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The seed bank of hemlock forests: implications for forest regeneration following hemlock decline[1]

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K. A. Sullivan and A. M. Ellison (Harvard Forest, 324 North Main Street, Petersham, MA 01366, USA). The seed bank of hemlock forests: implications for forest regeneration following hemlock decline. J. Torrey Bot. Soc. 133:393–402. 2006.—Soil seed banks are especially important for forest regeneration in stands with few understory species and individuals. The understory of hemlock (*Tsuga canadensis*)-dominated stands in New England primarily consists of hemlock seedlings and saplings, but all size classes of hemlock are attacked by the hemlock woolly adelgid (*Adelges tsugae*). Prior to the initiation of a large-scale manipulative experiment designed to examine the impact of the adelgid on hemlock forest ecology, we documented the seed bank composition of eight large (0.81 ha) experimental hemlock-dominated and young hardwood-dominated plots. The seed bank samples from the hemlock-dominated plots contained significantly fewer species (rarefied species richness = 24; 95% confidence interval = 20–28) than those from the hardwood-dominated plots (species richness = 30). Seed banks from all plots were dominated by *Betula lenta, Rubus* spp., and *Carex pensylvanica*. Among plots, there was little compositional relationship between the forest overstory and its understory on the one hand, and its seed bank on the other hand. Because seeds of hemlock and birch persist for only a few years in the seed bank, and because hemlock seedlings are readily attacked and killed by the adelgid, damaged hemlock stands are more likely to be replaced by stands of black birch and other hardwoods than by hemlock.

Key words: *Betula*, birch, hemlock, hemlock woolly adelgid, regeneration, seed bank, *Tsuga canadensis*.

The forests of central New England lie in the transition hardwood-white pine-hemlock region and are a heterogeneous mosaic of deciduous trees (principally red oak *Quercus rubra* L., red maple *Acer rubrum* L., and black birch *Betula lenta* L.) and conifers (principally white pine *Pinus strobus* L. and eastern hemlock *Tsuga canadensis* (L.) Carr.) (Cogbill et al. 2002). The species composition across the landscape reflects the interaction of centuries of land-use, including agriculture and forestry (Foster and Aber 2004), periodic insect outbreaks (Orwig and Foster 1998, Johnson et al. 2005), and occasional catastrophic storms (Foster and Boose 1992, Boose et al. 2001) with fine-scale environmental variation. After various types of disturbance, interactions among species, their environment, land-use history, and successional dynamics together contribute to the maintenance of the landscape-level variability in species composition.

At present, a novel disturbance agent is impacting eastern hemlock-dominated stands in the southern part of hemlock's natural range. From Massachusetts, southern New Hampshire, and southern Maine through the Carolinas and into Georgia, eastern hemlocks are declining and dying because of infestation by the hemlock woolly adelgid (*Adelges tsugae* Annand) and from pre-emptive salvage logging (Orwig et al. 2002). The woolly adelgid is a homopteran insect introduced from Japan to the mid-Atlantic states in the 1950s (McClure 1987, McClure and Cheah 1999) that began to heavily infest trees in New England in the mid-to-late 1980s (Orwig et al. 2002). This rapidly spreading insect kills trees of all sizes and age classes within 4–20 years after infestation (Orwig et al. 2002). Since the early 1990s, hemlock, which is of low economic value, has been logged by landowners throughout New England in anticipation of future infestation by the adelgid (Orwig et al. 2002).

Suppressed saplings and soil seed banks are an important source of forest regeneration

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following disturbances that cause death or removal of overstory trees (Thompson 1987, 1989, Lambers et al. 2005). The understory of hemlock stands in the northern portion of hemlock's range (from Pennsylvania northward into southern Canada) is relatively species-poor, and those species that are present grow at low densities (Rogers 1980, Mladenoff 1990, Yorks et al. 2000) and are likely to contribute little to forest regeneration. Following a disturbance, seedlings emerging from the seed bank are likely to experience little competition for light from these few suppressed saplings and thus seedlings are likely to contribute significantly to forest regeneration of declining hemlock stands. In contrast, hardwood stands have a relatively dense understory with suppressed saplings of trees and a dense herbaceous layer, both of which will likely outcompete seedlings emerging from the seed bank. In New England, hemlock stands lost to logging and the adelgid are being replaced by stands of black birch (*Betula lenta* L.) and other hardwoods (Orwig et al. 2002) that may alter both the supply of seeds into the seed bank and the subsequent regeneration of these former hemlock stands.

In small light gaps caused by single-tree treefall gaps, seeds near the top of the seed bank are most likely to germinate, and so seeds in the upper 5–10 cm of soil (O and A horizons) have been the focus of previous studies of seed banks and regeneration in hemlock stands (Mladenoff 1990, Catovsky and Bazzaz 2000, Yorks et al. 2000). These studies have found a relatively species-poor seed bank dominated by the tree *Betula alleghaniensis* Britton, the shrubs *Sambucus racemosa* L. ssp. *pubens* (Michx.) House and *Rubus* spp., and spores of various ferns, including *Dennstaedtia punctilobula* (Michx.) Moore and *Dryopteris intermedia* (Muhl.) A. Gray.

As hemlocks succumb to the adelgid, however, large-scale mortality of trees creates large, bright patches (Orwig and Foster 1998, Kizlinski et al. 2002), providing opportunities for establishment of more light-demanding species. Logging operations further scarify the soil, exposing seeds buried deeper in the soil to conditions suitable for germination (Kizlinski et al. 2002). Thus, seeds buried more deeply in the soil could contribute significantly to stand regeneration and reestablishment of the understory (Putz 1983, Thompson 1987, Chambers and MacMahon 1994).

In this study, we had three objectives: (1) to describe the seed bank composition of hemlock and young hardwood stands in north-central Massachusetts; (2) to determine how seed bank composition in these stands varied with depth; (3) to provide base-line data for a long-term manipulative experiment examining the impact of the hemlock woolly adelgid and logging on regeneration of hemlock stands.

Unlike previous studies of hemlock seed banks (Mladenoff 1990, Catovsky and Bazzaz 2000, Yorks et al. 2000), our soil samples extended well into the mineral soil (B horizon), allowing us to quantify seed bank composition as a function of soil depth. In order to assess regeneration potential of these stands, we compared seed banks among hemlock stands and nearby young hardwood stands, and contrasted the species pool of buried seeds with the existing understory and overstory layers in both hemlock and hardwood stands. Because this study was conducted in the context of a long-term manipulative experiment (described below), our results provide testable predictions of changes in species composition that may occur following loss of hemlock in New England forests.

Study Site. Field work was conducted within eight 90 × 90 m (0.81 ha) experimental plots within the 121 ha Simes Tract at the Harvard Forest Long-Term Ecological Research Site in Petersham, Massachusetts, USA (Figure 1). These plots are at the current northern range limit of the hemlock woolly adelgid, and are part of a long-term experiment in which we are examining the response of forest ecosystems to hemlock decline and increased harvesting (Barker-Plotkin et al. 2004). At the time of this study, there was no adelgid present in any of the plots. These eight plots are grouped in two blocks, each consisting of three plots dominated by hemlock and one plot of mixed northern hardwoods (Table 1). Block 1 (plots 1–3 and 8) is in undulating terrain bordered on its northern edge by a *Sphagnum*-dominated wetland. Block 2 (plots 4–7) is on a forested ridge. These plots comprise a hemlock removal experiment: each block consists of a hemlock control (unmanipulated) plot, a plot in which all hemlock trees were girdled in May 2005 to simulate death-by-adelgid, a plot in which all hemlocks >20 cm DBH and any merchantable hardwoods and white pine

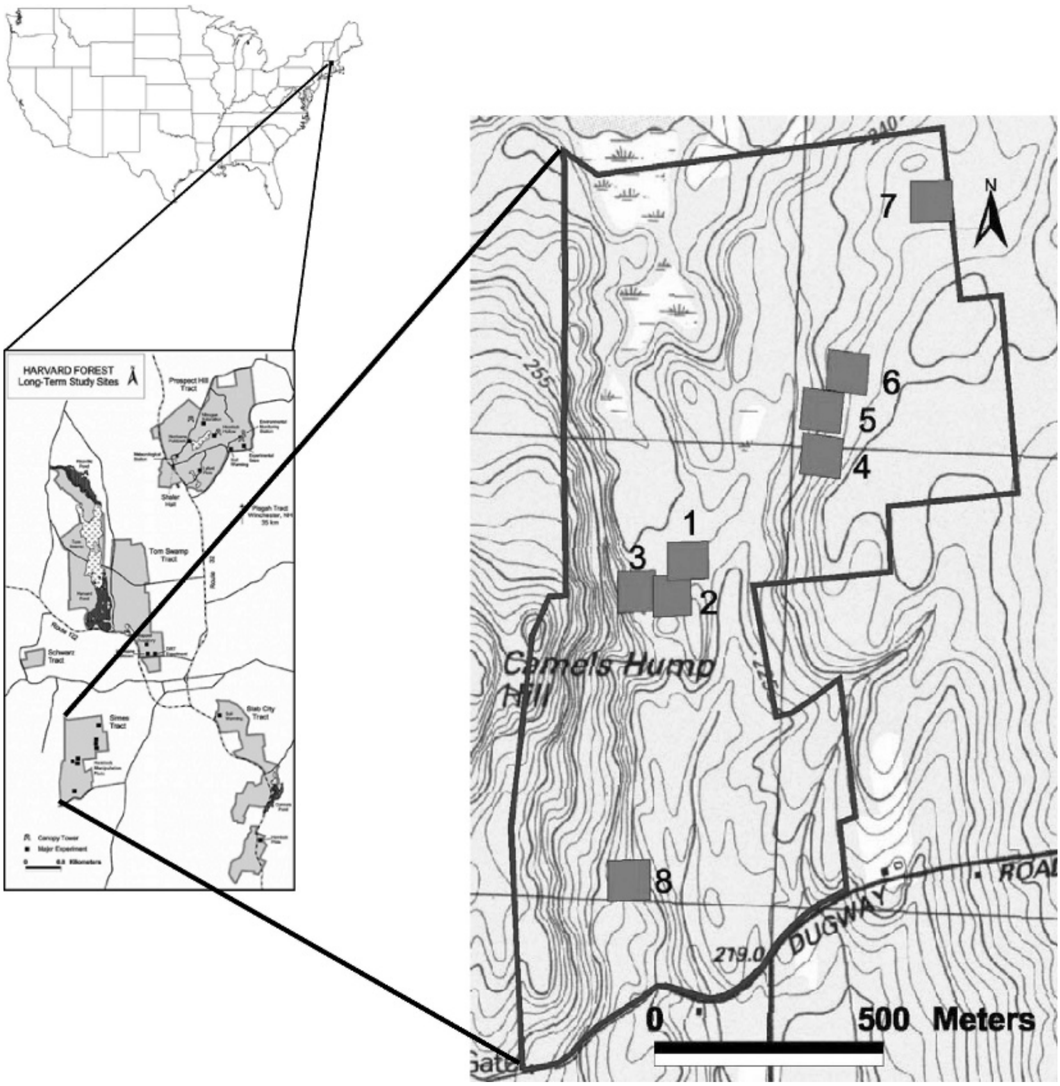

FIG. 1. Map of the study site at the Harvard Forest in north-central Massachusetts. Block 1 consists of hemlock plots 1–3 and hardwood plot 8, and Block 2 consists of hemlock plots 4–6 and hardwood plot 7.

(*Pinus strobus*) were logged and mechanically removed from the site in February–April 2005, and a hardwood control plot. The seed bank study described here was done in summer 2004, one year *before* the girdling and logging of the manipulated plots. Thus, the data presented here provide baseline data for the experimental treatments. Over the next several years to decades, we will be able to directly test the predictions of understory and overstory regeneration derived from our results.

Methods. COMPOSITION OF THE SEED BANK. In early June 2004, five soil samples were collected from the central 30 × 30 m area of each of the six hemlock and two hardwood study plots. Each sample was 60 × 60 cm in area and 20-cm deep. Sample location within each plot was determined using a random-number generator, and samples were separated by at least 10 m. Samples were divided into 2 cm depth increments (10 per sample). The top 2 cm (O horizon) was generally thick duff containing leaf litter, matted roots, and rocks; the next 4–8 cm (A horizon) consisted of a mix of duff, topsoil, and mineral soil clay; and the lower 10 cm (B horizon) was generally mineral soil with clay or sand. Below 20 cm, there was

Table 1. Overstory composition (percent basal area of each species) of the eight sampled 90 × 90 m plots at Harvard Forest's Simes Tract. The diameters of all trees in each plot were measured, so these data are a complete inventory, not a statistical sample. Data provided by Audrey Barker-Plotkin (Harvard Forest). Plot numbers in parentheses refer to numbers indicated on site map in Figure 1. "Other" species include *Acer saccharum* Marshall, *Betula alleghaniensis* Britton, *Betula papyrifera* Marshall, *Ostrya virginiana* (Miller) K. Koch., *Fraxinus americana* L., *Carya* spp., *Prunus serotina* Ehrh., and *Quercus velutina* Lam.

	Block 1				Block 2			
Tree species	Hemlock (Plot 1)	Hemlock (Plot 2)	Hemlock (Plot 3)	Hardwood (Plot 8)	Hemlock (Plot 4)	Hemlock (Plot 5)	Hemlock (Plot 6)	Hardwood (Plot 7)
Tsuga canadensis	82	68	56	0	77	78	70	6
Pinus strobus	13	10	16	0	0	0	9	36
Acer rubrum	2	2	8	14	3	8	11	9
Quercus rubra	1	20	9	33	2	6	5	13
Quercus alba	2	0	10	0	0	1	0	0
Betula lenta	0	1	0	45	19	6	2	24
Other	1	0	1	8	0	1	3	12
Total basal area (m^2 ha^{-1})	49.6	44.2	40.5	26.4	51.4	52.2	71.9	44.8

more rock than soil. We used the direct germination method (Gross 1990) in full light to determine seed bank composition in each 2-cm increment. In brief, each increment was hand-mixed and placed atop 1 cm of milled *Sphagnum* in a labeled cell of a divided potting tray. The trays were placed in full sun in a climate-controlled greenhouse (minimum nighttime temperature = 15°C; maximum daytime temperature = 30°C) at the Harvard Forest. The trays were watered daily. Seedlings that emerged were counted and, when they were large enough, identified to the lowest taxonomic level possible (normally species, but occasionally, e.g., *Rubus* and some *Carex*, only to genus). Seedlings of graminoids (sedges, rushes, grasses) and some forbs were transplanted into 10-cm pots and maintained in the greenhouse for another year until they flowered and could be identified to species. Because many ferns are also greenhouse weeds, we did not count or identify the few (<10) specimens of ferns in our samples. Nomenclature follows Flora of North America for species in completed treatments (see http://www.fna.org/FNA) or Gleason and Cronquist (1991).

COMPARISON WITH THE UNDERSTORY FLORA. Concurrent with collecting soil samples, we counted and identified all individual understory (< 1 m height) plants occurring in a 1 m^2 quadart centered on each soil sample point. We also counted all live saplings (trees > 1m in height and < 5 cm diameter) in the center 30 × 30 m of each plot.

DATA ANALYSIS. The unit of inference of this study is the central 30 × 30 m area of each 90 × 90 m plot in the Hemlock Removal Experiment. Thus, the five replicate soil samples from within each plot were pooled prior to comparisons between hemlock and hardwood plots. Because this results in an overall small sample size, we used rarefaction (Gotelli and Graves 1996) to account for differences in total abundance of emergent seed bank seedlings (384 seedlings in hemlock soil samples *versus* 207 seedlings in hardwood soil samples) and to more accurately compare species richness of the seed bank between the hemlock and hardwood plots. In brief, rarefaction estimates the number of species that would have been encountered in the more abundant samples (here, the hemlock plots with $N = 384$ seedlings) if the total number of seedlings was equivalent to that of the numerically smaller sample (here, the hardwood plots with $N = 207$ seedlings (Gotelli and Graves 1996)). Thus, by sampling without replacement, we create a rarefied sample of 207 seedlings from the hemlock plots. We used EcoSim 7.72 (Gotelli and Entsminger 2005) for our rarefaction calculations. One thousand such randomizations were run to generate average rarefied sample size and associated bootstrapped confidence intervals (Efron 1982). We used *t*-tests to compare hemlock and hardwood species richness values, and the Jaccard index ($J = \frac{c}{a + b + c}$, where c is the number of species common to the two forest types, a is the number of species unique to

Table 2. Species density (seeds/0.01 ha) in the seed bank of hemlock and hardwood plots. Values shown are based on pooled samples from the six hemlock and two hardwood plots. The raw data are available from the Harvard Forest Data Archive at http://harvardforest.fas.harvard.edu/data/archive.html, dataset HF-105.

Species	Seeds/0.01 ha in seed bank of: Hemlock	Hardwood
Trees		
Acer rubrum L.	0	25
Betula alleghaniensis Britton	83	0
Betula lenta L.	1333	1400
Betula papyrifera Marsh.	25	250
Prunus serotina Ehrh.	0	75
Tsuga canadensis (L.) Carr.	17	0
Shrubs		
Gaultheria procumbens L.	8	0
Mitchella repens L.	0	150
Rhus glabra L.	17	100
Rhus typhina L.	8	125
Rubus flagellaris Willd.	33	0
Rubus spp.	531	200
Spiraea spp.	0	25
Vaccinium angustifolium Ait.	8	0
Forbs		
Ambrosia artemisiifolia L.	8	75
Hedyotis caerulea (L.) Hook.	0	150
Hypericum canadense L.	0	50
Hypericum perforatum L.	0	25
Lobelia inflata L.	42	50
Lysimachia ciliata L.	25	0
Lysimachia quadrifolia L.	116	25
Maianthemum canadense Desf.	0	300
Mollugo verticillata L.	8	50
Verbascum thapsus L.	0	75
Viola sororia Willd.	8	50
Graminoids		
Carex atlantica L. Bailey	0	75
Carex debilis Michx. var. *rudgei* L. Bailey	8	0
Carex laxiflora Lam.	58	200
Carex pensylvanica Lam. var. *pensylvanica*	481	400
Carex spp.	17	75
Rhynchospora alba (L.) Vahl.	17	50
Scirpus cyperinus (L.) Kunth.	58	50
Juncus canadensis J. Gay	8	0
Juncus tenuis Willd.	25	250
Dicanthelium dichotomum (L.) Gould	8	25
Festuca rubra L.	17	0
Panicum clandestinum L.	8	0
Panicum lanuginosum Elliot	33	200
Poa annua L.	125	525
Other Poaceae	25	100

hemlock forest samples, and b is the number of species unique to hardwood forest samples) to assess similarity between forest plots. The Kolmogorov-Smirnov test was used to test whether the distribution of seeds within the soil profile varied between hemlock and hardwood plots. Gotelli and Ellison (2004) provide detailed descriptions of the Jaccard index and the Kolmogorov-Smirnov test. All other statistical tests were done using S-Plus 6.2 (Insightful Corporation, Seattle, WA).

Results. SEED BANK. *Species richness and composition.* Seedlings of 40 species emerged in the direct germination experiment (Table 2). In the six hemlock plots, an average of 13 ± 2.9 (SD) species germinated from the seed bank samples (all samples pooled within a plot), whereas in the two hardwood plots, 29 ± 3.5 species germinated ($t = 6.1$, df $= 6$, $P = 0.0008$). Despite having three times the volume of soil samples from the hemlock stands as from the hardwood stands, we recovered the same total number of species (30) from soils of each forest type. The species similarity of the two forest types (Jaccard index) equaled 0.5. The most common taxa recovered (Table 2) were birch (*Betula* spp.) (45% of the seedlings in the hemlock samples and 32% of the seedlings in the hardwood samples), *Rubus* spp. (19% of the hemlock sample and 4% of the hardwood sample), and *Carex* spp. (18% of the hemlock sample and 14% of the hardwood sample). In both forest types, black birch (*Betula lenta*) accounted for at least 85% of the birches and *C. pensylvanica* accounted for > 50% of the sedges.

Rarefaction showed that, given an abundance of seedlings equal to that in the hardwood samples, the expected species richness of the seed bank in the hemlock plots was 24 species (95% confidence interval equaled 20–28 species) *versus* 30 in the hardwood plots. Thus, we conclude that at $P < 0.05$, the seed banks of hemlock stands were significantly less species-rich than the seed banks of hardwood stands.

Species distribution by depth. In the seed banks of both hemlock and hardwood stands, tree seeds were most abundant in the upper 6 cm of the soil, shrubs were most abundant between 4 and 12 cm, and graminoids were most abundant between 8 and 18 cm; the density of germinated seedlings of each species at each 2-cm depth increment in each these groups did not differ between the two stand types (Kolmogorov-Smirnov test statistics = 0.1, 0.3, and 0.5, with $P = 1.0$, 0.79, and 0.17

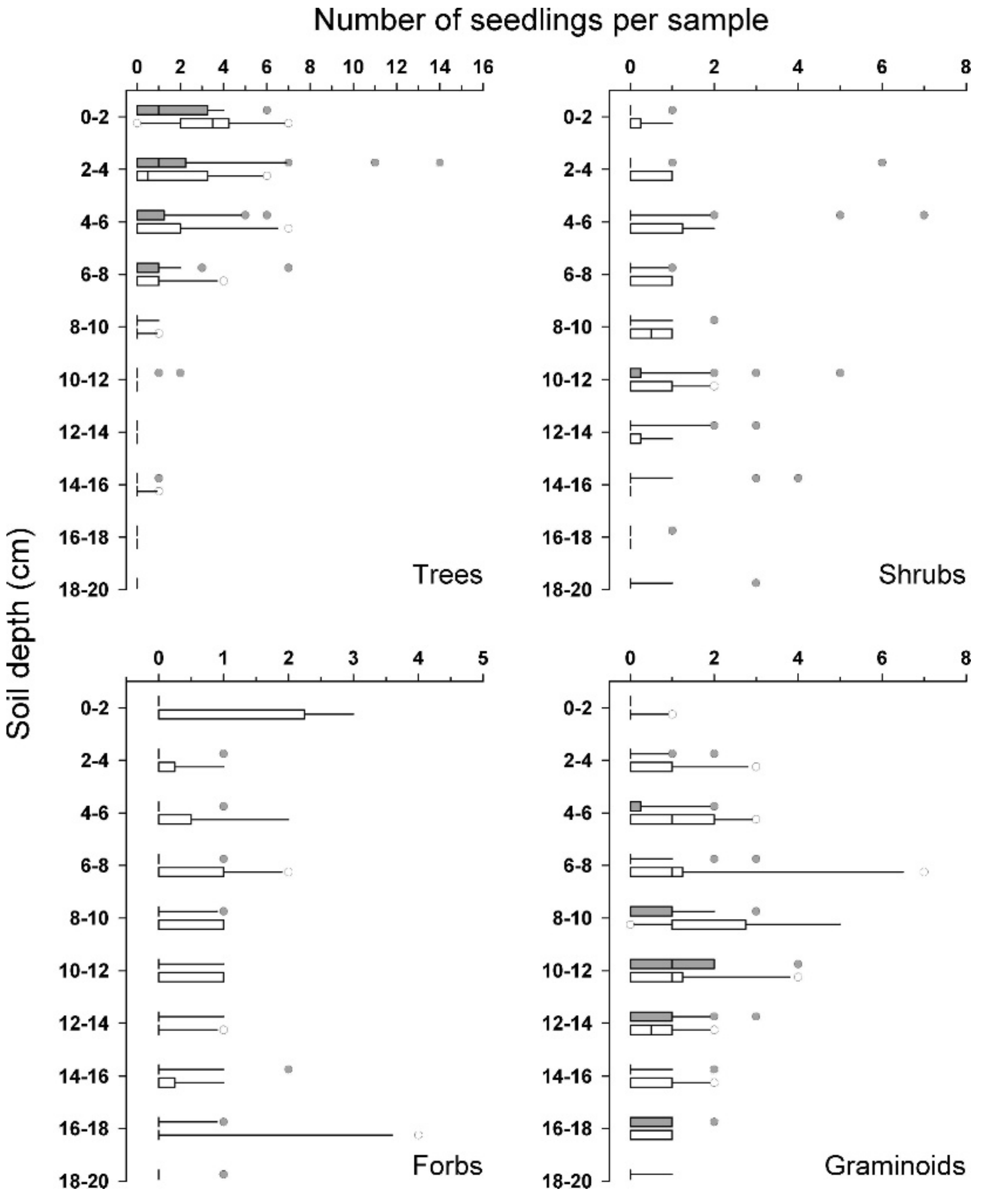

FIG. 2. Box plots illustrating the distribution of emergent seedlings of trees, shrubs, forbs, and graminoids in all the soil samples from hemlock stands (grey boxes and circles) and hardwood stands (white boxes and circles) at 2 cm depth intervals. Boxes enclose data from the 25th to the 75th percentiles, with the median number of seedlings (50th percentile) indicated by the central vertical line. Horizontal lines ("whiskers") extend to the 10th and 90th percentiles of the data; any points beyond that are indicated individually with circles. A single vertical line drawn at 0 indicates no seedlings emerging in that sample.

for trees, shrubs, and graminoids, respectively; Fig. 2). In contrast, distribution of forb seeds differed between the two stand types (Kolmogorov-Smirnov test statistic = 0.9, P = 0.0002). Forbs were common and uniformly distributed in the seed bank of hardwood stands but were rare in the seed bank of hemlock stands. Forb seedlings germinated

Table 3. Average density (± 1 SD) per 0.01 ha of understory species (< 1 m height, < 5 cm diameter) present at locations from which soil seed bank samples were taken. Values shown are means pooled across the 6 hemlock and 2 hardwood plots.

Species	Average density (± 1 SD)/0.01 ha in understory of: Hemlock	Hardwood
Tree seedlings		
Acer rubrum L.	158 ± 205.1	638 ± 583.4
Acer saccharum Marshall	0	13 ± 17.7
Betula lenta L.	3 ± 4.3	13 ± 17.7
Corylus cornuta Marshall	0	25 ± 30.4
Fraxinus americana L.	0	13 ± 17.7
Ostrya virginiana (Miller) K. Koch	1 ± 3.4	0
Pinus strobus L.	0	425 ± 601.0
Prunus serotina Ehrh.	0	38 ± 17.7
Quercus rubra L.	6 ± 4.3	25 ± 35.4
Tsuga canadensis (L.) Carr.	39 ± 40.9	0
Shrubs		
Rubus flagellaris Willd.	0	13 ± 17.7
Vaccinium angustifolium Ait.	0	425 ± 530.3
Forbs		
Aralia nudicaulis L.	0	25 ± 35.4
Maianthemum canadense Desf.	0	10838 ± 3270.4
Medeola virginiana L.	0	575 ± 353.6
Mitchella repens L.	12 ± 20.8	4225 ± 2545.6
Smilacina racemosa (L.) Desf.	0	338 ± 335.9
Graminoids		
Carex pensylvanica Lam. var. *pensylvanica*	0	813 ± 300.5
Juncus tenuis Willd.	0	38 ± 5.3
Danthonia sp.	0	113 ± 123.7
Ferns and fern-allies		
Dennstaedtia punctilobula (Michx.) Moore	0	425 ± 70.7
Dryopteris carthusiana (Villars) H. P. Fuchs	0	13 ± 17.7
Dendrolycopodium obscurum (L.) A. Haines	1 ± 3.4	188 ± 265.5

most abundantly in hemlock soil samples below 10 cm (Fig. 2).

UNDERSTORY. *Species richness and composition.* The understory vegetation of hemlock stands had markedly fewer species (7 species found in 60 plots) than that of hardwood stands (21 species found in 20 plots), and the overall density of understory individuals in hemlock forests was 1–4 orders of magnitude less than density of understory individuals in hardwood stands (Table 3). The hemlock understory consisted primarily of eastern hemlock seedlings (Table 3) and saplings (Table 4), 1-year-old red maple seedlings, and the occasional *Mitchella repens*. The hardwood understory was multi-layered, with many seedlings, abundant blueberry (*Vacci-*

Table 4. Number of saplings (tree species < 5 cm diameter) in the center 30 × 30 m area of the eight sampled plots at Harvard Forest's Simes Tract. This is the same area of each plot from which the seed bank was sampled. These data were collected January – May, 2005 by Audrey Barker-Plotkin.

	Block 1				Block 2			
Species	Hemlock (Plot 1)	Hemlock (Plot 2)	Hemlock (Plot 3)	Hardwood (Plot 8)	Hemlock (Plot 4)	Hemlock (Plot 5)	Hemlock (Plot 6)	Hardwood (Plot 7)
Tsuga canadensis	28	12	1	0	18	21	7	0
Pinus strobus	0	0	0	2	0	0	0	7
Acer rubrum	0	0	0	13	0	0	0	5
Acer saccharum	0	0	0	14	0	0	0	0
Prunus sp.	0	0	0	0	1	0	0	0
Betula lenta	1	0	0	0	0	0	0	0

nium angustifolium) bushes, a diverse herb layer with forbs, graminoids, ferns, and lycopods (Tables 3), and some maple and pine saplings (Table 4).

Comparison with the seed bank. There was little similarity between the species composition of the seed bank and the understory in either the hemlock (Jaccard index of similarity = 0.06) or the hardwood stands (Jaccard index = 0.15). Among the overstory tree species, only black birch was also represented in the seed bank to any significant degree (compare Tables 1 and 2). Among understory herbs, *Maianthemum canadense* was abundant in the hardwood understory and in its seedbank.

Discussion. In our study sites, as in temperate forests in general (Pickett and McDonnell 1989, Mladenoff 1990, Schiffman and Johnson 1992, Hanlon et al. 1998, Leckie et al. 2000, Yorks et al. 2000, Gilliam and Roberts 2003), there was little similarity between species composition of the aboveground vegetation and what is present in the seed bank (see also Hills and Morris 1992). Despite its dominance in the overstory, eastern hemlock was poorly represented in the seed bank. With its short-lived seeds, hemlock is a "transient" seed bank species (Bekker et al. 1998, Sutherland et al. 2000); its seeds remain in the seed bank for only a single season (Baskin and Baskin 1998) and it is rare in seed banks of most hemlock forests (Yorks et al. 2000). The two hemlock seeds that did germinate were both in the upper 2 cm of the soil cores. Consistent with its status as a late-successional dominant, hemlock was absent in the hardwood understory but was modestly abundant in the understory of hemlock-dominated plots (Table 4). Taken together, these data suggest that hemlock will be very slow to recolonize stands following removal of overstory hemlock by the adelgid or by logging, especially because the adelgid infests and kills hemlocks in all size classes.

Tree seeds in general, and black birch in particular, were uncommon in the soil below 8 cm (Fig. 2). Previous studies have also found that tree seeds are abundant in the duff layer and their abundance declines with depth (Pickett and McDonnell 1989, Schiffman and Johnson 1992). In seed banks of both the hemlock and hardwood stands, black birch was the most common tree species (Table 2). This small-seeded species is intermediate in shade tolerance and germinates readily when light levels increase (Catovsky and Bazzaz 2000); its seeds only persist in the seed bank for a few years (Sutherland et al. 2000). Large quantities of birch seeds disperse in autumn over a wide area. These seeds are transported by wind across great distances atop snowpack (Matlack 1989, Greene and Johnson 1997), and the seeds germinate readily the following summer (Catovsky and Bazzaz 2000, Sutherland et al. 2000). Hence, our collection of soil samples in early June (as suggested by Warr et al. (1994)) captured these seeds before they had germinated in the field. Six months after we experimentally logged two of our plots, the most abundant seedlings present were those of several birch species (A. M. Ellison, *personal observation*). It is not surprising that birch dominates stands where hemlock has recently been killed by the adelgid or logged off (Orwig et al. 2002), but its potential for long-term persistence in these forests has not yet been assessed.

After accounting for sample size through rarefaction, species richness of shrubs, forbs, and graminoids in the seed bank was significantly lower in hemlock plots than in hardwood plots (Table 2). This difference parallels the species-poor character of the understory in the hemlock plots (Tables 3 and 4). Similarly, the understory of the hardwood plots was rich in shrubs, forbs, and graminoids, but these species (except for *Maianthemum canadense*) were poorly represented in the seed bank. Overall, shrubs and forbs were most abundant in the top 10–12 cm, whereas graminoids were more common below that.

In contrast with the rich information we have for some tracts at the Harvard Forest (Raup 1966, Foster and Aber 2004), we have little information on land-use history at the Simes Tract. The stratification of the seed bank – tree seeds in the upper 0–6 cm, shrubs and forbs in the middle soil layers, and graminods below 14 cm – suggests that the history of the Simes Tract was qualitatively similar to other areas of north-central Massachusetts that are currently forested. Clearing of forest for pasture in the 18th and early 19th centuries provided an opportunity for colonization of graminoids, which were replaced by shrubs and a diversity of perennial forbs after abandonment of agriculture in the late 19th century (Livingston and Allessio 1968). Trees colonized slowly from surrounding wood lots and from further afield, as their seeds do not persist for long in the seed bank. However, interpreting land-use history from seed bank data alone is difficult as physical sorting can redistribute seeds throughout the soil profile. Independent data on site-specific land-use history are needed to determine how well the seed bank reflects land-use history at this site.

The moderate similarity between the seed bank of hemlock and hardwood plots reflected in our data suggests that the primary impact of removal of hemlock from New England forests will be homogenization of the landscape. Young stands of hardwoods, the primary forest type in southern New England, will continue to mature; regeneration in treefall gaps and other disturbances will simply reset the successional clock. As they succumb to the adelgid or are felled for pulp and timber, older hemlock stands are likely to be replaced by hardwoods. This floristic homogenization may be paralleled by the homogenization of the fauna (Tingley et al. 2002, Ellison et al. 2005b), and may result in a cascade of changes to ecosystem dynamics (Ellison et al. 2005a).

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