Management regime and field age affects species richness and cover of native forbs and exotic species in Virginia grasslands

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ABSTRACT

The majority of grasslands in the eastern United States are maintained through agricultural use (livestock grazing and hay production), intermittent management as fallow fields, or active management for ecological or recreational purposes. Management following agricultural use can follow a variety of practices from benign neglect to active planting of native grasses and forbs. We surveyed 64 grasslands in a 15-county region of northwestern Virginia to assess their plant species composition, with emphasis on the response of exotic species and native forb species richness to time since agricultural use. With regard to agricultural use, we found that livestock grazing resulted in low levels of native species richness and increased exotic species prevalence, while hay production increased native forb richness. In these fields, eutrophication (as measured by phosphorus levels) was a strong positive predictor of exotic species. Post-agricultural fields, maintained through mowing (fallow), retained native species but also experienced sharp increases in exotic species. When post-agricultural management included the establishment of native grasses and forbs a higher initial richness of native species resulted. However, fields disked during establishment lost native species and gained exotic species with increasing field age; an outcome not observed when field establishment did not involve disking. The management practices applied to post-agricultural fields significantly impact their ability to support biodiversity, their propensity to harbor exotic species, and their ability to maintain native diversity and resist invasions of exotic species with increasing age since abandonment.

RESTORATION RECAP

- The restoration of native forb species in post-agricultural fields is facilitated best by not disturbing the soil during the restoration
- Fields restored by planting native grasses and forbs lose many of the added forb species as the field ages
- Exotic species are controlled best by not disturbing the soil and not supplementing sites with phosphorus
- Of fields used as pasture or harvested for hay production, hay fields maintained more native forb species than did livestock pastures

INTRODUCTION

Grasslands are one of the most threatened ecosystems in North America, with estimates suggesting that native prairies have been reduced to less than 0.1% of their pre-European extent (Samson and Knopf 1994). Historically, agricultural conversion and livestock production were the leading causes of loss of native grasslands. However, during recent decades, agricultural abandonment has increased in the eastern United States (Flinn et al. 2005, Cramer et al. 2008), providing opportunities for restoration or creation of native grasslands.

Grasslands are a natural ecosystem throughout much of Virginia. Though primarily forested at the time of the arrival of Europeans, the Ridge and Valley and Piedmont physiographic provinces of Virginia also contained prairies and savannas that were maintained by natural and human-caused fires (Allard and Leonard 1962, Brown 2000). Extant prairies in Virginia are rare and semi-natural, maintained by human activities (Fleming and Coulling 2001). Isolated from the main extent of North American prairie, these eastern prairies have not been well-studied, especially in Virginia (Davis et al. 2002, Tompkins 2013, Benson 2011). Since the colonial period, Virginia grasslands have been maintained and expanded through agricultural use, which shifted from wheat farming and sheep ranching in the late 19th century (Kirby 1991) to primarily hay production and cattle ranching in the 20th century (USDA 2014). Currently, metropolitan centers in Virginia are expanding and replacing farmland with development, but large farms along the leading edge of these expanding exurban areas are also converting to estates and second homes, with reductions both in acreage and intensity of agricultural production (Waisanen and Bliss 2002, Ramankutty et al. 2010). This shift in land ownership and economy offers an opportunity to document how alternate prescriptions of grassland management, including conversion to native warm-season grasslands (NWSG), affects the richness of native and exotic species in the grassland community.

Tillage agriculture has created strong and lasting legacies in soil and plant communities, which include increased abundance and diversity of exotic species, and often, the complete loss of native specialists (Foster et al. 2003, Flinn et al. 2005, Cramer et al. 2008, Brudvig et al. 2013). The species composition of post-agricultural grasslands may be limited by the dispersal ability of propagules and the soil legacies of the site (Nsikani et al. 2018). In addition, traditional forage production that uses exotic grasses to maximize productivity has effects similar to those of tillage agriculture, including the reduction of native species richness via mechanical or chemical removal, eutrophication via fertilization, and modification of the soil seed bank (Smith et al. 2009, Teutsch 2009, Zylka et al. 2016). In eastern North America, this management regime included a shift to exotic, cool-season (C_3) grasses from native, warm-season (C_4) grasses, preferred for forage production because of increased yield (Peterson and Brann 2009). As a result of this shift, today's exotic, cool-season grasslands (ECSG) on post-agricultural soils have lower native species richness than do native warm-season grasslands (Miles and Knops 2009).

Eutrophication from fertilization is one legacy of agriculture, with phosphorus levels typically elevated in post-agricultural soils (Flinn and Vellend 2005). After cessation of fertilization, nitrogen is depleted rapidly, but phosphorus can remain relatively high for decades

(Marrs 1993). Eutrophication reduces plant diversity (Crawley et al. 2005, Suding et al. 2005, Hautier et al. 2014, Harpole et al. 2016), and biodiversity remains depressed longer on soils subjected to excess phosphorus than those subjected to excess nitrogen (Willems and van Nieuwstadt 1996). Exotic species tend to increase disproportionately in response to nutrient additions, even in native-dominated habitats (Huenneke et al. 1990, Morghan and Rice 2006, Seabloom et al. 2015,). Eutrophication can also increase the dominance of grasses (Inouye and Tilman 1995, Silvertown et al. 2006, Hejcman et al. 2007), often at the expense of forb diversity (McCain et al. 2010).

The species composition of post-agricultural grasslands depends to some extent on the intensity of the prior agricultural use. Moderately degraded grasslands, such as those without a history of tillage, may revert to a rich suite of native species once woody shrubs are removed, even without the addition of native propagules (Waldén and Lindborg 2016, Trowbridge et al. 2017). However, disturbing the soil following agricultural use (i.e., tillage) can stimulate the exotic seed bank and promote the establishment of early-successional exotic species (Jauni et al. 2015). As an alternative, herbicides can be used to remove dominant exotic grasses (Bakker et al. 2003, Huddleston and Young 2005) or they can be applied after soil disturbance to control exotic species (Masters et al. 1996).

Post-agricultural management, which generally requires sporadic or periodic disturbance (i.e.., mowing, spot herbicide, mulching or burning) to prevent woody encroachment and maintain the open field, can include re-establishing the dominance of native grass species, including a suite of native forbs (Rowe 2010). Native forbs have high conservation value, both for aesthetic appeal and as a component of biodiversity. Grasses dominate the productivity of native prairies, but forbs contribute overwhelmingly to both species and functional diversity in eastern Piedmont and midwestern tallgrass prairies (Reichman 1987, Davis et al. 2002).

Here we evaluate the effects of grassland management during and following agricultural use on the total herbaceous species richness, native forb richness and cover, and dominance of grasses and exotic species under four different management prescriptions: 1) standard ECSG forage and pasture grasslands; 2) ECSG grasslands maintained for post-agricultural use (fallow); and grasslands converted to NWSG for post-agricultural use to promote biodiversity, either 3) with or 4) without soil disturbance. Our hypotheses were: 1) Total herbaceous species richness, native forb richness and abundance, and exotic species richness and cover will be higher in post-agricultural grasslands than in grasslands under active agricultural management; 2) Total herbaceous species richness and both native forb species richness and abundance will be highest in post-agricultural grasslands converted to NWSG using protocols that include seed additions of native forb species; 3) Tillage during post-agricultural management will lead to a decline in native forb richness and abundance and increases in exotic species; 4) Both native grasses and exotic species will increase in post-agricultural fields in response to high nutrient (phosphorus) levels, with a concurrent reduction in the richness and cover of native forbs; and 5) Both herbaceous species richness and native forb richness will be reduced as grass dominance increases, regardless of its origin (NWSG or ECSG).

METHODS

Study area and site selection

We selected 62 grasslands in 15 counties in the Blue Ridge, Ridge and Valley, and Piedmont ecoregions of Northern Virginia. (37°43’ N to 39°27’ N; 77°16’ W to 79°28’ W) (Table 1). To the west of the Blue Ridge Mountains, the soils are underlain with sedimentary rocks and include karst topography, while igneous and sedimentary rocks underlie the Piedmont (Weakley et al. 2013). The region is classified as humid subtropical climate (Woodward and Hoffman 1991), receiving an average of 107 cm of precipitation annually, with a slight decline in the winter months compared to other seasons. The warm summers have an average maximum July temperature of 30° C, and the mild winters have an average minimum January temperature of -5° C.

We selected grasslands for surveys in cooperation with Virginia Working Landscapes, a partnership of private landowners, non-governmental organizations, public agencies, and volunteers dedicated to promoting biodiversity and native plants and wildlife (VWL 2019). Grasslands in this region are embedded in a matrix of forests, row-crop agricultural fields, and old fields, with only small, scattered populations of native grassland species persisting in forest clearings and ruderal habitats. All selected grasslands had a history of tillage agriculture and/or had been tilled and planted with ECSG in the mid-20th century. We separated grasslands into five management categories based on information provided by land managers through questionnaires and interviews. ECSG Hay grasslands (n=8) had been mowed one to two times annually, with biomass removed. ECSG Pasture grasslands (n=10) had not been mowed for hay but were rotationally grazed, primarily by cattle. ECSG Fallow grasslands (n=15) had been removed from agricultural production and their management varied, either being mulched (mowed with biomass not removed), spot-treated with herbicide, or burned, or a combination of these, with management intervals ranging from one to five years. NWSG Disked grasslands (n=12) were seeded with native grasses and forbs after turning over the soil, then maintained with mulching, fire, or spot herbicide. NWSG Undisked grasslands (n=17) were seeded with native grasses and forbs either after multiple herbicide applications or following no-till row-crop agriculture, then maintained with mulching, fire, or spot herbicide application. Seeds of native species were commercially-sourced as cultivars or regional genotypes and were either drilled or broadcast, depending on the grassland. We assigned grasslands an age based on the number of years between the establishment of the current grassland management and the year of the vegetation survey.

Plant biodiversity surveys

We surveyed plant biodiversity in an average of ten 8-ha grasslands per year, with the earliest survey on July 12 and the latest September 7. Some grasslands were visited in multiple years, but only the final survey year (between 2011 and 2017) was used for analysis. For each survey, three poles were spaced a minimum of 200 m apart within the field, a 100 m transect was placed in a random direction from each pole, and seven 1-m^2 quadrats were placed at random intervals along each transect. In some grasslands, land managers changed management regimes of areas containing one or two transects after the transects were established, meaning that in the final survey year, these were considered multiple grasslands with different management regimes. This resulted in several grasslands with only one or two transects (see Table 1 for the number of transects and grasslands in each management regime). Individual transects that spanned multiple management regimes were excluded from the analysis. This selection process resulted in the analysis of 141, 100-m transects across the 62 grasslands.

Within each 1-m^2 quadrat, all plant species were identified and the percent cover of all herbaceous vascular plant species was visually estimated to within 10%. Species with less than 10% cover were assigned a conservative value of 1% cover for analysis. Records of individuals that could not be identified to species (3.2% of records) were removed unless they could be identified to a genus or family not represented by any other individuals within the transect. Vegetation surveys were either led by the authors (22%) or citizen scientists with substantial botanical expertise. Citizen scientists were vetted by one of the authors, attended a one-day training session before each survey season, and collected specimens of any unknown species for later identification by professional staff.

Soil sampling

We collected eight 15-cm soil cores per survey transect at points 25 and 75 meters in each cardinal direction from either the center of the survey area (2011 surveys) or one end of the survey transect (all other years) and composited them into a single sample per transect. Soils were sent to a commercial laboratory (Waypoint Analytical, Richmond, VA) for sieving and chemical analyses, including pH , Mehlich-3 phosphorus (Sims et al. 2002), organic matter, potassium, magnesium, calcium, and cation exchange capacity.

Statistical analyses

We calculated the observed herbaceous species richness and native forb species richness per transect, based on the presence of each species in any 1 m^2 quadrat along the transect. We determined species to be native or exotic to the United States using the Flora of Virginia (Weakley et al. 2013). To estimate percent coverage of native forbs, grasses and exotic species along a transect, we summed the percent cover of each native forb, grass, and exotic species within each quadrat. We then converted these values to proportions by dividing the percent cover value for each species by the total percent cover of all species in each quadrat. Finally, we averaged the proportion values for all quadrats along each transect to obtain a single value for each metric at each transect.

Our initial examination of means and variance for each management type, did indicate substantial differences in species richness and average cover values (Table 2), however the data did not meet assumptions for a normal distribution regardless of data transformations performed. Subsequently we assumed non-normal distributions of data and used generalized linear mixed models to evaluate the effects of grassland management, age, pH, phosphorus (ppm) and the interaction of age and management on these metrics (herbaceous species richness, native forb species richness, native forb cover, exotic species cover, grass cover). We also included grass cover as a main effect for richness responses. We scaled as Pearson residuals all continuous variables (pH, ppm, grass cover and age). We specified a Poisson distribution with a log link for richness and a binomial distribution with a logit link for the proportion of total cover. We used field site as a random effect to account for among-grassland heterogeneity. We used the R statistical software version 3.4.2 (R Core Team 2017), with the packages *lme4* for generalized linear mixed models, *car* for Wald χ^2 effects tests, and *multcomp* for multiple comparisons for our analyses.

RESULTS

Species Richness

Average herbaceous species richness showed considerable variation among grasslands, ranging from 7-42 species (Table 1). Using a multivariate analysis based on a Poisson distribution of data, we detected significant differences in plant communities within management types if we incorporated field age into the analysis. In this multivariate analysis, total herbaceous species richness did not vary among management regimes (Wald $\chi^2 = 0.51$, $p = 0.97$) (Table 3). There was, however, a decline in total species richness with the age of the grassland in both ECSG Pasture (-0.74 species/year; z = -2.15, $p = 0.032$) and NWSG Disked (-0.65 species/year; z = -2.13, $p = 0.033$) grasslands. In contrast to our hypothesis, native forb richness also did not vary in response to management category (Wald $\chi^2 = 5.97$, $p = 0.20$), but native forbs declined by 0.47 species/year in NWSG Disked grasslands (z = -2.64, $p = 0.008$). Species richness for both herbaceous (Wald $\chi^2 = 6.95$, $p = 0.008$) and native forbs (Wald $\chi^2 = 9.39$, $p = 0.002$) were reduced as the proportion of grass cover increased, but neither was affected by pH or phosphorus.

Relative Abundance

A multivariate analysis of the fields based on a binomial distribution of data did show the proportional cover of native forbs varied among grassland management categories (Wald $\chi^2 = 20.03$, $p < 0.001$), being higher in NWSG Undisked (40%) than in grasslands still used for forage production, i.e., ECSG Hay (6%; z = 3.50, $p = 0.039$), and ECSG Pasture (6%; z = 3.51, $p = 0.004$) (Table 3). There were no other differences among management categories in the proportional cover of native forbs.

Exotic species made up a larger proportional cover in ECSG Pasture (0.85) than in any grassland restored to NWSG (Wald $\chi^2 = 28.80$, $p < 0.0001$) (Table 3). In the multivariate analysis, the proportional cover of exotic species was higher in both ECSG Fallow (0.62) and ECSG Hay (0.58) than in NWSG Undisked (0.33). Using ECSG Fallow as a reference, ECSG Pasture had higher levels of exotic species cover (z = 3.38, p < 0.001). Disking during the establishment of NWSG grasslands was marginally better in controlling exotic species invasion when compared to ECSG Fallow (z = -1.98, $p = 0.047$), while NWSG Undisked clearly promoted less exotic species cover relative to ECSG Fallow (z = -2.90, p = 0.004). Exotic species cover declined with age in both NWSG Undisked (z = -2.54, $p = 0.011$) and ECSG Pastures (z = -2.19, $p = 0.029$), but not the remaining management types.

In the multivariate analysis, the proportional cover of native forbs decreased with increased levels of phosphorus (Wald $\chi^2 = 50.77$, $p < 0.001$), while the proportional cover of both exotic (Wald $\chi^2 = 20.14$, $p < 0.001$) and grass (Wald $\chi^2 = 18.33$, $p < 0.001$) species increased with higher levels of phosphorous. Grass cover was the only cover variable that responded to pH, with the proportional cover of grass increasing with higher pH (Wald $\chi^2 = 12.13$, $p < 0.001$).

Field Age

The multivariate analysis allowed us to identify a significant interaction between management practice and field age for three of our grassland metrics (Herbaceous species richness, native forb richness and native forb cover) (Table 3). Figure 1 shows variation with field age of each management type for each of our metrics. ECSG Pasture fields declined or were stable in these measures over time, and NWSG fields disked during establishment showed significant declines in these measures following the initial high levels in natural forb richness and cover (Figure 1). In contrast, NWSG fields not disked during establishment increased in species richness and cover with increased age. ECSG Hay fields either maintained or showed a slight increase in our richness and cover measures. With regards to exotic species, fallow fields showed the largest increase in exotic species over time while NWSG fields not disked during establishment showed the largest decline in exotic species with increasing age (Figure 1).

DISCUSSION

Two major criteria for grassland integrity are native species richness and diversity, and the dominance of native species relative to exotic species (Rowe 2010). Whether post-agricultural grasslands reduce, maintain, or increase plant diversity relative to agricultural grasslands can vary based on field management (Martin et al. 2005), but success also depends on the environmental conditions, relative diversity prior to restoration, and the availability of propagules (Baker et al. 2003, Zylka et al. 2016, Matthews et al. 2017). Because forbs account for the majority of species in North American prairies (Reichman 1987, Davis et al. 2002), native forb abundance and diversity are crucial to evaluating the status of grassland plant communities.

Native forbs also support the abundance and diversity of native arthropod herbivores and pollinators (Whiles and Charlton 2006), and the establishment of native forbs can mitigate the decline of native pollinators (Cameron et al. 2011, Blaauw and Isaacs 2014). However, native forbs are unlikely to colonize grasslands in the absence of abundant source populations (Winsa et al. 2015). Due to this, seeds of native forbs are often included in restoration protocols, even though establishment success can be relatively low (Hillhouse and Zedler 2011, Middleton et al. 2010), see Millikin et al. 2016 as an exception). For example, Baer et al. (2002) found that native forbs established readily when added during the restoration of a tallgrass prairie, but then declined rapidly, from more than 50% of cover during the second year after establishment to less than 10% of cover by the sixth year. Our examination of fields that differed in both management and age provides evidence that protocols during post-agricultural management make a significant difference; initial species richness for both herbaceous species and native forbs declined over time for NWSG plantings that included turning over the soil but did not decline for NWSG planted without turning over the soil. In our study, all agricultural fields were maintained for hay or pasture using ECSG species; we have no data on how abandoned NWSG agricultural fields would respond to tilling during initial treatment.

Although our initial examination of native forbs (both richness and percent cover) for each of the management types indicated restoration to NWSG increased native forb species (Table 2), a more nuanced examination of the data found our first two hypotheses were too broad to be supported (Table 3). We observed no sustained increase in species richness for fallow fields or conversion to NWSG for either herbaceous or native forb species. We did find, however, that proportional cover of native forbs was higher in NWSG Undisked than in all the grasslands used for forage production, (i.e. ECSG Hay, and ECSG Pasture). We also did not find that fallow fields or conversion to NWSG always shifted dominance from exotic to native species; again, the exception was when establishment did not include turning over the soil. While proportional cover of exotics increased with field age for fallow fields and stayed constant for fields disked during NWSG establishment, it declined markedly in NWSG fields that were not disked during establishment.

The link between disturbance and invasion of exotic plant species is well established (Alpert et al. 2000, Myers and Harms 2009, Jauni et al. 2015). Schnoor et al. (2015) conducted a meta-analysis of grassland restoration projects and found heavy disturbance (i.e., disking) was detrimental to restoration of native species, while light disturbance (i.e., rotavation) was beneficial. For both hypotheses, soil disturbance is the dominant factor facilitating exotic species colonization or persistence, and not grass type or management method.

Eutrophication with phosphorus has been shown to favor exotic grassland species over natives (Seabloom et al. 2015), and to reduce plant species richness in grasslands by promoting grasses over forbs (Janssens et al. 1998). In this study, relatively high phosphorus levels were associated with grass dominance, and the proportional cover of both exotic species and grasses increased with increased phosphorus in our grasslands. Phosphorus amounts between 50 and 100 ppm are considered optimum for crop yield in the Mid-Atlantic region (Sims et al. 2002). Shifts in plant communities in response to eutrophication are widely documented (Suding et al. 2005, Stevens et al. 2010), but often as shifts in stability and not species richness (Adler et al. 2011, Hauitier et al. 2014). We did not find direct evidence that elevated phosphorus reduces species richness; however, phosphorus promoted grass dominance, and grass dominance, in turn, reduced both total and native forb species richness. Reducing nutrients in grassland restoration is widely recommended (Bakker and Berendse 1999, Morghan and Seastedt 1999, Tilman and Isbell 2015). A recommended method for reducing grassland nutrients is the repeated removal of above-ground biomass via mowing (Maron and Jeffries 2001) or fire (Jones et al. 2012, Boughton et al. 2017).

Grassland management to restore grassland integrity (i.e., high species richness and maintenance of a native community) relies on active management. Some prescriptions are clearly better than others at achieving these conservation targets. First, the simple annual mowing of abandoned agricultural fields does not facilitate grassland integrity due to the decline in native species and the marked increase in exotic species over time. Second, grasslands managed for biodiversity should be established without turning the soil, as the relative abundance and cover of native forbs is more sustainable than either fallow or plantings involving disking. This has important implications for the arthropod and pollinator biodiversity that depend on native forbs (Cameron et al. 2011, Blaauw and Isaacs 2014). In addition, when native grasslands were managed without disking, exotic species cover declined with grassland age; an effect not observed when fields were left fallow as ECSG or converted to NWSG through disking. Turning the soil, therefore, appears to reduce species richness whereas minimizing disturbance can help shift the community towards native composition. Third, eutrophication can reduce total species richness through promotion of exotic species and dominant grasses. Common fertilization practices impede maintaining native grasslands. Therefore, we recommend active management when restoring post-agricultural grasslands in Virginia, and these actions should include the following: 1) no turning of the soil to reduce the impact of exotic species proliferation and avoid losing native species over time, and 2) elimination or reduction of eutrophication through fertilization (especially phosphorous) in order to promote native forbs and avoid domination by exotic and grass species. In conclusion, the abandonment of agriculture in the eastern United States provides an opportunity to create native grasslands but only when managed appropriately.

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Figure 1. Responses of herbaceous species richness (A), native forb species richness (B), native forb cover (C) and exotic species cover (D) to management type and grassland age. Categories not sharing the same lowercase letter were different at = 0.05. * denotes a significant interaction with age of grassland. Shaded region represents 95% confidence interval.