RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Seeding is not always necessary to restore native early successional plant communities

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Restoration of native early successional plant communities in the eastern United States is a conservation priority because of declining populations of associated plants and wildlife. Restoration typically involves seeding native species and is often fraught with problems including weedy competition, expensive seed, and slow establishment. Pairing seed bank response with strategic herbicide applications may be an alternative approach for restoring these plant communities. We compared early successional plant communities established by seeding (SD) paired with selective herbicide use to natural revegetation (NR) from the seed bank paired with selective herbicide use at 18 locations that were previously row-crop or tall fescue (*Schedonorus arundinaceus*) fields in Tennessee, Alabama, and Kentucky, the United States. We did not detect differences in species diversity and richness, coverage of non-native grasses and forbs, or number and coverage of native flowering forbs by season between NR and SD treatments at tall fescue or fallow crop sites. Species evenness was greatest in NR and coverage of native-warm-season grasses in SD. Species richness and coverage of native forbs were least in untreated tall fescue units (CNTL). More flexibility to use herbicides with NR reduced coverage of sericea lespedeza (*Lespedeza cuneata*) in NR units compared to SD units at tall fescue sites. NR was 3.7 times cheaper than seeding. Land managers should consider using an NR approach to establish native early successional plant communities.

Key words: herbicides, native species plantings, non-native species control, pollinators, seed bank, tall fescue

Implications for Practice

- Native early successional plant communities can be restored in fields dominated by tall fescue (*Schedonorus arundinaceus*) and in fallow row-crop fields in the eastern United States using seed bank response and strategic herbicide applications.
- Seeding is expensive, subject to establishment failure, and is not necessary on many sites to restore native early successional plant communities. Funds used to seed an area could be used to restore >3X as much area with natural revegetation (NR) and positively impact declining populations of plant and wildlife species.
- Restoration of native early successional plant communities through NR contained similar structural, compositional, and diversity metrices, and should be considered over seeding on sites dominated by previously seeded non-native plant species.

Introduction

Restoring native early successional plant communities has become a conservation priority throughout the United States and other countries (Washburn et al. 2000; Askins 2001; Van Diggelen & Marrs 2003; Brennan & Kuvlesky Jr. 2005; Reid et al. 2009). From 1982–2015, approximately 5.7 million hectares of early successional plant communities were lost to development in the United States (USDA 2018) and remaining early successional communities have undergone substantial declines in quality (Noss et al. 1995). Many wildlife species are associated with these plant communities, and many have experienced population declines (Brennan 1991; Knopf 1994; Brennan & Kuvlesky Jr. 2005; USDA 2009). More specifically, habitat loss is a threat to global pollinator populations, triggering widespread interest in converting non-native plant communities to native plant communities (NRC 2007; Potts et al. 2010).

In the eastern United States, retired production agriculture fields are dominated by non-native species that were seeded for livestock forage or erosion control, often through

Author contributions: CH conceived the research idea; CH, WG developed the field design; WG collected data and with assistance from JZ performed statistical analyses; WG, CH, with contributions from DB and CM, wrote the manuscript; all authors discussed the results and contributed edits and comments on the manuscript.

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doi: 10.1111/rec.13249
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13249/suppinfo

government-sponsored programs (Carmichael Jr 1997; Houck 2009). Most of these non-native species outcompete native plants and arrest ecological succession. Tall fescue (*Schedonorus arundinaceus*) is the most common non-native grass in the eastern United States and was widely established through the Natural Resources Conservation Service's (NRCS) Conservation Reserve Program (CRP) (Buckner et al. 1979; Carmichael Jr 1997; Rogers & Locke 2013). Fields dominated by non-native species typically are restored by spraying non-native species with herbicides followed by seeding native species (Barnes 2004; Burger Jr. 2005; Mittelhauser et al. 2011; Wortley et al. 2013). Seeding is perceived necessary for restoration because of lack of persistence of some native species or because tillage and herbicides are assumed to have altered seed bank composition (Menalled et al. 2001; Koger et al. 2004; McLauchlan 2006; Janika 2016; Li et al. 2017). In addition, programs such as CRP and the Environmental Quality Incentives Program (EQIP) prioritize funding to contracts that use seeding, ultimately making seeding a requirement.

Although seeding is the ubiquitous method for restoring retired agricultural production fields, several issues complicate success. Competition with plants arising from the seed bank is considered the number one reason for seeding failure (Barnes 2004; Rowe 2010). Sericea lespedeza (*Lespedeza cuneata*) and bermudagrass (*Cynodon dactylon*) are two non-native species common in the seed banks of retired production fields in the southeastern United States that are very difficult to control (Bond et al. 2005; Ferrell et al. 2005; Brooke & Harper 2016). In fact, no control options exist for these species that will not also harm seeded native species. Other issues that complicate success via seeding include inadequate seedbed preparation (Rushing 2014), availability of local genotypic seed (Kiehl et al. 2010), and multi-year seedling establishment, which landowners consider a seeding failure (Harper et al. 2007; Rushing 2014). Last, native plant seed used in conservation programs are expensive, commonly costing >$1,000/ha.

Seeding native plant species in retired production fields may not be necessary (Middleton 2003; Harper & Gruchy 2009). Natural revegetation (NR) from the seed bank may be a viable option, giving land managers more options to control invasive species without fear of harming seeded species and losing investment of seed (Liu et al. 2009; Prach et al. 2018). Selective herbicides and strategic applications could be used to promote a desirable native plant community from the seed bank and support focal wildlife species or those of conservation need, meet site-specific management objectives, and minimize coverage of undesirable non-native species (Harper 2017). Because an NR approach would eliminate seed purchases, money saved could be allocated to restoring more and larger areas.

We conducted a field experiment across a large geographical area to compare restoration of native plant communities established via NR to those established by seeding on fields dominated by tall fescue or recently retired from row-crop agriculture. We analyzed data from fallow crop fields and tall fescue fields separately because of different management histories and because fallow crop fields did not have a tall fescue control. Our research objectives were to determine if using NR from the seed bank paired with strategic herbicide applications would produce a plant community dominated by native herbaceous plants and have species diversity, evenness, and richness similar to fields established by seeding and strategic herbicide applications. We hypothesized seeded fields would have greater coverage of non-native species because of fewer options to control competing plants germinating from the seed bank without harming seeded species. We hypothesized naturally revegetated fields would have less coverage of native grasses and greater coverage of native forbs than seeded fields. Lastly, we hypothesized tall fescue-dominated controls would have the least plant diversity, evenness, and richness because of its competitive nature, which limits germination from the seed bank and slows ecological succession.

Methods

Site Characteristics

We collected data at 18 study sites (15 tall fescue-dominated and three fallow crop sites) in Tennessee, Alabama, and Kentucky (Fig. 1). Study sites ranged in size from 2.2 to 5.3 ha. All fields had previously been maintained in an open condition by mowing, haying, or row-crop agriculture for at least 15 years. Eight study sites were on Tennessee Wildlife Resources Agency (TWRA) property in Cocke, Cumberland, Lawrence, Roane, Union, White, Williamson, and Wilson counties. Six study sites were located on Tennessee Valley Authority properties in Bedford, Hamblen, Jefferson, Monroe, and Sevier counties, Tennessee, and Franklin County, Alabama. One study site was on Alabama Department of Conservation and Natural Resources (ADCNR) property in Jackson County, one was in Cades Cove within the Great Smoky Mountains National Park (hereafter Park) in Blount County, Tennessee, one on United States Fish and Wildlife Service property in Fulton County, Kentucky, and one on private property in Haywood County, Tennessee. Elevations ranged from 86 to 658 m. Mean daily temperature across the study area ranged from −4 to 33°C with mean annual precipitation from 114 to 152 cm (National Oceanic and Atmospheric Administration 2019). Soils at 17 of the 18 sites were loam or silt/loam with one site (Jackson County, Alabama) with silt clay (Soil Survey Staff 2019).

Study Design

We selected fields in 2015 dominated by tall fescue or crop fields that were fallowed within the previous 2 years. Tall fescue sites were divided into three similar-sized treatment units and each randomly assigned one of three treatments (control [CNTL], NR, and seeded [SD]) and fallow crop sites were divided into two similar-sized treatment units and each randomly assigned one of two treatments (NR and SD). Controls at tall fescue sites averaged 75% coverage of tall fescue. We collected data June–August (once at each site each year) 2016–2018 along five systematically-assigned transects in each unit maintaining 10-m buffers between transects and unit edges. Although CNTL units were dominated by tall fescue, they were

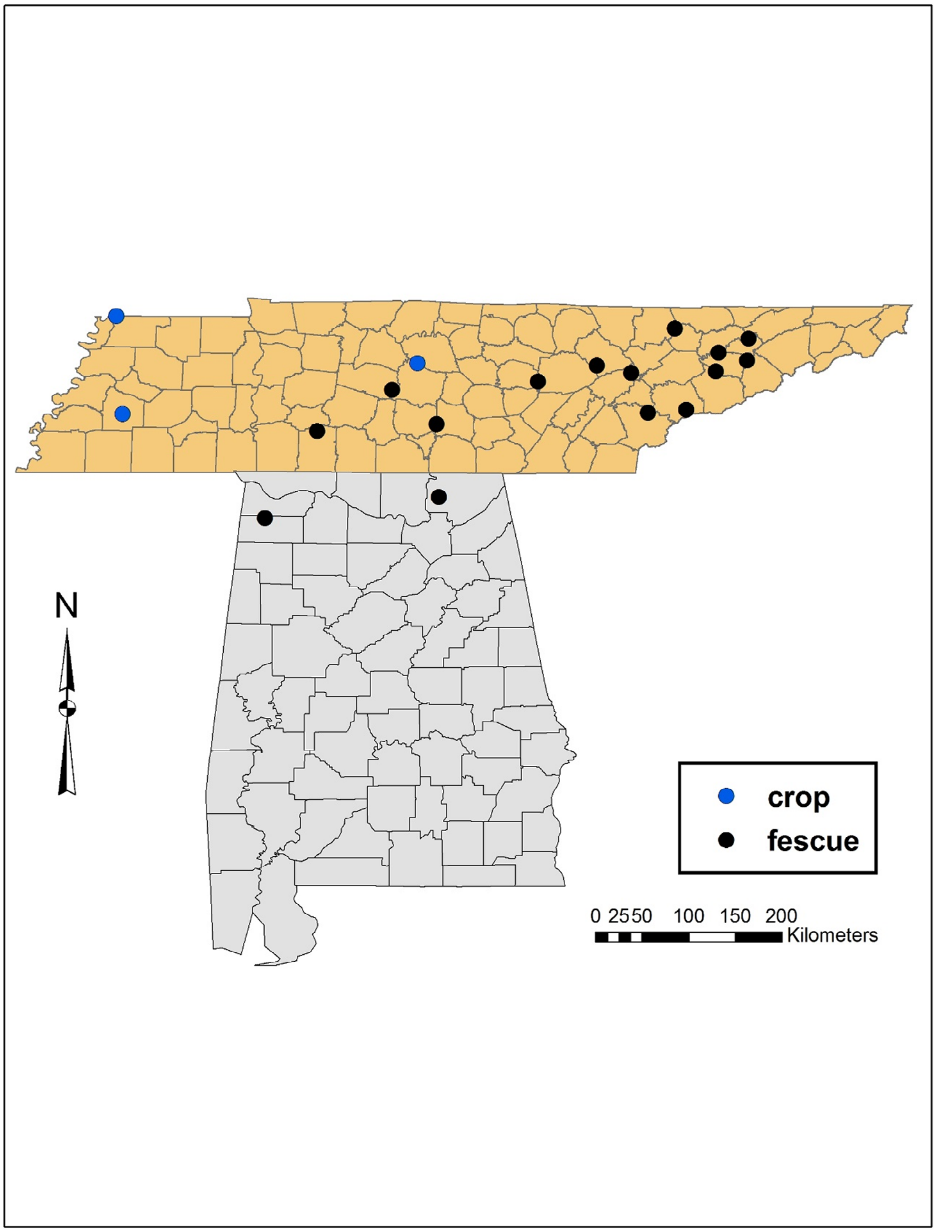

Figure 1. Map of 18 study site locations in Tennessee, Alabama, and Kentucky, U.S.A. (2016–2018).

undergoing succession with various forbs and brambles pioneering from the seed bank, which produced a different species composition than would be found in tall fescue fields maintained for hay or pasture.

Treatments

Initial Mowing and Herbicide Applications to Control Tall Fescue. We mowed each of the 15 fields in September–October 2015 and allowed them to regrow to 15.2–25.4 cm. We applied glyphosate (2.8 kg ai ha^{-1}) with broadcast applications in SD and NR to control tall fescue in November–December 2015. Herbicide applications were made when temperatures were at or above 10°C to ensure effectiveness because tall fescue actively grows at temperatures as low as 3°C (Gastal et al. 1992; Rogers & Locke 2013).

Seeding Treatment. We seeded a native warm-season grass (NWSG) and forb seed mixture in SD treatment units in April–May 2016 following recommendations from Private Lands Wildlife Biologists (PLWB) with TWRA and ADCNR who implement their conservation programs. We seeded all sites with the same seed mixture (Table 1) excluding the Park site because of restrictions on introduction of outside genotypic seed sources. Seed used at the Park were collected from within Cades Cove by National Park

Table 1. Species and seeding rate used for all study sites excluding Blount County, TN. Rates are pure live seed (PLS). Seed source: Roundstone Native Seed, LLC (Upton, KY, U.S.A.).

Common Name	*Scientific Name*	*Seeding Rate (seed/m^2)*
Little bluestem	*Schizachyrium scoparium*	178.7
Sideoats grama	*Bouteloua curtipendula*	39.3
Switchgrass	*Panicum virgatum*	32.0
Partridge pea	*Chamaecrista fasciculata*	10.1
Purple coneflower	*Echinacea purpurea*	21.4
Illinois bundleflower	*Desmanthus illinoensis*	4.0
Gray-headed coneflower	*Ratibida pinnata*	26.4
Black-eyed susan	*Rudbeckia hirta*	73.9

Table 2. Plant species and seeding rate used at Blount County, TN study site. Rates are pure live seed (PLS). Seed collected within the Great Smoky Mountains National Park (Blount County, TN, U.S.A.)

Common Name	*Scientific Name*	*Seeding Rate (seed/m^2)*
Big bluestem	*Andropogon gerardii*	30.2
Little bluestem	*Schizachyrium scoparium*	39.8
Swamp sunflower	*Helianthus angustifolius*	10.0
Mountain mint	*Pycnanthemum* sp.	87.2
Sneezeweed	*Helenium autumnale*	108.7
Wild bergamot	*Monarda fistulosa*	65.7
Wild quinine	*Parthenium integrifolium*	10.0
Roundhead lespedeza	*Lespedeza capitata*	17.7

Service personnel (Table 2). No-till drills (Truax Flex II Series drills [Truax Company Inc., New Hope, MN, U.S.A.] and Haybuster drills [Duratech Industries International Inc., Jamestown, ND, U.S.A.]) were used to plant seed. We calibrated and adjusted drills to ensure the recommended seeding rate of 7.3 kg/ha pure live seed (PLS) and seeding depth was ≤0.6 cm (Harper et al. 2007). Because seeded species were tolerant of imazapic herbicide (Plateau, BASF) we made preemergence applications (0.07–0.105 kg ai ha^{-1}) within 7 days of seeding to control competition (Washburn et al. 1999; Harper et al. 2007).

Natural Revegetation Treatment. We allowed the seed bank to revegetate NR units following initial tall fescue control. We then used strategic herbicide applications to remove non-native invasive species (i.e. undesirable) and to promote a native (i.e. desirable) early successional plant community in NR treatment units. Undesirable vegetation most often was classified as species identified by the Southeast Exotic Pest Plant Council as non-native invasive species. Areas opened by herbicide applications naturally revegetated. This cycle of herbicide application and NR continued until desirable species established.

Maintenance Herbicide Applications in NR and SD Treatment Units. We made spot-spray applications using 15-L backpack sprayers (Solo U.S.A., Newport News, Virginia) and/or a 95-L ATV sprayer (Cabelas, Sydney, Nebraska) equipped with a spray gun (Green Garde, H.D. Hudson Manufacturing Company, Chicago, Illinois). Spot-spray applications were used most often (69% [48 of 70] and 86% [12 of 14] of all applications across 18 sites and 3 years in NR and SD, respectively), impacting ≤20% of any treatment unit. Broadcast applications impacted 100% of a treatment unit (31% [22 of 70] and 14% [2 of 14] of all applications made in NR and SD, respectively). We made broadcast applications with boom sprayer attachments on a tractor or an ATV.

We determined herbicide (Table 3) and application rate based on undesirable species present and herbicide labels. SD treatment units were the same as seedings conducted on lands enrolled in conservation programs (e.g. CRP and EQIP), and management activities (i.e. mowing and herbicide applications) followed PLWB recommendations to comply with conservation program rules. Biologists recommended spot-spraying SD treatment units containing ≥30% coverage of johnsongrass (*Sorghum halepense*), crabgrass (*Digitaria* spp.), and/or Japanese stiltgrass (*Microstegium vimineum*) with imazapic because seeded species were imazapic tolerant. Sericea lespedeza was spot-sprayed at ≥30% coverage though seeded species were susceptible to those applications. Bermudagrass is problematic when establishing early successional plant communities and was sprayed regardless of coverage. Woody species (i.e. trees and shrubs) were controlled if coverage increased above 5% according to biologists' recommendations.

We sprayed undesirable plants in NR treatment units regardless of coverage. Non-native species not labeled as invasive but increased in coverage ≥30% also were considered undesirable. Certain native species, such as blackberry (*Rubus* spp.) and black locust (*Robinia pseudoacacia*), were considered undesirable once they represented 30% coverage and were thinned by spot-spraying to prevent dominance.

Mowing for Management. We maintained CNTL units by mowing annually in late winter (February), representing default management practices common in fallow tall fescue fields (Dykes 2005). Annual mowing was not used in NR or SD treatment units. Five of 18 SD units were mown once according to biologist recommendations to prepare for broadcast herbicide applications or to release seeded species from weedy competition. No mowing for management was used in NR units.

Variable Measurements

Measuring Vegetation Composition. We conducted line-point intercept sampling to quantify vegetation composition in all treatments (Herrick et al. 2009). We established five 50-m transects in each treatment unit beginning at predetermined locations that were systematically assigned using Google Earth. Every plant species that intercepted each transect was recorded

Table 3. Herbicides and adjuvants used for control of undesirable plant species in natural revegetation and seeded treatment units.

Active Ingredient	*Trade Name*	*Manufacturer*	*Selectivity*
Herbicides			
Imazapic	Plateau	BASF	Broad-spectrum selective
Glyphosate	Accord XRT II	Dow AgroSciences	Broad-spectrum
Imazapyr	Arsenal AC Arsenal PowerLine	BASF	Broad-spectrum selective
Clethodim	Clethodim 2E	Agri Star	Grass-selective
Triclopyr	Garlon 3A Remedy Ultra	Dow AgroSciences	Forb-selective Woody
Triclopyr + fluroxypyr	Pasturegard	Dow AgroSciences	Forb-selective Woody
Adjuvants			
Alkylarypolyoxyethlene glycols, free fatty acids, and IPA	90/10 Surfactant	ProSolutions LLC	
Paraffin oil, surface active compounds and coupling agents	Basal oil	Alligare	
Phytobland paraffinic oil	Prime oil	Agrisolutions	
Methylated seed oil	MSO	Alligare	

at 2-m intervals. We calculated percent coverage of species and vegetative life forms (bramble, forb, grass, and woody) by dividing the number of hits of each species or life form by the total number of sampling points per transect. We then averaged percent coverage of each species or life form across all transects for each treatment to calculate percent coverage.

Measuring Spatial and Temporal Coverage of Flowering Forbs Important to Pollinators. We compared treatment effects against seeding requirements of conservation programs such as CP–42 (Pollinator Habitat, USDA Farm Service Agency), which requires seeding ≥3 flowering species for each season (spring, summer, and fall). We calculated average number and coverage of native forbs in each treatment, and to better understand the temporal continuum of bee food resources, we calculated the average number and coverage of spring- (NSPFF), summer- (NSUFF), and fall-flowering forbs (NFFF) (Steffan-Dewenter & Tscharntke 2001).

Measuring Success of Seeding and Restoration. Seeding native species is common throughout the restoration ecology literature (Foster et al. 2007; Freeman et al. 2017; Behringer et al. 2019; Lesica & Cooper 2019). However, seeding or restoration success is vaguely defined (Zedler 2007; Wortley et al. 2013). There are no clearly defined standards of seeding success or failure for conservation programs such as CRP and EQIP (Mayberry 2019, Natural Resources Conservation Service, personal communication). Gauging and defining success of restoration projects should be important considerations for decision making, planning future projects, and research. Since there is no accepted standard for seeding success or overall successful restoration, we set quantitative benchmarks to define success for our research as emphasized by Zedler (2007). Several studies have reported ≤10% coverage of seeded species 2–3 years after seeding (Wilson et al. 2004; Buisson et al. 2006; Holl et al. 2014). However, we chose to define a successful seeding for our research as having ≥25% coverage of seeded species by the third growing season (2018). We believed 25% coverage should be a minimum goal when seeding is carefully conducted with high-quality seed, properly calibrated equipment, and appropriate competition control.

Diversity indices are one of the most commonly used metrics to gauge overall restoration success (Ruiz-Jaen & Aide 2005; Wortley et al. 2013). Therefore, we defined successful restoration as having statistically greater species diversity, evenness, and richness than CNTL units and ≥80% coverage of native species. The prolific and widespread nature of non-native species across the landscape is likely to comprise some percentage of most plant communities (Ricciardi 2007; Lemke et al. 2013). Since fallow crop fields did not have CNTL units, we were unable to compare NR and SD treatment units to a CNTL. As suggested by Applestein et al. (2018), success should be based on long-term monitoring, and a single assessment within a few years after restoration should be used cautiously.

Measuring Costs and Effort. We recorded the amount and type of herbicide applied, the cost of herbicides, and the number of visits to each site to establish early successional plant communities dominated by native grasses and forbs in NR and SD. We calculated average costs and effort required for each treatment unit.

Statistical Methods

We used a randomized complete block design with replication for analysis of tall fescue site data. We conducted one-way analyses of variance (ANOVA) blocking on site using program R version 3.5.1 (R Development Core Team 2016) to compare means of plant species richness, diversity, and evenness, percent coverage of native and non-native plants, and coverage and number of species of native spring-, summer-, and fall-flowering forbs among the three treatments at $\alpha = 0.05$. We used post hoc Tukey HSD tests to compare treatments when a significant effect of treatment was observed. We used arcsine square root, square root, and fourth root transformations on non-normal data to meet assumptions of normality and equal variance. We analyzed 2018 data (third growing season) to compare treatment effects and the resulting plant communities because NWSG and forb communities often require 2–3 years to establish (Fransen et al. 2006; Harper et al. 2007; Rushing 2014), and because we used mowing and/or herbicides to promote native species-dominated plant communities in SD and NR treatment units during 2016–2017.

We used a randomized complete block design with repeated measures for analysis of fallow crop site data. The limited number of fallow crop sites ($n = 3$), and because these fields lacked a tall fescue control, limited the amount of data available for analysis. We used a repeated-measures study design to increase sample size and statistical power compared to analyzing 2018 data alone. Because of the small sample size and differences in analytical procedures, comparisons between fallow crop sites and tall fescue sites should be interpreted with caution.

We calculated the average Shannon-Weiner index and Simpson's E index values for each treatment to determine plant species diversity and evenness, respectively. The Shannon-Weiner index was scored from zero to four, with greater values implying greater plant diversity. The maximum value for Simpson's E index is one, with index values nearer one representing greater plant community evenness (i.e. how evenly abundance is distributed among species).

Results

Diversity, Evenness, and Species Richness

Tall Fescue Sites. We detected a treatment effect for diversity ($p \le 0.01$), evenness ($p \le 0.01$), and species richness ($p \le 0.01$). However, posthoc analyses indicated no difference for Shannon diversity index (NR = 2.7 ± 0.01[SE], SD = 2.6 ± 0.01; $p = 0.65$) or richness (NR = 31 ± 1, SD 32 ± 1; $p = 0.78$). The Simpson's evenness index value was different between NR and SD ($p = 0.03$) (Table S1).

Fallow Crop Sites. No differences were detected between NR and SD for Shannon diversity index values (NR = 2.3 ± 0.2, SD = 2.6 ± 0.1; $p = 0.31$), Simpson's evenness index values (NR = 0.28 ± 0.05, SD = 0.31 ± 0.02; $p = 0.46$), or species richness (NR = 24 ± 3, SD = 28 ± 3; $p = 0.44$).

Native and Non-native Species Coverage

Tall Fescue Sites. We detected a treatment effect ($p \le 0.01$) for coverage of native and non-native species, tall fescue, native forb coverage, and native and non-native grasses. We did not detect a treatment effect for non-native forb coverage ($p = 0.29$). The treatment effects resulted from CNTL because no treatment differences were detected between NR and SD except for native grass coverage which was greater in SD (NR = 49 ± 4%, SD = 61 ± 3%; $p = 0.05$; Table S2). Tall fescue, purpletop (*Tridens flavus*), and little bluestem (*Schizachyrium scoparium*) were the most detected species in CNTL, NR, and SD, respectively (Table S3). Black-eyed susan was the most detected forb seeded in SD but was 13th out of 87 forb species detected, indicating most forbs established from the seed bank. We detected 4, 2, and 6% coverage of bermudagrass in CNTL, NR, and SD, respectively ($p = 0.25$). Sericea lespedeza coverage was less in NR than SD ($p = 0.04$).

Fallow Crop Sites. We did not detect a treatment effect for native species coverage, non-native species coverage, native grass coverage, non-native grass coverage, native forb coverage, or non-native forb coverage (Table S4). Neither sericea lespedeza (NR = 2 ± 0.6%, SD = 2 ± 0.6%; $p = 0.83$) or bermudagrass coverage (NR = 0 ± 0%, SD = 0.1 ± 0.1%; $p = 0.422$) was different between treatments. There was greater non-native species coverage ($p = 0.03$) in 2017 (36 ± 5%) than in 2018 (8 ± 2%), and greater non-native grass coverage ($p = 0.02$) in 2017 (15 ± 4%) than in 2018 (5 ± 2%) indicating our spot-spray applications were effective. Broomsedge bluestem was the most detected species in NR and SD (Table S3).

Coverage of Native Flowering Forbs Important to Pollinators

Tall Fescue Sites. We detected a treatment effect for coverage of NSPFF ($p \le 0.01$), but not for NSUFF ($p = 0.13$), or NFFF ($p = 0.16$). However, the treatment effect for NSPFF was a result of CNTL and no differences in coverage among any of the three response variables was detected between NR and SD. We also detected treatment effects for the number of spring ($p \le 0.01$), summer ($p \le 0.01$), and fall ($p \le 0.01$) flowering forbs. Again, these differences were a result of CNTL, and we did not detect any difference between NR and SD for any of the three response variables. (Table S5).

Fallow Crop Sites. We did not detect any difference for coverage of NSPFF ($p = 0.30$), NSUFF ($p = 0.27$), or NFFF ($p = 0.48$) species between NR and SD (Table S6).

Treatment Costs and Effort

Average cost for the SD treatment was $468.98/ha. The glyphosate applications to prepare SD treatments ($20.26/ha), the pre-emergence imazapic application ($16.61/ha), and seed costs ($400.38/ha) were standard across all sites. Post-seeding herbicide applications for weed control in SD averaged $31.73 and ranged $1.58–$198.57/ha, and costs of treatment (herbicide) applications in NR averaged $126.69/ha and ranged $55.74–$289.28/ha across all years, including the initial $20.26/ha glyphosate application. On average, SD treatment units required 0.4 visits per site per year for seeding, mowing, and herbicide applications, whereas NR treatment units required 1.3 visits per site per year excluding the initial herbicide treatment to control tall fescue in SD and NR. We estimated our average time per visit to implement treatments was 1.2 person-hours per hectare. Seed bank response, not treatment unit size, dictated the time needed to implement treatments.

Discussion

Both NR and SD treatments were effective in converting tall fescue-dominated fields and fallow crop fields into a native species-dominated early successional plant community. NR and SD treatment units did not differ from each other in 14 of the 17 variables measured at tall fescue sites, and no variable differed between treatments at fallow crop sites. We did not detect any differences in non-native species coverage or native forb coverage between NR and SD as we hypothesized. Our hypotheses of less coverage of native grasses in NR than in SD and CNTL having the least plant diversity, evenness, and richness was supported by our results. Our data indicate no plant community benefits were gained from seeding compared to natural revegetation, and seeding was 3.7 times more expensive than natural revegetation.

Our results indicate properly timed and applied glyphosate can nearly eradicate tall fescue coverage with a single application. Previous studies also reported tall fescue is effectively controlled with fall glyphosate applications (Fribourgh et al. 1988; Vogel & Waller 1990; Harper & Gruchy 2009). We detected only 2 and 6% coverage of tall fescue in SD and NR treatment units, respectively, in the third growing season, compared to 75% in CNTL units.

Native grasses were plentiful in the seed bank and seeding native grasses led to the greatest coverage of NWSG in SD units. Seeding native grasses may increase their coverage above that needed for many objectives, especially when managing for certain wildlife species that require no more than 35% coverage of grass (Brooke et al. 2016). The 61% coverage of native grasses in SD treatment units at tall fescue sites resulted in a lower evenness index score in SD compared to NR units.

Native plant species dominated NR and SD treatment units at both tall fescue and fallow crop sites. Strategic herbicide applications in NR units promoted species composition evenly represented by grasses and forbs, whereas seeding native grasses in SD units resulted in a plant community more strongly represented by grasses. Native species dominance in NR at tall fescue sites also was influenced by herbicide applications that reduced coverage of sericea lespedeza. Fallow crop sites had relatively little sericea lespedeza, and changes in coverage would have been difficult to detect. Forb species diversity provides important nectar and pollen resources for pollinators and contributes to increased plant community diversity, evenness, and richness (Steffan-Dewenter & Tscharntke 2001; Dickson & Busby 2009; Mader et al. 2011). However, forb abundance and plant diversity often decline over time in seeded fields because of dominance of seeded grasses (Dickson & Busby 2009; Carter & Blair 2011; Willand et al. 2013).

Availability of floral resources (coverage and number of species) throughout the growing season is important in restoration projects focusing on pollinators (Steffan-Dewenter & Tscharntke 2001). We expected NSUFF to comprise the greatest coverage of native flowering forbs because all seeded forbs were summer-flowering species. However, only 4 of 17% coverage of NSUFF in SD units at tall fescue sites and 2 of 18% coverage at fallow crop sites were from seeded species. Overall, we expected greater coverage of NSPFF and NFFF in SD and NR treatment units at tall fescue and fallow crop sites. However, with native grass coverage ≥49% across all treatments and sites, forb coverage was suppressed as described by Weber (1999) and Dickson and Busby (2009). Seed bank suppression caused by active tall fescue growth in spring decreased coverage of NSPFF in CNTL compared to NR and SD.

We quantified the number of native flowering forb species by flowering season to compare our treatments with NRCS pollinator seedings. Interestingly, even CNTL met the NRCS 3-species requirement for summer- and fall-flowering periods at tall fescue sites, and no treatment at either site type met the 3-species requirement for the spring-flowering period. Although the seed mixture we used was not as diverse as some pollinator or ecosystem restoration seedings (Foster et al. 2007), it was a mixture commonly used in conservation programs and was developed by state and NRCS wildlife biologists responsible for carrying out conservation programs on private lands. However, there is evidence that more diverse seed mixtures may not lead to more diverse plant communities (Wood et al. 2015; Geaumont et al. 2019). Moreover, Wood et al. (2015) reported many pollinators preferred "wild plants" arising from the seed bank over those seeded. Regardless, pollinators clearly can benefit from species occurring naturally, and seeding is not necessarily requisite to increase food or nesting opportunities.

Our results contradict other studies that indicate seeding is necessary to restore degraded ecosystems, and that seed banks may not be a viable option for most restoration projects (Foster & Tilman 2003; Foster et al. 2007; Bossuyt & Honnay 2008; Sharma et al. 2018). Liu et al. (2009), however, documented seed banks at degraded sites were sufficient to allow successful revegetation, and that seeding may introduce unintended species that outcompete native species. Our data also indicate fallow crop sites with a history of herbicide applications and tillage contain seed banks sufficient for restoring native plant communities. A key component in our study that is lacking in others is that we paired seed bank response with continued spot-spray herbicide applications to remove non-native vegetation as it established. Herbicides are commonly used only for site preparation prior to seeding (Barnes 2004; Carter & Blair 2011). However, problematic species, such as bermudagrass and sericea lespedeza, have long-lived seed that allow them to establish well after site preparation with herbicides (Offutt & Baldridge 1973; Carey 1995). In addition, it is important to recognize that non-native species will continue to colonize any area over time as they are brought in by wind, water, and/or animals. Management through some type of disturbance is requisite to maintain early successional plant communities (Harper 2007).

We discovered multiple spot-spray herbicide applications in NR treatment units removed "layers" of non-native plants in the seed bank, corroborating with Warr et al. (1993) and Sharma et al. (2018) who reported seed bank composition may vary in depth in the soil profile. By visiting fields and spot-spraying on average once per year, we were able to significantly reduce or control coverage of undesirable species and increase coverage of desirable species. This minimal effort led to less coverage of sericea lespedeza in NR compared to SD units that were not spot-sprayed unless coverage exceeded 30%. We emphasize that spot-spray applications were key to establishing native early successional communities that were ecologically functional and provided habitat for many declining wildlife species.

Natural revegetation units at all tall fescue sites had ≥80% coverage of native species and species diversity, richness, and evenness that was greater than that recorded in CNTL units. Therefore, NR treatment units met our criteria for successful restoration. Evenness in the SD treatment units at tall fescue sites was not different from CNTL units and was the variable preventing SD treatment units to be considered successfully restored. Dominance of little bluestem and broomsedge bluestem in SD treatment units reduced evenness index values. We believe evenness would continue to decline and plateau at a relatively low-index value in SD treatments because of the seeded NWSG. We detected an average of 33 and 38% coverage of seeded species at tall fescue and fallow crop sites, respectively. Therefore, SD units at both site types met our ≥25% coverage of seeded species success metric.

In our study, diverse native early successional plant communities could have been restored on 3.7 times more land using an NR approach compared to seeding, suggesting seeding may not be the best use of restoration funding. The most expensive herbicide cost per hectare incurred at a single NR treatment unit was still 2.6 times less expensive than the average cost to plant 1 ha. Although average visits per year were greater in NR than SD, we believe a slight increase in time investment using the NR approach during the initial 2 years of establishment is negligible considering the flexibility in herbicide use to remove undesirable vegetation. Using the NR approach, restorationists can avoid common seeding errors, weather variability, seeding equipment failures, and other variables that may be problematic with seeding establishment. The costs, effort, and plant community characteristics in SD versus NR treatments suggest that few, if any, benefits are gained by seeding expensive seed mixtures to restore native early successional plant communities.

Seed bank composition can be highly variable from site to site. The level of non-native species control is objective-driven and depends upon the species that respond. Some of the most common problematic species (narrowleaf plantain [*Plantago lanceolata*], johnsongrass, and musk thistle [*Carduus nutans*]) in our NR treatments could have been partially or completely controlled with a preemergence imazapic application, which would have reduced the number of follow-up herbicide applications. Prior to application, it is important to consider potential impacts of soil-active herbicides on both native and non-native species. Proper field preparation, proactive monitoring, and targeted herbicide applications over at least two growing seasons should produce a diverse native early successional plant community without seeding. Monitoring and herbicide applications should be conducted for both cool- and warm-season undesirable species. The herbicides we used to control undesirable plants are labeled in the United States for rangeland or wildlife management applications, making this technique lawful and usable in most areas throughout the United States. Although we studied tall fescue and fallow crop fields in the eastern United States, the NR approach using the seed bank and strategic herbicide applications to reduce undesirable plant coverage should be applicable in many regions of other countries, especially where undesirable non-native grasses have been previously seeded and resulted in reduced plant diversity and unfavorable conditions for native wildlife.

Acknowledgments

We acknowledge the field technicians that aided with data collections. We thank the National Park Service, U. S. Fish and Wildlife Service, and L. McCool for logistical support. In addition, we thank the Tennessee Valley Authority, Tennessee Wildlife Resources Agency, and Alabama Department of Conservation and Natural Resources for financial and logistical support.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Species diversity (Shannon-Wiener index), evenness (Simpson's E index) and richness (mean ± SE) across treatments at tall fescue sites (n = 15), June–August 2018.
Table S2. Percent coverage of native and non-native species (mean ± SE) by treatment at tall fescue sites (n = 15), July–August 2018.
Table S3. Percent coverage (mean ± SE) of the 10 most detected plant species (common and scientific names) by treatment at tall fescue (n = 15) and fallow crop sites (n = 3), July–August 2018.
Table S4. Percent coverage of native and non-native species (mean ± SE) by treatment at fallow crop sites (n = 3), July–August 2018.
Table S5. Percent coverage and number of species (mean ± SE) of native spring-, summer-, and fall-flowering forbs by treatment at tall fescue sites (n = 15), June–August 2018.
Table S6. Percent coverage and number of species (mean ± SE) of native spring-, summer-, and fall-flowering forbs by treatment at fallow crop sites (n = 3), June–August 2018.
Table S7. Plant species detected along line-point intercept transects across all sites (n = 18) and treatments (control [CNTL], natural revegetation [NR], and seeded [PL]), June–August 2018.

Coordinating Editor: Mark Paschke

Received: 14 October, 2019; First decision: 2 December, 2019; Revised: 28 February, 2020; Accepted: 17 July, 2020