

Seed-bank characteristics in mixed-mesophytic forest clearcuts and edges: Does “edge effect” extend to the seed bank?

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Abstract: Little is known about the seed banks of mixed-mesophytic forest clearcuts or their associated forest edges. Seed banks were described and compared to better understand how seed density, species richness, and composition change with increasing distance from clearcuts. Thirty-two taxa were found in the seed bank of clearcuts, and 44 were found in adjacent forest edges. Annuals represented 41% of seeds in clearcuts, but only 8% in edges, while trees and shrubs represented 3% in both areas. Seed-bank density and species richness varied significantly within and between clearcuts, but clearcuts were no different in seed-bank density and richness from interior forest seed banks. Seed-bank density declined significantly with distance from clearcuts on west-facing forest edges, but demonstrated no discernable spatial pattern on south-facing edges. Overall, edge effects from clearcutting on adjacent forest seed banks were demonstrated in total seed density and in several common wind-dispersed, early-successional herbaceous species, including *Erechtites hieraciifolia* (L.) Raf. and *Lobelia inflata* L., and *Vitis*, a common ingestion-dispersed species. The seed-shadow edge effect may influence both current and future community characteristics and population dynamics of vegetation in mixed-mesophytic forest edges adjacent to clearcuts.

Key words: seed banks, clearcutting, edge effects, mixed-mesophytic forest, West Virginia.

Résumé : On connaît peu de choses sur les banques de graines des forêts mixtes mésophytes coupées à blanc et de leurs bordures associées. Les auteurs décrivent et comparent les banques de graines pour mieux comprendre comment la densité des graines, la richesse en espèces et la composition changent avec une augmentation de la distance à partir de la coupe à blanc. Les auteurs ont retrouvé trente-deux taxons dans la banque de graine d'une coupe à blanc alors qu'à l'orée de la forêt adjacente, ils en retrouvent 44. Les annuelles constituent 41 % des graines sur la coupe à blanc, mais seulement 8 % dans les bordures, alors que les arbres et les arbustes en représentent 3 % dans les deux cas. La densité et la richesse en espèces des deux banques varient significativement à l'intérieur et entre les coupes à blanc, mais les banques de graines des sites coupés à blanc ne diffèrent ni en densité ni en richesse des banques de graines de l'intérieur des forêts. La densité des banques de graines diminue significativement avec la distance à partir de la coupe à blanc, sur les bordures faisant face à l'ouest, mais ne montrent aucun patron spatial distinct sur les bordures faisant face au sud. En général, on démontre des effets de bordure de la coupe à blanc sur les banques de graines de la forêt adjacente, en termes de densité totale des graines et de plusieurs espèces herbacées communes de début de succession dispersées par le vent, incluant l'*Erechtites hieraciifolia* (L.) Raf. et le *Lobelia inflata* L., ainsi que le *Vitis*, une espèce commune dispersée par ingestion. L'effet de bordure ombragée pourrait influencer les caractéristiques courantes et futures de la communauté et la dynamique des populations végétales des bordures adjacentes aux coupes à blanc pratiquées en forêts mixtes mésophytes.

Mots clés : banque de graines, coupe à blanc, effet de bordure, forêt mixte mésophyte, West Virginia.

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Introduction

The forest soil seed bank can be defined as the aggregation of viable seeds in a volume of soil at a specific time (Simpson et al. 1989). Seed-bank density and richness vary, because the

factors that influence them, such as disturbance type and intensity, successional stage, soil chemistry, and microclimate, vary over space and time. For example, seed banks vary along environmental gradients of resource availability and disturbance (Thompson 1978), including successional sequences (Oosting and Humphreys 1940; Bicknell 1979; Roberts and Vankat 1991), chemical and nutrient gradients (Van der Valk and Rosburg 1997), soil moisture gradients (Bakker et al. 1996), and topographic gradients (Ashton et al. 1998). The resulting spatial array of seeds in the soil seed bank determine spatial and temporal patterns of vegetation.

Several studies have described change in tropical forest seed banks across forest edges, the area of transition between a relatively bright, warm, and dry opening and a shaded, cool, and humid interior forest (Wales 1967; Chen et

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al. 1990; Matlack 1993). In an undisturbed tropical forest, Soderstrom (1986) attributed a negative correlation between seed-bank density and distance from a recently disturbed second-growth forest to a combination of local seed rain from edge-associated colonizing species and dispersal of seeds from the adjacent second-growth stand. Saulei and Swaine (1988) found that the majority of seeds in the seed bank of a remnant tropical forest stand originated from fruit-bearing pioneer trees in the surrounding logged area, and speculated that frugivorous birds were responsible for their dispersal and deposition. As expected on the basis of the high reproductive potential and dispersal ability of many early-successional, disturbance-associated species (Harper 1977; Noble 1989), both studies demonstrated an effect of a logged stand on the seed bank of an adjacent forest edge. Very little, however, is known about how timber harvesting may affect seed banks of temperate deciduous forest edges.

Because seed-bank density and richness are most meaningful as relative measures, their description and assessment requires an analysis of the seed banks of both the opening and the adjacent intact forest. Contributions to the forest edge seed bank could come from resident species or from the seed rain originating in the recently harvested area, or from both residents and dispersers. It is known, for instance, that stands of edge plants are relatively dense and diverse compared with closed-canopy interior forest, with species characteristic of both early-successional forest and interior forest habitat types (Wales 1972; Ranney et al. 1981; Matlack 1994a; Landenberger 1999). Consequently, forest edge seed banks should be relatively dense and diverse, composed of species characteristic of both openings and interior forest, and should decline in density and richness with increasing distance from the opening. Description of such patterns of seeds in the forest soil seed bank would provide compelling evidence of an edge effect on an intact forest.

To date, no studies have described either the extent, shape, or species composition of the edge effect on seed-bank communities in the temperate mixed-mesophytic forest. We address the following questions: First, do the seed banks of recent clearcuts differ from adjacent closed-canopy forest seed banks in size and composition? Second, do the effects of clearcutting on the forest seed-bank stop at the edge of the clearcut, or is there evidence of an edge effect on the adjacent forest seed bank? Third, do adjacent forest edges with different aspects differ in seed-bank response to clearcutting? Finally, is there a pattern in seed density over distance for common species that are dispersed differently? Because many early-successional and weedy species have long periods of seed dormancy (Oosting and Humphreys 1940; Baskin and Baskin 1985; Nakagoshi 1985), alteration of the seed bank adjacent to clearcuts could influence species composition and diversity of forest vegetation long after clearcuts have regenerated to forest. Further, such impacts could mean that adjacent forest communities may respond to future disturbance in unexpected ways because of their altered seed pools.

Materials and methods

Study sites

We worked in and adjacent to two 6-ha clearcuts dating

from 1990. The cuts were generally rectangular, with straight edges along the northern and eastern boundaries, termed "south-facing edge" and "west-facing edge", respectively. Clearcuts and their adjacent edge zones (hereafter called "sites" and referred to specifically as "Rock Camp Run" and "Little Black Fork") were selected on the basis of similarity in overstory and understory vegetation type, age, aspect, and elevation. Both clearcuts had a precutting overstory dominated by sugar maple and red oak and had a precutting structure and species composition similar to the adjacent forest (Landenberger 1999). Sites were approximately 1 km apart and were located at approximately 900 m a.s.l. in Randolph County, West Virginia, in the unglaciated Allegheny Mountain section of Braun's (1950) mixed-mesophytic forest region. Clearcuts and the adjacent forest were surrounded by intact, mature second-growth deciduous forest, although both cuts were accessible by a logging road.

Clearcut vegetation was characterized by a spatially heterogeneous mixture of trees, shrubs, and herbs. Regenerating tree species included *Robinia pseudoacacia* L., *Prunus serotina* Ehrh., *Liriodendron tulipifera* L., *Acer pensylvanicum* L., and others. Common shrubs included *Aralia spinosa* L., *Sambucus canadensis* L., *Rubus* spp., and *Smilax* spp. Common herbs included *Potentilla simplex* Michx., *Phytolacca americana* L., *Eupatorium rugosum* Houtt., *Erechtites hieraciifolia*, *Oxalis stricta* L., *Carex* spp., *Dennstaedtia punctilobula* (Michx.) Moore, and other herbs, including a variety of spring ephemerals (Landenberger 1999).

Adjacent forest edges were characterized by the overstory species *Acer saccharum* (Marsh.), *Quercus rubra* L., *Tilia americana* L., *Liriodendron tulipifera*, and *Fagus grandifolia* Ehrh.. Forest shrubs and vines included *Lindera benzoin* (L.) Blume, *Sambucus*, *Rubus*, and *Aristolochia macrophylla* Lam., *Vitis* sp., and others. The edge herb layer was rich and varied (Landenberger 1999) and included species typical of the mixed-mesophytic forest (Braun 1950).

Seed-bank sampling

Samples were taken in March 1997. Beginning at the center of each clearcut, five sampling locations were selected by taking and following a random compass bearing a random distance between 0 and 100 m. At each location, four replicate samples (15 cm × 15 cm × 4 cm deep) were taken using a sharp knife. Five sampling locations, with four replicates per location, resulted in 20 samples per clearcut.

Sampling also occurred adjacent to clearcuts in west-facing and south-facing forest edges, the two aspects that we inferred would show the most pronounced edge effect on the seed bank (Matlack 1993). Edges were defined as 150 m × 45 m areas, bounded by the clearcut and terminating 45 m from the clearcut within the forest (0.67 ha). Edge boundaries were located at least 30 m from any clearcut corners. Linear borders reduced the variability in light patterns caused by an undulating or indistinct boundary and created a fixed linear distance from which to locate edge soil samples. Edges showed no evidence of overstory gaps caused by dominant or codominant canopy tree mortality.

Within edges, 10 transects were established parallel to the clearcut boundary at 5-m intervals beginning on the forest-clearcut boundary (0 m) to a distance of 45 m into the adjacent forest. Four randomly located samples (15 cm ×

15 cm × 4 cm deep) per transect were taken on all 10 transects, for a total of 40 soil samples per edge. South-facing and west-facing aspects were sampled identically, for a total of 80 edge samples per site and a total edge sample of 160 (2 sites × 2 edges per site × 40 samples per edge). Seed densities are expressed as seed number per sample (0.9 L) and, to compare between studies, seeds per square metre.

Seed germination

The germinable fraction of the seed bank, hereafter referred to as the seed bank, was quantified by seedling emergence. Samples were taken to the West Virginia University Plant Sciences greenhouse within 48 h and prepared for germination. Materials were sieved through a 1.0-cm mesh screen to remove rocks, twigs, and leaves. Larger material was rinsed and the rinse effluent captured to collect seeds that would otherwise have been lost. Soils were spread over a sterile medium of 75% peat and 25% sand (by volume) in plastic germination trays (30 cm × 30 cm × 8 cm), placed on greenhouse benches, and watered daily. Ten control trays were placed randomly across the bench to detect contamination. There was no germination in any control flat. Tray locations on the bench were randomized every 2 weeks, at which time plants were identified and removed; if identification was not possible, plants were maintained until identification was possible (some species were kept through the entire summer until they flowered). The experiment was terminated after 12 weeks on 15 June 1997. Species nomenclature follows Gleason and Cronquist (1991).

Data analysis

The composition of the seed bank was compared among locations within clearcuts, between clearcuts, between clearcuts and interior forest transects, between transects within edges, and between edges with contrasting aspects. The dependent variable measured on each sampling unit included seed-bank density, species richness, and Shannon–Weiner diversity (H' , Barbour et al. 1987).

The comparison of the two clearcuts was done in the context of a mixed-model nested analysis of variance, with random locations nested within sites (clearcuts). A two-way analysis of variance with replication was used to test for differences in mean density, mean richness, and mean diversity between the seed bank of clearcuts and the seed bank of interior forest transects. Means were analyzed from each clearcut sample location ($n = 4$ samples per location; 5 locations per clearcut), and for each 40- and 45-m transect on both aspects at each site ($n = 4$ samples per transect; 4 transects per site) to avoid pseudoreplication (Hurlbert 1984). Seed-bank density was log transformed to normalize residuals. Species richness and diversity did not require transformation.

A three-way mixed-model analysis of variance of the edge seed-bank data was used to analyze seed-bank density, richness, and Shannon–Weiner diversity as a function of site, edge aspect, and distance from clearcut boundaries ($n = 160$). Site was treated as a random factor, and F tests were made accordingly (Sokal and Rohlf 1998). Treating site as a random factor resulted in a more conservative set of F tests. Edge aspect, a nominal variable, and distance, a continuous

variable, were fixed factors. Seed-bank density was square-root transformed to normalize residuals. Species richness and diversity did not require transformation. Because of the conservative F tests applied in the factorial model, regression was also used to examine the pattern of seed density variation with distance within each edge.

Common species, defined as those occurring in all four edges and having mean values of 1.0 or greater per soil sample (>4 seeds·m⁻²), were grouped by mode of dispersal. Six dispersal categories were defined a priori: wind, adhesion, ingestion, ants, ejection, and none (gravity), using categories developed by Beattie and Culver (1981) and Matlack (1994b). There were no ant-, ejection-, or gravity-dispersed seeds fulfilling the category requirements, so these groups were eliminated from further analysis. This resulted in a total of nine common species, three each in the wind, adhesion, and ingestion categories. Wind-dispersed species included *Erechtites hieracifolia*, *Eupatorium rugosum*, and *Lobelia inflata*; adhesion-dispersed species included *Galium aparine* L., *Muhlenbergia schreberi* J.F. Gmelin., and *Panicum clandestinum* L.; ingestion-dispersed species included *Phytolacca americana*, *Rubus*, and *Vitis*. Data for each species were combined by distance from clearcut boundaries ($n = 10$ distance categories), and means of seed density were regressed on distance. The model having the best empirical fit was selected.

Results

Species composition of the seed bank

A high diversity of herbaceous taxa were documented in clearcut and edge seed banks (Table 1). Twenty species occurred in the seed bank of one clearcut, and 15 were documented in the other, with 13 species existing in common between the two clearcuts. Four of these were composites in the family Asteraceae (*Anaphalis margaritacea* (L.) Clark, *Erechtites hieracifolia*, *Eupatorium rugosum*, and *Taraxacum officinale* Weber.). Other herbaceous taxa shared between the clearcuts included *Galium aparine*, *Oxalis stricta*, *Phytolacca americana*, and *Lobelia inflata*. Few shrubs, vines, and trees were documented in the seed bank of either clearcut.

Forty-nine taxa were documented in the seed bank of edges. Fifteen occurred at all four edge locations, including the Asteraceae (*Anaphalis*, *Erechtites*, and *Eupatorium*), and three additional herbs (*Galium aparine*, *Lobelia inflata*, and *Phytolacca americana*). Forest herbs and grasses represented in all edge samples included *Sanicula gregaria* Bicknell, *Viola papilionacea* Pursh., *Carex laxiflora* Lam., and *Muhlenbergia schreberi*; shrubs and vines included *Rubus* spp., *Sambucus canadensis*, and *Vitis* spp. Of the seven tree species found in edge seed banks, only *Liriodendron tulipifera* was represented at all four edge locations. Three species, all composites in the Asteraceae, were represented in the two clearcuts and all four edges (*Anaphalis*, *Erechtites*, and *Eupatorium*) and represented 34% of the total sample.

Seed-bank variation within and between clearcuts

Seed-bank density varied markedly between locations within clearcuts ($F = 4.35$; $p = 0.001$) and between clearcuts

Table 1. Total number of seed germinations by species and life form for each sampling location.

Species	Family	Rock Camp clearcut	Little Black clearcut	Rock Camp		Little Black	
				West edge	South edge	West edge	South edge
Herbs							
<i>Amphicarpa bracteata</i> (L.) Fernald	Leguminosae	0	1	1	0	12	0
<i>Anaphalis margaritacea</i> (L.) Clark	Asteraceae	22	1	5	4	13	6
<i>Arisaema triphyllum</i> (L.) Schott	Aracea	0	0	0	7	6	0
<i>Aster divaricatus</i> L.	Asteraceae	8	0	0	5	0	0
<i>Cicuta maculata</i> L.	Umbelliferae	0	0	0	1	0	0
<i>Circaea alpina</i> L.	Onagraceae	10	0	0	0	0	0
<i>Cirsium</i> spp.	Asteraceae	0	0	0	0	16	0
<i>Erechtites hieraciifolia</i> (L.) Raf.	Asteraceae	286	65	102	9	48	72
<i>Eupatorium rugosum</i> (L.) Houtt.	Asteraceae	167	38	69	1676	100	131
<i>Dentaria diphylla</i> Michx.	Brassicaceae	2	6	9	2	0	0
<i>Dentaria laciniata</i> Muhl.	Brassicaceae	0	0	4	0	2	12
<i>Dicentra canadensis</i> (Goldie) Walp.	Fumariaceae	0	0	1	8	0	0
<i>Galium aparine</i> L.	Rubiaceae	9	5	60	249	29	12
<i>Geranium maculatum</i> L.	Geraniaceae	0	0	0	0	0	2
<i>Glechoma hederacea</i> L.	Lamiaceae	0	0	0	1	0	0
<i>Hypericum</i> spp.	Clusiaceae	759	14	1	1	0	1
<i>Impatiens pallida</i> Nutt.	Balsaminaceae	0	0	0	0	0	2
<i>Oxalis stricta</i> L.	Oxalidaceae	235	2	4	13	0	1
<i>Laportea canadensis</i> (L.) Wedd.	Urticaceae	3	1	6	39	0	2
<i>Lobelia inflata</i> L.	Campanulaceae	240	4	45	16	9	3
<i>Phytolacca americana</i> L.	Phytolaccaceae	80	12	118	119	5	6
<i>Pilea pumila</i> (L.) Gray	Urticaceae	54	0	6	73	0	0
<i>Plantago major</i> L.	Plantaginaceae	2	0	0	0	0	0
<i>Polystichum acrostichoides</i> Michx.	Onocleaceae	0	0	1	0	0	0
<i>Potentilla simplex</i> Michx.	Rosaceae	88	0	0	2	0	0
<i>Sanicula gregaria</i> Bicknell	Umbelliferae	0	0	5	14	3	3
<i>Sedum ternatum</i> Michx.	Crassulaceae	29	1	0	4	0	0
<i>Sonchus asper</i> (L.) Hill.	Asteraceae	0	1	0	79	0	3
<i>Solidago caesia</i> L.	Asteraceae	103	0	1	36	0	0
<i>Stellaria pubera</i> Michx.	Caryophyllaceae	2	0	0	2	1	0
<i>Taraxacum officinale</i> Weber.	Asteraceae	99	1	1	1	0	0
<i>Thalictrum dioicum</i> L.	Ranunculaceae	0	0	2	0	0	0
<i>Viola papilionacea</i> Pursh.	Violaceae	14	21	29	30	52	22
Total number of herb germinations		2212	173	470	2391	296	278
Grasses							
<i>Carex laxiflora</i> Lam.	Cyperaceae	49	20	30	3	12	15
<i>Carex plantaginea</i> Lam.	Cyperaceae	0	0	2	0	0	0
<i>Muhlenbergia schreberi</i> J.F. Gmelin.	Poaceae	17	14	38	43	521	212
<i>Panicum clandestinum</i> L.	Poaceae	45	0	9	6	719	92
Total number of grass germinations		111	34	79	52	1252	319
Shrubs							
<i>Aralia spinosa</i> L.	Araliaceae	0	0	2	6	0	1
<i>Ribes rotundifolium</i> Michx.	Grossulariaceae	0	0	0	1	0	0
<i>Rubus</i> spp.	Rosaceae	3	26	6	37	12	34
<i>Sambucus canadensis</i> L.	Caprifoliaceae	37	1	2	5	1	2
<i>Smilax rotundifolia</i> L.	Smilacaceae	0	1	0	0	0	0
Total number of shrub germinations		40	28	10	49	13	37

Table 1 (concluded).

Species	Family	Rock Camp clearcut	Little Black clearcut	Rock Camp		Little Black	
				West edge	South edge	West edge	South edge
Vines							
<i>Aristolochia macrophylla</i> Lam.	Aristolochiaceae	0	0	6	2	0	3
<i>Parthenocissus quinquefolia</i> (L.) Planchon.	Vitaceae	0	0	0	2	0	0
<i>Vitis</i> spp.	Vitaceae	2	35	79	65	17	13
Total number of vine germinations		2	35	85	67	17	16
Trees							
<i>Acer saccharum</i> Marshall.	Aceraceae	0	0	3	3	0	0
<i>Betula lenta</i> L.	Corylaceae	0	0	0	1	1	0
<i>Liriodendron tulipifera</i> L.	Magnoliaceae	0	19	3	12	25	20
<i>Magnolia acuminata</i> (L.) L.	Magnoliaceae	0	0	0	0	0	1
<i>Prunus serotina</i> Ehrh.	Rosaceae	0	0	4	4	2	0
<i>Robinia pseudoacacia</i> L.	Leguminosea	0	2	0	0	6	0
<i>Quercus rubra</i> L.	Fagaceae	0	0	0	0	0	1
Total number of tree germinations		0	21	10	20	34	22
Total germinations of all species by location		2365	291	654	2579	1612	672

($F = 23.99$; $p = 0.001$). Seed-bank richness also varied between locations within clearcuts ($F = 3.12$; $p = 0.05$) and between clearcuts ($F = 5.62$; $p = 0.01$), while Shannon–Weiner diversity varied only between locations within clearcuts ($F = 3.84$; $p = 0.003$). The Rock Camp Run clearcut had a higher mean seed-bank density (525.7 vs. 64.7 seeds·m⁻²) and richness (8.0 vs. 5.3). Rock Camp Run had over twice the density of graminoid seeds (24.6 vs. 9.1 seeds·m⁻²) and over six times the density of seeds in the Asteraceae (152 vs. 23.5 seeds·m⁻²). Additionally, seed densities of the eight species that were unique to Rock Camp Run averaged 17 seeds·m⁻², indicating a wide distribution in the seed bank throughout the clearcut compared with a mean of only 2 seeds·m⁻² of the five species restricted to the Little Black Fork clearcut, indicating the relative rarity of that site's unique species. Of the eight species restricted to the Rock Camp Run clearcut, only two were represented in a single sample (*Panicum clandestinum* and *Plantago major* L.). Conversely, three of the five species restricted to the Little Black Fork clearcut were represented in a single sample.

Seed-bank variation between clearcuts and forest

There was little consistent pattern in density, richness, or diversity between clearcut and interior forest seed banks. Although overall the seed bank at Rock Camp Run was larger ($F = 29.32$; $p < 0.001$) and had a higher richness than Little Black Fork ($F = 6.60$; $p < 0.022$), clearcuts did not have a larger seed bank than the forest stands. The only consistent pattern between clearcut and interior forest seed banks was that, of common species, the annual *Erechtites* had a higher seed density in clearcuts, and the perennials *Eupatorium* and *Muhlenbergia* had a higher density in the forests.

Seed-bank variation in edge

Edges had 19 species that were not represented in clearcuts. In contrast with the relationship between the two clearcut seed banks, seed-bank density did not differ between edge sites. Most importantly, seed-bank density de-

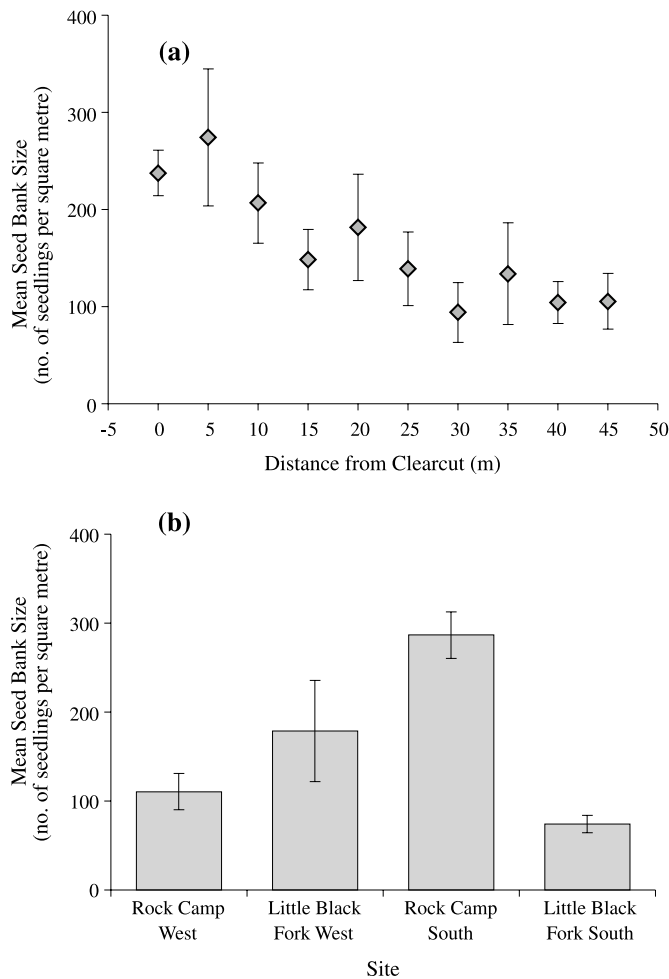
clined significantly with distance from clearcut boundaries (Fig. 1a), and this pattern was not dependent upon site or aspect (no site × distance or site × aspect interaction; Table 2). Had the more liberal model been applied (if site was not a random factor), the aspect × distance and site × distance interactions would have been significant, however. The relationships between aspect and distance were further examined using regression.

Aspects differed at the two sites (a site × aspect interaction, $p < 0.001$). At the Rock Camp Run site, the south-facing aspect had approximately twice the mean seed density of the west-facing aspect (286.4 south vs. 132.3 seeds·m⁻² west) (Fig. 1b). Much of the difference was explained by the mean density of *Eupatorium* seeds at the south-facing aspect (186.0 vs. 67.5 seeds·m⁻²). The reverse was true at the Little Black Fork site. Here, *Eupatorium* was common in the seed bank of both aspects; the difference was largely explained by the high mean density of the two grasses, *Panicum* and *Muhlenbergia*, on the west-facing aspect.

Species richness did not vary significantly with site, aspect, or distance, but like seed density, did demonstrate a significant site × aspect interaction ($p < 0.001$). The Rock Camp Run south-facing aspect had a higher mean richness than Rock Camp Run west (south mean, 8.0; west mean, 4.7), while the opposite was true at Little Black Fork (south mean, 4.8; west mean, 5.3). Diversity did not differ by any single treatment effect, nor did it demonstrate an interaction.

Separate linear regressions of seed-bank density on distance were highly significant on both west-facing aspects, but not significant on south-facing aspects (Fig. 2). The most common species in edges were *Eupatorium rugosum*, *Erechtites hieraciifolia*, and *Lobelia inflata* in the wind group, *Galium aparine*, *Panicum clandestinum*, and *Muhlenbergia schreberi* in the adhesion group, and *Phytolacca americana*, *Vitis* sp., and *Rubus* sp. in the ingestion group. Distance explained a significant amount of the variation in two of the three common wind-dispersed species and one of the ingestion-dispersed species (Fig. 3). Seed densities of both

Fig. 1. Mean seed-bank size (no. of seedlings per square metre) as a function of (a) distance from clearcut boundary and (b) aspect at each site. Error bars represent one standard error of the mean.



Erechtites and *Lobelia* were best described by a logarithmic model. Of the wind-dispersed species common in each edge, *Eupatorium* ($R^2 = 0.54$, $p = 0.07$, not shown) demonstrated a higher average seed density at 45 m from clearcuts (mean = 45.2 seeds·m⁻²) than the seed density of both *Lobelia* and *Erechtites* at the clearcut boundary (Figs. 3a and 3b). The three graminoid adhesion-dispersed species demonstrated no significant effect of distance on seed density. In the ingestion group, *Vitis* increased linearly with distance (Fig. 3c).

Discussion

Temperate deciduous forest seed banks are frequently dominated by early-successional species (Pickett and McDonnell 1989). This pattern of dominance by disturbance-associated colonizers accurately characterizes the seed bank of both clearcuts and their associated south- and west-facing forest edges. Six years after logging, the seed bank at each location was dominated by native “weedy” herbs (Radosevich 1998), including *Erechtites*, *Eupatorium*, *Phytolacca*, *Panicum*, *Muhlenbergia*, and *Carex*, species characteristic of recently disturbed mixed-mesophytic forest and edges (Braun 1950).

Erechtites and *Eupatorium*, two examples of common native opportunists (Baskin and Baskin 1996; Landenberger and Ostergren 2002), were distributed throughout each clearcut, although their average densities were five times higher at Rock Camp Run. The between-site variation demonstrated by these two species was typical of variation in patterns of relative seed density and species richness of other herbs and grasses at the two clearcuts. Yet forest stand type, harvest method, and harvest timing were the same for both clearcuts and provide unlikely explanations for higher richness and abundance at Rock Camp Run. Higher soil pH could, in part, explain Rock Camp Run’s larger average seed bank (Brown and Oosterhuis 1981), although differences in the preclearcut seed bank may also have influenced post-clearcutting seed densities. Considerable variation in herbaceous and woody species richness and abundance at the forest stand spatial scale (1–10 ha) is characteristic of mixed-mesophytic forests (Braun 1950; Muller 1981), a pattern that would reasonably be expected to extend to the early-successional community seed bank.

The size and richness of clearcut seed banks was no different, on average, from that of the most distant transects sampled under 85-year-old, mid-successional interior forest stands. The majority of seeds in the seed bank of the interior forest were species associated with forest borders, canopy gaps, and other types of temporary openings (Marks 1983). A reasonable explanation for the similarity between these two contrasting environments is that interior forest seed banks have experienced significant seed dispersal from either clearcuts or from vegetation growing immediately adjacent to the clearcuts, although it is reasonable to expect that seeds came from both locations (Clark et al. 1999; Levin et al. 2003). Seed dispersal from clearcuts and forest edges (De Foresta and Prevost 1986; Saulei and Swaine 1988) offers an ecologically relevant exception to our current understanding that seed input into mid-successional temperate forest seed banks is low following canopy closure, when early-successional species are rare or absent (Pickett and McDonnell 1989; Hyatt 1996).

Although clearcuts themselves are discrete, their effect on adjacent forest seed banks may not be, and may depend, in part, on edge aspect. One such effect is the seed shadow created in part by common early-successional herbaceous species in the clearcut. Our findings of a dramatic decline in seed-bank density with increasing distance from west-facing edges provides evidence for such a claim in mixed-mesophytic forests. In contrast, south-facing aspects showed no decline across the edge zone, suggesting that either the seed-shadow is absent on south-facing edges or that declining seed density occurs beyond 45 m from the clearcuts. The latter case is unlikely, however, because any decline in seed density would tend to occur near the clearcut for wind-dispersed species that dominated the seed bank (Green and Johnson 1989; Clark et al. 1999).

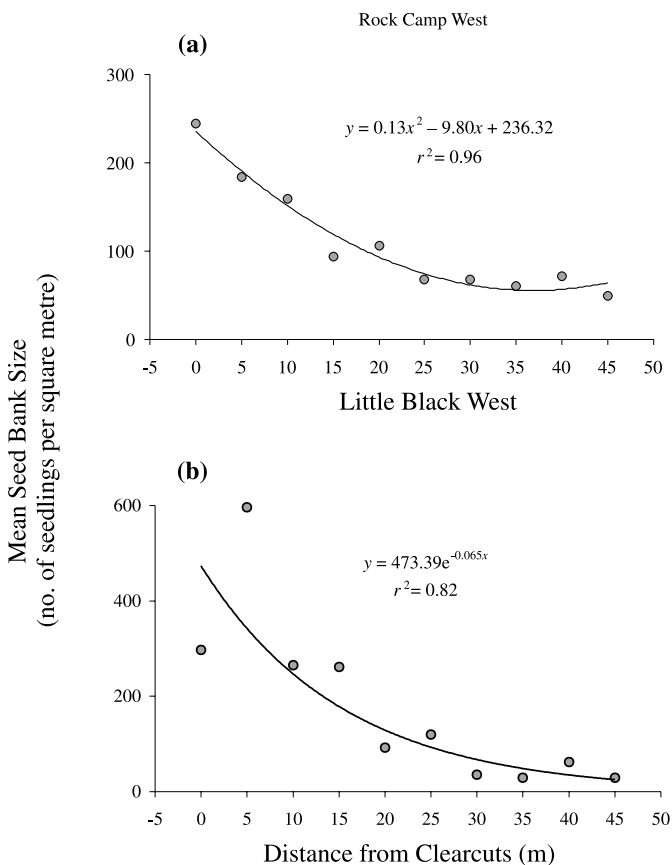
Given the longevity of seeds of many early-successional temperate forest species (Pickett and McDonnell 1989), effects on the forest seed bank from adjacent clearcutting may influence the composition and structure of forest flora in edges long after the adjacent clearcuts have regenerated. Furthermore, because stands adjacent to clearcuts are particularly prone to canopy disturbances and gap formation

Table 2. Three-way factorial mixed-model analysis of variance of seed-bank size.

Source of variation	df	SS	MS	F ratio	p value
Site	1	2.62	40.46	0.02	0.904
Aspect	1	40.46	40.46	0.35	0.658
Distance	1	112.09	112.09	22.38	<0.001
Site × aspect	1	113.89	113.89	22.67	<0.001
Site × distance	1	26.01	26.01	1.73	0.414
Aspect × distance	1	102.95	102.95	6.85	0.232
Site × aspect × distance	1	15.03	15.03	3.00	0.085
Error	152	761.32	5.01		

Note: The two sites are the forest stands on south-facing and west-facing edges immediately adjacent to Rock Camp Run and Little Black Fork clearcuts. Clearcut seed banks were not considered in this analysis. SS, sum of squares; MS, mean square.

Fig. 2. Best-fit regressions of mean seed-bank size (no. of seedlings per square metre) as a function of distance from clear-cut forest boundaries on the west-facing edges of (a) Rock Camp and (b) Little Black sites. Nonsignificant regressions on the south-facing edges of the two sites are not shown.



(DeWalle 1983), disturbed forest edges provide substantial habitat for colonization of early-successional trees (Kupfer 1996; Kupfer and Runkle 1996; Knapp and Canham 2000) and herbs (Goldblum 1997; Goldblum and Beatty 1999; Landenberger 1999) soon after clearcutting. Depending on species-specific germination requirements and longevity, seeds would remain dormant until a gap forms, creating conditions necessary for germination, growth, reproduction, and further dispersal (Mladenoff 1990; Nakagoshi 1985; Vasquez-Yanes and Orozco-Segovia 1994).

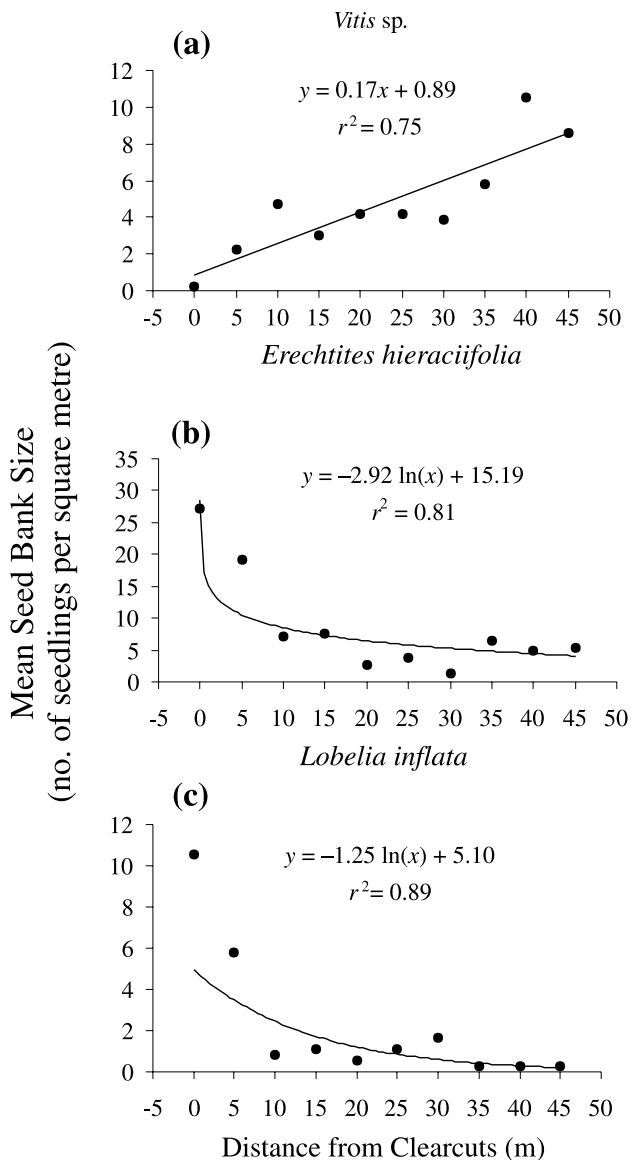
Consequently, the seed-bank edge effect may have both immediate and long-term consequences for edge communities, increasing the abundance of certain species near clearcuts, while others remain unaffected. Such impacts are most likely to occur on west-facing edges and in the more common seed-bank species. For these, seed densities tended to decline over distance from clearcuts, albeit at different rates. Wind-dispersed species, in particular, demonstrated that adjacent clearcutting influences seed densities over a range of distances, but particularly near the clearcut boundary. *Erechtites* and *Lobelia* showed rapid declines in seed density from 0 to 10 m into the forest, indicating that either dispersal is limited by the edge canopy or that rates of reproduction beyond 10 m from the forest boundary are very low. The underlying mechanisms for the consistent and strong patterns of decline in seed densities with increasing distance from clearcuts is likely a combination of limited dispersal into the adjacent forest and low seed production across the forest edge (Landenberger and Ostergren 2002). Conversely, the common vine *Vitis* increased with increasing distance from clearcuts, suggesting that it may be more abundant in interior forest stands.

If these or similar patterns of altered seed banks in forest stands adjacent to clearcuts are replicated, our understanding of the spatial patterns of forest flora near clearcuts, and perhaps other temporary openings, such as occur in insect defoliations, ice storms, or windthrow events, will improve significantly. Given that forest edge habitat is rapidly increasing in the eastern US as well as in forests throughout the world (Murcia 1995), this information would add considerably to our understanding of forest dynamics in an increasingly important forest habitat type.

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Fig. 3. Significant best-fit regressions of mean seed-bank size (no. of seedlings per square metre) for common species. Common species are defined as those occurring in all four edge locations and having mean values of ≥ 1.0 seeds per sample (≥ 4.0 seeds·m⁻²). *Erechtites hieraciifolia* and *Lobelia inflata* are wind-dispersed species, and *Vitis* is an ingestion-dispersed species. Nonsignificant ($p > 0.05$) regressions of other common species are not shown.



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