Effects of Prescribed Fire on the Buried Seed Bank in Mixed-Hardwood Forests of the Southern Appalachian Mountains

Tara L. Keyser[1,*], Tracy Roof[1], Jacquelyne L. Adams[1], Dean Simon[2], and Gordon Warburton[3]

Abstract - This study characterizes the seed bank prior to and immediately following dormant-season prescribed fire in mature, mixed-*Quercus* spp. (oak) forests in the southern Appalachian Mountains. Thirty samples from the litter/duff (LD) and the top 5 cm of the mineral soil (MS) were collected from five 5-ha burn units (6 plots per experimental unit) before and immediately after low-intensity prescribed fires, where maximum fire temperatures varied from <79 to 316 °C. A split-plot ANOVA and multi-response permutation procedures (MRBP) were utilized to assess the effects of burn treatment (pre- or post-fire) and seed bank layer (LD and MS) on the diversity and density of the buried seed bank. An average of 471 emergents/m^2 was observed in the buried seed bank comprising 133 identifiable taxa. No differences in total seed-bank density, Shannon-Weiner's diversity index (H′), or overall species composition between pre- and post-fire sampling or between the LD and MS layers were observed. Species richness (S) of the seed bank, however, was slightly greater pre-fire than post-fire, regardless of layer. Similarity, as defined by Sørenson's index, of species common to the seed bank and aboveground forest understory was low, with a slight increase in Sørenson's index observed during post-fire sampling of the seed bank and aboveground vegetation. Although we observed only negligible effects of a once-applied, low-intensity prescribed fire on the buried seed bank, the effects of a low-intensity prescribed fire management regime—one that involves repeated low intensity burns—on the buried seed bank are unknown and should be a focus of future studies across mixed-oak forests in the eastern US.

Introduction

The composition and contribution of the buried seed bank to post-disturbance species composition of the arborescent and herbaceous vegetation layers in mixed-*Quercus* spp. (oak) forests in the eastern US has been little studied. Results from the few studies to quantify and describe the seed bank of mixed-oak forests suggest the density and composition of the seed bank is spatially and temporally variable. For example, a depauperate seed bank containing an average of only 0.4 seeds/m^2 was found by Schiffman and Johnson (1992) in mature, ridge-top forests of the Ridge and Valley physiographic province of the southern Appalachians, while Schuler et al. (2010) observed a density of 248 arborescent emergents/m^2 in the seed bank of a second-growth mixed-oak forest in the central

[1]USDA Forest Service, Southern Research Station, Bent Creek Experimental Forest, 1577 Brevard Road, Asheville, NC 28806. [2]North Carolina Wildlife Resources Commission, 8676 Will Hudson Road, Lawndale, NC 28090. [3]North Carolina Wildlife Resources Commission, 783 Deep Woods Drive, Marion, NC 28752. [*]Corresponding author - tkeyser@fs.fed.us.

Appalachians. Although across-site differences in the density of the seed bank are common, within-site differences in the density and composition of the seed bank have also been observed across topographic positions and areas of varying site quality within a given forest stand, further emphasizing the heterogeneity inherent to the buried seed bank (Ashton et al. 1998, Leckie et al. 2000, Singhakumara et al. 2000, Small and McCarthy 2010).

Time since disturbance or the stage of stand development (Oliver and Larson 1996) has been shown to affect the characteristics and potential contribution of the buried seed bank to the structure and composition of the forest understory (Graber and Thompson 1978, Grandin 2001, Plue et al. 2010). For example, in a chronosequence of old-field to old-growth *Acer-Fagus* (maple-beech) stands in Ohio, Roberts and Vankat (1991) found that richness, diversity, and density of the seed bank decreased as time since disturbance increased, as did the similarity between the composition of the seed bank and aboveground vegetation. Factors associated with changes in seed-bank characteristics over time include (1) changes in life-history types in aboveground vegetation (e.g., change from shade-intolerant annual/biennial species early in stand development to shade-tolerant perennial species during later stages of stand development) (Bossuyt and Hermy 2001, Brown and Oosterhuis 1981, Warr et al. 1994); (2) decreased seed viability after prolonged periods without disturbance (Bossuyt and Hermy 2001, Warr et al. 1994); and (3) decreased input to the seed bank from aboveground vegetation (Plue et al. 2010). As such, while aboveground vegetation in mature second-growth forests may consist primarily of shade-tolerant species, the buried seed bank is generally dominated by highly persistent shade-intolerant annual and biennials species common to recently disturbed forest conditions (e.g., young-forest habitats; Korb et al. 2005, Thompson et al. 1998), which under the more conducive environmental conditions (e.g., high light) may germinate and contribute to the development and composition of the post-disturbance community.

The paradigm that the buried seed bank of mature, second-growth forests is dominated by shade-intolerant species characteristic of the early stages of stand development (e.g., Grandin and Rydin 1998, Korb et al. 2005) has implications regarding the restoration of oak ecosystems in the southern Appalachians. Several researchers have suggested a change in the disturbance regime (e.g., cessation of anthropogenic burning) has promoted the conversion of mixed-oak forests to forests dominated by shade-tolerant species, such as *Acer rubrum* (Red Maple) (e.g., Abrams 1992, Brose et al. 2001, Orwig and Abrams 1994), while even-aged forest management practices have resulted in a conversion of oak-dominated forests to stands dominated by shade-intolerant species, such as *Liriodendron tulipifera* (Yellow-Poplar) (e.g., Beck and Hooper 1986, Loftis 1983). Despite evidence suggesting that seed banking of arborescent species is of only a minor importance in the regeneration of temperate forests (Bossuyt et al. 2002, Meadows et al. 2006), in high-quality, mixed-oak forests, mesophytic tree species that often interfere with oak regeneration (e.g., Yellow-Poplar, *Betula lenta* [Sweet Birch], and Red Maple), are capable of regenerating from seed stored in the long-term (e.g., Yellow-Poplar) or transient (e.g., Sweet Birch and Red Maple) seed bank following disturbance (Clark and Boyce 1964, Hille Ris Lambers and Clark 2005, Sander and Clark 1971, Sullivan and Ellison 2006).

In the southern Appalachian Mountains, prescribed fire is increasingly used by land managers to promote the regeneration of ecologically valuable oak species by controlling competition from both shade-tolerant (Abrams 1992, Orwing and Abrams 1994) and shade-intolerant (Brose et al. 2001) arborescent species, decrease hazardous fuel loadings, enhance wildlife habitat, and increase understory species diversity and structural heterogeneity (Vose 2000). Upland hardwood forests of the southern Appalachian Mountains possess some of the highest levels of tree and understory vegetation diversity in the US. The role of the buried seed bank is often overlooked despite the known contribution the seed bank has in shaping post-disturbance ecosystem structure and composition (Leck et al. 1989). The density of composition of viable seed remaining in the seed bank following prescribed fire can affect post-disturbance community dynamics (Auld and Denham 2006). In this study, we (1) quantify and describe the buried seed bank on intermediate to high-quality mixed-hardwood forests in the southern Appalachian Mountains, (2) examine the effects of prescribed fire on the density and composition of the buried seed bank, and (3) identify the relationship between aboveground species composition and that of the buried seed bank prior to and following prescribed fire.

Methods

Field site description

This study was conducted on the North Carolina Wildlife Resource Commission's Cold Mountain Game Lands (CMGL) in Haywood County in western North Carolina. The CMGL encompass 1333 ha and are located on the Blue Ridge physiographic province of the southern Appalachian Mountains. Past land use consisted primarily of exploitive logging (e.g., widespread clearcutting) during the mid-20th century, making age of the stands within CMGL approximately 80 years. Terrain is mountainous with steep slopes. Slopes of areas used in this study range from approximately 35 to 55 percent. Elevations within the study area range from 975 m to 1280 m. Average annual temperature ranges from 3 °C in January to 24 °C in July (McNab and Avers 1994). Average precipitation approximates 1200 mm annually and is evenly distributed throughout the year (McNab and Avers 1994). Vegetation on CMGL consists of mature, second-growth, upland mixed-hardwood forests. Oak and *Carya* spp. (hickory) species along with Yellow-Poplar are the predominant overstory trees, while the midstory consists primarily of shade-tolerant species, including *Oxydendrum arboreum* (Sourwood), *Cornus florida* L. (Flowering Dogwood), *Nyssa sylvatica* Marsh. (Blackgum), *Halesia tetraptera* Ellis (Silverbell), and Red Maple (Schafale and Weakley 1990).

Field methods

During the summer of 2008, five 5-ha replicate units (approximately 225 x 225 m) were located throughout the CMGL. Each replicate consisted of fully stocked stands of mixed-species composition. Within each of the 5 replicates, 2 transects were established. Transects were parallel to and >30 m from a unit boundary, and positioned across a slope gradient. The first transect was located by picking a random distance along the boundary line from the farthest downslope corner of each burn unit.

Along each of the 2 transects per experimental unit, three 0.05-ha permanent circular plots (12.6-m radius) were established at 50 m, 112 m, and 175 m (Fig. 1). Within each 0.05-ha permanent plot, all overstory trees ≥25 cm diameter at breast height (dbh) were inventoried and tagged. Midstory trees ≥5 cm and <25 cm dbh were inventoried and tagged within a 0.01-ha (5.6-m radius) subplot concentrically nested within each plot. For all tagged trees, species, dbh, and crown class was recorded. Tree regeneration was sampled using two 0.004-ha circular regeneration subplots originating 8 m from plot center at bearings of

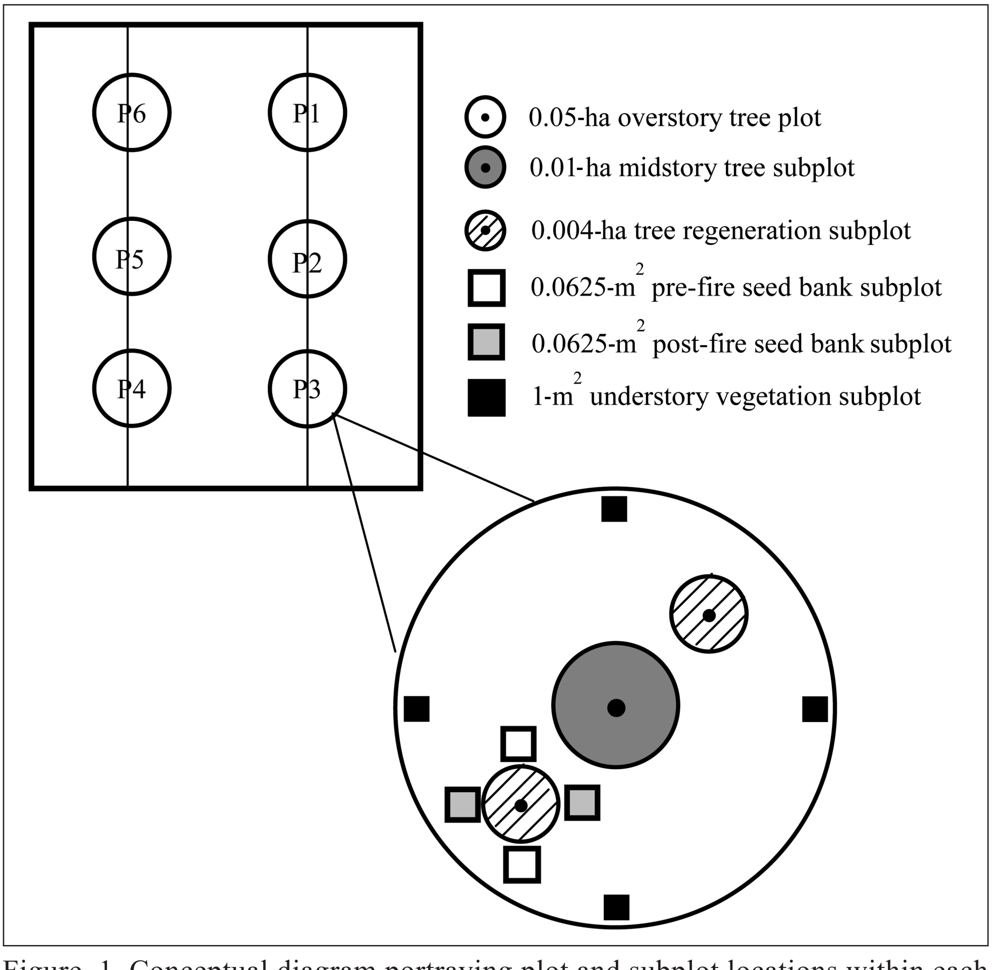

Figure. 1. Conceptual diagram portraying plot and subplot locations within each of the five 5-ha replicates. Replicates contained 2 parallel transects approximately 225 m in length along which plots were established. Transects within replicates were separated by ≥30 m. Vegetation plots were located at approximately 50 m, 112 m, and 175 m along each transect.

45° and 225°. In the regeneration subplots, advance reproduction (arborescent species <3.8 cm dbh) was enumerated by species in 5 height/diameter classes: (1) <0.3 m tall; (2) ≥0.3 m to <0.6 m tall; (3) ≥0.6 m to <0.9 m tall; (4) ≥0.9 m to <1.2 m tall; and (5) ≥1.2 m tall to <3.8 cm dbh. Information on forest understory vegetation, including species presence/absence, and percent cover was collected using four 1-m^2 subplots located 12 m from plot center in the north, south, east, and west directions (Fig. 1). Percent cover by species was determined via ocular estimation. Collection of forest understory vegetation data occurred in 2008, prior to the fire and again during the first growing season post-fire.

Seed-bank samples were collected at 5 m north and 5 m south of the regeneration subplot located at the 225° azimuth in each of the 5 replicates prior to the fire and again at 5 m east and 5 m west of the tree regeneration subplot immediately following the fire (Fig. 1). Samples of the seed bank from the litter and duff (O_i + O_e + O_a) and mineral soil to a depth of 5 cm were collected separately using a 25-cm by 25-cm (0.0625-m^2) sampling frame. The litter and duff layer was easily distinguishable from the mineral soil layer. During each pre- and post-fire sampling period, the 2 litter/duff (LD) seed-bank subsamples collected from each 0.05-ha plot were combined. Similarly, during each pre- and post-fire sampling period, the 2 mineral soil (MS) seed-bank subsamples collected from each 0.05-ha plot were combined. Pooling resulted in a total of 30 subsamples from each pre- and post-fire LD layer (6 LD subsamples per replicate and sampling period) and 30 subsamples from each pre- and post-fire MS layer (6 MS subsamples per replicate and sampling period). The 6 subsamples per replicate, seed-bank layer (LD and MS), and sampling period (pre- and post-fire) combination were averaged for all analyses (n = 5), making the 5-ha replicate the experimental unit.

On 25 February 2009, the North Carolina Wildlife Resources Commission implemented a prescribed burn on 2 of the 5 replicate units. Because these 2 replicates were located in close proximity to one another, the burn was conducted as a single prescribed fire. However, because of the buffers (≥50 m) between replicate units, we considered these units to be two independent replicates. Due to poor burning conditions, the remaining 3 replicates were left unburned until 1 April 2010. In the 2010 burns, 2 of the 3 replicates were burned by a single prescribed fire due to the proximity of the replicates, while the last replicate was burned during a separate fire on the same day. Because of buffers (≥50 m), we consider all replicate units to be independent. The prescribed fires were cool, backing fires ignited with short, strip lighting and/or flanking strip lighting. Ten-hour fuel moisture on the burn days ranged from 9 to 11%, and relative humidity was between 20 and 40%, with wind speeds <12 km/hr. Maximum temperature at surface level was quantified at the regeneration subplot closest to seed-bank sampling using Tempilaq® temperature sensitive paints (Tempil, Inc., South Plainfield, NJ).

Greenhouse methods

In the case of the 2009 prescribed fire in which only 2 of the 5 replicates were burned, pre-fire seed-bank samples were collected during the first 2 weeks of December, 2008. Post-fire seed-bank samples were collected on 25 February and 26 February 2009. For these 2 replicates, pre-fire seed-bank samples were collected prior to completion of the cold-stratification period characteristic of the study area. Consequently, pre-fire seed-bank samples for these 2 replicates were cold stratified at 4 °C for an additional 60 days prior to further processing and germination. Post-fire seed-bank samples for these 2 replicates were cold stratified along with the pre-fire seed-bank samples. In the case of the 2010 prescribed fires, pre- and post-fire seed-bank samples were collected on 1 April and 5 April 2010, respectively, after completion of the normal cold-stratification period. Consequently, samples from these 3 replicates received no further cold stratification. Although collection of seed-bank samples from the 3 replicates burned in 2010 were collected later in the year than the 2009 samples, no seedling germination was observed in the field prior to collection. An unseasonably cold winter with considerable snow cover late into 2010 likely delayed the start of the growing season. Consequently, the timing of collection as well as differences in cold-stratification periods likely had little effect on the results presented here.

In the greenhouse, seed-bank samples were sieved through a 6-mm-mesh screen. This removed vegetative material (e.g., roots, rhizomes, tubers, etc.) that could have added to the germination potential of the samples. When large seeds (>6 mm diameter) were encountered (e.g., acorns, Hickory nuts, etc.), we manually placed them into the sieved sample. Once sieved, we placed the seed-bank samples into 28- x 53-cm flats in combination with soil medium (Premier Pro-mix Bx). Flats were placed in the greenhouse and watered 3 to 4 days per week. The seed bank was identified by using the seedling germination technique (Brown 1991). We checked for new germinants 3 days per week over a 6-month period. Control trays containing only soil medium were placed in the greenhouse to check for contamination.

Statistical analyses

The similarity between species observed in aboveground understory sampling and the LD and MS seed-bank layers was assessed using Sørenson's similarity index. Using presence or absence of species, Sørenson's index was calculated as: $2w / (A + B)$, where A = the number of species in aboveground vegetation, B = the number of species in the seed bank, and w = the number of shared species in common in above- and belowground samples. Sørenson's index ranges from 0 to 1, with 0 indicating a lack of similarity between species present aboveground versus the seed bank and 1 indicating complete agreement between aboveground and seed-bank species. Pre-fire Sørenson similarity index values were calculated using pre-fire aboveground vegetation and pre-fire seed-bank data. Post-fire Sørenson similarity index values were calculated using the post-fire aboveground vegetation and post-fire seed-bank data. Sørenson's index was calculated separately for each of the 0.05-ha plots and averaged by replicate. Sørenson's similarity index was used because of its widespread use in the seed-bank literature (e.g., Hopfensperger 2007).

Differences in total seed-bank density (determined by the number of individuals that germinated), seed-bank density by lifeform (i.e., forb, graminoid, shrub, arborescent, vine), species richness (S), Shannon-Weiner's diversity index (H′), and Sørenson's index between the LD and MS layers and burn treatment (pre- and post-fire) were analyzed using a mixed-effects split-plot analysis of variance (ANOVA), where seed-bank layer (LD and MS) was the main-plot factor and burn treatment (pre- and post-fire) was the split-plot factor. In addition to the main effects, the interaction between seed-bank layer and burn treatment was included in the ANOVA. Seed-bank layer and burn treatment were fixed effects and replicate and replicate*seed-bank layer were random effects. Because the primary objective of the prescribed burns was to control competition from some of oaks' main competitors, we performed a similar ANOVA on seed-bank density of species known to interfere with oak regeneration, including Yellow-Poplar, Sweet Birch, and Red Maple, on mid- to high-quality sites. Seed-bank collections were equally correlated (i.e., only one repeated measurement). Therefore, the split-plot design rather than a repeated-measures design was employed as suggested by Littell et al. 1998. Following significant *F*-tests in the split-plot ANOVA, pairwise comparisons of least-square means were performed using Tukey's honestly significant test. Some density data were square-root or $\log_e(y + 1)$ transformed to achieve normality and homoscedasticity. Analyses of seed-bank density, diversity, and similarity were conducted using the Proc Mixed procedure in SAS (SAS Institute, Inc.).

We used blocked multi-response permutation procedures (MRBP) on presence/absence data to test for differences in species composition using PC-ORD v. 5.0 (McCune and Grace 2002). Permutation procedures were used to test the null hypothesis that there were no significant differences in species composition among defined groups (McCune and Grace 2002). Because MRBP can only accommodate relatively simple experimental designs, the data were sliced (McCune and Grace 2002) to test the following hypotheses: (1) there is no difference between pre- and post-fire species composition in the LD layer, (2) there is no difference between pre- and post-fire species composition in the MS layer, and (3) there is no difference in species composition between the LD and MS seed-bank layers. For all analyses, an alpha = 0.05 was used to assess significance.

Results

Stands used in this study were mature, fully stocked, second-growth stands. Mean (SE) basal area (m^2/ha) and stems per hectare prior to burning was 36.2 (4.2) and 719 (27), respectively, with 60% of the pre-fire basal area (m^2/ha) comprised of oak and hickory species. The first growing season post-fire, mean (SE) basal area and stems per hectare was 35.6 (4.2) and 702 (28), respectively.

The seed bank within the fully stocked mixed-hardwood stands was abundant and diverse. At the end of the study, 7058 germinants from the LD and MS layers comprising 133 identifiable taxa were observed. In order of relative abundance, the LD layer was dominated by forb, arborescent, shrub, graminoid, and vine species, while the MS layer was dominated by the seeds of forb, shrub, graminoid, arborescent, and vine species. In the combined LD and MS layers from both the pre- and post-fire sampling periods, we observed 70 forb species (15 annuals/biennials, 43 perennials, and 15 identified to only the genus level), 22 graminoid species (19 perennials and 3 identified to only the genus level), 12 shrub species, 5 vine species, 24 arborescent species, and 1 group of unknown species.

Of the 133 identifiable species, approximately 30 were categorized as ruderal species. Some of the more frequently observed ruderal species included *Rubus* spp. (brambles) (average 192 emergents/m^2), *Phytolacca americana* (Pokeweed) (average 9 emergents/m^2), *Oxalis* spp. (Wood Sorrel) (average 52 emergents/m^2), and *Erechtites hieraciifolia* (Fireweed) (average 3 emergents/m^2) (Table 1). Of the species that could be categorized, annual and perennial species possessed average (SE) densities of 5.7 (1.1) and 361.5 (27.1) emergents/m^2, respectively. The only non-native species encountered in the seed bank was *Paulownia tomentosa* (Thunb.) Siebold & Zucc. Ex Steud. (Princess Tree) (average 0.3 emergents/m^2), which occurred on only 7% of sampling locations pre-fire. Most species were not uniformly distributed across the study area, with only 51 species observed on ≥10% of the sample locations (Table 1).

The prescribed fires conducted in this study were of low intensity. Maximum temperature at the litter surface 5 m from where pre- and post-fire seed-bank subsamples were collected ranged from <79 to 316 °C. Average (SE) scorch height on overstory and midstory trees was 0.3 m (0.1). Litter consumption reflected the low fire intensity, with litter depth (cm) averaging (SE) 5.1 (0.6) cm prior to the fire and 2.7 (0.5) cm post-fire.

Results of the split-plot ANOVA revealed no statistical difference in total seed-bank density or Shannon-Weiner's diversity index (H′) between the LD and MS layers or between pre- and post-burn sampling periods ($P > 0.05$). There was, however, a significant effect of burn treatment on species richness (S), with slightly greater richness pre-fire than post-fire ($F = 11.68$; df = 1,4; $P = 0.0091$). Overall, seed-bank density was highly variable, with density averaged across replicates ranging from 144 to 1274 seeds/m^2 (Table 2).

At the lifeform level, the split-plot ANOVA revealed a significant effect of seed-bank layer on the density of arborescent species ($F = 15.8$; df = 1,4; $P = 0.0165$). The seed bank of arborescent species was characterized by significantly greater density in the LD than MS layer, with mean densities (SE) of 139 (28.1) and 43 (10.4) emergents/m^2 in the LD and MS layers, respectively. No significant effect of seed-bank layer or burn treatment was observed for forbs, graminoids, shrubs, and vines ($P > 0.05$). Similarly, no significant effect of seed-bank layer or burn treatment was observed for the arborescent species of interest, including Yellow-Poplar, Sweet Birch, and Red Maple ($P > 0.05$).

After averaging data across groups defined by the specific hypotheses, results from the MRBP analyses revealed no significant differences in species composition between pre- and post-fire sampling periods for the LD and MS layers, nor did we observe any significant differences in species composition between the LD and MS layers (Table 3).

Table 1. Frequency of occurrence (%) and average density (emergents/m^2) observed in the buried seed bank. Frequency relates to 0.05-ha plots nested within replicates (*n* = 30). Only species occurring on ≥10% of the plots are listed. For lifeform: F = forb, T = arborescent, S = shrub, G = graminoid, and V = vine. For life history: A = annual, P = perennial, and B = biennial. Lifeform and life history were determined in accordance with the USDA Plants Database (USDA, NRCS 2011). Species listed as annual/biennial by were classified as annuals.

	Pre-fire		Post-fire		Life-	Life
Species	Litter/duff	Mineral soil	Litter/duff	Mineral soil	form	history
Acer rubrum L. (Red Maple)	40 (22.0/m^2)	3 (0.7/m^2)	23 (4.7/m^2)	3 (1.3/m^2)	T	P
Ageratina altissima (L.) King & H. Rob. (White Snakeroot)	10 (2.7/m^2)	10 (2.0/m^2)	17 (3.3/m^2)	23 (9.3/m^2)	F	P
Aruncus dioicus (Waleter) Fernald (Bride's Feathers)	7 (2.0/m^2)	10 (4.0/m^2)	13 (3.3/m^2)	7 (3.3/m^2)	F	P
Aristolochia macrophylla Lam. (Pipevine)	13 (4.0/m^2)	3 (0.7/m^2)	13 (3.3/m^2)	7 (1.3/m^2)	V	P
Arisaema triphyllum (L.) Schott (Jack In The Pulpit)	7 (1.3/m^2)	0 (0.0/m^2)	13 (3.3/m^2)	7 (2.0/m^2)	F	P
Betula lenta L. (Sweet Birch)	73 (245.3/m^2)	63 (57.3/m^2)	73 (160.0/m^2)	67 (49.3/m^2)	T	P
Campanula divaricata Michx. (Small Bonny Bellflower)	10 (2.0/m^2)	17 (4.0/m^2)	0 (0.0/m^2)	7 (2.0/m^2)	F	P
Carex digitalis Willd. (Slender Woodland Sedge)	7 (3.0/m^2)	17 (4.0/m^2)	13 (6.0/m^2)	3 (0.7/m^2)	G	P
Carex spp. (sedge)	17 (3.0/m^2)	13 (5.3/m^2)	33 (19.3/m^2)	30 (28.0/m^2)	G	P
Carex virescens Muhl. Ex Willd. (Ribbed Sedge)	17 (7.3/m^2)	27 (14.7/m^2)	23 (10.0/m^2)	20 (30.7/m^2)	G	P
Conyza Canadensis (L.) Cronquist (Canadian Horseweed)	1 (5.3/m^2)	7 (1.3/m^2)	27 (8.7/m^2)	20 (14.0/m^2)	F	A
Dichanthelium boscii (Poir.) Gould & C.A. Clark (Bosc's Panicgrass)	0 (0.0/m^2)	7 (6.7/m^2)	7 (2.0/m^2)	17 (5.3/m^2)	G	P
Dichanthelium spp. (rosette grass)	27 (12.7/m^2)	17 (8.0/m^2)	7 (3.3/m^2)	3 (1.3/m^2)	F	-
Dichanthelium commutatum (Schult..) Gould (Variable Panicgrass)	40 (46.7/m^2)	43 (70.7/m^2)	37 (26.0/m^2)	37 (64.7/m^2)	G	P
Dichanthelium dichotomum (L.) Gould (Cyoress Panicgrass)	10 (2.7/m^2)	23 (37.3/m^2)	20 (24.0/m^2)	23 (22.0/m^2)	F	P
Erechtites hieraciifolia (L.) Raf. ex DC. (American Burnweed)	30 (6.0/m^2)	7 (1.3/m^2)	13 (2.7/m^2)	3 (0.7/m^2)	F	A
Eupatorium purpureum L. (Sweetscented Joe Pye Weed)	20 (6.0/m^2)	10 (5.3/m^2)	7 (2.0/m^2)	10 (2.0/m^2)	F	P
Fraxinus americana L. (White Ash)	3 (0.7/m^2)	0 (0.0/m^2)	17 (3.3/m^2)	0 (0.0/m^2)	T	P
Gnaphalium obtusifolium L. (Rabbit-Tobacco)	13 (6.7/m^2)	7 (1.3/m^2)	0 (0.0/m^2)	3 (0.7/m^2)	F	A
Hieracium spp. (hawkweed)	10 (6.0/m^2)	7 (4.0/m^2)	7 (1.3/m^2)	0 (0.0/m^2)	F	-
Hieracium paniculatum L. (Allegheny Hawkweed)	3 (2.0/m^2)	7 (2.0/m^2)	7 (2.0/m^2)	17 (9.3/m^2)	F	P
Houstonia purpurea L. var. *purpurea* (Venus' Pride)	17 (23.3/m^2)	17 (14.7/m^2)	27 (12.0/m^2)	40 (26.7/m^2)	F	P
Hydrangea arborescens L. (Wild Hydrangea)	43 (81.3/m^2)	43 (60.0/m^2)	23 (36.0/m^2)	40 (68.7/m^2)	S	P
Juncus spp. (rush)	17 (3.3/m^2)	3 (0.7/m^2)	13 (3.3/m^2)	20 (4.0/m^2)	G	-

Table 1, continued.

Species	Pre-fire		Post-fire		Life-form	Life history
	Litter/duff	Mineral soil	Litter/duff	Mineral soil		
Juncus tenuis Willd. (Poverty Rush)	10 (2.7/m^2)	10 (10.0/m^2)	7 (2.0/m^2)	13 (3.3/m^2)	G	P
Liriodendron tulipifera L. (Yellow-Poplar)	57 (41.3/m^2)	47 (28.0/m^2)	40 (58.7/m^2)	37 (19.3/m^2)	T	P
Lobelia inflata L. (Indian-Tobacco)	3 (0.7/m^2)	10 (2.7/m^2)	13 (8.0/m^2)	17 (11.3/m^2)	F	A
Lysimachia quadrifolia L.(Whorled Yellow Loosestrife)	3 (0.7/m^2)	13 (7.3/m^2)	3 (1.3/m^2)	7 (4.7/m^2)	F	P
Melampyrum lineare Desr. (Narrowleaf Cowwheat)	10 (2.0/m^2)	7 (2.0/m^2)	0 (0.0/m^2)	3 (0.7/m^2)	F	A
Oxalis stricta L. (Common Yellow Oxalis)	17 (88.7/m^2)	7 (1.3/m^2)	27 (7.3/m^2)	13 (4.7/m^2)	F	P
Oxydendrum arboreum (L.) DC. (Sourwood)	40 (87.3/m^2)	27 (20.0/m^2)	20 (6.0/m^2)	10 (2.0/m^2)	T	P
Phytolacca americana L. (Pokeweed)	17 (3.3/m^2)	33 (14.7/m^2)	17 (10.7/m^2)	23 (7.3/m^2)	F	P
Potentilla canadensis L. (Dwarf Cinquefoil)	7 (2.0/m^2)	27 (14.7/m^2)	13 (7.3/m^2)	23 (26.7/m^2)	F	P
Prenanthes altissima L. (Tall Rattlesnakeroot)	3 (0.7/m^2)	7 (1.3/m^2)	10 (3.3/m^2)	0 (0.0/m^2)	F	P
Pycnanthemum montanum Michx. (Thinleaf Mountainmint)	10 (3.3/m^2)	17 (5.3/m^2)	10 (4.0/m^2)	13 (10.7/m^2)	F	P
Robinia pseudoacacia L. (Black Locust)	30 (10.0/m^2)	37 (14.0/m^2)	40 (10.7/m^2)	40 (13.3/m^2)	T	P
Rubus allegheniensis Porter (Allegheny Blackberry)	57 (184.7/m^2)	57 (253.3/m^2)	63 (103.3/m^2)	70 (205.3/m^2)	S	P
Rubus odoratus L. (Purpleflowering Raspberry)	0 (0.0/m^2)	3 (0.0/m^2)	20 (8.7/m^2)	10 (0.7/m^2)	S	P
Salix nigra Marsh. (Black Willow)	30 (11.3/m^2)	10 (2.0/m^2)	7 (0.9/m^2)	7 (0.9/m^2)	T	P
Scirpus cyperinus (L.) Kunth (Woolgrass)	13 (2.7/m^2)	3 (0.7/m^2)	7 (2.0/m^2)	3 (0.7/m^2)	G	P
Smilax rotundifolia L. (Roundleaf Greenbrier)	7 (1.3/m^2)	10 (6.0/m^2)	3 (0.7/m^2)	0 (0.0/m^2)	V	P
Solidago curtisii Torr. & A. Gray (Mountain Decumbent Goldenrod)	17 (4.7/m^2)	17 (3.3/m^2)	27 (8.7/m^2)	13 (4.0/m^2)	F	P
Solidago puberula Nutt. (Downy Goldenrod)	17 (6.0/m^2)	7 (2.7/m^2)	7 (2.0/m^2)	10 (2.0/m^2)	F	P
Sonchus asper (L.) Hill (Spiny Sowthistle)	13 (4.7/m^2)	0 (0.7/m^2)	0 (0.0/m^2)	0 (0.0/m^2)	F	A
Unknown	47 (48.0/m^2)	50 (27.3/m^2)	47 (16.0/m^2)	40 (18.0/m^2)	N/A	-
Viola spp. (Violet)	23 (8.0/m^2)	17 (4.7/m^2)	23 (13.3/m^2)	27 (15.3/m^2)	F	-
Viola blanda Willd. (Sweet White Violet)	27 (79.3/m^2)	17 (39.3/m^2)	27 (56.0/m^2)	17 (41.3/m^2)	F	P
Viola rotundifolia Michx. (Roundleaf Yellow Violet)	37 (84.0/m^2)	33 (30.7/m^2)	33 (58.7/m^2)	30 (39.3/m^2)	F	P
Viola sororia Willd. (Common Blue Violet)	60 (72.0/m^2)	83 (96.0/m^2)	80 (78.0/m^2)	87 (99.3/m^2)	F	A
Vitis aestivalis Michx. (Summer Grape)	67 (76.7/m^2)	63 (46.7/m^2)	67 (56.0/m^2)	53 (38.0/m^2)	V	P
Zizia trifoliata (Michx.) Fernald (Meadow Alexanders)	10 (6.7/m^2)	10 (3.3/m^2)	7 (2.0/m^2)	7 (1.3/m^2)	F	P

We observed 147 and 143 species during the sampling of aboveground forest understory vegetation pre- and post-fire, respectively. Perennial forbs dominated the forest understory vegetation. The split-plot ANOVA revealed slightly greater similarity between species common to the aboveground vegetation and post-fire seed bank than species common to the aboveground vegetation and pre-fire seed bank, regardless of the seed-bank layer sampled (F = 14.6; df = 1,8; P = 0.0051). Despite the significant effect of the prescribed fire, similarity between the species observed in the aboveground vegetation and the buried seed bank was low. Sørenson values ranged from 0.12 to 0.28 (mean = 0.16) prior to the fire and 0.16 to 0.34 (mean = 0.25) post-fire. Pre-fire, the number of species common to the seed bank and aboveground vegetation was 29 and 25 for the LD and MS layers, respectively (Table 4). Post-fire, the number of species represented in both the seed bank and aboveground vegetation was 34 and 31 for the LD and MS layers, respectively (Table 4). Most of the species responsible for the increase in similarity between the buried seed bank and aboveground understory vegetation were perennial forbs and perennial graminoids (Table 4).

Table 2. Summary statistics for seed-bank propagule density (emergents/m^2), species richness (S), and Shannon-Weiner's diversity index (H′) pre- and post-fire for the litter/duff (LD) and mineral soil (MS) layers averaged across replicates (n = 5). Data presented are from raw, untransformed data.

	LD (n = 5)				MS (n = 5)			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Seed-bank density								
Pre-fire	603	417	299	1274	435	124	304	585
Post-fire	424	248	144	692	419	137	272	573
Species richness (S)								
Pre-fire	12.3	1.6	10.0	14.3	12.1	1.1	11.0	14.0
Post-fire	11.3	1.5	9.2	13.2	11.0	1.2	10.0	12.8
Weiner's diversity index (H′)								
Pre-fire	1.9	0.1	1.8	2.0	2.1	0.1	1.9	2.1
Post-fire	1.9	0.2	1.6	2.1	1.9	0.1	1.7	2.0

Table 3. Test statistics related to the multi-response permutation procedure (MRBP) for seed-bank species composition. $\delta_{observed}$ and $\delta_{predicted}$ = observed and expected weighted mean within-group distance, respectively, A = chance-corrected within-group homogeneity, and P = the probability of observing a smaller or equal $d_{observed}$.

MRBP analysis	$\delta_{observed}$	$\delta_{expected}$	A	P
1. Test for differences between pre- and post-fire species composition in the litter/duff layer	3.7058	3.7843	0.0207	0.1011
2. Test for differences between pre- and post-fire species composition in the mineral soil layer	3.5638	3.5525	-0.0032	0.5896
3. Test for differences between species composition in the litter/duff and mineral soil seed bank layers	3.6409	3.7196	0.0212	0.0926

Table 4. Species common to the buried seed bank and aboveground vegetation for the litter/duff (LD) and mineral soil (MS) seed-bank layers, pre- and post-fire. L = litter/duff, M = mineral soil. P = present, A = absent.

	Pre-fire		Post-fire	
Species	L	M	L	M
Acer rubrum (Red Maple)	P	P	P	P
Amphicarpaea bracteata L. Fernald (American Hogpeanut)	A	A	A	P
Aristolochia macrophylla (Pipevine)	P	P	P	P
Arisaema triphyllum (Jack In The Pulpit)	P	A	P	P
Betula lenta (Sweet Birch)	P	P	P	P
Campanula divaricata (Small Bonny Bellflower)	A	A	A	P
Carex spp. (sedges)	P	P	P	P
Carex digitalis (Slender Woodland Sedge)	A	A	P	P
Carya glabra (Mill.) Sweet (Pignut Hickory)	P	A	A	P
Chelone lyonii Pursh (Pink Turtlehead)	A	P	P	A
Circaea lutetiana L. (Broadleaf Enchanter's Nightshade)	P	P	A	A
Dichanthelium spp. (rosette grass)	P	P	P	A
Dichanthelium boscii (Bosc's Panicgrass)	A	A	P	P
Dichanthelium commutatum (Variable Panicgrass)	A	A	P	P
Dichanthelium dichotomum (Cypress Panicgrass)	A	A	P	P
Eupatorium purpureum (Sweetscented Joe Pye Weed)	P	P	P	P
Fraxinum americana (White Ash)	P	A	P	A
Galium triflorum Michx. (Gragrant Bedstraw)	A	A	P	A
Hieracium paniculatum (Allegheny Hawkweed)	P	P	P	P
Houstonia purpurea var. *purpurea* (Venus' Pride)	A	A	P	P
Hydrangea arborescens (Wild Hydrangea)	A	A	P	P
Kalmia latifolia L. (Mountain Laurel)	P	A	A	A
Laportea canadensis (L.) Weddell (Canadian Woodnettle)	A	A	P	A
Liriodendron tulipifera (Yellow-Poplar)	P	P	P	P
Lysimachia quadrifolia (Whorled Yellow Loosestrife)	A	P	A	P
Melampyrum lineare (Narrlowleaf Cowwheat)	A	A	A	P
Oxydendrum arboreum (Sourwood)	P	P	A	P
Potentilla canadensis (Dward Cinquefoil)	P	P	P	P
Prenanthes altissima (Tall Rattlesnakeroot)	A	A	P	A
Prunus serotina Ehrh. (Black Cherry)	P	A	P	P
Pycnanthemum montanum (Thinleaf Mountainmint)	A	P	A	A
Robinia pseudoacacia (Black Locust)	P	P	P	P
Rubus allegheniensis (Allegheny Blackberry)	A	A	P	P
Sassafras albidum (Nutt.) Nees (Sassafras)	P	A	A	A
Sambucus nigra L. ssp. *canadensis*) (L.) R. Bolli (American Elderberry)	P	P	A	A
Sanguinaria canadensis L. (Bloodroot)	A	A	P	A
Sanicula spp. (sanicle)	A	A	P	A
Smilax glauca Walter (Cat Greenbrier)	A	P	A	A
Solidago curtisii Torr. & A. Gray (Mountain Decumbent Goldenrod)	P	P	P	P
Thalictrum dioicum L. (Early Meadow-Rue)	P	A	P	P
Vaccinium pallidum Aiton (Blue Ridge Blueberry)	A	P	A	A
Vitis aestivalis Michx. (Summer Grape)	A	P	P	P
Viola blanda (Sweet White Violet)	P	P	P	P
Vicia caroliniana Walter (Carolina Vetch)	A	A	A	P
Viola rotundifolia (Roundleaf Yellow Violet)	P	P	P	P
Viola sororia (Common Blue Violet)	P	P	P	P
Zizia trifoliata (Meadow Alexanders)	P	P	P	P

Discussion

Despite the abundance of information characterizing the distribution and diversity of species across the landscape and the effects of forest management on understory community composition, little is known about the diversity and density of the buried seed bank in the southern Appalachians. Outside of studies that describe the importance of the seed bank for a limited number of shrub and arborescent species (e.g., Hille Ris Lambers and Clark 2005, Hille Ris Lambers et al. 2005), this study was the first to our knowledge to describe and quantify both the woody and non-woody buried seed bank in the Blue Ridge Province of the southern Appalachian Mountains, an area possessing the highest levels of diversity of arborescent and herbaceous vegetation in the US. We found the forest floor (LD) and the upper portions of the mineral soil (MS) contained, on average, 514 and 427 seeds/m^2, respectively, representing 133 identifiable taxa. Although the density of the seed bank in this study substantially exceeds that in xeric ridge-top oak forests of the southern Appalachians (Schiffman and Johnson 1992), the density of the seed bank is less than that reported in other mixed-oak and mixed-mesophytic eastern hardwood forests (Ashton et al. 1998). Species richness of the buried seed bank in this study, however, was far greater than reported for other temperate hardwood forests (Schelling and McCarthy 2007, Small and McCarthy 2010), likely reflecting the diversity inherent to productive southern Appalachian forests.

The overall experimental design used in this study was not specifically developed to address the effects of controlled burns on the seed bank. Rather, the experimental design, including the location of plots within experimental units as well as the vegetation sampling within the experimental units, was designed to address a larger question of how vegetation (both arborescent and understory vegetation), as opposed to strictly the buried seed bank, responds to 3 recommended oak-regeneration treatments, one of which included the prescribed burn treatments conducted in this seed-bank study. The clustering of seed-bank sampling around a single regeneration subplot nested within the larger 0.05-ha plot (Fig. 1) was performed because (1) of the proximity to a location where fire intensity was set to be recorded, and (2) to avoid disturbing areas within the permanent plot where other vegetation and fuels data were being collected. In regards to both the density and diversity of the buried seed bank reported in this study, the clustering of seed-bank sampling around one tree-regeneration subplot, as opposed to sampling being conducted throughout the entire 0.05-ha plot, may have affected our estimates of seed-bank diversity and/or density (Bigwood and Inouye 1988, Csontos 2007). Had the sampling been more widely distributed, it is possible the number of parent plants contributing to the seed-bank subplots would have increased, thereby potentially increasing seed-bank density and/or diversity. With that caveat in mind, this study does provide new and detailed information that not only characterizes the seed bank in productive forests of the southern Appalachians, but also provides information as to the potential effects of prescribed fire on the density and diversity of the seed bank.

The composition of the soil seed bank in previously disturbed systems is often dominated by non-native, shade-intolerant annual, and/or ruderal species (Korb et al. 2005, Pickett and McDonnell 1989), which can dominate the early stages of stand development following disturbance. Species frequently observed following substantial canopy-reducing disturbances, including brambles, Pokeweed, and other shade-intolerant annual forbs (e.g., Fireweed) were present in the buried seed bank both pre- and post-fire. However, unlike the seed bank of other temperate forests (e.g., Bossuyt and Hermy 2001, Bossuyt and Honnay 2008, Halpern et al. 1999), the seed bank of the mixed-oak stands sampled in this study also contained numerous perennial species. This finding supports Leckie et al. (2000) who report the seed bank of a temperate deciduous forest in Québec, Canada contained a high proportion of both annual and shade-tolerant perennial species. This study confirms that ruderal and/or annual species can form a persistent seed bank (Korb et al. 2005, Tsuyuzaki and Kanda 1996, Whitney 1986), but questions the generalization that the seed bank of mature, closed-canopied forests is dominated by "early-successional" species.

With the exception of the arborescent seed bank, where emergent density was ≈225% greater in the LD than MS layer, we found no effect of seed-bank layer, which is a proxy for soil depth, on the overall density and species composition of the buried seed bank. Many studies document a reduction in the density of the buried seed bank with increased soil depth (Blodgett et al. 2000, McGee and Feller 1993, Pratt et al. 1984, Qi and Scarratt 1998) as well as varying composition between upper and lower seed-bank depths (Halpern et al. 1999, Rydgren and Hestmark 1997). Shade-intolerant perennial and annual species characteristic of the early stages of stand development are often located lower in the forest floor profile suggesting a more persistent seed bank (Pratt et al. 1984, Qi and Scarratt 1998), while shade-tolerant perennial forest species are predominantly located in the upper portions of the seed bank and represent more of a transient seed bank (Bossuyt et al. 2002). The fact that this study found no significant difference in the density or composition of the LD and MS layers could imply that even with increased fire intensity and increased duff consumption, the contribution of the seed bank to the aboveground vegetation may not change, as the LD and MS layers were similar in density and composition.

In the southern Appalachians, prescribed fire is utilized to restore structure and composition, reduce hazardous fuel loadings, promote the regeneration of desirable tree species, and increase understory production and diversity (Vose 2000). We found no significant effect of a single prescribed burn on the density, composition, and relative abundance of life forms within the buried seed bank. This finding is in contrast to studies reporting both increased (Allen et al. 2008, Schuler and Liechty 2008) and decreased (Blodgett et al. 2000, Clark and Wilson 1994, Schuler et al. 2010) seed-bank emergence following fire and/or experimental heating. The fires conducted in this study were of low intensity, which is characteristic of winter burns in eastern US oak forests (e.g., Glasgow and Matlack 2007; Hutchinson et al. 2005a, b). Heat transfer through the soil profile decreases with increasing depth (Steuter and McPherson 1995). Consequently, incomplete consumption of the litter layer coupled with insulation of seeds stored in the duff and mineral soil likely inhibited seed mortality during the fire (Cain and Shelton 1998, Greenberg et al. 2012).

In general, low-intensity prescribed fires in mixed-oak forests of the eastern US have little to no effect on aboveground species composition (e.g., Elliott and Vose 2005, 2010; Elliott et al. 1999; Hutchinson et al. 2005a). The lack of similarity between species composition in the seed bank and aboveground vegetation is well documented (e.g., Grandin 2001, Hopfensperger 2007, Plue et al. 2010, Roberts and Vankat 1991). In this study, the small, but significant increase in similarity between the seed bank and aboveground vegetation following a one-time low intensity burn suggests the seed bank has a limited role in contributing to community dynamics in mixed-oak forests following typical dormant-season prescribed fires. Our results confirm studies that document little to no change in the seed-bank composition following both intermediate silvicultural treatments (e.g., forest thinning; Korb et al. 2005) and prescribed fire (Schelling and McCarthy 2007). However, evidence suggests that prescribed fires of greater intensity or multiple fires may affect not only the density of the buried seed bank, but also alter the composition by consuming seeds directly or exhausting the seed bank through increased post-fire germination (Allen et al. 2008, Schuler et al. 2010). It is within the immediate years following more intense, canopy-reducing disturbances, where environmental conditions may be more conducive to the germination and establishment of individuals from the seed bank (i.e., ruderal and other shade-intolerant species), when similarity between aboveground vegetation and the buried seed bank increases (Bossuyt et al. 2002).

In the context of oak restoration, the lack of an overall effect of prescribed fire on the density of the seed bank of known oak competitors, including Sweet Birch and Yellow-Poplar is informative. Studies in other mixed-oak forests have suggested the use of prescribed fire to reduce the abundance of oak competitors in the seed bank and thus improve oak regeneration success (e.g., Hutchinson et al. 2005b, Schuler et al. 2010). Either the prescribed fires in this study were not of high enough intensity to initiate mortality in the Sweet Birch or Yellow-Poplar seed banks, or these species are fairly resistant to the effects of low-intensity fire. Results from Schuler et al. (2010) suggest that either multiple burns are required to deplete the seed bank of these mesophytic species and/or that prescribed fires must be of greater intensity than the ones implemented in this study. The concentration of the arborescent seed bank in the LD layer suggests the seed bank of these species is especially susceptible to fire-induced mortality (Auld and Denham 2006, Tozer 1998). However, prescribed burns aimed at promoting oak regeneration are generally conducted with low intensity, and generally consume only a proportion of the leaf-litter layer and aboveground biomass (e.g., Glasgow and Matlock 2007, Hutchinson et al. 2005b). Therefore, seed stored in the duff, which was included in the LD layer in this study, may be protected from mortality during these low-intensity fires (Greenberg et al. 2012). Yellow-Poplar, which is a particularly aggressive competitor with oak on moderate- to high-quality sites (Beck and Della-Bianca 1981), can remain viable up to 8 years in the seed bank (Clark and Boyce

1964, Sander and Clark 1971), and is a prolific seed producer on an almost annual basis (Beck and Della-Bianca 1981). Consequently, if restoration goals include reducing the seed source of Yellow-Poplar from mixed-oak stands in order to reduce competitive pressures during the oak-regeneration process, removal of nearby seed-producing individuals coupled with repeated, higher-intensity prescribed burns that consume the litter and duff layers as well as heat the mineral soil may play a role in reducing competition from Yellow-Poplar seedlings. Although we observed only negligible effects of a once-applied, low-intensity prescribed fire on the buried seed bank, the effects of a low-intensity prescribed fire management regime—one that involves repeated low-intensity burns for the purposes of promoting oak regeneration (e.g., Brose et al. 2001)—on the buried seed bank are unknown and should be a focus of future studies across mixed-oak forests in the eastern US.

Acknowledgments

This is a contribution of the Regional Oak Study (ROS). This research was initiated by the Forest Service, USDA, Southern Research Station, Upland Hardwood Ecology and Management Research Work Unit (RWU-4157) in partnership with the USDA Northern Research Station, the North Carolina Wildlife Resources Commission, the Stevenson Land Company, and the Mark Twain National Forest. The authors express their gratitude to Mark Williams and other members of the North Carolina Wildlife Resources Commission for preparing and implementing the prescribed burns. In addition, the authors thank Kenny Frick for assistance in collecting seed-bank samples as well as assisting on the prescribed burn; Alisha Goodman and Andrea Hinek for assistance in sample collection, processing, and data collection; Josh Bronson from the USDA Forest Service for providing greenhouse space and equipment; Dave Dannelly for assistance in identification; and Beverly Collins from Western Carolina University for providing details regarding seed-bank sampling protocols. Comments from Stan Zarnoch, Dan Dey, Tom Schuler, and two anonymous reviewers greatly improved this manuscript.

Literature Cited

Abrams, M.D. 1992. Fire and the development of oak forests. BioScience 42:346–353.

Allen, E.A., J.C. Chambers, and R.S. Nowak. 2008. Effects of a spring prescribed burn on the soil seed bank in a sagebrush steppe exhibiting pinyon-juniper expansion. Western North American Naturalist 68:265–277.

Ashton, P.M.S., P.G. Harris, and R. Thadani. 1998. Soil seed-bank dynamics in relation to topographic position of a mixed-deciduous forest in southern New England, USA. Forest Ecology and Management 111:15–22.

Auld, T.D., and A.J. Denham. 2006. How much seed remains in the soil after a fire? Plant Ecology 187:15–24.

Beck, D.E., and L. Della-Bianca. 1981. Yellow-Poplar: Characteristics and management. USDA Forest Service Agriculture Handbook no. 583, Washington, DC. 91 pp.

Beck, D.E., and R.M. Hooper. 1986. Development of a southern Appalachian hardwood stand after clearcutting. Southern Journal of Applied Forestry 10:168–172.

Bigwood, D.W., and D.W. Inouye. 1988. Spatial pattern analysis of seed banks: An improved method and optimized sampling. Ecology 69:497–507.

Blodgett, H., G. Hart, and M. Stanislaw. 2000. Annual burning decreases seed density in the upper soil layers of the seed bank. Tillers 2:31–38.

Bossuyt, B., and O. Honnay. 2008. Can the seed bank be used for ecological restoration? An overview of seed-bank characteristics in European communities. Journal of Vegetation Science 19:875–884.

Bossuyt, B., and M. Hermy. 2001. Influence of land-use history on seed banks in European temperate forest ecosystems: A review. Ecography 24:225–238.

Bossuyt, B., M. Hey, and M. Hermy. 2002. Seed bank and vegetation composition of forest stands of varying age in central Belgium: Consequences for regeneration of ancient forest vegetation. Plant Ecology 162:33–48.

Brose, P., T. Schuler, D. Van Lear, and J. Berst. 2001. Bring fire back: The changing regimes of the Appalachian mixed-oak forests. Journal of Forestry 99:30–35.

Brown, A.H.F., and L. Oosterhuis. 1981. The role of the buried seed bank in coppicewoods. Biological Conservation 21:19–38.

Brown, D. 1991. Estimating the composition of a forest seed bank: A comparison of the seed-extraction and seedling-emergence methods. Canadian Journal of Botany 70:1603–1612.

Cain, M.D., and M.G. Shelton. 1998. Viability of litter-stored *Quercus faclcata* Michx. acorns after simulated prescribed winter burns. International Journal of Wildland Fire 8:199–203.

Clark, D.L., and M.V. Wilson. 1994. Heat-treatment effects on seed-bank species of an old-growth Douglas-Fir forest. Northwest Science 68:1–5.

Clark, F.B., and S.G. Boyce. 1964. Yellow-Poplar seed remains viable in the forest litter. Journal of Forestry 62:564–576.

Csontos, P. 2007. Seed banks: Ecological definitions and sampling considerations. Community Ecology 8:75–85.

Elliott, K.J., and J.M. Vose. 2005. Effects of understory prescribed burning on Shortleaf Pine (*Pinus enchinata* Mill.)/mixed hardwood forests. Journal of the Torrey Botanical Society 132:236–251.

Elliott, K.J., and J.M. Vose. 2010. Short-term effects of a prescribed fire on mixed oak forests in the southern Appalachians: Vegetation response. Journal of the Torrey Botanical Society 137:49–66.

Elliott, K.J., R.L. Hendrick, A.E. Major, J.M. Vose, and W.T. Swank. 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. Forest Ecology and Management 114:199–213.

Glasgow, L.S., and G.R. Matlack. 2007. Prescribed burning and understory composition in a temperate deciduous forest, Ohio, USA. Forest Ecology and Management 238:54–64.

Graber, R.E., and D.F. Thompson. 1978. Seeds in the organic layers and soil of four beech-birch-maple stands. USDA Forest Service Research Paper NE-401, Northeastern Forest Experiment Station, Broomall, PA. 8 pp.

Grandin, U. 2001. Short-term and long-term variation in seed bank/vegetation relations along an environmental and successional gradient. Ecography 24:731–741.

Grandin, U., and H. Rydin. 1998. Attributes of the seed bank after a century of primary succession on islands in Lake Hyälmaren, Sweden. Journal of Ecology 86:293–303.

Greenberg, C.H., T.L. Keyser, S.J. Zarnoch, K. Connor, G. Warburton, and D. Simon. 2012. Acorn viability following prescribed fire in upland hardwood forests. Forest Ecology and Management 275:79–86.

Halpern, C.B., S.A. Evans, and S. Nielson. 1999. Soil seed banks in young, closed-canopy forests of the Olympic Peninsula, Washington: Potential contributions to understory reinitiation. Canadian Journal of Botany 77:922–935.

Hille Ris lambers, J., and J.S. Clark. 2005. The benefits of seed banking for Red Maple (*Acer rubrum*): Maximizing seedling recruitment. Canadian Journal of Forest Research 35:806–813.

Hille Ris Lambers, J., J.S. Clark, and M. Lavine. 2005. Implications of seed banking for recruitment of southern Appalachian woody species. Ecology 86:85–95.

Hopfensperger, K.N. 2007. A review of similarity between seed bank and standing vegetation across ecosystems. Oikos 116:1438–1448.

Hutchinson, T.F., E.K. Sutherland, and D.A. Yaussy. 2005a. Effects of repeated prescribed fire on the structure, composition, and regeneration of mixed-oak forests in Ohio. Forest Ecology and Management 218:210–228.

Hutchinson, T.F., R E.J. Boerner, S. Sutherland, E.K. Sutherland, M. Ortt, and L.R. Iverson. 2005b. Prescribed fire effects on the herbaceous layer of mixed-oak forests. Canadian Journal of Forest Research 35:877–890.

Korb, J.E., J.D. Springer, S.T. Powers, and M.M. Moore. 2005. Soil seed banks in *Pinus ponderosa* forests in Arizona: Clues to site history and restoration potential. Applied Vegetation Science 8:103–112.

Leck, M.A., V.T. Parker, and R.L. Simpson. 1989. Ecology of soil seed banks. Academic Press, San Diego, CA. 462 pp.

Leckie, S., M. Vellend, G. Bell, M.J. Waterway, and M.J. Lechowicz. 2000. The seed bank in an old-growth, temperate deciduous forest. Canadian Journal of Botany 78:181–192.

Littell, R.C., P.R. Henry, and C.B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. Journal of Animal Science 76:1216–1231.

Loftis, D.L. 1983. Regenerating southern Appalachian mixed hardwood stands with the shelterwood method. Southern Journal of Applied Forestry 7:212–217.

McGee, A., and M.C. Feller. 1993. Seed banks of forested and disturbed soils in southwestern British Columbia. Canadian Journal of Botany 71:1574–1583.

McCune, B., and J.B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR. 300 pp.

McNab, W.H., and P.E. Avers. 1994. Ecological subregions of the United States: Section descriptions. USDA Forest Service Administrative Publication WO-WSA-5, Washington, DC.

Meadows, J.S., F.T. Bonner, and J.D. Haywood. 2006. Soil seed-bank survival in forests of the southern United States. New Forests 32:335–345.

Oliver, C.D., and B.C. Larson. 1996. Forest Stand Dynamics, Update Edition. John Wiley and Sons, Inc. New York, NY. 520 pp.

Orwing, D.A., and M.D. Abrams. 1994. Land-use history (1720–1992), composition, and dynamics of oak-pine forests within the Piedmont and coastal Plain of northern Virginia. Canadian Journal of Forest Research 24:1216–1225.

Pickett, S.T.A., and M.J. McDonnell. 1989. Seed-bank dynamics in temperate deciduous forest. Pp. 123–148, *In* M.D. Leck, V.T. Parker, and R.L. Simpson (Eds.). Ecology of Soil Seed Banks. Academic Press, San Diego, CA. 462 pp.

Plue, J.K., H. Verheyen, D Van Calster, K. Marage, R. Thompson, M. Kalamees, B. Jankowska-Blaszczuk, B. Bossuyt, and M. Hermy. 2010. Seed banks of temperate deciduous forests during secondary succession. Journal of Vegetation Science 21:965–978.

Pratt, D.W., R.A. Black, and B.A. Zamora. 1984. Buried viable seed in a Ponderosa Pine community. Canadian Journal of Botany 62:44–52.

Qi, M., and J. B. Scarratt. 1998. Effect of harvesting method on seed-bank dynamics in a boreal mixedwood forest in northwestern Ontario. Canadian Journal of Botany 76:872–883.

Roberts, T.L., and J.L. Vankat. 1991. Floristics of a chronosequence corresponding to old field-deciduous forest succession in southwestern Ohio. II. Seed banks. Journal of the Torrey Botanical Society 118:377–384.

Rydgren, K., and G. Hestmark. 1997. The soil propagule bank in a boreal old-growth spruce forest: Changes with depth and relationship to aboveground vegetation. Canadian Journal of Forest Research 75:121–128.

Sander, I.L., and B.C. Clark. 1971. Reproduction of upland hardwood forests in the central States. USDA Forest Service Agriculture Handbook no. 405, Washington, DC. 25 pp.

Schafale, M.P., and A.S. Weakley. 1990. Classification of the natural communities of North Carolina—third approximation. NC Department of Environment, Health, and Natural Resources, Division of Parks and Recreation, Natural Heritage Program. Raleigh, NC.

Schelling, L.R., and B.C. McCarthy. 2007. Effects of a prescribed fire and thinning on the spatial heterogeneity of the seed bank in a mixed-oak forest. Natural Areas Journal 27:320–331.

Schiffman, P.M., and W.C. Johnson. 1992. Sparse buried seed bank in a southern Appalachian oak forest: Implications for succession. American Midland Naturalist 127:258–267.

Schuler, J.L., and H.O. Liechty. 2008. Seed-bank emergence following prescribed burning in the Ozark Highlands. Pp. 516–524, *In* D.F. Jacobs, and C.H. Michler (Eds.). Proceedings of the 16th Central Hardwoods Forest Conference. USDA Forest Service General Technical Report GTR-NRS-P-24, Northern Research Station, Newton Square, PA. 595 pp.

Schuler, T.M., M.T. Van-Gundy, M.B. Adams, and W.M. Ford. 2010. Seed-bank response to prescribed fire in the central Appalachians. USDA Forest Service Research Paper NRS-9, Northern Research Station, Newton Square, PA. 9 pp.

Singhakumara, B.M.P., R.S.J.P. Uduporuwa, and P.M.S. Ashton. 2000. Soil seed banks in relation to light and topographic position of a hill dipterocarp forest in Sri Lanka. Biotropica 32:190–196.

Small, C.J., and B.C. McCarthy. 2010. Seed-bank variation under contrasting site-quality conditions in mixed-oak forests of southeastern Ohio, USA. International Journal of Forestry Article ID 419482, 13 pp. Available online at doi:10.1155/2010/419482.

Steuter, A.A., and G.R. McPherson. 1995. Fire as a physical stress. Pp. 550–579, D.J. Bedunah and R.E. Sosebee (Eds.). *In* Wildland Plants: Physiological Ecology and Developmental Morphology. Society for Range Management, Denver, CO.

Sullivan, K.A., and A.M. Ellison. 2006. The seed bank of hemlock forests: Implications for forest regeneration following hemlock decline. Journal of the Torrey Botanical Society 133:393–402.

Thompson, K., J.P. Bakker, R.M. Bekker, and J.G. Hodgson. 1998. Ecological correlates of seed persistence in soil in the NW European flora. Journal of Ecology 86:163–169.

Tozer, M.G. 1998. Distribution of the soil seed bank and influence of fire on seedling emergence in *Acacia saligna* growing on the central coast of New South Wales. Australian Journal of Botany 46:743–755.

Tsuyuzaki, S., and F. Kanda. 1996. Revegetation patterns and seed-bank structure on abandoned pastures in northern Japan. American Journal of Botany 83:1422–1428.

US Department of Agriculture, Natural Resource Conservation Service (USDA, NRCS). 2011. The PLANTS Database. National Plant Data Center, Baton Rouge, LA. Available online at http://plants.usda.gov. Accessed 20 April 2012.

Vose, J.M. 2000. Perspectives on using prescribed fire to achieve desired ecosystem conditions. Pp. 12–17, *In* W.K. Moser, and C.F. Moser (Eds.). Tall Timbers Fire Ecology Conference Proceedings, No. 21: Fire and Forest Ecology: Innovative Silviculture and Vegetation Management. Tall Timbers Research Station, Tallahassee, FL.

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

Whitney, G.G. 1986. A demographic analysis of *Rubus idaeus* and *Rubus pubescens*. Canadian Journal of Botany 64:2916–2921.