba</i>	5	15.6	3	1.6	3	0.6	5	10.3	4	6.0	4	1.4		
<i>Quercus ilicifolia</i>	4	1.7	4	6.4	5	52.5	5	6.0	5	6.0	4	0.7	1	0.1
<i>Quercus prinoides</i>	1	0.1	2	0.2	4	2.1	4	0.4	2	0.5	2	0.2		
<i>Quercus stellata</i>					2	0.2	3	1.3	1	0.4	1	0.1		
<i>Quercus velutina</i>	4	1.4	2	1.2	4	1.0	5	6.8	5	10.3	2	0.2		
<i>Rhus copallinum</i>			2	0.5							1	0.1		
<i>Rosa carolina</i>			1	0.1							3	0.3	2	0.2
<i>Rubus allegheniensis</i>					1	0.1					1	0.1		
<i>Rubus flagellaris</i>	1	0.1	1	0.1	1	0.1			2	0.2	3	0.6	1	0.8
<i>Rubus hispidus</i>											2	0.9		
<i>Rubus occidentalis</i>			1	0.1										
<i>Rubus recurvicaulis</i>			2	0.2	1	0.1	1	0.1			2	0.9	2	0.5
<i>Schizachyrium scoparium</i>					2	0.9					4	1.7	3	7.7
<i>Sisyrinchium angustifolium</i>											1	0.1		
<i>Sisyrinchium spp.</i>													1	0.1
<i>Smilax glauca</i>	1	0.1												
<i>Smilax rotundifolia</i>									1	0.1	1	0.1		
<i>Solidago odora</i>			2	0.2	1	0.1					4	1.1		
<i>Solidago puberula</i>											1	0.1		
<i>Solidago rugosa</i>			1	0.1	1	0.1			1	0.1	4	0.4	2	0.2

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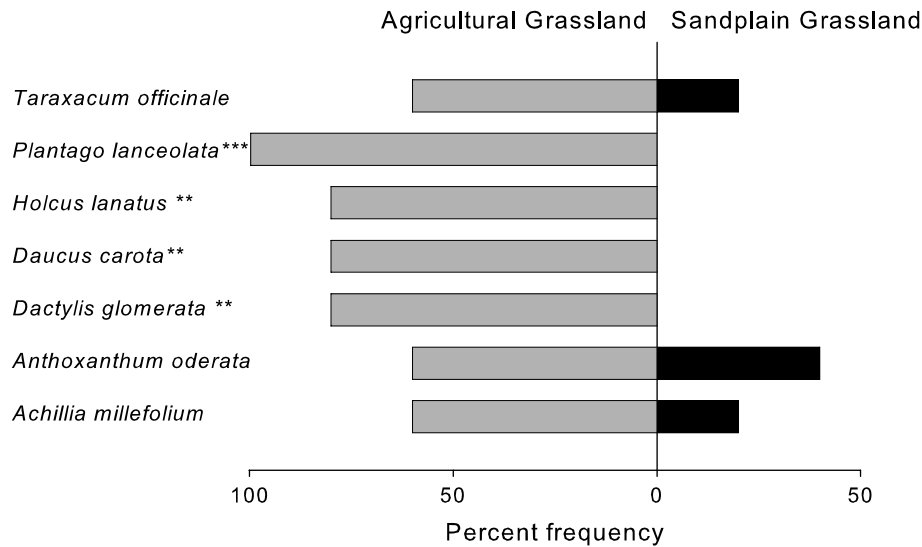


Fig. 4 – Test for differences in cover of major species in agricultural grasslands and sandplain grasslands. These species were the most widespread and were selected because they were the only ones to occur in four or more study plots. G-test: nonsignificant (unmarked), $P > 0.05$; *, $0.05 \geq P > 0.01$, **, $0.01 \geq P > 0.001$; and ***, $P < 0.0001$.

(*Daucus carota*), and orchard grass (*Dactylis glomerata*) were significantly associated with agricultural grasslands compared with sandplain grasslands (Fig. 4).

When the agricultural grasslands were removed from the NMDS, scrub oak shrublands and a group containing pine plantations and previously-tilled pine plantations were distinct (Fig. 3b). Sandplain grasslands, tree oak woodlands and burned tree oak woodlands were broadly similar in species composition despite their large differences in structure, largely because they shared fairly high abundance of many shrub species, such as *Gaylussacia baccata* and *Vaccinium angustifolium*. No native species had statistically significant associations with either agricultural grasslands or sandplain grasslands; however *Q. alba*, *Q. ilicifolia*, licorice goldenrod (*Solidago odora*), and *V. angustifolium* showed weak associations with sandplain grasslands and butterfly-weed (*Asclepias tuberosa*) and common yellow wood-sorrel (*Oxalis stricta*) tended to be associated with agricultural grasslands.

3.2. Soils

Soil surface horizons in sandplain grasslands and agricultural grasslands were either absent or thinner than in the other land cover categories (Table 3). Surface soil bulk densities were highest in the agricultural grasslands, higher in sandplain grasslands than the other sites but not different among non-grassland land cover categories (Table 3). The bulk density in the mineral soil A horizon was higher than in the surface horizon, but it did not differ among land cover categories (Table 3).

The pH in both surface and mineral horizons was highest in the agricultural grasslands but differed little among the land cover categories (Table 3). Differences in exchangeable Ca^{2+} , Mg^{2+} , K^+ , Na^+ and the sum of base cations in the surface horizon were relatively small. Notable differences were a trend toward lower Ca^{2+} in sandplain grasslands and lower K^+ in sandplain grasslands and in agricultural grasslands (Table 3). Exchangeable cations in the mineral horizon were very

low, but Ca^{2+} and Mg^{2+} were significantly higher in the agricultural grasslands (Table 3). Soil stocks of exchangeable cations followed the same patterns, with higher total Ca^{2+} and Mg^{2+} stocks in agricultural grasslands compared with all other sites.

Soil C concentrations in the surface horizon were lowest in the agricultural grasslands (Table 3). Soil N concentration in the surface horizon showed a similar general pattern but differences between agricultural grasslands and other sites were not statistically significant. Differences in C and N concentration in the mineral horizon among land cover categories were small and not significant (Table 3). Total C stocks were higher in burned oak woodlands than in any other sites ($P < 0.031$) but N stocks did not differ across land cover categories. The C:N ratios in mineral and surface horizons showed similar patterns, with generally lower values in sandplain grasslands and agricultural grasslands (Table 3). In the surface horizon, soil respiration rate was highest in the agricultural grassland but overall differences among land cover categories were small (Table 3). In the mineral horizon, respiration rate was higher in the agricultural grasslands than in any other land cover category.

There were no differences in NO_3^- and NH_4^+ stocks among land cover categories in either surface or mineral horizons. However, there was a trend for higher concentrations of NO_3^- in agricultural grasslands (Table 3). In the surface horizon, sandplain grasslands and agricultural grasslands had a lower rate of net N mineralization than the land cover categories (Table 3). However, the mineral horizon of agricultural grasslands had the highest rate of net N mineralization, but this variable was not significantly different from the other sites. In both the surface and mineral horizons, net nitrification rates were higher in the agricultural grasslands than in the other categories (Table 3). Potential nitrification rate was highest in the agricultural grasslands in both surface and mineral horizons and was significantly higher in the mineral horizon (Table 3).

Table 3 – Soil characteristics in land cover categories with different land use history and current vegetation on the outwash sandplain of Martha's Vineyard

Characteristic	Units	Horizon	Land cover category							P
			Pine	Tilled pine	Scrub oak	Tree oak	Burned oak	Sandplain grassland	Agricultural grasslands	
Horizon depth	cm	Surface	4.0 ^a	3.9 ^a	4.0 ^a	4.9 ^a	3.9 ^a	1.0 ^b	0.0 ^b	<0.0001
Bulk density	g cm ⁻³	Surface	0.13 ^a	0.21 ^a	0.17 ^a	0.13 ^a	0.17 ^a	0.70 ^b	1.14 ^c	<0.0001
pH		Surface	3.8 ^a	4.4 ^{a,b}	3.9 ^a	3.9 ^a	5.0 ^{b,c}	4.2 ^a	5.5 ^{b,c}	<0.0001
Extractable Ca ²⁺	cmol (+) kg ⁻¹ dry soil	Surface	8.5 ^a	5.1 ^a	7.7 ^a	9.3 ^a	10.0 ^a	0.8 ^a	4.7 ^a	<0.0069
Extractable Mg ²⁺	cmol (+) kg ⁻¹ dry soil	Surface	4.2 ^{a,b}	2.49 ^{a,c}	2.1 ^{b,c}	5.5 ^a	5.2 ^a	0.9 ^c	1.5 ^c	<0.0002
Extractable K ⁺	cmol (+) kg ⁻¹ dry soil	Surface	1.6 ^{a,b}	0.9 ^{b,c}	1.3 ^{b,c}	2.1 ^a	0.8 ^c	0.6 ^c	0.6 ^c	<0.0008
Extractable Na ⁺	cmol (+) kg ⁻¹ dry soil	Surface	1.8 ^{a,b}	1.5 ^{a,b}	1.7 ^{a,b}	2.6 ^a	0.5 ^b	1.5 ^{a,b}	1.4 ^{a,b}	<0.0196
Sum cations	cmol (+) kg ⁻¹ dry soil	Surface	16.1 ^a	9.9 ^{a,b}	12.8 ^{a,b}	19.5 ^a	16.5 ^a	3.8 ^b	8.1 ^{a,b}	<0.0006
Carbon	mg g ⁻¹	Surface	351 ^a	344 ^a	232 ^{a,b}	345 ^{a,b}	336 ^{a,b}	156 ^b	32 ^c	<0.0001
Nitrogen	mg g ⁻¹	Surface	12 ^a	12 ^a	9 ^{a,b}	20 ^a	15 ^a	8 ^{a,b}	2 ^{a,b}	<0.0015
C:N ratio		Surface	35 ^a	34 ^a	28 ^{a,b}	26 ^{a,b}	27 ^{a,b}	22 ^{b,c}	16 ^c	<0.0001
Respiration rate	mg C g ⁻¹ C h ⁻¹	Surface	0.7 ^{a,b}	0.5 ^{a,b}	1.0 ^{a,b}	0.5 ^{a,b}	0.4 ^b	0.8 ^{a,b}	1.3 ^a	<0.0199
Extractable NH ₄ ⁺	μg N g ⁻¹ dry soil	Surface	1.2 ^a	1.1 ^a	0.9 ^a	0.8 ^a	1.8 ^a	1.0 ^a	3.0 ^a	NS
Extractable NO ₃ ⁻	μg N g ⁻¹ dry soil	Surface	0.1 ^a	0.1 ^a	0.1 ^a	0.1 ^a	0.1 ^a	0.1 ^a	1.1 ^a	NS
Net N mineralization	μg N g ⁻¹ dry soil d ⁻¹	Surface	21.4 ^a	12.6 ^a	10.6 ^a	12.1 ^a	17.1 ^a	1.6 ^b	2.4 ^b	<0.0001
Net nitrification	μg N g ⁻¹ dry soil d ⁻¹	Surface	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0.5 ^{a,b}	1.4 ^b	<0.0005
Potential nitrification	μg N g ⁻¹ dry soil d ⁻¹	Surface	—	—	—	0.20 ^a	1.2 ^a	1.2 ^a	17.3 ^a	NS
Bulk density	g cm ⁻³	Mineral	0.78 ^a	0.89 ^a	0.97 ^a	0.94 ^a	0.82 ^a	1.03 ^a	0.99 ^a	NS
pH		Mineral	4.5 ^a	4.6 ^a	4.4 ^a	4.5 ^a	4.7 ^a	4.7 ^a	5.8 ^b	<0.0001
Extractable Ca ²⁺	cmol (+) kg ⁻¹ dry soil	Mineral	0.1 ^a	0.1 ^a	0.1 ^a	0.1 ^a	0.1 ^a	0.0 ^a	2.9 ^b	<0.0001
Extractable Mg ²⁺	cmol (+) kg ⁻¹ dry soil	Mineral	0.1 ^{a,b}	0.1 ^{a,b}	0.1 ^{a,b}	0.2 ^a	0 ^b	0.1 ^a	0.5 ^c	<0.0001
Extractable K ⁺	cmol (+) kg ⁻¹ dry soil	Mineral	0.2 ^a	0.2 ^a	0.1 ^a	0.2 ^a	0 ^a	0.1 ^a	0.4 ^a	NS
Extractable Na ⁺	cmol (+) kg ⁻¹ dry soil	Mineral	0.5 ^a	0.4 ^a	0.3 ^a	0.3 ^a	0.2 ^a	0.4 ^a	0.3 ^a	NS
Sum cations	cmol (+) kg ⁻¹ dry soil	Mineral	1.0 ^a	0.8 ^a	0.5 ^a	0.7 ^a	0.3 ^b	0.6 ^a	4.1 ^c	<0.0001
Carbon	mg g ⁻¹	Mineral	31 ^a	28 ^a	15 ^a	17 ^a	16 ^a	21 ^a	22 ^a	NS
Nitrogen	mg g ⁻¹	Mineral	1 ^{a,b,c}	1 ^{a,b,c}	1 ^c	1 ^{b,c}	1 ^c	2 ^{a,b}	2 ^a	<0.0010
C:N ratio		Mineral	35 ^a	25 ^{a,b}	32 ^a	30 ^a	32 ^a	18 ^b	16 ^b	<0.0001
Respiration rate	mg C g ⁻¹ C h ⁻¹	Mineral	0.2 ^a	0.2 ^a	0.7 ^{a,b}	0.3 ^a	0.4 ^a	0.3 ^b	1.1 ^b	<0.0023
Extractable NH ₄ ⁺	μg N g ⁻¹ dry soil	Mineral	1.1 ^a	1.6 ^a	1.5 ^a	0.5 ^a	0.8 ^a	2.2 ^a	0.4 ^a	NS
Extractable NO ₃ ⁻	μg N g ⁻¹ dry soil	Mineral	0.0 ^a	0.0 ^a	0.0 ^a	0.0 ^a	0.0 ^a	0.0 ^a	1.1 ^a	NS
Net N mineralization	μg N g ⁻¹ dry soil d ⁻¹	Mineral	0.9 ^a	0.6 ^a	0.7 ^a	0.4 ^a	0.6 ^a	0.3 ^a	1.3 ^a	NS
Net nitrification	μg N g ⁻¹ dry soil d ⁻¹	Mineral	0 ^a	0 ^a	0 ^a	0 ^a	0.1 ^a	0.1 ^a	0.8 ^b	<0.0004
Potential nitrification	μg N g ⁻¹ dry soil d ⁻¹	Mineral	—	—	—	1.2 ^a	0.4 ^a	1.3 ^a	19.4 ^b	<0.0026

Values within rows with similar subscripts were not significantly different (Bonferroni t-tests). Potential nitrification was not analyzed for all sites and sites with missing data are indicated by (—).

3.3. Soils and vegetation relationships

Species richness of native and nonnative species was significantly related to different suites of soil characteristics. Non-native species richness was positively related to soil density ($P < 0.01$), pH ($P < 0.05$), and sodium ($P < 0.05$) but negatively related to soil potassium. Native species richness was significantly lower in soils with higher rates of net nitrification ($P < 0.001$), rates, extractable soil Ca^{2+} ($P < 0.05$) and extractable soil Mg^{2+} ($P < 0.05$).

4. Discussion

4.1. Vegetation patterns

On the Martha's Vineyard sandplain, there was broad overlap in species composition of pine plantations, scrub oak shrublands, tree oak and burned tree oak woodlands and sandplain grassland that differed in their historical tillage, dominant overstory vegetation and occurrence of recent fire. The similarity of species composition was caused primarily by the wide distribution of dominant plant species. The occurrence of similar dominant tree and shrub species across a variety of habitats ranging from wooded to shrubby to predominantly open has been noted for Martha's Vineyard, Nantucket, and Cape Cod sandplains (Dunwiddie et al., 1996, 1997). In addition, recent prescribed burning of the understory resulted in no dramatic shifts in the species composition of the vegetation. Sandplain grasslands had more species primarily because of additions of grasses and forbs not present in the more wooded land cover categories. All of these land cover categories had relatively low numbers and cover of nonnative species, although there was a weak trend toward more nonnative species in previously-tilled pine plantations and in sandplain grasslands.

Our results contrasted somewhat with previous studies in which previous tillage was strongly correlated with lower abundances of some native plant species (Motzkin et al., 1996, 2002; Eberhardt et al., 2003). Several factors may have caused this result. We sampled a relatively small number of sites (5) for each land cover category (total $n = 35$), compared with the 89–344 plots surveyed in these earlier studies. This could have limited our ability to discriminate some statistical differences among land cover classes, especially for understory species that were patchily distributed and typically occurred on both tilled and untilled woodland sites even there was a significant probability they occurred more frequently in one land use or the other. Similar to these earlier studies, we found some native species such as *Q. alba*, *Q. ilicifolia*, *S. odora*, and *V. angustifolia*, were less common in tilled sites but these differences were not statistically significant when included in multiple Bonferroni comparisons among the seven land use categories.

We could not discount the possibility that the effect of tilling had a smaller effect on Martha's Vineyard than elsewhere, either because tilling occurred in relatively small patches compared with other coastal locations (Foster and Motzkin, 1999), because the history of agricultural disturbance may have been shorter or less intense. Our results were consistent with Dunwiddie et al. (1996) who found that sandplain grasslands shared both native and nonnative species with agricul-

tural grasslands. Also on the Martha's Vineyard sandplain, Lezberg et al. (2006) showed that mechanical land clearing to promote early-successional grassland and shrubland increased the richness of grasses and forbs but did not result in the elimination of any woody species present before the manipulation, and produced patterns of species cover and frequency similar to that we observed in the sandplain grasslands.

In contrast to the broad overlap in species composition among pine plantations, scrub oak shrublands, oak woodlands, burned oak woodlands and sandplain grasslands, the agricultural grasslands had very different vegetation that contained a high richness and cover of nonnative species and low richness and cover of the native species that predominated in the other land cover categories. The combination of the absence of native shrubs and the presence of European agricultural weeds such as *P. lanceolata*, *H. lanatus*, *D. carota*, and *D. glomerata* helped to distinguish agricultural grasslands from all of the other land cover categories (Fig. 3). This result was broadly consistent with other studies that found that recent agricultural fields are frequently dominated by nonnative species (Pickett, 1982; Ogden and Rejmanek, 2005).

4.2. Soil characteristics

Soil physical properties, cation concentrations and carbon and nitrogen concentrations and turnover rates showed the same broad similarity among pine plantations, tilled pine plantations, scrub oak shrublands, oak woodlands, burned oak woodlands and sandplain grasslands and the same large differences between agricultural grasslands and the other land cover categories. On the sandplain, the similarity of these soil characteristics across different woodland types and sandplain grasslands with different land-use histories and current vegetation suggested that the influence of these factors on soil chemistry and biogeochemical function in the sandplain landscape was relatively small. Several factors may account for this pattern. Vegetation in the range of pine plantations, oak woodlands and sandplain grasslands may not have differed substantially enough in the presence of the major species or species groups, such as oaks (*Quercus* spp.), sugar maple (*Acer saccharum*) or Ericaceous shrubs, that have been linked to differences in soil nutrient status and nitrogen cycling in other forest locations in the Northeastern US (Finzi et al., 1998; Gilliam et al., 2001). Our soil results were generally similar to the findings of Compton et al. (1998) who found that previous tillage had a relatively minor effect on soil C and N stocks and rates of soil nitrogen cycling in a New England sandplain. The turnover time of soil organic matter in the very sandy soils of Martha's Vineyard sandplain of about 50 years (Peterson and Neill, 2002) is shorter than the turnover time of organic matter turnover in soils from similar latitudes with even slightly greater clay content (Arrouays et al., 1995; Hooker et al., 2005) and less than the approximately 70 years since the tillage of our formerly tilled pine plantations. This likely reduced or eliminated any ability to detect differences in soil properties between old tilled and non-tilled sites. The absence of a major effect of burning on any soil properties was consistent with other studies that have measured few long-term changes to C or N stocks or N

cycling rates following prescribed burns in oak woodlands (Boerner et al., 2000; Phillips et al., 2000; Hubbard et al., 2004).

The largest differences in soil characteristics occurred between the various woodlands and the agricultural grasslands, with sandplain grasslands showing intermediate characteristics. Several features of the agricultural and sandplain grassland soils stood out. The absence of a true organic Oea horizon was correlated with the higher bulk densities in the grasslands. The common practice of liming plowed land and hayfields was likely responsible for elevated pH in the agricultural grasslands. Soil pH on former agricultural soils is commonly elevated compared with non-tilled forest soils (Compton and Boone, 2000). Higher pH in our agricultural grasslands compared with the formerly tilled pine plantations probably reflected the much shorter time since cultivation. Higher concentrations of Ca^{++} and Mg^{++} in the mineral soil of the agricultural grasslands also probably reflected recent history of lime additions in these sites. The close proximity to the ocean was also likely the cause of similar and relatively high Na^+ concentrations in all land cover categories.

Differences in soil N concentrations and cycling rates also stood out in the agricultural grasslands. Rates of net nitrification in all the wooded land cover categories and of sandplain grasslands were low and generally resembled patterns typical in the relatively acid soils of oak and pine woodlands (Compton et al., 1998; Finzi et al., 1998). High rates of net nitrification and potential nitrification suggested a fundamental shift toward greater inorganic nitrogen availability and greater production of soil NO_3^- in the agricultural grassland soils. Higher rates of net nitrification in cultivated compared with grassland soils has been reported from both North America (Schimel, 1986) and Europe (Jassy et al., 2002).

By comparing hardwood forests with previous tillage and similar forest on soils never tilled, Compton et al. (1998) found higher rates of net nitrification in formerly tilled soils that mirrored the increases in net nitrification from native to plowed grasslands that we found in this study. However, they found that plant species composition, specifically the difference between pine and oak forests, affected N dynamics. We found no differences in N dynamics between formerly tilled pine plantations and never tilled pine plantations, which could reflect the relatively short legacy of former tillage in these sandy soils that have high organic matter turnover rates and relative similarity of acid-loving oak and Ericaceous vegetation.

4.3. Implications for conservation and management

Restoration or expansion of the open, disturbance-dependent grasslands and shrublands that support most rare and regionally-restricted plants and insects are conservation land management priorities on the New England coastal sandplain. Our results suggest that the history of land use, current vegetation and soil characteristics do not pose major barriers to management strategies that would involve conversion among any of these vegetation types with the specific objective of maintaining some habitat for particular rare plants or insects (Wagner et al., 2003; Clarke and Patterson, 2006). Such management might involve maintaining a mosaic of vegetation types or promoting specific species-rich shrubland or grassland communities within larger largely forested mosaics. For example,

based on the low richness of nonnative plants and the similarity of soils, removal of all or a portion of the approximately 259 ha of nonnative red and white pines that now exist in the MFCSF in the central portion of Martha's Vineyard to promote native plants or Lepidoptera (Foster and Motzkin, 1999; Dunlop, 2004) would be unlikely to cause significant increases in nonnative plants. Plantations that were never tilled would appear to be somewhat better candidates for this management compared with formerly-tilled plantations based on their slightly lower (but not statistically significant) richness and cover of nonnative species in non-tilled sites. Across the wider sandplain region, several smaller-scale experiments that examined mechanical tree clearing in oak woodlands (Lezberg et al., 2006), oak, pitch pine and scrub oak woodlands on Martha's Vineyard (Patterson and Clark, 2006) and scrub oak shrublands on Nantucket (K. Beattie, pers. comm.) all found that manipulations were not followed by significant increases in nonnative species, suggesting that sites that have similar soils and no previous history of nonnative species can promote grasslands or shrublands without significant risk of invasion by nonnative species. Expansion of sandplain grassland habitat to promote native sandplain plants must be balanced against the relatively greater value of oak woodlands and oak shrublands for many rare Lepidoptera (Goldstein, 1997; Wagner et al., 2003).

Because they are already cleared and because of their visual resemblance, agricultural grasslands are potential candidates for management to reestablish cover of native-species rich sandplain grasslands. Attempts to promote sandplain grasslands or native species-rich shrublands on recently-tilled agricultural grasslands, however, may face other hurdles. Although vegetation structure (predominance of grasses and forbs) in agricultural grasslands and sandplain grasslands is superficially similar, agricultural grasslands: (1) lack many of the native shrubs, forbs and grasses that are present in all of the woodland land cover categories, and (2) contain a high richness and cover of nonnative forbs and grasses. Based on studies from other locations that suggest restoration of native grassland vegetation on recently-abandoned agricultural lands can be jeopardized by the persistence of nonnative grasses (Bakker and Wilson, 2004), promotion of native species-rich plant communities on Northeastern US sandplain agricultural grasslands may require measures to eliminate nonnative grasses, seeding or planting with native plants, or both. Because many typical and rare Northeastern US sandplain forbs and grasses reach greatest abundance on soils with low pH, low moisture, and low nutrient status (Farnsworth, 2006), and because low soil nutrient status may be required to favor native or desired plants at the expense of nonnative or less desired species (Marrs et al., 1991; Ehrenfeld and Toth, 1997; Owen and Marrs, 2000), the higher soil pH and Ca and Mg concentrations in the agricultural grasslands may also represent a barrier to the reestablishment of native plants. Further experiments to test the relative performance of target native sandplain plants in competition with nonnative species and tests of the effects of pH-lowering soil amendments or nutrient removal strategies would provide valuable information that could enhance future promotion of native vegetation on these anthropogenically-enriched areas.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2006.10.046](https://doi.org/10.1016/j.biocon.2006.10.046).

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