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Soil seed bank dynamics in relation to topographic position of a mixed-deciduous forest in southern New England, USA

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Abstract

We examined the floristic significance of soil seed banks in relation to valley, midslope and ridge sites in a 70–90-year old forest in northeastern Connecticut. A-horizon mineral soils were collected to 5 cm depth in the early spring from forest understory sites across the topography. Samples from each of the sites were exposed to full sun within a greenhouse. Records of germination were made at regular intervals over a 60-day period. These showed significant differences among sites in number of species and total number of germinants. Greatest numbers of species and germinants were recorded from valley sites and these progressively declined from midslope to ridgetop. Twenty-five different species were identified. Species were grouped into growth habits – graminoids, herbs, shrubs, trees, and vines. Over 61% of all germinants across all sites were graminoids. Seventy-four percent of all germinants in the valley sites were graminoids, with over 93% of them represented by two sedge species, *Carex glaucodea* and *C. lupulina*. On the ridgetop sites graminoids were more evenly distributed among six different species. The percentage in each growth habit changed rank across topographic position with germinants of graminoids and trees most abundant on valley sites; herbs, on midslopes, and shrubs, on ridgetops. All germinants, except for those of the trees, *Carex* spp., and two herb species were weedy species that were not characteristic of the existing vegetation. Germinants of the trees, *Carex* spp., and herbs that were characteristic of the existing vegetation were mostly confined to soils from the valley sites. Two weedy herbs, *Plantago major* and *Verbascum thapsus*, are exotic introductions that originally came from Europe. Only one vine, *Vitis aestivalis*, from a midslope site germinated. Species diversity is higher on midslope sites than valleys and ridgetops. The significance of these findings in relation to site productivity and disturbance history is discussed. © 1998 Elsevier Science B.V.

Keywords: Buried seed; *Carex* spp.; Connecticut; Forest understory; Land use; Slope position; regeneration

1. Introduction

Soil seed banks have been defined as those seeds that can remain dormant for a period of time in the surface soil until their germination is triggered by an

environmental change (Grime, 1989; Simpson et al., 1989). The number of soil seed bank studies that have been done in moist temperate deciduous forests are fewer than in other ecosystems. For these kinds of forests past studies have demonstrated the importance of buried seed for regeneration following infrequent but severe disturbances (Marks, 1974). Seed banks are

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rich during early stages of stand development or just after agricultural abandonment (Oosting and Humpreys, 1940; Livingston and Alessio, 1968; Roberts et al., 1984). The amount of seeds in soil progressively declines with the development of close-canopied forests but increases can occur when stands enter the old-growth stage (as defined after Oliver and Larson, 1995) when the forest canopy begins to break up (Olmstead and Curtis, 1947; Marquis, 1975; Moore and Wein, 1977; Bicknell, 1979; Nakagoshi, 1985; Mladenoff, 1985). All these studies have demonstrated that the soil seed banks of these forests include mostly early successional ‘intolerant’ species (e.g. *Betula* spp., *Carex* spp., *Juncus* spp., *Prunus* spp., *Rubus* spp.) that differ from the existing forest composition (Oosting and Humpreys, 1940; Hill and Stevens, 1981; Nakagoshi, 1985).

No studies in these moist temperate forest regions have documented how the amount and composition of the soil seed bank vary with topography across the landscape of mature closed-canopied forest. This kind of information can provide a better understanding of the ecological role of seed banks and their contribution to vegetation establishment after disturbance on different sites. Differences in the amounts of viable seeds among sites suggest varying abilities of forests to recover after severe disturbance.

The objective of this study was to document the soil seed bank dynamics of mid-successional moist temperate forest in relation to ridgetop, midslope, and valley sites situated on glacial till topography. We hypothesized that valley sites might have greater numbers and species of germinants than ridgetop sites. Evidence for this had been deduced from observations that weed abundance (particularly of early succes-

sional herbs and graminoids) after canopy disturbance was much greater on valley sites than ridgetop sites.

2. Study site

The experiment was conducted at the 3160 ha Yale–Myers Forest in northeastern Connecticut (41°55′N, 72°05′W). The topography of the forest is undulating with parallel ridges and valleys that range between 200 and 350 m above msl. Sites were located in 70–90-year old mixed deciduous stands that had arisen from advanced regeneration released by removal of old-field pine. The pine had colonized abandoned pastures after 1850.

Nine sites were selected, three from each topographic position (valley, midslope, ridgetop). All sites were stony silty loam soils derived from thin glacial tills that were classified as Typic and Lithic Dystrachrepts (USDA Soil Conserv. Serv., 1981). The depth to bedrock increased with progression from ridge to valley. Sites had all been previously used for pasture but none showed an Ap horizon indicating tillage. Samples were collected from the surface mineral soil (0–5 cm depth) of each of the ridgetop, midslope and valley sites to measure soil carbon, soil nitrogen and available aluminum (Al), potassium (K), magnesium (Mg) and calcium (Ca). Available soil nutrients were extracted using a neutral salt (ammonium chloride) following standard procedures by Suarez (1996). Valley sites were significantly higher than midslope and ridgetop sites in percentage of carbon, nitrogen, potassium, magnesium and calcium (Table 1). Ridgetop and midslope sites were significantly higher in amounts of aluminum than the valley sites.

Table 1

Soil carbon, soil nitrogen and available aluminum (Al), potassium (K), phosphorous (P), magnesium (Mg) and calcium (Ca) for surface mineral soil (0–5 cm depth) of ridgetop, midslope and valley sites collected from the same sample locations as soil containing the buried seed

	Sites		
	Valley	Midslope	Ridgetop
Carbon (%)	16.07 a	9.15 b	9.34 b
Nitrogen (%)	1.06 a	0.51 b	0.58 b
Al (mg/Kg)	142.42 b	335.58 a	370.58 a
K (mg/Kg)	295.25 a	138.50 b	111.16 b
Mg (mg/Kg)	395.05 a	49.33 b	27.00 c
Ca (mg/Kg)	1525.08 a	521.00 b	521.00 b

Note: Letters qualitatively indicate significant differences among sites according to Duncan’s multiple range test ($P < 0.05$).

Table 2

Overstorey basal area of forest sites for all woody plants greater than 2.5 cm at diameter breast height (dbh). Fixed area sample plots (8 m radius) were positioned at each point around which buried seed soil samples had been taken

Species	Sites		
	Valley	Midslope	Ridgetop
White oaks ^a	—	1.75	3.29
Red oaks ^b	5.95	14.93	8.99
Upland hickories ^c	—	0.53	9.95
Shagbark hickory	3.62	1.78	1.72
Sugar maple	6.06	1.16	—
Red maple	2.04	2.30	0.04
Tolerant birches ^d	5.64	1.51	—
Tulip poplar	5.87	—	—
White ash	5.34	0.10	0.20
Eastern hemlock	1.08	—	1.51
Other canopy trees ^e	0.07	0.88	0.15
Understorey treelets ^f	0.29	0.04	0.02
Total overstorey			
Basal area (m ² /ha)	35.96 g	24.98 h	25.87 h

Note: Letters in a row qualitatively indicate significant differences in total overstorey basal area (m²/ha) among sites according to Duncan's multiple range test ($P < 0.05$).

^aChestnut oak (*Q. prinus*); white oak (*Q. alba*).

^bRed oak (*Q. rubra*); black oak (*Q. velutina*).

^cPignut hickory (*C. glabra*); mockernut hickory (*C. tormentosa*).

^dBlack birch (*B. lenta*); yellow birch (*B. alleghaniensis*).

^eAmerican elm (*Ulmus americana*); white birch (*B. papyrifera*); white pine (*Pinus strobus*).

Ridgetop sites had an overstorey of white oaks (chestnut oak, *Quercus prinus* L.; white oak, *Q. alba* L.) and red oaks (red oak, *Quercus rubra* L.; black oak, *Q. velutina* Lam.), with a subcanopy of more shade tolerant hickories (pignut hickory, *Carya glabra* [Mill] Sweet.; mockernut hickory, *C. tormentosa* (Poir.) Nutt.) (see Table 2) and a groundstorey primarily of sedges (*Carex* spp.) and lowbush blue-berry (*Vaccinium angustifolium* Ait.). There was a noticeable absence of understorey tree species.

Midslope sites had an overstorey of red oak (*Q. rubra* L.) and black birch (*Betula lenta* L.) with a subcanopy and understorey of maples (sugar maple, *A. saccharum* Marsh.; red maple, *A. rubrum* L.) and shagbark hickory (*Carya ovata* (Mill) K. Koch). Wild sarsaparilla (*Aralia nudicaulis* L.), Canada mayflower (*Maianthemum canadense* Desf.), starflower (*Trientalis borealis* Raf.) and hay-scented fern (*Dennstaedtia punctiloba* (Michx.) Moore) were the dominant groundstorey plants on the midslope.

Valley sites had an emergent canopy of tulip poplar (*Liriodendron tulipifera* L.), white ash (*Fraxinus americana* L.) and red oak, a main canopy of sugar maple and shade tolerant birch (black birch; yellow birch, *B. alleghaniensis* Britton), a subcanopy of sugar maple and eastern hemlock (*Tsuga canadensis* (L.) Carr.), and an understorey of ironwood (*Carpinus caroliniana* Walt.) and witchhazel (*Hamamelis virginiana* L.). The groundstorey included advanced regeneration of sugar maple, herbs such as violets (*Viola* spp.), wood anemone (*Anemone thalictroides* L.), and jack-in-the-pulpit (*Arisaema triphyl- lum* (L.) Schott.), and maidenhair-fern (*Adiantum pedatum* L.) and cinnamon fern (*Osmunda cinnamo- nea* L.).

3. Methods

Four surface soil samples were collected beneath closed-canopied stands on each of the nine sites. Sample positions were selected from around single points by randomly choosing a distance (less than 5 m) and an azimuth. For each soil sample the litter layer was scraped away and the surface mineral soil (A horizon) was collected to a depth of 5 cm in a 10 cm × 10 cm area. Soil from each sample was added in equal volumes to two trays of dimensions 10 cm × 20 cm with 5 cm depth. Trays were first filled half way with sterilized sand. Seeds in the soil samples were allowed to germinate under full sun and moist conditions in a greenhouse. There were, therefore, a total of 24 trays (three replicate sites × four samples/site × two trays/sample) that represented a single topographic position. All trays were maintained at field capacity by watering. Germination was recorded every third day over a 60-day period (1 June–1 August 1995). When the seedlings were large enough to be recognized, a voucher specimen was collected and pressed for each species, all other individuals were recorded by species and then discarded. Germinants were counted for each species, by habit (herb, graminoid, vine, shrub, tree) and by topographic position. Numbers of germinants were compared for all species using the Kruskal–Wallis test (Proc Npar1way, SAS Institute, 1988). Diversity statistics were calculated separately for each topographic position for herbs, grasses/sedges, shrubs, trees, and all species

combined. Simpson's (1989) diversity (D) and equability (E) were calculated as (Begon et al., 1986)

$$D = \left[\sum_{i=1}^S \left(\frac{n_i}{N} \right)^2 \right]^{-1}, \quad E = \frac{D}{S}$$

where S is the number of species observed, N the total number of individuals, and n_i is the number of individuals of species i . Shannon–Weaver diversity (H) and equality (J) were calculated in the following way as described by Begon et al. (1986):

$$H = - \sum_{i=1}^S \frac{n_i}{N} \ln \frac{n_i}{N}, \quad J = \frac{H}{\ln S}$$

4. Results

A total of twenty-five species were recorded as germinants from soils collected from all the sites. The majority of the species comprised herbs (23%) and graminoids (61%) (Table 3). Most germinants of tree species were *Betula* spp. that were found on all sites. Number of germinants of paper birch (*B. papyrifera* Marsh) increased with progression from valley to midslope to ridgetop sites, while the reverse was the case for black birch. Germinants of other tree species were mesic-loving (tulip poplar, eastern hemlock) and restricted to valley sites. Graminoids, particularly *Carex* spp., predominated on the valley sites, herbs predominated on midslope sites, and shrubs predominated on ridgetop sites. All species combined, the sedges (*Carex glaucoidea* Tuckerm.; *C. lupulina* Muhl.) represented over 59% of all germinants.

Only the trees, the *Carex* spp., and two species of herbs, represented species that were presently on the sites. The two species of herbs, meadow violet (*Viola papilionacea* Pursh.) and meadow-rue (*Thalictrum polygamum* Muhl.), are restricted to forest understories of mesic sites. Interestingly, *Carex* spp. are one of the dominant components of the existing groundstorey of the upland forest (ridge, midslope), but the greatest number of germinants from the soil samples are from the valley sites. Germinants of all other species are considered weeds of disturbed sites of which two, mullein (*Verbascum thapsus* L.), and plantain (*Plantago major* L.) are exotic introductions from Europe. Germinants of mullein and plantain

appeared only on the midslope and ridgetop sites. Germinants of only one species of vine was recorded (wild grape, *Vitis aestivalis* Michx.) and they were restricted to midslope sites.

Diversity statistics reveal that overall, there are greater numbers of species with greater measures of diversity on the midslope site than valleys and ridgetop sites (Table 4). Diversity and equability statistics for herbs were highest on midslope sites but other growth habits showed no strong trends across sites.

5. Discussion

The species richness, as measured by total number of species, for our study (25 taxa) was high compared to other studies. Northern hardwood forests of New Hampshire, Maine and the Allegheny forests of Pennsylvania recorded three taxa (Bicknell, 1979), 8–10 taxa Olmstead and Curtis (1947) and 6–7 taxa (Marquis, 1975), respectively.

One reason for this might be related to differences in past land use. Our forests, like most in southern New England (Raup, 1966) originated from pasture that was abandoned by farmers more than 100 years ago. Forests in northern New England and the Alleghenies of Pennsylvania were usually on lands that were repeatedly cutover for timber, and used for charcoal and wood chemical production, but were never actually cleared and farmed for a period of time. The fact that the lands were never converted to pasture perhaps prevented the establishment of many of the weedy species common to early seral habitats. This is supported by the buried seed bank studies conducted by Livingston and Alessio (1968) in central Massachusetts. The number of species recorded in their studies of 5–80-year old pine plantations that were established on old fields ranged between 21 to 25. Also, further west in Ohio, Roberts et al. (1984) recorded 21 species from a 90-year-old maple–elm stand that originated from an abandoned field. Another reason is that the colder Northern hardwood forests and their Alleghany variant are less species rich than the more maritime forests of southern New England.

Total numbers of germinants in our study were comparable with other second growth oak–hickory forests of eastern North America that had similar land

Table 3
Density (number/m²) of germinants for each site by species and growth habit

Species by group	Family	Valley	Midslope	Ridge	Sig
<i>Herbs</i>					
<i>Bidens aristosa</i> (Michx.) Britt.	Compositae	0	92	25	**
<i>Desmodium nudiflorum</i> (L.) DC	Fabaceae	4	0	0	
<i>Draba reptans</i> (Lam.) Fern.	Brassicaceae	0	25	0	
<i>Houstonia longifolia</i> Gaertn.	Rubiaceae	25	67	0	**
<i>Krigia virginica</i> (L.) Willd.	Asteraceae	8	158	0	**
<i>Potentilla canadensis</i> L.	Rosaceae	42	83	75	***
<i>Plantago major</i> L.	Plantaginaceae	0	8	0	
<i>Thalictrum polygamum</i> Muhl.	Ranunculaceae	4	0	0	
<i>Verbascum thapsus</i> L.	Scrophulariaceae	0	33	17	*
<i>Viola papilionacea</i> Pursh.	Violaceae	108	17	17	**
Total number of herbs		191 b	483 a	134 b	***
<i>Graminoids</i>					
<i>Carex brevior</i> (Dewey) Mackenzie	Cyperaceae	58	17	42	**
<i>Carex glaucoidea</i> Tuckerm.	Cyperaceae	783	333	242	**
<i>Carex lupulina</i> Muhl.	Cyperaceae	308	233	33	***
<i>Carex rosea</i> Schk.	Cyperaceae	0	8	8	
<i>Hypoxis hirsuta</i> L. (Cov.)	Amarylidaceae	17	0	0	
<i>Panicum auburne</i> Ashe.	Poaceae	0	0	8	
<i>Panicum lanuginosum</i> Ell.	Poaceae	0	0	25	
Total number of grasses		1166 a	591 b	358 c	***
<i>Shrubs</i>					
<i>Amelanchier sanguinea</i> (Pursh.)DC	Rosaceae	0	8	0	
<i>Rubus allegheniensis</i> Porter	Rosaceae	25	42	92	**
<i>Rubus idaeus</i> L.	Rosaceae	17	0	42	**
Total number of shrubs		42 a	50 b	134 a	***
<i>Trees</i>					
<i>Betula lenta</i> L.	Betulaceae	142	108	8	***
<i>Betula papyrifera</i> Marsh.	Betulaceae	8	17	25	**
<i>Liriodendron tulipifera</i> L.	Magnoliaceae	8	0	0	
<i>Tsuga canadensis</i> (L.) Carr.	Pinaceae	8	0	0	
Total number of trees		166 a	125 b	33 c	***
<i>Liana</i>					
<i>Vitis aestivalis</i> Michx.	Vitaceae	0	8	0	
Total number of germinants		1565 a	1257 b	659 c	***

Row entries followed by the same letter are not significantly different at $P < 0.05$.

use histories. For example, the study by Oosting and Humphreys (1940) in the Piedmont had approximately 3318 germinants per m² for an 85-year old stand, but this number declined to 1181 for older forest (>200 years). Also, the old field pine plantations studied by Livingston and Allesio (1968) recorded between 1248 and 5014 germinants per m².

Second-growth Northern hardwood forests of New Hampshire and the Alleghenies had germinant densities per m² of 117 (Bicknell, 1979) and 30–61

(Marquis, 1975), respectively. Studies of old growth hemlock–maple–birch forests in Michigan recorded only 2–4 germinants per m², while for Maine old growth sugar maple–beech had 0.17–1.50 per m². The overall trends among these different studies suggest that buried seed in mature or old-growth forest is generally small, but increases with degree and kind of disturbance. The cutover forests, therefore, have moderately sized buried seed banks, and the second growth forests that originated after the land had been

Table 4
Diversity statistics by growth habit and site

	Valley	Midslope	Ridge
<i>Herbs (10)</i>			
Number of species	6	8	4
Number of site restricted species	2	2	0
Simpson's <i>D</i>	2.579	4.978	2.629
Simpson's <i>E</i>	0.430	0.622	0.657
Shannon–Weaver <i>H</i>	1.215	1.781	1.164
Shannon–Weaver <i>J</i>	0.678	0.857	0.840
<i>Graminoids (7)</i>			
Number of species	4	4	6
Number of site restricted species	1	0	2
Simpson's <i>D</i>	1.911	2.010	2.061
Simpson's <i>E</i>	0.478	0.528	0.344
Shannon–Weaver <i>H</i>	0.830	0.877	1.091
Shannon–Weaver <i>J</i>	0.599	0.633	0.609
<i>Shrub species (3)</i>			
Number of species	2	2	2
Number of site restricted species	0	0	0
Simpson's <i>D</i>	1.930	1.368	1.755
Simpson's <i>E</i>	0.965	0.684	0.878
Shannon–Weaver <i>H</i>	0.675	0.440	0.622
Shannon–Weaver <i>J</i>	0.974	0.634	0.897
<i>Tree species (4)</i>			
Number of species	4	2	2
Number of site restricted species	2	0	0
Simpson's <i>D</i>	1.354	1.301	1.580
Simpson's <i>E</i>	0.338	0.654	0.790
Shannon–Weaver <i>H</i>	0.572	0.398	0.554
Shannon–Weaver <i>J</i>	0.413	0.574	0.799
<i>All species (25)</i>			
Number of species	14	17	16
Simpson's <i>D</i>	3.278	6.983	5.435
Simpson's <i>E</i>	0.205	0.411	0.388
Shannon–Weaver <i>H</i>	2.230	2.254	1.728
Shannon–Weaver <i>J</i>	0.845	0.796	0.623

Total number of species by growth habit are given in parentheses.

farmed for a period have the greatest amount of buried seed (Pickett and McDonnell, 1989). Studies of old fields themselves showed that this period of succession has the highest numbers of buried seed compared to other sites (Livingston and Alessio, 1968).

In our study, nine of the 25 species were growing in the present forest. Four of these species were trees, of which the majority of germinants were either paper or black birch. The germinants of black birch, with tulip poplar and eastern hemlock predominated in soils from the valley site. This result corresponds with their

known autecology of shade-tolerant, mesic-loving species (Burns and Honkala, 1991). This is dramatically illustrated by trends in current overstorey basal area distribution across the sites for the tolerant birches (Table 2).

The paper birch showed the reverse trend with an increase in number of germinants with progression upslope from valley, to midslope, to ridge. The lower overstorey basal area at upslope sites (Table 2), and therefore the lower leaf area index, is probably because the upland soils are more droughty (see

Ashton and Larson, 1996) and less fertile (Table 1). The capacity of dormant paper birch seed to endure drier and more fire prone soils, and still remain viable, perhaps is one reason why this species has a greater soil seed bank in ridge sites than the more mesic-loving black and yellow birches. Also, dormant paper birch seed probably requires greater amounts of irradiance than that of the understory sites in ridge sites for germination, while this might not be the case for the other birch species. However, no studies that we are aware of have actually tested this.

The two species that germinated from the buried seed bank and were also present as herbs in the existing forest understory – meadow violet (*Viola papilionacea* Pursh.) and meadow-rue (*Thalictrum polygamum* Muhl.) – are characteristic of mesic valley sites and are disseminated by small birds and ants. The sedges (*Carex* spp.) also showed interesting trends across sites. Buried seed banks appear largest for sedge species in the valley sites but their current dominance is mostly restricted to the forest understories of midslope and ridgetop sites. The dark shade and adequate moisture of the valley sites might be the one factor inhibiting the germination of sedge species and promoting their dormancy in the soil. All the other species that germinated from the soil samples are weedy early-seral plants that colonize disturbed soils. The two exotic escapees from Europe – plantain (*Plantago major* L.) and mullein (*Verbascum thapsus* L.) – probably colonized the sites during the farming period and have remained in the seed bank.

There are clear differences in dispersal agents among the growth habits. The shrubs (raspberries, *Rubus* spp. ; shadbush, *Amelanchier sanguinea* (Pursh) DC) and vine (wild grape, *Vitis aestivalis* Michx.) are bird dispersed, the trees are wind dispersed, the graminoids are mostly wind and small mammal dispersed, and the herbs are dispersed by ejection (dehiscent capsules), ants, or on the feathers or fur of small birds and mammals.

Different growth habits predominated on different sites with the shrubs preferring the ridges, the herbs preferring the midslopes, and the grasses/sedges and trees preferring the valley sites. The dominance of the uplands by shrubs supports an argument that they are more drought tolerant because of their woody morphology. The richness and dominance of the herbs on midslopes might suggest a position within the soil

catena that allows enough overstory light and below-ground soil moisture to promote the existence of herbs, at least those that are more ephemeral.

In general, there were many more germinants from soils of valley sites than those for midslope and ridgetop. This may explain why competition for tree regeneration by weedy vegetation is high on valley sites. Also, the greatest proportion of buried seed on these sites is from several species of sedge that are probably strong competitors of tree regeneration.

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