Research Article

Seed Bank Variation under Contrasting Site Quality Conditions in Mixed Oak Forests of Southeastern Ohio, USA

Christine J. Small¹ and Brian C. McCarthy²

¹ Department of Biology, Radford University, Radford, P.O. Box 6931, VA 24142, USA

² Department of Environmental and Plant Biology, Ohio University, Athens, OH 45701, USA

Correspondence should be addressed to Christine J. Small, cjsmall@radford.edu

Received 31 August 2009; Accepted 3 February 2010

Academic Editor: Marc D. Abrams

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Seed bank composition was sampled in 192–2.5 m² quadrats, established in six regenerating clearcut (~7 years) and six second-growth (~125 years) mixed-oak forest stands in southeastern Ohio. Seed bank and aboveground composition diverged markedly (Sørensen's coefficient <10%), emphasizing the importance of fast-growing, early-successional germinants to early ecosystem recovery. Seed richness was significantly ($P < .01$) higher in clearcut stands, suggesting declining richness with stand age. Richness estimations 28%–60% higher than observed values demonstrated high seed bank heterogeneity, emphasizing the need for intensive sampling to assess temperate forest seed bank variation. Site quality (topographic aspect) strongly influenced seed bank composition, with greater importance of early-successional trees, thicket-forming shrubs, and nonnative species on mesic sites. Thus, forest seed banks are likely to play an important, site-dependent role in shaping competitive environments for commercially important timber species after harvesting and soil disturbance and have the potential for marked influence on postharvest forest development.

1. Introduction

Management priorities in US National Forests have changed markedly over the past century, with current policy emphasizing management of forests as intact and functioning ecosystems [1, 2]. This ecosystem-based approach seeks to maintain forest productivity and production of goods and services, while protecting the physical, chemical, and biological processes associated with healthy ecosystem function (e.g., soil and water quality, nutrient cycling, and biological diversity) [2–4]. As disturbance is an essential component of forested ecosystems, influencing forest structure, function, and development, it follows that management practices based on a comprehensive understanding of forest disturbance and recovery processes should be the most successful in regenerating preharvest forest structure and composition and minimizing ecosystem impacts [1, 5].

Designing ecosystem-based management plans for large-scale, stand-initiating harvests are particularly challenging, as postharvest conditions may be quite different from similarly

scaled natural disturbances [3, 6]. Like natural canopy-opening disturbance, stand-level harvest substantially alters site conditions (e.g., light availability, air and soil temperatures, soil moisture, nitrification, organic content), which in turn influences survival and reservoirs of plant species diversity in the postharvest community [7–9]. However, complete removal of overstory trees and soil disturbance during traditional stem-only or whole-tree clearcutting has the potential to significantly alter stand development patterns by reducing or eliminating advance regeneration (e.g., formerly suppressed seedlings and saplings and root- and stump-sprouts) and increasing the importance of germinating seeds during early ecosystem recovery [3, 10, 11].

The importance of the soil seed bank to temperate forest recovery following large-scale disturbance is widely recognized. Early-successional, short-lived species typically dominate forest seed banks and germinate quickly in response to increased light, fluctuating temperatures, and low CO₂ concentrations, facilitating rapid revegetation and resource capture (esp. water and nutrient runoff) [7, 12–14].

Yet the seed bank contributes little to the direct regeneration of late successional deciduous forest species, as trees and forest herbs rarely form long-term persistent seed banks [15–18]. Nonetheless, significant seed bank contributions to early-successional seres suggest that seed composition may have pronounced influences on the development of postharvest forest communities. Early-successional, herbaceous-dominated understories have been shown to act as species-specific “filters” to forest regeneration, inhibiting the establishment and growth of many commercially-important and shade-intolerant hardwood seedlings [19, 20]. Even when advanced regeneration of target species is present, dense layers of understory vegetation can severely inhibit hardwood regeneration [6, 21]. This issue has been well studied in oaks (*Quercus* spp.), where understory competition for above- and below ground resources (esp. light) is considered a primary cause of postharvest regeneration failure, particularly on high quality sites [22, 23].

Whereas the importance of understory competition to forest regeneration is widely recognized, the potential for buried seeds to influence postharvest forest dynamics—through the shaping of early-successional communities and resulting competitive interactions—has received little attention, especially within the compositionally diverse mixed mesophytic forest region [15, 24–26]. In particular, little is known about the potential for buried seeds to influence postharvest forest regeneration under differing site quality conditions (e.g., [27]). It is widely recognized that much of the site quality variation that occurs across topographically dissected landscapes (e.g., moisture, temperature, radiation, soil depth, and fertility) can be accounted for by slope aspect, with generally more mesic conditions (e.g., moisture, fertility) on NE slopes and more xeric conditions on SW slopes in north temperate regions [28–32]. Given the pronounced influence of site quality on both understory [33–37] and overstory [12, 22, 23, 38] composition, productivity, and regeneration success, similar variation in seed bank composition and diversity may be expected across the landscape. Thus, our objectives were to examine variations in seed bank and aboveground vegetation relative to topographic aspect in recently clearcut and mature second-growth mixed oak forests and evaluate potential contributions of the seed bank to postharvest forest development under these contrasting site quality conditions.

2. Materials and Methods

2.1. Study Site. Field sampling was conducted at the Waterloo Wildlife Research Station (WWRS; 39° 21' 8" N, 82° 16' 57" W), a 505 ha state-owned research area in the Low Hills Belt section [39] of the Unglaciaded Allegheny Plateau of southeastern Ohio, USA [40]. Topographically, this region is highly dissected, with moderate to steep slopes (20%–70%) and ridgetop elevations of 280 to 320 m. The vegetation of WWRS lies in the mixed mesophytic forest association of the unglaciaded eastern deciduous forest region [39]. Mature second-growth forests are dominated by mixed oaks (*Quercus* spp.) and hickories (*Carya* spp.) on ridgetops and south-facing slopes and mesophytic species (e.g., *Fagus*

grandifolia, *Liriodendron tulipifera*, *Acer saccharum*, *Fraxinus americana*, and *Prunus serotina*) on lower and north-facing slopes [41].

Prior to anthropogenic disturbance, the land occupied by WWRS was heavily forested. By the late 1800s and early 1900s, however, much of the region (including WWRS) was under cultivation or pasture and large areas experienced heavy timber harvesting [32]. Today, the overstory at WWRS is relatively even-aged (~125 years). In our study sites, these second-growth stands are dominated by *Acer rubrum*, *Quercus prinus*, *Q. alba*, *Q. velutina*, *Q. coccinea*, *Fagus grandifolia*, and *Nyssa sylvatica*. Young revegetating clearcut stands also are present (~7 years), similarly dominated by *A. rubrum* and *Q. prinus*, but with greater importance of *Liriodendron tulipifera*, *Prunus serotina*, and *Sassafras albidum* [41].

2.2. Field and Greenhouse Methods. To sample seed bank and aboveground vegetation characteristics, permanent 2.5 m² circular quadrats were established in six upland, naturally regenerating clearcut stands (CC, ~7 years; late stand initiation stage) and six upland second-growth forest stands (SG, ~125 years; understory reinitiation stage) [5]. Sixteen replicate quadrats ($n = 16$) were established in each of the 12 stands, in a stratified-random arrangement ($N = 192$) [41]. Each stand had a minimum area of 1.75 ha (100 × 175 m) and was uniformly treated (entirely CC or SG). Each clearcut stand was located within 100 m of one of the six second-growth forest stands (minimum 50 m buffer between CC and SG quadrats) and displayed similar ranges of elevation, slope angle, and topographic aspect. These pairs of clearcut and second-growth stands were treated as statistical blocks when examining species-site relationships relative to stand age.

Each quadrat was assigned to one of three aspect categories, shown to represent gradients of soil moisture, depth, and fertility across this study site [37, 41]. Aspect categories were as follows: northeast (NE) = 345.5° to 104.5° aspect (119° range around due NE (45°)), southwest (SW) = 165.5° to 284.5° aspect (119° range around due SW (225°)), and intermediate (INT) = 105° to 165° and 285° to 345° aspect (60° ranges around due SE (135°) and NW (315°)). Thus, six aspect/stand age classes were evaluated: NE-SG ($n = 28$), INT-SG ($n = 27$), SW-SG ($n = 41$), NE-CC ($n = 29$), INT-CC ($n = 34$), and SW-CC ($n = 33$). In each 2.5 m² quadrat, all vascular plant species were inventoried in late April 1998 and late June 1998, to capture peak growth of spring ephemeral herbs and graminoids/composites, respectively. One seed bank sample, including soil and leaf litter, was collected immediately adjacent to each vegetation quadrat ($n = 192$) in early March 1999, to allow natural cold stratification of seeds from the 1998 growing season. Samples were extracted using a 10 × 10 × 5 cm deep (500 cm³) metal frame. Collected seed bank samples were placed in plastic bags and stored at 4°C until all samples were obtained.

Seed bank composition was assessed using the seedling emergence method. This technique is considered relatively accurate and the most appropriate for plant communities in which high seed richness is expected ([13, 42, 43], but see Baskin and Baskin [44]). Collected samples were

TABLE 1: Mean, total, and Jackknife estimated species richness of aboveground vegetation in 192 quadrats established in six revegetating clearcut (CC; ~7 years) and six second-growth (SG; ~125 years) forest stands at WWRS. Asterisk (*) indicates significant difference in CC and SG richness ($P < .05$). Letters indicate significant difference among CC/SG topographic aspect classes ($P < .05$).

	Mean Richness*	Mean Richness by Aspect Class			Total Richness	Jackknife 1	Jackknife 2
		SW	INT	NE		Total Richness	Total Richness
CC	14.7	14.1 ^(ac)	16.0 ^(a)	13.9 ^(ac)	118	134.8	120.8
SG	12.8	11.3 ^(b)	15.9 ^(a)	12.1 ^(bc)	104	135.0	124.9
Total					132		

concentrated using an 8 mm sieve to remove vegetative propagules, leaf litter, and other coarse materials and increase emerging seedling density, as suggested by Ter Heerd et al. [45]. Samples were spread over 2–3 cm of vermiculite/potting medium in $20 \times 20 \times 6$ cm aluminum trays. Four trays containing only vermiculite/potting medium were used to detect the presence of wind-borne seeds. Trays were placed on greenhouse benches and watered as necessary to maintain soil moisture. Seedling emergence was monitored from March through November 1999. As seedlings emerged, each was identified to species and removed. If identification was not possible, seedlings were transplanted to pots and grown to maturity. Voucher specimens were retained for all species. Each month, dilute liquid fertilizer was applied to stimulate seedling growth and trays were randomly rearranged to control location effects [13]. After completion of emergence studies, five trays were randomly selected from each aspect/stand age class (5 trays $\times$ 6 aspect/stand age classes; thus, $n = 30$) and soil examined for ungerminated seeds. Seeds located were soaked in water (20 hours), seed coats were punctured, and seeds were immersed in 1% neotetrazolium chloride solution (48 hours) to test for viability [46, 47]. All ungerminated seeds found to be viable were represented by emerged species. Nomenclature for aboveground and seed bank species follows Gleason and Cronquist [48].

2.3. Data Analysis. Mean frequency was calculated for each seed bank and aboveground species by aspect/stand age class. Revegetating clearcut and second-growth forest diversity were assessed as mean (per seed bank sample or aboveground quadrat) and total species richness. Two-way ANOVA tests were used to examine the effects of stand age (CC versus SG; fixed effect), aspect position (NE, INT, SW; fixed effect), and the interaction of these on seed bank and aboveground richness. Stand was treated as a random effect (block). Richness data were $\log_{10}$ transformed to meet normality and equal variance assumptions. Treatment means for significant ANOVAs were compared using a *posteriori* Bonferroni multiple comparison procedures. All ANOVAs were conducted using NCSS software [49].

To evaluate the adequacy of seed bank and understory sampling, bootstrap-derived species-area curves were created by subsampling the data set to determine mean richness at each possible subsample size. In addition, total clearcut and second-growth seed bank and understory richness values were compared to two nonparametric, incidence-based richness estimators: (1) first-order Jackknife, which

incorporates the number of uniques (species occurring in a single quadrat) and the number of quadrats sampled [50, 51], and (2) second-order Jackknife, which incorporates the number of uniques, duplicates (species occurring in exactly two quadrats), and sample quadrats [52, 53]. In accordance with Palmer [51, 53], Chazdon et al. [54], and others, these resampling techniques were used to reduce sampling bias and create more robust richness estimations by more heavily weighting rare or infrequent species for a given sample size. Species-area curves and estimated richness values were calculated using PC-ORD software [55].

Compositional variation among aboveground and seed bank samples was examined using hierarchical, polythetic, and agglomerative cluster analysis, with UPGMA group linkage and Sørensen's dissimilarity method ([56]; PC-ORD software [55]). Sørensen's Community Coefficient was used to estimate the compositional similarity of seed bank versus aboveground samples in clearcut and second-growth forest stands. The index is calculated as $2c/(a + b + 2c)$, where a is the number of species unique to sample a , b is the number of species unique to sample b , and c is the number of species shared by both samples. The relationship of seed bank composition to vegetation, topography, and microenvironmental variables was examined using Canonical Correspondence Analysis (CCA [55]). CCA is a direct ordination technique that provides simultaneous evaluation of vegetation and environmental data [57]. Variables included in the initial CCA were aspect, slope angle, leaf litter depth, air temperature, relative humidity, spring light availability, soil NO_3 , P, K, Ca, Mg, and Al, soil moisture, organic matter content, silt, clay, C, N, and C:N, pH, soil compaction, tree basal area and density, and sapling, seedling, herbaceous cover. (See Small and McCarthy [41] for complete descriptions of soil analyses and vegetation measures.) Quadrat aspect was cosine transformed to range from 0 (SW) to 2 (NE) for use in CCA [58]. All variables were $\log_{10}$ transformed to reduce outlier influence and provide greater weight to changes in resource availability (e.g., soil nutrients) at low concentrations [59]. Highly correlated variables and those only weakly associated with the first three CCA axes were removed from final CCAs to produce the most parsimonious ordinations, in accordance with Ter Braak [57] and Palmer [59].

3. Results

3.1. Species Richness. Plant species richness aboveground was more than twice that of the seed bank (132 versus 63 spp.) and, in both strata, appeared to decline with stand age (Tables 1 and 2; Figure 1). Mean richness per quadrat/sample

FIGURE 1: Bootstrap-derived species-area curves (± 2 SD; dotted lines) for 96–2.5 m² aboveground (AG) and seed bank (SB) samples in revegetating clearcut (CC; ~7 years) and second-growth (SG; ~125 years) forest stands at WWRS, Athens County, Ohio, USA.

for both aboveground vegetation and the seed bank were significantly higher in younger revegetating clearcuts than in more mature forests ($P < .05$ aboveground, $P < .01$ seed bank; Tables 1 and 2). Similarly, total richness aboveground (CC = 118 versus SG = 104 spp.) and in the seed bank (CC = 49 versus SG = 46 spp.) was slightly lower in mature stands. Richness estimators (Jackknife 1, Jackknife 2) supported these differences aboveground (greater richness in younger stands) and suggested that a relatively small proportion of species remained unaccounted for based on our sampling efforts (2%–12% in CC; 17%–23% in SG; Table 1). In contrast, Jackknife estimations of seed bank richness were markedly higher than observed values, suggesting that our samples failed to account for one quarter to one third of the species likely present (22%–28% in CC; 29%–38% in SG; Table 2). Further, richness estimators suggested *higher* seed bank richness in later successional stands. Convergence of species-area curves for clearcut and forest seed banks also suggests that greater sampling may produce higher belowground richness values in mature stands (Figure 1).

3.2. Species Composition. Species composition differed markedly between seed bank and aboveground samples (Sørensen's coefficient of similarity <10%) and suggested increasing compositional divergence with stand age. In both clearcut and second-growth stands, cluster analysis showed nearly complete divergence of seed bank and aboveground vegetation although above- to belowground similarity was slightly higher in younger stands (Sørensen's coefficient CC =

FIGURE 2: Dendrogram representing UPGMA cluster analysis of aboveground (broken) and seed bank (solid) samples in revegetating clearcut and second-growth forest quadrats at WWRS.

26.6%, SG = 21.6%; Figure 2). Compositional separation of seed bank and aboveground vegetation resulted largely from high frequency of early-successional annuals (e.g., *Erechtites hieraciifolia*, *Acalypha rhomboidea*, *Solanum nigrum*, *Verbascum thapsus*) and graminoids (*Carex* spp., *Juncus tenuis*, and *Panicum* spp.) in the seed bank and increased frequency of shade-tolerant perennial herbs (e.g., *Aster* spp., *Desmodium glutinosum*, *Lysimachia quadrifolia*, *Polygonatum pubescens*, *Polystichum acrostichoides*, and *Potentilla simplex*), shrubs (*Rubus pensilvanicus*, *Smilax rotundifolia*), and trees (*Acer rubrum*, *Quercus prinus*, *Sassafras albidum*) aboveground (Figure 3, Table 3).

Compositional trends within the seed bank (CCA ordination; Figure 4) showed marked influence of both stand age and topographic aspect, with revegetating clearcuts and second-growth forests separated along CCA Axis 1 ($\lambda = 0.349$) and aspect categories grading from most mesic (NE) to most xeric (SW) along Axis 2 ($\lambda = 0.267$). Of our measured site variables, aspect had the most pronounced correlation with seed bank composition (Axis 2, $r = -0.923$). Other important variables, each correlated with compositional variation along Axis 1 and reaching the greatest extent in young clearcut stands, were temperature

TABLE 2: Mean, total, and Jackknife estimated species richness in 192 seed bank samples collected from six revegetating clearcut (CC; ~7 years) and six second-growth (SG; ~125 years) forest stands at WWRS. Double asterisk (**) indicates significant difference in CC and SG richness ($P < .01$). Letters indicate significant difference among CC/SG topographic aspect classes ($P < .05$).

	Mean Richness**	Mean Richness by Aspect Class			Total Richness	Jackknife 1	Jackknife 2
		SW	INT	NE		Total Richness	Total Richness
CC	2.7	2.3 ^(a)	3.1 ^(a)	2.6 ^(a)	49	62.9	67.8
SG	1.9	1.4 ^(b)	2.3 ^(a)	2.1 ^(a)	46	64.8	73.7
Total					63		

($r = 0.849$), light availability ($r = 0.513$), and tree density ($r = 0.665$; Figure 4). Cluster analysis of samples in our six-stand age/aspect classes emphasized topographic influences on seed bank and aboveground composition. After early divergence of seed bank and aboveground samples, cluster analysis showed consistent separation of samples from NE and SW aspect positions, both above- and belowground, regardless of stand age (Figure 5). Aboveground, these compositional variations were associated with increased frequency of *Amphicarpaea bracteata*, *Anemonella thalictroides*, *Arisaema triphyllum*, *Cardamine concatenata*, *Cimicifuga racemosa*, *Geranium maculatum*, *Osmorhiza claytonii*, *Fraxinus americana*, and *Viburnum acerifolium* from SW to NE slopes (both CC and SG stands), and higher frequency of graminoids and most woody seedlings (e.g., *Lysimachia quadrifolia*, *Carex digitalis*, *Panicum* spp., *Liriodendron tulipifera*, *Quercus* spp., *Sassafras albidum*, *Vaccinium* spp., and *Smilax* spp.) on SW slopes (Figure 3, Table 3). In the seed bank, species such as *Phytolacca americana*, *Carex laxiflora*, *Rhus glabra*, and *Rubus* spp. were more common on NE slopes (esp. CC); grasses (esp. *Panicum* spp.) were more widely distributed on SW slopes (Table 3).

3.3. Nonnative Species. The distribution of nonnative plant species was also strongly influenced by aspect, with remarkably similar trends aboveground and in the seed bank (Figure 6). Greater nonnative richness was found in the seed bank (9 spp., *Cardamine hirsuta*, *Digitaria ischaemum*, *Glechoma hederacea*, *Polygonum convolvulus*, *Sida spinosa*, *Solanum nigrum*, *Trifolium pratense*, *T. repens*, and *Verbascum thapsus*) than aboveground (6 spp., *Cardamine hirsuta*, *Celastrus orbiculatus*, *Potentilla recta*, *Rosa multiflora*, *Taraxacum officinale*, and *Tussilago farfara*; Table 3), yet nonnative plants were more common in aboveground quadrats (Figure 6). Recent harvesting appeared to increase the frequency of nonnative species, both aboveground and in the seed bank (Figure 6). The most pronounced influence, however, appeared to be that of site quality, with more mesic sites (INT and NE aspects) supporting greater frequencies of nonnative species, especially in younger stands, whereas more xeric sites (SW) had consistently low nonnative abundance (Figure 6).

4. Discussion

Our examination of buried seed distribution across naturally regenerating (stand initiating) and mature second-growth mixed oak stands showed four pronounced trends: (1) seed

bank composition diverged markedly from that of aboveground vegetation, (2) observed seed bank richness was lower in later successional forests than in recently harvested stands, (3) despite intensive sampling (relative to most seed bank studies), richness estimators and species-area curves indicated high seed bank variability, supporting previous assertions that temperate forest seed banks often are under-sampled, and (4) topographic aspect strongly influenced seed bank composition, including the prevalence of nonnative plant species. We discuss each of these findings and consider implications for postharvest forest regeneration below.

4.1. Compositional Divergence of Seed Bank and Aboveground Vegetation. One of the most widely supported generalizations concerning forest seed banks is that the composition of buried seeds diverges from that of aboveground vegetation [14, 15, 60–62]. Low compositional similarity of above- and belowground vegetation (<10%) at our study site supports this generalization and suggests that mixed oak forests in the mixed mesophytic forest region are likely to follow this pattern. Furthermore, while younger stands (~7 years) showed slightly greater above- versus belowground compositional similarity, even the short time since clearcutting was sufficient for marked differentiation to occur (Figure 2; Table 3). As in other forest regions, the prevalence of fast-growing, early-successional species in the seed bank emphasizes the importance of buried seeds to ecosystem recovery following large-scale disturbance (Figure 3) [8, 12]. In contrast, the markedly lower frequency and diversity of later successional species (trees and herbaceous perennials) reflects the inability of many of these species to form persistent seed banks and highlights the role of vegetative reproduction and postdisturbance seed dispersal in the regeneration of mature forest species [17, 44, 63].

4.2. Increased Seed Bank Richness in Young Forests. Our results showed higher seed bank and aboveground richness in younger, revegetating clearcut stands than in later successional, second-growth forests, due primarily to greater importance of graminoids and nonnative species. Increases in aboveground diversity following clearcutting are consistent with Roberts and Gilliam ([9]; mesic sites), Bormann and Likens [8], Small and McCarthy [37], and others and have been linked to greater habitat heterogeneity and resource availability following disturbance [5, 64, 65]. Disturbance and associated heterogeneity also have been shown to increase ecosystem susceptibility to nonnative

FIGURE 3: Aboveground and seed bank richness by life form in revegetating clearcut and second-growth forest samples at southwest (SW), intermediate (NW/SE; INT), and northeast (NE) aspect positions at WWRS. Note different scales of y-axes. See text for definitions of stand type/aspect classes. Life form designations follow Gleason and Cronquist [48].

species, reducing resource use and competition by resident vegetation and increasing the availability of resources to opportunistic invading species [66, 67]. While the influence of microenvironmental variability on aboveground vegetation is widely recognized [9, 41, 68], our results suggest comparable influences on seed dispersal and storage in the soil seed bank.

In contrast to generalizations about above- and below-ground compositional divergence, generalizations about changes in seed bank diversity during forest succession have received limited support. Like our study, Pickett and McDonnell [15] suggest seed bank diversity to be higher early in forest succession and decline with canopy closure. Several chronosequence studies also have examined seed bank dynamics during deciduous forest succession [12, 60, 69].

FIGURE 4: Canonical correspondence analysis (CCA) ordination of 192 seed bank samples by aspect class (see text) in revegetating clearcut and mature second-growth forest samples. See text for description of variables.

Whereas many of these studies document declines in seed bank *density* over time [14, 15], trends in seed bank richness vary widely. For example, Roberts and Vankat [69] found seed bank richness to decline during succession, yet indicated that seed bank richness may not decline if aboveground vegetation diversity is especially high. Stark et al. [70] indicate that changes in seed bank richness and heterogeneity depend more on spatial scale than time since disturbance. Trends in seed bank diversity during succession were similarly unclear at our study site, as Jackknife richness estimators contradicted observed trends and suggested that additional sampling may produce higher seed bank richness values in older forests (Table 2). If this is the case, the high diversity of aboveground vegetation at our study site (>100 species in SG forest quadrats) may limit successional declines in seed bank diversity, as suggested by Roberts and Vankat [69].

4.3. Sampling Considerations for Seed Bank Variability. As in many seed bank studies, we found considerably lower richness in the seed bank than aboveground. Yet the 63 species of buried seeds we observed were markedly higher than those reported for most temperate forest communities [15]. This increased richness may reflect the relatively small number of seed bank studies conducted in the mixed mesophytic forest region [15, 25] or correspond to the exceptionally high aboveground diversity for which this region is noted [39, 69]. An examination of experimentally thinned, burned, and untreated mixed oak stands in southeastern Ohio found similarly high seed emergence from samples collected in early spring (70 spp. in 80–0.01 m² samples [26]). However, as in our study, poor representation of aboveground species in the seed bank suggests that aboveground diversity is not

TABLE 3: Frequency of occurrence (% of samples) for aboveground understory (herbaceous and woody seedling) and seed bank species in revegetating clearcut (CC) and second-growth (SG) forest samples by aspect category at WWSR. Only species with frequencies >12% across all stand/aspect categories are shown. Asterisk (*) indicates a nonnative species.

	Aboveground						Seed Bank					
	CC		SG		CC		SG					
Species	SW	INT	NE	SW	INT	NE	SW	INT	NE	SW	INT	NE
Annual or Biennial Herbs												
<i>Acalypha rhomboidea</i>								2.9		4.9	18.5	14.3
<i>Amphicarpaea bracteata</i>	24.2	32.4	34.5	26.8	44.4	46.4					3.7	
<i>Erechtites hieracifolia</i>							39.4	26.5	31.0	29.3	18.5	39.3
<i>Galium aparine</i>	3.0	14.7	82.8	4.9	51.9	25.0						
<i>Lobelia inflata</i>		11.8	3.5									
* <i>Solanum nigrum</i>							3.0		13.8	2.4	3.7	
* <i>Verbascum thapsus</i>							3.0		6.9			3.6
Perennial Herbs												
<i>Anemonella thalictroides</i>	3.0	5.9	17.2	2.4	7.4	17.9						
<i>Antennaria plantaginifolia</i>		5.9						2.9	24.1			
<i>Arisaema triphyllum</i>		2.9	34.5		18.5	21.4						
<i>Aristolochia serpentaria</i>		8.8	3.5		14.8	3.6						
<i>Aster divaricatus</i>	51.5	55.9	3.5	29.3	37.0	50.0						
<i>Aster lateriflorus</i>	57.6	76.5	24.1	24.4	33.3	7.1						
<i>Aster undulatus</i>	15.2	14.7		4.9	14.8	7.1						
<i>Boehmeria cylindrica</i>	3.0	5.9	17.2	9.8	40.7	17.9						
<i>Botrychium dissectum</i>		2.9	6.9		11.1							
<i>Cardamine concatenata</i>		5.9	13.8	2.4	7.4	35.7						
* <i>Cardamine hirsuta</i>		14.7	34.5						6.0			
<i>Cimicifuga racemosa</i>		2.9	10.3		3.7	50.0						
<i>Circaea lutetiana</i>			13.8		3.7							
<i>Cunila organoides</i>		23.5		12.2								
<i>Desmodium glutinosum</i>	33.3	35.3	44.8	31.7	74.1	64.3						
<i>Dioscorea villosa</i>		2.9	3.5			14.3						
<i>Dryopteris marginalis</i>	6.1	2.9	3.5			7.1						
<i>Eupatorium serotinum</i>		5.9			33.3			11.8	3.5	2.4	11.1	
<i>Galium circaezans</i>		5.9	27.6	9.8	40.7	28.6						
<i>Geranium maculatum</i>		8.8	24.1	4.9	18.5	35.7						
<i>Geum canadense</i>			3.5	2.4	40.7							
<i>Goodyera pubescens</i>		11.8		7.3								
<i>Hedyotis caerulea</i>	9.1	5.9		4.9								
<i>Helianthus divaricatus</i>		11.8	3.5		7.4							
<i>Heuchera americana</i>	3.0	14.7	13.8									3.5
<i>Hieracium venosum</i>	9.1			4.9								
<i>Hydrophyllum macrophyllum</i>				2.4	3.7							
<i>Lespedeza hirta</i>	18.2	5.9										
<i>Lysimachia quadrifolia</i>	30.3	32.4	6.9	29.3	18.5	14.3						
<i>Monotropa uniflora</i>				2.4	3.7	10.7						
<i>Onoclea sensibilis</i>	3.0	8.8	6.9			3.6						
<i>Orchis spectabilis</i>			3.5		11.1							
<i>Osmorhiza claytonii</i>			37.9		29.6	32.1						
<i>Oxalis violacea</i>		2.9			11.1							
<i>Phytolacca americana</i>	3.0		3.5				3.0	11.8	20.7	2.4		3.6
<i>Podophyllum peltatum</i>		11.8	13.8		14.1	7.1						
<i>Polygonatum pubescens</i>	15.2	23.5	17.2	31.7	18.5	53.6						
<i>Polygonum virginianum</i>		5.9	6.9									

TABLE 3: Continued.

Species	Aboveground						Seed Bank					
	SW	CC INT	NE	SW	SG INT	NE	SW	CC INT	NE	SW	SG INT	NE
<i>Polystichum acrostichoides</i>	27.3	38.2	34.5	2.4	37.4	21.4						
<i>Porteranthus stipulatus</i>	12.1	2.9		4.9								
<i>Potentilla simplex</i>	45.5	61.8	20.7	26.8	29.3	7.1		5.9		4.9	7.4	3.6
<i>Prenanthes altissima</i>	3.0	14.7	6.9	4.9	18.2	10.7						3.6
<i>Sanicula canadensis</i>			3.5	4.9	37.0							
<i>Smilacina racemosa</i>	9.1	17.7	17.2	19.5	11.1	25.0						
<i>Solidago canadensis</i>							6.0	11.8	6.9			
* <i>Taraxacum officinale</i>	6.1	14.7	3.5	2.4								
<i>Tiarella cordifolia</i>			6.9		3.7	21.4						
* <i>Trifolium repens</i>							3.0	23.5			3.7	
<i>Trillium grandiflorum</i>		2.9	3.5			10.7						
<i>Uvularia perfoliata</i>		11.8	10.3	7.3	22.2	25.0						
<i>Vicia caroliniana</i>		23.5	17.2									
<i>Viola palmata</i>	3.0	5.9	17.2									
<i>Viola sororia</i>	30.3	44.1	44.8	22.0	48.2	14.3	3.0	2.9	3.5		3.7	7.1
Graminoids												
<i>Agrostis perennans</i>							6.1	14.7	3.5			
<i>Bromus pubescens</i>		8.8	13.8	4.9	11.1	10.7						
<i>Carex digitalis</i>	60.6	61.8	6.9	31.7	18.5	3.6	12.1	29.4	3.5	4.9	18.5	10.7
<i>Carex laxiflora</i>	12.1	35.3	51.7	7.3	25.9	21.4	9.1	5.9	24.1	4.9	7.4	17.9
<i>Juncus tenuis</i>		11.8					9.1	26.5	3.5	2.4	7.4	
<i>Luzula echinata</i>		5.9		7.3								
<i>Muhlenbergia schreberi</i>								2.9	6.9	2.4	3.7	
<i>Panicum boscii</i>							3.0	8.8		12.2	7.4	
<i>Panicum clandestinum</i>	39.4	35.3	10.3	12.2	18.5		27.3	14.7	10.3	14.6		
<i>Panicum dichotomum</i>	24.2	5.9		17.1	3.7	3.6	45.5	17.7	3.5	14.6	7.4	10.7
<i>Poa sp.</i>	18.2	26.5	3.5	19.5	22.2	7.1						
Shrubs and Trees												
<i>Acer rubrum</i>	48.5	55.9	41.4	85.4	70.4	75.0				2.4		
<i>Amelanchier arborea</i>	3.0	2.9		7.3	7.4	7.1						
<i>Carya spp.</i>	18.2	2.9	13.8	14.6	14.8	14.3						
<i>Cornus florida</i>	9.1	20.6	3.5	12.2	3.7	3.6		2.9				
<i>Fagus grandifolia</i>	12.1	2.9		2.4								
<i>Fraxinus americana</i>			10.3	2.4	3.7	25.0						
<i>Gaylussacia baccata</i>	18.2			7.3								
<i>Lindera benzoin</i>		5.9	44.8		14.8							
<i>Liriodendron tulipifera</i>	66.7	61.8	34.5	29.3	33.3	10.7	6.1	5.9	3.5	2.4	25.9	35.7
<i>Nyssa sylvatica</i>	27.3	8.8	10.3	17.1	18.5	14.3		2.9				
<i>Prunus serotina</i>	6.1	20.6	17.2	9.8	7.4	7.1						
<i>Quercus alba</i>	18.2			4.9								
<i>Quercus prinus</i>	36.4	26.5	13.8	51.2	25.9	21.4		2.9		2.4		3.6
<i>Quercus rubra</i>	24.2	26.5	24.1	39.0	29.6	21.4						
<i>Quercus velutina</i>	30.3		13.8									
<i>Rhus copallinum</i>	15.2	14.7	3.5					8.8	3.5		7.4	
<i>Rhus glabra</i>	3.0	5.9					3.0	5.9	6.9	4.9	11.1	14.3
* <i>Rosa multiflora</i>	3.0	23.5	27.6	9.8	18.5	7.1						
<i>Rubus occidentalis</i>							3.0	14.7	31.0		7.4	3.6
<i>Rubus pensilvanicus</i>	78.8	73.5	51.7	14.6	33.3	14.3	6.1	5.9	20.7			7.1
<i>Sassafras albidum</i>	66.7	55.9	20.7	80.5	70.4	28.6				2.4	7.4	3.6

TABLE 3: Continued.

Species	Aboveground						Seed Bank					
	SW	CC INT	NE	SW	SG INT	NE	SW	CC INT	NE	SW	SG INT	NE
<i>Ulmus rubra</i>					40.7	3.6						
<i>Vaccinium pallidum</i>	75.8	23.5		43.9								
<i>Vaccinium stamineum</i>	27.3	14.7		43.9	14.8	3.6						
<i>Viburnum acerifolium</i>	3.0	11.8	41.4	9.8	37.0	60.7						
Woody Vines												
<i>*Celastrus orbiculatus</i>		5.9	6.9	2.4	7.4	7.1						
<i>Parthenocissus quinquefolia</i>	12.1	44.1	44.8	19.5	51.9	50.0		2.9				
<i>Smilax glauca</i>	30.3	17.7	13.8	43.9	44.4	3.6						
<i>Smilax rotundifolia</i>	81.8	55.9	48.3	70.7	44.4	32.1	6.1				3.7	3.6
<i>Toxicodendron radicans</i>		8.8	3.5		3.7	10.7						
<i>Vitis vulpina</i>	42.4	35.3	58.6	19.5	14.8	14.3	6.1	2.9	3.5	7.3	14.8	7.1

FIGURE 5: Summary dendrogram representing UPGMA cluster analysis of aboveground (AG; solid) and seed bank (SB; broken) samples across the six stand age/aspect classes examined. (See text for description of aspect/stand age classes.)

the primary influence on seed bank richness, but that seeds are likely to persist from earlier land use disturbances (esp. former cultivation or pasturing) or dispersal from nearby open habitats [15, 16]. Supporting this view, Schiffman and Johnson [24] attribute notably low seed diversity and density in mature oak-dominated forests of the southern Appalachians to the absence of such disturbance history and neighboring seed sources.

Alternative explanations for the high seed bank richness found at our study site support assertions of undersampling in many temperate forest seed bank studies. High variability in seed bank composition, density, and diversity is frequently

FIGURE 6: Frequency of nonnative plant species in aboveground and seed bank samples across the six stand age/aspect classes examined. (See text for description of classes.)

reported, coupled with low observed richness values [15]. However, assessments of sampling adequacy are rarely performed [70–72]. In our study, nearly 200 seed bank samples (96 per stand type; 0.01 m²) were insufficient (based on Jackknife richness estimations) to fully capture seed bank heterogeneity, yet we sampled much more intensively than many similar studies. For example, Olmsted and Curtis [61] found 10, 12, and 8 seed bank species in 50, 110, and 150 year beech-sugar maple stands in Maine, but their study included only four 0.09 m² samples from each stand. Ashton et al. [27] found 25 seed bank species in 70–90 year deciduous forests of southern New England, based on 36–0.01 m² samples. Similarly, Roberts and Vankat [69] reported 29 taxa in a 10-year-old field, 21 taxa in a 90 year, and 14 taxa in an old-growth beech-maple forest in western Ohio, based on 10–0.008 m² samples from each sere. Like our study, each of these reflects seed bank samples collected in winter or early

spring, before spring germination, and therefore includes both transient seed bank species (those viable only in the first year after maturation and dispersal) and persistent seed bank species (viable seeds persisting in the seed bank for more than one year [44]). Given the high compositional variation of our seed bank samples (Figures 2 and 5) and failure of our species-area curves to reach plateaus (Figure 1), sample sizes such as these would have severely decreased observed richness values (e.g., a sample size of $n = 10$ would have resulted in only 14 and 20 spp., instead of the 46 (SG) and 49 (CC) spp. observed) and potentially biased observed trends. Similar conclusions were reached by Qi and Scarratt [72], in a study of clearcut and undisturbed boreal mixedwood forest of Ontario, and Stark et al. [70], in an evaluation of seed bank variability and sampling adequacy in Douglas-fir forests of British Columbia, each emphasizing the need for intensive sampling to represent seed bank heterogeneity and the pronounced influence of infrequent (unique) species.

4.4. Influence of Topography on Seed Bank Composition. We found seed bank composition, including the prevalence of nonnative species, to vary markedly with topographic aspect position (i.e., SW versus NE slopes; Figure 5). All aspect/stand age classes were dominated by ruderal herbs (e.g., *Erechtites hieraciifolia*, *Acalypha rhomboidea*, and *Solanum nigrum*), but grasses (esp. *Panicum* spp.) were especially common in the soils of SW slopes; thicket-forming shrubs (*Rubus* spp., *Rhus* spp.) were better represented in NE and INT slope soils. Two early-successional, shade-intolerant trees (*Liriodendron tulipifera* and *Sassafras albidum*) were also important in NE and INT forest seed banks. As in many north temperate regions, aspect differences across our study site are associated with edaphic variations, with drier, more acidic, and less fertile soils on SW slopes (lower organic matter, nutrient content (esp. Ca, K, Mg), Ca:Al ratio, and higher C:N ratio) versus INT or NE slopes, regardless of stand age [37, 41]. The highest soil nutrient concentrations occur in NE-CC soils and INT-SG soils; [41]. Like Jenkins and Parker [34, 38] in hardwood forests of central Indiana and Hutchinson et al. [33] in nearby oak forests of southern Ohio, we found site quality (slope aspect) to be a primary influence on aboveground structure and composition, with greater woody seedling abundance, lower herbaceous richness and abundance, and lower canopy tree density and basal area on SW slopes [41] (Figure 4).

Similar variations in seed bank size and composition have been noted relative to specific soil or site factors (e.g., soil pH, moisture, and organic content [13, 17]), yet few studies have considered the implications of broader scale landscape variations. An exception is Ashton et al. [27], who examined seed bank dynamics along topographic gradients from ridgetop to valley bottom and reported differences in seed density, diversity, and life form frequency relative to slope position. Such differences in seed bank composition across the landscape, as found in our study (Figures 4 and 5), should be expected to produce compositional and potentially structural differences in early-successional communities following disturbance. These initial communities, in turn,

play an important role in shaping the competitive environment for overstory regeneration. George and Bazzaz [19] demonstrated this pronounced influence of ground layer competition (intense fern competition) on tree seedlings in mixed hardwood forests of central Massachusetts. They concluded that understory vegetation can act as a species-specific “filter” to tree seedling emergence, growth, and survival, shaping the structure and composition of seedling communities and potentially driving compositional shifts in tree regeneration. Similar effects on sapling growth and survival have been noted under thick shrub (*Rhododendron maximum*) cover in the southern Appalachians [19, 73]. While perennial herbs were relatively infrequent in our seed bank samples, greater prevalence of thicket-forming shrubs and early-successional trees on NE slopes suggests greater potential for regeneration inhibition on these mesic sites.

The effects of understory competition on regeneration of desired timber species, especially during stand initiation, are considered critical aspects of forest management [23, 74]. Successful canopy reestablishment is dependent on a number of factors, including the availability of advance regeneration, understory density and composition, and site conditions [21, 22, 74–76]. In eastern deciduous forests, poor oak regeneration (esp. *Quercus rubra* and *Q. alba*) has become a major concern, with intense understory competition considered a primary cause of regeneration failure after harvesting, particularly on high quality sites [22, 23]. Dense understories of shade-tolerant and faster-growing saplings (e.g., *Acer saccharum*, *A. rubrum*, *Liriodendron tulipifera*, *Fraxinus americana*, *Nyssa sylvatica*, and *Sassafras albidum*), shrubs (e.g., *Rhododendron maximum*), and taller, broad-leaved herbs have been shown to slow growth and increase mortality of oak seedlings and encourage replacement of oak-dominated stands by more mesophytic species [23, 38, 73, 74, 77]. On mesic sites, logging and canopy-opening disturbances tend to accelerate this transition by releasing shade-tolerant species already present in the understory [38, 74, 78].

Our results similarly suggest that canopy removal and soil disturbance may be more problematic in mesic and intermediate stands (NE/INT slopes) at our study site, where they are likely to favor emergence of rapid growing and highly competitive saplings (e.g., *Liriodendron tulipifera*, *Sassafras albidum*), shrubs (e.g., *Rubus* spp., *Rhus* spp., and *Smilax rotundifolia*), and broad-leaved herbs (versus grasses) from the soil seed bank (Table 3). Disturbance of mesic sites also appears to encourage nonnative species establishment, with the greatest frequencies of nonnatives on sites of higher soil moisture and fertility (NE and INT slopes) and more recent disturbance (CC) at our study site (Figure 6, Table 3). Increased frequency of nonnative seeds and aboveground species on mesic, disturbed sites supports the results of McNab and Loftis [79] and Neary et al. [80], who emphasize the importance of minimizing soil disturbance on richer sites, where the potential for aggressive competitors is especially high during stand initiation.

Our findings generally support the results of other temperate forest seed bank studies, suggesting similar dynamics but potentially greater seed bank diversity in the mixed

mesophytic forest region. Yet our study also emphasizes the need for increased attention to sources of ecological heterogeneity, their assessment, and their influences on seed bank dynamics, as these may have important implications for postharvest regeneration in eastern forests. Dech et al. [23] describe variations in initial understory composition, including oak seedling competitors, with harvesting intensity and topographically driven gradients of soil fertility and similarly emphasize the importance of ecosystem-specific considerations in the management of overstory regeneration. Understanding controls on understory development after forest clearing, particularly factors influencing the density and composition of competing ground layer vegetation, is one of the most important knowledge gaps in our understanding of oak regeneration. Seed bank communities are likely to play an important, site-dependent role in shaping the competitive environment for oaks and other commercially important timber species after harvesting and, thereby, have the potential to influence postharvest forest development. As seed bank contributions are expected to increase with soil disturbance and seed composition has been shown to vary with the specific properties of the forest system, our results emphasize the importance of site-specific management in assessing the potential for soil disturbance and resulting understory competition to inhibit overstory regeneration success.

Acknowledgments

The authors wish to thank the Ohio Biological Survey, Ohio University Houk Memorial Research Fund, and the Department of Environmental and Plant Biology at Ohio University for financial support, the Waterloo Wildlife Research Station, ODNR for permission to conduct this study, and J. E. Brown, D. C. White, and R. G. Verb for field assistance.

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