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The soil seed bank and its relationship to the aboveground vegetation in deciduous forests in New York City

FAITH KOSTEL-HUGHES* and TRUMAN P. YOUNG§
Department of Biological Sciences, Louis Calder Center, Fordham University, P.O. Drawer K, Armonk, NY 10504, USA

MARK J. McDONNELL
The Australian Research Centre for Urban Ecology, Royal Botanic Garden-Melbourne, c/o School of Botany, University of Melbourne, Parkville 3052, Australia

The soil seed bank was studied in two deciduous forests in Bronx (New York City), NY. The purpose of this study was to determine how the biotic and abiotic differences between urban and rural forests are reflected in urban forest seed banks. Soil samples were collected in two consecutive years and monitored for emergence in the greenhouse over two years. In 1993, the mean number of emergents ranged from 4636 to 5373 m^{-2} (excluding ferns), or from 6972 to 9651 m^{-2} (including ferns). In 1994, the mean number of emergents ranged from 1656 to 2013 m^{-2} (excluding ferns), or from 5019 to 5992 m^{-2} (including ferns). Graminoids and ferns combined accounted for approximately 70% of all emergents each year. Three taxa, *Rubus* spp., *Betula lenta,* and *Liriodendron tulipifera,* comprised 60–80% of the woody emergents and were the only woody taxa to exhibit delayed germination. A substantial number of forbs, graminoids and ferns (15–50%) exhibited delayed germination. The nonnative woody species *Ailanthus altissima, Morus alba,* and *Celastrus orbiculatus* were absent from the aboveground vegetation of some forest plots yet were present at low densities in the seed bank. A greater mean density of emergents and the presence of nonnative species are the main differences between the seed banks of these urban forests and those reported for similar nonurban forests in this region.

Keywords: soil seed bank, urban forests, urban–rural gradient, nonnative species, New York City

Introduction

Urban forests are subject to unique sets of environmental conditions, both biotic and abiotic (Airola and Buchholz, 1984; Dorney *et al.*, 1984; Yost *et al.*, 1991; Matlack, 1993; Young, 1995; Bowers and Breland, 1996; McDonnell *et al.*, 1997; Pouyat *et al.*, 1997). Unfortunately, few studies of urban forests have been carried out. If we are successfully to manage and restore these communities, we need better documentation of the ways in which they differ from better studied rural forests. In particular, we need better information on the regeneration ability of the dominant woody species, both natives and nonnatives. Factors affecting regeneration, specifically the availability of seeds and/or safe sites (Harper, 1977), may differ between urban and rural plant communities. Soil seed bank studies are a common means of estimating the availability of seeds within a community (Leck *et al.*, 1989).

Soil seed bank composition is the product of factors affecting introduction and removal of seeds into and out of the seed bank. These include the seed rain, secondary dispersal, predation, pathogens, burial, and microsite conditions affecting dormancy and germination (Simpson *et al.*, 1989). Disturbances associated with urbanization may affect some of these factors and consequently affect the seed bank composition of urban plant communities. Differences in bird community composition in response to urban land use (Blair,

* To whom correspondence should be addressed, at Department of Ecology, Evolution, and Natural Resources, Rutgers University, 1 College Farm Road, New Brunswick, NJ 08901, USA.
§Present address: Department of Environmental Horticulture, University of California, Davis, CA 95616, USA.

1996) and greater proximity of urban forests to nonforest seed sources due to fragmentation (Yost *et al.*, 1991) may affect seed rain contribution to the seed bank. Foraging differences among gray squirrels in response to urbanization (Bowers and Breland, 1996) may affect secondary dispersal, burial and predation. Urban forests in New York City, in comparison with rural forests, have somewhat hydrophobic soil (White and McDonnell, 1988), higher organic matter and total N concentrations in the mineral soils (A horizon) (White and McDonnell, 1988; Pouyat *et al.*, 1994b), lower leaf litter depth, mass and density (Kostel-Hughes, 1995), greater densities of nonnative earthworm species (Steinberg *et al.*, 1997) and frequent anthropogenic fires (Kostel-Hughes, personal observation). These differences, combined with elevated mean monthly temperatures (2–3°C) and increased average annual precipitation (5 cm) (McDonnell *et al.*, 1993), have the potential to affect microsite conditions significantly in urban forests.

Numerous studies have examined the soil seed bank composition of temperate deciduous forests (see review by Pickett and McDonnell, 1989), but none, to our knowledge, have included forests embedded within an urban setting. We conducted a soil seed bank study in two temperate deciduous forests in New York City to determine the extent to which the soil seed banks of these urban forests exhibit the same general density, depth and growth form composition patterns reported for seed banks of nonurban temperate forests in this region.

Materials and methods

Study area

This study was conducted in 1993 to 1995 in Van Cortlandt Park (464 ha) and Pelham Bay Park (1119 ha), located in the north-central and northeastern Bronx (New York City), NY, adjacent to the southern border of Westchester County, NY (Fig. 1). Forested areas in these two parks are substantial: 243 ha in Van Cortlandt Park and 316 ha in Pelham Bay Park (McDonnell *et al.*, 1990). Van Cortlandt and Pelham Bay Parks are among the urban sites included in a number of studies of forests along an urban–rural transect in the New York City metropolitan area (White and McDonnell, 1988; Pouyat and McDonnell, 1991; McDonnell *et al.*, 1993; Pouyat *et al.*, 1994a; Pouyat *et al.*, 1994b; Kostel-Hughes, 1995; McDonnell *et al.*, 1997; Pouyat *et al.*, 1997).

Ten permanent forest reference plots (20 m $\times$ 20 m) were established in each of these parks in 1986 to monitor long-term vegetation changes in forest ecosystems in response to urbanization (McDonnell *et al.*, 1990). Sites were subjectively chosen to represent different types of forest communities present in these parks and were approximately 80 to 100 years old (McDonnell *et al.*, 1990). Quantitative vegetation surveys were conducted in each of these plots in 1987 and 1992 (McDonnell *et al.*, 1990; and in preparation). The tree species composition of these forest plots is typical of mid- to late-successional northeastern deciduous forests, and it includes both native and nonnative plant species. See Appendix 1 for a list of all species that were identified in these forest plots during a 1992 vegetation survey.

Sampling methods

Because of time and greenhouse space limitations, we were able to sample only nine of the twenty permanent plots (six in Van Cortlandt Park and three in Pelham Bay Park). Only plots containing *Acer* species in the seedling, sapling, and/or adult stages were sampled. This was designed to complement laboratory experiments being conducted that compared germination rates and seedling growth of native and nonnative *Acer* species in response to different litter treatments (Kostel-Hughes, 1995).

Soil samples were collected in these nine 400 m^2 forest plots in May 1993 and May 1994. Soil samples were collected using a stratified random sampling design. In 1993, ten cylindrical soil cores, 5 cm in diameter and 10 cm deep, were collected from each of four 10 $\times$ 10 m subplots for a total of 40 soil cores per plot. The ten soil cores from each subplot were pooled into two subsamples of five cores each for a total of eight subsamples per plot. By using an aluminum core liner modified to split lengthwise, soil cores were separated into two fractions, 0 to 5 cm deep (including litter) and 5 to 10 cm deep.

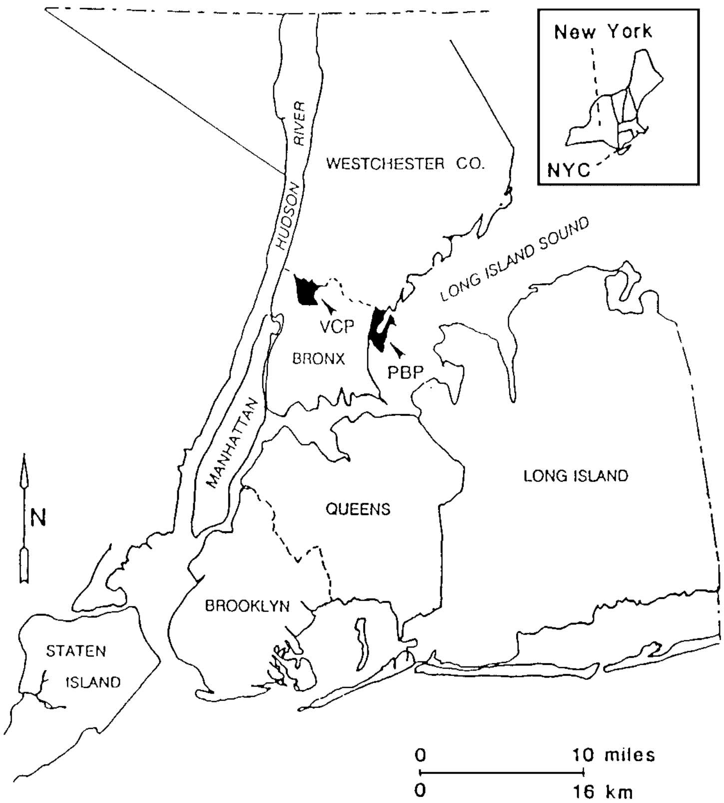

Figure 1. Map of the New York City metropolitan area showing the location of Van Cortlandt Park (VCP) and Pelham Bay Park (PBP) in Bronx, New York. (Adapted from McDonnell *et al.*, 1990.)

After completing the first season of germination trials for the samples collected in 1993, performance curves were created for each of the nine plots (Fig. 2) to determine if the sampling design was adequate for estimating seed density of woody species. We calculated the cumulative number of seeds of woody species in the 0 to 5 cm depth fraction for one through eight subsamples. In each plot, the mean number of seeds of woody species per subsample was reached, or nearly so, by the fourth of the eight total subsamples. Based on the 1993 results, the sampling protocol was modified in 1994, and only five soil cores (pooled into one subsample) were collected from each of the four subplots for a total of 20 cores (four subsamples) per plot. Also, based on our finding that the vast majority (78%) of seeds of woody taxa were concentrated in the 0 to 5 cm fraction in 1993, in 1994 we resampled the plots to a depth of 5 cm rather than 10 cm.

Greenhouse methods

The soil seed bank was estimated using the seedling emergence method, in which the samples are subjected to conditions that are generally favorable to germination (Simpson *et al.*, 1989). Soil samples were processed on the day of collection. Soil samples were layered no more than 2.5 cm deep on top of 4.0 cm sterilized seedling soil mix that had been thoroughly wetted down in plastic flats. Shallow layering of soil samples has been shown to enhance overall germination rates (Kjellsson, 1992). Control flats filled with sterilized seedling soil mix (6.5 cm deep) were interspersed among the seed bank sample flats on the greenhouse bench at a ratio of one control flat for every four sample flats. This provided a means for detecting potential contaminant seeds introduced to sample flats within the greenhouse. The number of hours of

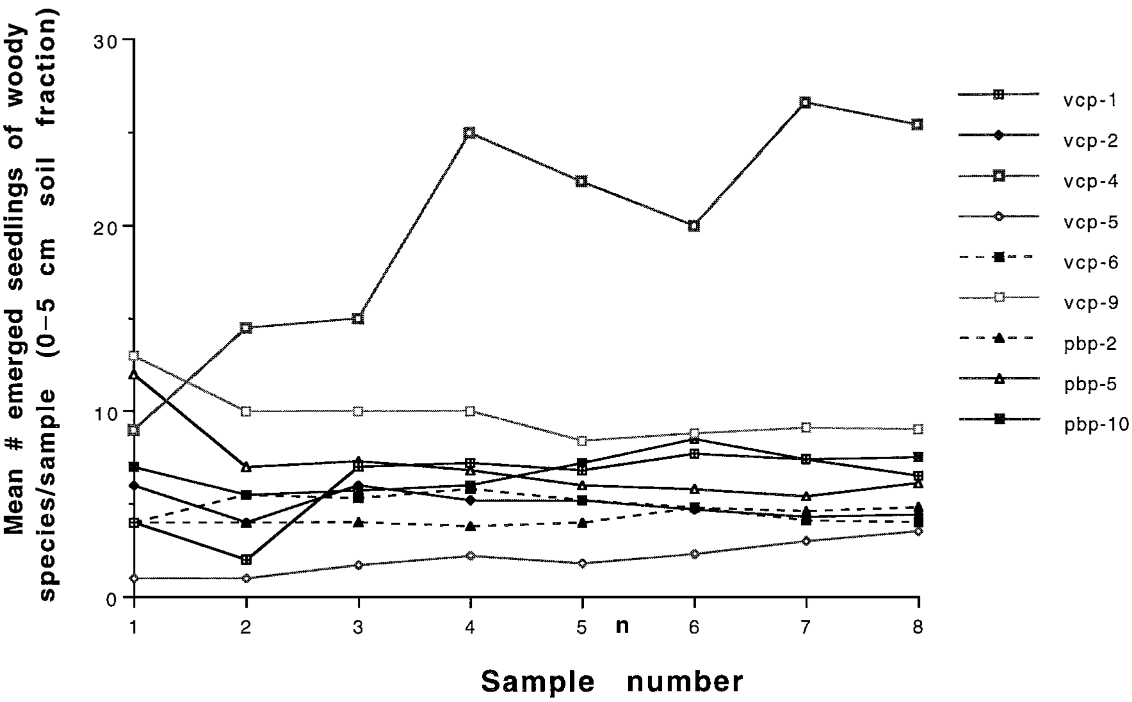

Figure 2. Performance curves for the seed bank sampling method used in 1993. The mean number of seeds of trees, shrubs and vines in the 0–5 cm soil core fraction was plotted for each subsample for each of the nine plots sampled to determine the effectiveness of this sampling regime for estimating the size of the seed bank for woody species. Plots in Van Cortlandt Park are abbreviated as VCP and those in Pelham Bay Park are abbreviated as PBP and are numbered as in McDonnell *et al.*, 1990.

daylight ranged from 14 to 16 hours per day. Natural lighting was supplemented with artificial lighting during prolonged overcast periods, and as daylight decreased during the autumn months. Greenhouse temperatures generally ranged between 15°C and 35°C during the summer months. Occasionally temperatures rose as high as 50°C in the greenhouse. These incidents of high temperatures were infrequent and brief (1–2 hours). Since the flats did not dry out and there was no subsequent reduction in number of emergents nor any loss of seedlings, we are confident that this did not have any significant effect on our findings.

Flats were watered daily, or as needed, and the location of every flat on the greenhouse bench was shifted twice a month. Seedling emergence was monitored daily through two growing seasons. Each week seedlings were identified and removed from the flats. If they were not yet identifiable, each was transplanted to another pot for future identification. Taxonomy follows Gleason and Cronquist (1991). Approximately every month, the upper 2.5 cm of soil in the flats was stirred to stimulate germination (Forcella, 1984). In December, all flats were moved outdoors (covered) to provide any remaining seeds with a winter stratification treatment in case this was required to break dormancy. The flats were returned to the greenhouse the following May and seedling emergence was monitored through another growing season. The samples collected in 1993 were monitored in the greenhouse May through November of 1993 and 1994. Likewise, the samples collected in 1994 were monitored in the greenhouse May through November of 1994 and 1995. Following the second year of monitoring germination, 10% of the samples were sieved to look for seeds that may have been present but failed to germinate.

Data analyses

Seedlings of *Oxalis* spp. were considered contaminants and excluded from the data set because of their emergence in the control flats. We use the term “the soil seed bank” to refer to all seeds and spores contained in the soil and litter of the samples collected. Our interests were in the woody species because they are the floristic and biomass dominants of these communities. Therefore we made no attempt to identify graminoids or ferns to species, and all were grouped into one of these two categories. Similarly, although we made tentative identification of many herbaceous emergents, they were not vouchered nor intended to be described analytically at the genus or species level. Therefore we grouped all of these herbs together as “forbs” for analysis. Vine, shrub and tree seedlings were identified to species, unless noted, and were analyzed separately. See Appendix 1 for a list of those species that were identified in these seed bank samples. To be comparative with other seed bank studies, separate density values were calculated both with and without ferns included.

To reduce the number of zero values in the data set, and therefore improve normality, all subsamples (eight in 1993 and four in 1994) in each plot were pooled, resulting in a single total value for each 20 $\times$ 20 m plot (six plots in Van Cortlandt Park and three plots in Pelham Bay Park). To reduce skewness, 0.5 was added to all values, which were then square root transformed (Sokal and Rohlf, 1981). Skewness (g_1) was calculated for each taxon in each plot before and after transformation. After square root transformation, skewness for most taxa did not exceed $(6/n)^{-2}$, which indicates that the data were not distributed sufficiently differently from normal to bias statistical analyses (Snedecor and Cochran, 1980). Mean emergent seedling number per square meter was calculated for each taxon for each park, for each soil depth fraction, and for each sampling year. Using t-tests, comparisons were made of mean seed number m^{-2} among different growth forms and among different woody species between parks and between depth fractions within each park. To relate seed bank composition to that of the standing vegetation across the nine plots, we performed a regression of the total number of emergents for 1993 and 1994 combined against the Importance Value (sum of relative density, relative dominance, and relative frequency) of shrubs, vines and adult trees ($dbh > 2.54$ cm) for species that were recorded in both the seed bank samples and the 1992 vegetation survey for at least three plots. Prior to performing the regression analyses, both the seed bank and the Importance Value data were $\log(x + 1)$ transformed, which effectively reduced skewness.

Results

1993 seed bank samples

A total of 6190 germinants emerged from the soil samples collected in 1993: 4548 from the six forest plots in Van Cortlandt Park and 1642 from the three forest plots in Pelham Bay Park. Ferns and graminoids comprised the two largest groups of germinants, with between 31% and 44% of the total in both parks (Table 1). Forbs comprised 8 to 11% of all emergents in both parks (Table 1). Trees comprised 8 to 10% of all emergents, while shrubs and vines comprised only 2.5 to 4% and $<$1% of total emergents, respectively (Table 1).

In 1993, in both parks, *Betula lenta* seedlings accounted for the greatest number of tree emergents, followed by *Liriodendron tulipifera* (Table 2). *Liquidambar styraciflua* and *Ailanthus altissima* seedlings emerged at relatively low densities (a few dozen per m^2), while the other three tree species had only a dozen or fewer emergents per m^2 (Table 2). *Rubus* spp. was the only shrub taxon common to the seed banks of both parks and had the second-to-third greatest emergent density of all the woody taxa in each park (Table 2). The only other shrub species, *Aralia spinosa*, was found in only a single plot in Van Cortlandt Park, where it was present at densities $\leq$ 21/m^2 (Table 2). The three vine species that emerged from the seed bank samples had densities ranging from 13 to 42 per m^2 (Table 2). The estimated total germinant density in Van Cortlandt Park was 5373 m^{-2} without ferns and 9651 m^{-2} with ferns included (Table 3).

Table 1. Total number and percent total of emergents of each growth form for seed bank samples collected in 1993 and 1994 from forest plots in Van Cortlandt Park and Pelham Bay Park in New York City. For 1993 samples, both soil depth fractions are combined. For 1994 samples, only the 0–5 cm depth fraction was collected (see Sampling Methods). Percent totals of each growth form were calculated both including and excluding ferns

	Van Cortlandt Park 1993			Pelham Bay Park 1993			Van Cortlandt Park 1994			Pelham Bay Park 1994		
Growth form	*N*	% inc. ferns	% not inc. ferns	*N*	% inc. ferns	% not inc. ferns	*N*	% inc. ferns	% not inc. ferns	*N*	% inc. ferns	% not inc. ferns
Graminoids	1423	31.5	56	732	44.5	67	200	21.5	42	73	18.5	37.5
Forbs	511	11	20	137	8	12.5	132	14	27.5	39	10	20.5
Vines	34	<1	1.5	12	0.5	1	10	1	2.5	10	2.5	5
Shrubs	184	4	7	41	2.5	4	60	6.5	12.5	5	1.5	2.5
Trees	381	8	15	170	10	15.5	72	7.5	15	67	17	34.5
Ferns	2015	44	NA	550	33.5	NA	462	49.5	NA	201	50.5	NA
Total inc. ferns	4548			1642			936			395		
Total not inc. ferns	2533			1092			420			194		

Table 2. Mean number of emergents m^{-2} ($\pm$SE) of each woody species in each soil depth fraction for seed bank samples collected in 1993 and 1994 from forest plots in Van Cortlandt Park (VCP) and Pelham Bay Park (PBP). In 1994, only the 0–5 cm depth fraction was collected (see Sampling Methods)

	VCP 1993		PBP 1993		VCP 1994	PBP 1994
Species	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	0–5 cm
Trees						
Ailanthus altissima	28 ± 13	9 ± 4	17 ± 4	9 ± 9	38 ± 29	25 ± 15
Betula lenta	529 ± 300	45 ± 25	302 ± 155	55 ± 28	106 ± 48	178 ± 92
Carya cordiformis	—	—	—	—	4 ± 4	—
Liquidambar styraciflua	25 ± 14	—	59 ± 59	—	21 ± 17	43 ± 43
Liriodendron tulipifera	125 ± 55	21 ± 8	238 ± 108	25 ± 19	127 ± 53	204 ± 97
Morus alba	4 ± 3	13 ± 13	4 ± 4	4 ± 4	9 ± 5	—
Rhus spp.	4 ± 3	4 ± 3	—	4 ± 4	—	—
Robinia pseudoacacia	—	—	—	4 ± 4	—	—
Ulmus americana	—	—	—	—	—	119 ± 47
Shrubs						
Aralia spinosa	9 ± 9	—	—	—	21 ± 21	—
Rubus spp.	231 ± 104	151 ± 71	81 ± 33	93 ± 11	233 ± 130	43 ± 23
Vines						
Celastrus orbiculatus	19 ± 5	23 ± 18	13 ± 7	9 ± 9	25 ± 21	9 ± 9
Lonicera japonica	—	—	17 ± 17	—	—	17 ± 17
Parthenocissus quinquefolia	23 ± 13	4 ± 4	13 ± 13	—	17 ± 13	59 ± 59

Table 3. Mean number of emergents m^{-2} (±SE) for each growth form and soil depth for seed bank samples collected in 1993 and 1994 from forest plots in Van Cortlandt Park (VCP) and Pelham Bay Park (PBP). In 1994, only the 0–5 cm depth fraction was collected (see Sampling Methods)

	VCP 1993		PBP 1993		VCP 1994	PBP 1994
Growth form	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	0–5 cm
Graminoids	1236 ± 662	1786 ± 686	968 ± 360	2140 ± 1177	849 ± 339	620 ± 242
Forbs	592 ± 85	484 ± 98	314 ± 88	267 ± 53	552 ± 184	340 ± 174
Vines	47 ± 10	32 ± 18	43 ± 11	9 ± 9	51 ± 26	85 ± 73
Shrubs	240 ± 104	151 ± 71	81 ± 33	93 ± 11	255 ± 126	43 ± 23
Trees	715 ± 311[a]	91 ± 27[a]	620 ± 99[b]	102 ± 0[b]	306 ± 49[c]	569 ± 90[c]
Ferns	3055 ± 705	1223 ± 476	1580 ± 1505	756 ± 706	1966 ± 763	1707 ± 1644
Total inc. ferns	5885 ± 725	3766 ± 420	3605 ± 874	3367 ± 883	3979 ± 737	3363 ± 1719
Total not inc. ferns	2830 ± 384	2543 ± 381	2025 ± 198	2611 ± 538	2013 ± 345	1656 ± 195

[a]Indicates significant difference between soil depth fractions for Van Cortlandt Park 1993 samples.
[b]Indicates significant difference between soil depth fractions for Pelham Bay Park 1993 samples.
[c]Indicates significant difference in 1994 tree seed density between Van Cortlandt Park and Pelham Bay Park.

For Pelham Bay Park the total germinant density was 4637 m^{-2} without ferns and 6972 m^{-2} including ferns (Table 3).

Depth distribution

A total of 3622 individuals (58.5%) emerged from the 0–5 cm soil depth fraction and 2568 (41.5%) from the 5–10 cm fraction. The two parks had very similar patterns of depth distribution of growth forms (Table 3) and woody species (Table 2). Trees were the only growth form in which emergent density differed significantly between depths ($t = 2.74$; $p = .033$) with 89% of seedlings emerging from the 0–5 cm fraction in Van Cortlandt Park and 86% in Pelham Bay Park ($t = 7.24$; $p = .019$). There were no significant differences between Van Cortlandt Park and Pelham Bay Park in the mean number of emergents of any growth form or woody species in either depth fraction.

Delayed germination

One-half to three-quarters of all ferns, graminoids and forbs emerged during the first year of the two years of germination trials (Table 4). Ferns exhibited a great range in delayed germination, with 86% emerging in the first year in Van Cortlandt Park but only 48% emerging in the first year in Pelham Bay Park. The woody growth forms exhibited much less delayed germination, with 85–100% of the total seeds of trees, shrubs and vines emerging during the first year of the germination trials (Table 4). *Betula lenta*, *L. tulipifera* and *Rubus* spp. are the only woody taxa that exhibited delayed germination (Table 4). Fewer than a dozen seeds (mostly *L. tulipifera*) were found in the course of sieving the seed bank samples following two years of germination trials. None of these seeds were viable.

1994 seed bank samples

A total of 1331 germinants emerged from the (fewer) soil samples collected in 1994: 936 from Van Cortlandt Park and 395 from Pelham Bay Park. The relative abundance and mean density of the different growth forms were fairly similar to those in the 1993 samples (Tables 1 and 3). Ferns and graminoids were the

Table 4. Total number and percentage of individuals that emerged during the first of two years of germination trials from 1993 seed bank samples collected from Van Cortlandt Park and Pelham Bay Park. Data calculated for each plant growth form and each woody taxon that had less than 100% germination in the first year of the trials

	Van Cortlandt Park		Pelham Bay Park	
Growth form	%	*N*	%	*N*
Graminoids	73	1042	68	501
Forbs	54	277	51	70
Vines	97	33	100	12
Shrubs	91	168	90	37
Trees	87	333	85	144
Ferns	86	1725	48	265
Woody taxa				
Betula lenta	88	237	85	71
Liriodendron tulipifera	78	54	79	49
Rubus spp.	91	164	90	37

two largest groups again in 1994, but their relative abundances were somewhat different from 1993. Fern numbers increased from 33 to 44% in 1993 to 50% in 1994, whereas graminoids decreased from 31 to 45% in 1993 to approximately 20% of the total in 1994 (Table 1). Forbs, comprising 10 to 14% of all emergents, remained fairly consistent in their mean density estimates, species composition, and relative contribution to the seed bank from one year to the next. While no forb species were abundant in the seed bank, some of the more common forbs to emerge from the seed bank include the natives *Collinsonia canadensis*, *Eupatorium* spp., *Phytolacca americana*, *Solidago* spp., and the nonnatives *Alliaria petiolata*, *Commelina communis*, *Linaria vulgaris* and *Verbascum thapsus*. Some noteworthy native forest herb taxa that were present at relatively low densities ($<20\,m^{-2}$) include *Aster divaricatus*, *Erythronium* spp. and *Viola* spp.

Shrubs and vines, again, had the fewest emergents, comprising 1.5–6.5% of the total emergents (Table 1). Trees increased in Pelham Bay Park from 10% of total emergents in 1993 to 17% in 1994 (Table 1). Trees were also the only growth form that differed significantly between the two parks in 1994, with nearly twice the mean number of emergents in Pelham Bay Park as in Van Cortlandt Park (Table 3; $t = 2.73$; $p = .044$). This is largely due to the abundance of seeds of *Ulmus americana* in Pelham Bay Park samples in 1994 (Table 2). There were no significant differences between sampling years 1993 and 1994 in the mean number of emergents of any growth form or woody species for either park. The total germinant density in Van Cortlandt Park was 2013 m^{-2} excluding ferns and 3979 m^{-2} with ferns included (Table 3). For Pelham Bay Park, the total germinant density was 1656 m^{-2} excluding ferns and 3363 m^{-2} including ferns (Table 3).

Effectiveness of sampling design

The modified sampling design used in 1994 was associated with total seed density estimates that were lower, but not significantly so, than the estimates based on the 0–5 cm soil samples collected in 1993 (Table 3). However, in eight of the nine forest plots sampled, there were fewer woody taxa represented in the seed bank samples collected in 1994 than there were in those collected in 1993 (Table 5). Despite this decrease in species richness, four forest plots had one or two species present in the 1994 seed bank samples that had not been present in the 1993 samples. Of the fourteen woody taxa that emerged from the seed bank samples over the course of this entire study, the seeds of the three most abundant taxa, *B. lenta*, *L. tulipifera* and *Rubus* spp., accounted for 60–86% of all emergents.

Table 5. Total number of woody taxa identified from soil seed bank samples collected from each plot in Van Cortlandt Park (VCP) and Pelham Bay Park (PBP) in 1993 and 1994

Plot	1993	1994
VCP-1	7	5
VCP-2	5	4
VCP-4	7	5
VCP-5	6	6
VCP-6	8	4
VCP-9	8	5
PBP-2	6	5
PBP-5	7	6
PBP-10	7	5

Relationship between woody species in the seed bank and the vegetation: comparisons across nine plots

Most of the woody species (27 out of 39) that were present in the vegetation among these nine plots did not emerge from the seed bank samples. For each of the twelve woody species that did emerge from the seed bank, regression (correlation) analysis across all plots compared Importance Value of adult trees to abundance in the seed bank. For two native tree species, there was a significant positive correlation between Importance Values of adult trees and the number of emergents from the seed bank: *Lirodendron tulipifera* ($r^2 = 0.65$, $p < .005$, Fig. 3a) and *Liquidambar styraciflua* ($r^2 = 0.73$, $p < .002$, Fig. 3b). For *Betula lenta*, another native tree species, there was no significant correlation between Importance Values of adult trees and the number of emergents from the seed bank ($r^2 = 0.31$).

Rubus spp., one of the two shrub taxa in the seed bank, emerged from the samples of all nine plots. It was present in the vegetation of only four of the nine plots, yet there was a significant positive relationship between the seed bank and the aboveground vegetation ($r^2 = 0.66$; $p < .005$; Fig. 3c).

Two nonnative tree species occurred in the seed banks of the forest stands in these parks, *Ailanthus altissima* and *Morus alba*. Seedlings of *A. altissima* emerged from the seed bank samples from every plot even though it was present among adult trees of only two plots. There was no significant correlation between Importance Values of adult trees and the number of emergents from the seed bank for *A. altissima* ($r^2 < 0.001$). Similarly, seedlings of *M. alba* emerged from the seed bank samples of five plots yet was not present among adult trees of any plot and so was not analyzed by regression. Both of these species had some seedlings emerge from both the 0–5 cm and the 5–10 cm depth fractions.

Two nonnative vine species occurred in the seed banks of the forest stands in these parks, *Celastrus orbiculatus* and *Lonicera japonica*. Seedlings of *C. orbiculatus* emerged from the seed bank samples from seven of the nine plots and was present in the vegetation of six plots. But there was no significant relationship between the seed bank and the vegetation ($r^2 = 0.22$). By contrast, *L. japonica* seedlings emerged from the seed bank samples of only two plots, and it was present in the vegetation of four plots, yet there was a significant positive relationship between the seed bank and the vegetation ($r^2 = 0.58$; $p < .02$; Fig. 3d).

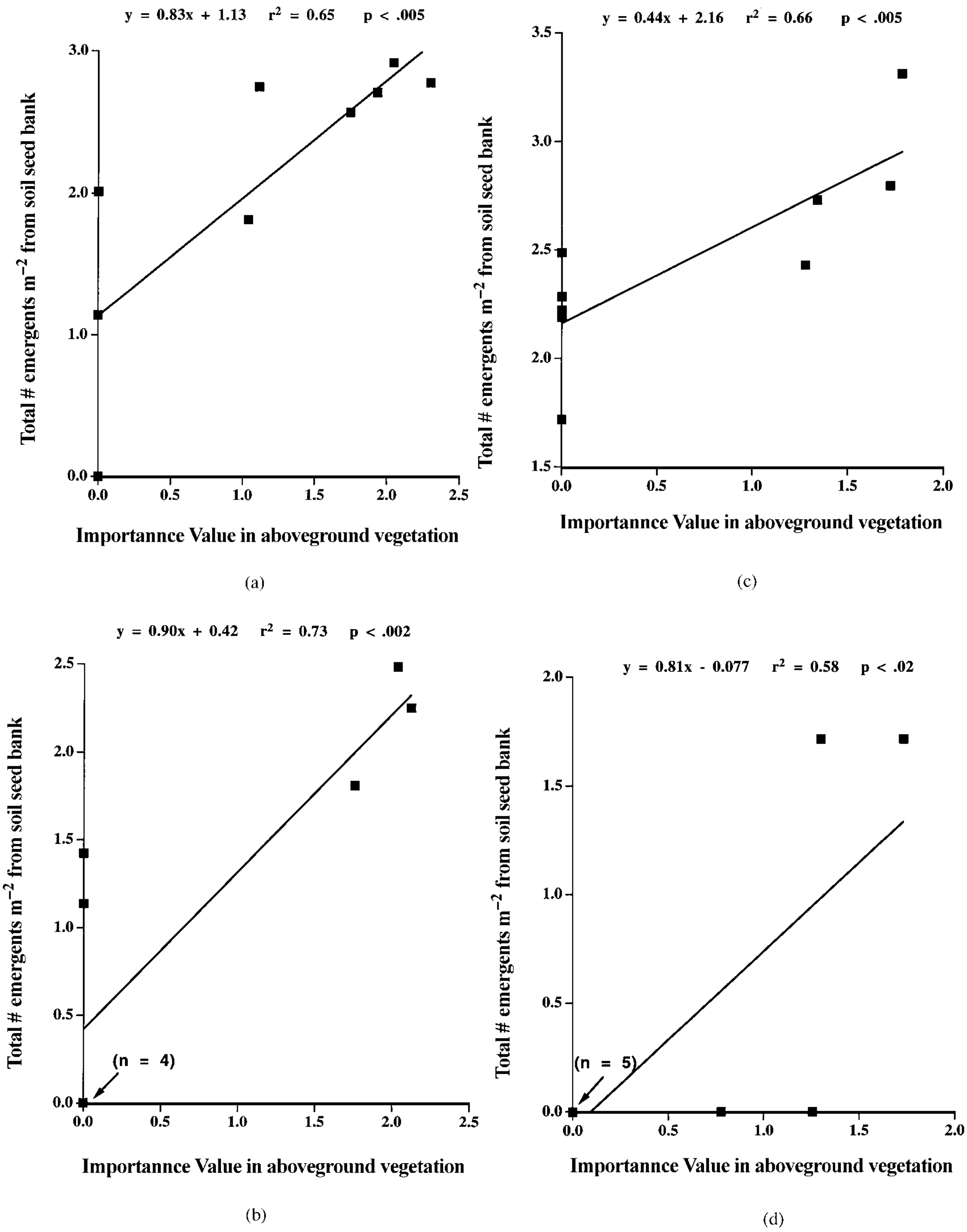

Figure 3a–d. Regression of the total number of emergents of (a) *Liriodendron tulipifera*, (b) *Liquidambar styraciflua*, (c) *Rubus* spp. and (d) *Lonicera japonica* from the seed bank against Importance Value of the species in the aboveground vegetation. Each point represents a different plot in either Van Cortlandt Park or Pelham Bay Park, Bronx, NY. Importance Values are from McDonnell *et al.*, (in prep.). (Seed bank and Importance Value data were log($x+1$) transformed prior to analysis.)

Discussion

The forests of Van Cortlandt Park and Pelham Bay Park were very similar in soil seed bank composition and density for each of the two years of this study. Graminoids and ferns, combined, consistently accounted for at least 70% of all germinants in each year, and there were no significant differences in their mean densities between parks or years. However, the shift in relative abundance of these two groups (ferns increased from 33 to 44% in 1993 to 50% in 1994, while the graminoids decreased from 31 to 45% in 1993 to 20% in 1994) may be a consequence of the modified sampling method used in 1994, in which only the 0–5 cm soil fraction was collected. Based on our 1993 findings, ferns tended to be more concentrated in the 0–5 cm soil fraction, whereas graminoids tended to be more concentrated in the 5–10 cm soil fraction. By collecting only the top 5 cm of soil in 1994, we may have biased our sampling to include more ferns and fewer graminoids.

Some temperate fern species form persistent soil spore banks that may contribute to their spatial and temporal dispersal (Dyer and Lindsay, 1992). While some recent seed bank studies have included data on ferns (Mladenoff, 1990; Beatty, 1991; McGee and Feller, 1993), most have not. Since hundreds to thousands of ferns may emerge from soil samples (McGee and Feller, 1993), they can greatly influence seed/spore bank density estimates, as evidenced by this study, and should be similarly reported in future seed bank studies. We also found a low correspondence between the density of ferns in the seed/spore bank and the Importance Value of ferns in the aboveground vegetation. This is consistent with an ability to form persistent soil spore banks.

Trees were, by far, the most abundant of the woody growth forms in the seed banks of these forests. This is also the growth form that exhibited the greatest differences in depth distribution (0–5 cm > 5–10 cm in both parks) and site location (PBP > VCP in 1994). *Betula lenta*, *Liriodendron tulipifera* and *Rubus* spp. were the three most abundant woody taxa and were also the only woody taxa to exhibit delayed germination. All three of these species were also present in the seed bank of one-half to twice as many more plots as those in which they were present in the vegetation, an indication of their dispersal abilities.

Liriodendron tulipifera and *Rubus* spp., along with *Liquidambar styraciflua*, had positive relationships between their abundance in the seed bank and their Importance Value in the vegetation. None of these taxa were present in the vegetation of any plot without also being in the seed bank. However, this method of determining correspondence may be rather limited based on the other five taxa that exhibited no relationship between the vegetation and the seed bank.

Of the fourteen woody taxa represented in the seed banks of these forests, four were nonnative (two trees and two vines). Three of these species, *A. altissima*, *M. alba* and *C. orbiculatus*, were present in the seed bank of more plots than those in which they were present in the vegetation. Only *L. japonica* was in the vegetation of more plots than it was in the seed bank. It was also the only nonnative species that had a positive correlation between the seed bank and the vegetation. This relationship was most likely driven by its absence from both the seed bank and the vegetation in five of the nine plots. Its greater presence in the vegetation than in the seed bank suggests that *L. japonica* may spread more by vegetative growth than by dispersal of its seeds within these forests.

Comparisons to other seed bank studies

We compared the results of our seed bank study to those of other deciduous forests of similar age (70 to approximately 100 years old) located in the northeastern U.S. and southeastern Canada (Table 6). The predominant species of the forests differ somewhat among these studies, and from our own, but we feel that the similarities in age, geographical region, and deciduous nature are sufficient for looking at general patterns of seed bank properties.

The methods used in a seed bank study can affect density estimates and should be taken into consideration when comparing studies (Simpson *et al.*, 1989). Among the studies we used, the area of the samples collected ranges over two orders of magnitude but does not correspond to any particular pattern of estimated seed density or woody species richness.

Table 6. Summary of seed density estimates (# m^{-2}), sample area and depth from studies of soil seed banks in temperate deciduous forests in northeastern U.S. Included are the age (years) of the stands studied and the total area of soil samples collected per site. Ranges of values are presented for studies that included more than one community

Reference	Dominant forest taxa	Stand age (years)	Mean seed density (# m^{-2})	Total area sampled (m^2)	Sample depth	Method	Woody seed density (# m^{-2})	Woody species richness
Moore and Wein 1977	Betula-Fagus Acer-Fagus	90 90	3400 ± 970 1950 ± 620	0.1	10 cm organic + 6 cm mineral soil	emergence 5 wks sieving & viability	>90% *Rubus* spp.	3
Graber and Thompson 1978	Fagus-Betula-Acer Fraxinus	95	1615	0.0447	L - F, H horizons +5 cm mineral soil	emergence 3 yrs	1599	15
Olmsted and Curtis 1947	Fagus-Betula-Acer	110	91	0.3716	duff, humus, top layer mineral soil	sorting and counting germination 60 days	82	2
Marquis 1975	Prunus-Acer	70 100+	302 110	2.32	10 cm deep	emergence 16+ wks sieving, germ. 30 days	291 105	7
Beatty 1991	Acer-Fraxinus-Ostrya (mounds vs. pits)	100–150	mound = 162 pit = 133	1.8	5 cm deep	emergence 2 yrs	13 10	2
Roberts and Vankat 1991	Acer-Ulmus	90	2776	0.0785	12 cm deep	emergence 12+ wks	~38	1
Kostel-Hughes *et al.* (this study)	Quercus-Carya-Acer-Liriodendron-Liquidambar	80–100	1993 4636–5373 (no ferns) 6972–9651 (with ferns) 1994 1656–2013 (no ferns) 5019–5992 (with ferns)	1993 0.0785/stand 0.706 total 1994 0.0393/stand 0.353 total	1993 10 cm deep 1994 5 cm deep	emergence 2 yrs	1993 948–1276 1994 612–697	1993 5–8 1994 4–6

The depth to which samples are collected can be based on soil horizons (Olmsted and Curtis, 1947; Graber and Thompson, 1978), vertical measurement (Marquis, 1975; Beatty, 1991; Roberts and Vankat, 1991; this study), or both (Moore and Wein, 1977), and researchers may include or exclude litter. Again, there is no consistent correspondence between sampling depth and density or species richness of the seed banks we compared. In contrast to other studies that reported a tendency for overall density of emergents to decline with depth (Moore and Wein, 1977; Graber and Thompson, 1978), we found that this was significant only for tree seeds in our study, although there was a similar trend for ferns as well. Graminoid density, on the other hand, tended to increase with depth. Our urban forests have an abundance of nonnative earthworm species, including some lumbricids (Steinberg *et al*., 1997), which forage at the surface and form deep permanent burrows (Edwards and Bohlen, 1996). These activities may result in greater vertical mixing of the soil and the seeds/spores therein. This would more greatly affect small, smooth and compact seeds than the larger seeds of most tree species (Thompson, 1987).

Another concern is the method of determining seed bank density – direct counting with viability testing versus seedling emergence. All the studies in our comparison utilized the emergence method to some degree. Duration of germination trials ranged widely among studies, lasting from five weeks (Moore and Wein, 1977) to three years (Graber and Thompson, 1978). The other studies that monitored emergence for more than one year found that most germination ($>$90%) occurred in the first year (Graber and Thompson, 1978; Beatty, 1991). Similar to our findings, Marquis (1975) and Graber and Thompson (1978) reported *Betula* spp., *Rubus* spp. and *L. tulipifera* among the woody taxa exhibiting delayed germination. In our study, 21–37% of total emergents, mostly ferns, forbs and graminoids, germinated in the second year of our trials, which increased the overall estimates of seed bank density for these parks by thousands per square meter. This suggests that the duration of germination trials may be at least as important as the total area sampled in estimating seed bank density by the emergence method.

The estimated mean densities (with and without ferns) of the soil seed banks of the urban forests in our study tended to be above the range found in the other studies. This difference can be attributed to the large numbers of both fern and graminoid germinants from our forests. Of the studies that reported seed bank densities in the thousands per m^2, only Roberts and Vankat (1991) had a large percentage of graminoids (65% of seed bank was *Juncus* spp.). Only Beatty (1991) reported ferns in her study, and although they comprised large percentages of the emergents (76% in mounds and 46% in pits), mean density of ferns was one-hundredth of the fern mean densities in our study.

Rubus spp. and *Betula* spp., both of early successional status, often comprise large percentages of the seed bank in temperate deciduous forests (see review by Pickett and McDonnell, 1989). In our study, as well as those by Marquis (1975), Moore and Wein (1977), and Graber and Thompson (1978), *Betula* spp. seeds comprised the majority of tree seeds in the seed banks, regardless of presence or absence in the vegetation. Likewise, in all the studies but one (Roberts and Vankat, 1991), *Rubus* spp. was the sole or dominant shrub taxon present in the seed bank.

Species that were not among the emergents in this study despite their presence in the vegetation include *Acer* spp., *Quercus* spp., *Fraxinus americana*, *Cornus florida* and *Sassafras albidum*. In fact, *Quercus rubra* exhibited a mast year in the fall of 1993 (A. Emmerich, City Parks Foundation, personal communication). Since these species produce relatively large seeds and fruits that are often preferred by vertebrates, seed predation may partly account for their absence from the seed bank. These findings are similar to those of other studies in which these tree species are absent or at very low densities in seed banks, even when dominant in the vegetation (Olmsted and Curtis, 1947; Marquis, 1975; Moore and Wein, 1977; Graber and Thompson, 1978; Beatty, 1991; Roberts and Vankat, 1991).

One of the more widely held generalizations about seed banks in temperate deciduous forests is their lack of correspondence with the aboveground vegetation (Pickett and McDonnell, 1989; Warr *et al*., 1993). This is usually based on the comparatively low number of species shared by both the seed bank and the vegetation (Staaf *et al*., 1987; Beatty, 1991; McGee and Feller, 1993; Warr *et al*., 1994) and/or divergence in the relative contribution of a species to the seed bank (number of emergents/total) and the vegetation (percent cover) (Pratt *et al*., 1984; Morgan and Neuenschwander, 1988; Warr *et al*., 1993). Plant species exhibit a wide range of reproductive strategies, especially with regard to seed production and dormancy, which tend to decline with successional age (Roberts and Vankat, 1991). Consequently, it should not be surprising that the relative abundance of many late successional species may not correspond to their relative abundance in the seed bank. Therefore, rather than base correspondence on the abundance of a species relative to all others in the seed bank and vegetation (across species, within sites), we determined the relationship between the contribution of each species to the seed bank (based on number/m^2) and the vegetation (based on Importance Values) among different sites (within species, across sites). Using a similar approach, Marquis (1975) found significant positive correlations between the number of seed bank emergents and the overstory basal area for four of six tree species in his study. However, only four of nine woody taxa in our study exhibited any relationship.

Compared to the other seed bank studies in northeastern deciduous forests, the seed banks of Van Cortlandt Park and Pelham Bay Park had the second greatest woody species richness, after Graber and Thompson (1978) with fifteen taxa. The Van Cortlandt Park seed bank had eleven woody taxa total, but species richness for the individual plots ranged from 5 to 8 taxa. The seed bank of Pelham Bay Park had a total of twelve woody taxa with a range of 6 to 7 taxa per plot. Marquis (1975) reported seven woody taxa in the seed banks of the 70 year stand and the 100+ year stand, while the other studies reported three or fewer. However, the comparatively high species richness of the urban forests is partly due to the four nonnative species present, which increased woody species richness of these forests by 40%. None of the other seed bank studies reported nonnative species in the seed bank, although two nonnative species were present in the vegetation of the site studied by Roberts and Vankat (1991). In a companion study, Vankat and Snyder (1991) report *Lonicera maackii* as having importance percentages of 24 in the ground layer and 39 in the understory, while *L. japonica* had an importance percentage of 4 in the ground layer. These findings, in addition to our own, suggest that *L. japonica* and *L. maackii* may not depend as heavily on reproduction by seed in these stands and so may be uncommon in the seed bank. In fact, Luken and Mattimiro (1991) found that forest-grown *L. maackii* had an average of one-third as many seeds in the soil seed bank as open-grown *L. maackii*, and they suggest that resources allocated to an annual release of large stem cohorts in the forest-grown *L. maackii* are not available for seed production.

Conclusions and management implications

The seed banks of the urban forests in this study are similar in many ways to those of nonurban northeastern deciduous forests reported in the literature. The primary difference is the presence of seeds of invasive nonnative woody species in the urban forest seed banks. Efforts by managers to eliminate these species from forests typically include clearing them from large areas where they have grown over much of the other vegetation. However, these efforts tend to disturb the forest floor and increase light levels. Therefore, such management strategies could prove counterproductive if they encourage germination of these nonnative species from the seed bank. Care should be taken to minimize such disturbance, possibly by clearing areas more gradually. Some of these species, particularly *A. altissima*, *C. orbiculatus* and *L. japonica*, can also dominate a community because of their ability to spread vegetatively. This study indicates that these species can also spread into other stands via their seeds. Therefore, if resources allow, managers should remove individuals of these species before they become reproductive (even at some distance from the site) and recognize that ongoing attention to potential recruitment from seeds may be needed.

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Appendix 1. Species in the aboveground vegetation (according to a 1992 survey) of selected forest plots (included in this study) in Van Cortlandt Park and Pelham Bay Park, Bronx, NY. An * indicates species that were also identified in the seed bank of these parks

Trees, shrubs and vines	Herbs	Graminoids	Ferns
Acer negundo	*Alliaria petiolata**	*Carex* spp.*	*Athyrium filix-femina*
Acer platanoides	*Amphicarpaea bracteata**	*Panicum* spp.*	*Onoclea sensibilis*
Acer rubrum	*Apocynum cannabinum*	*Panicum clandestinum*	*Thelypteris noveboracensis*
Acer saccharum	*Aralia nudicaulis*	*Poa* spp.	
*Ailanthus altissima**	*Aralia racemosa*		
*Aralia spinosa**	*Arisaema triphyllum*		
*Betula lenta**	*Aster cordifolius*		
Carpinus caroliniana	*Aster divaricatus**		
*Carya cordiformis**	*Boehmeria cylindrica*		
Carya glabra	*Cimicifuga racemosa*		
Carya tomentosa	*Circaea lutetiana**		
*Celastrus orbiculatus**	*Collinsonia canadensis**		
Cornus florida	*Commelina communis**		
Cornus racemosa	*Desmodium canescens*		
Euonymus alatus	*Desmodium paniculatum**		
Fagus grandifolia	*Duchesnea indica*		
Fraxinus americana	*Eupatorium dubium*		
Juglans cinerea	*Eupatorium maculatum*		
Lindera benzoin	*Eupatorium purpureum*		
*Liquidambar styraciflua**	*Eupatorium rugosum*		
*Liriodendron tulipifera**	*Eupatorium* spp.*		
*Lonicera japonica**	*Fragaria* spp.*		
*Morus alba**	*Fragaria vesca*		
Morus rubra	*Fragaria virginiana*		
Nyssa sylvatica	*Galium* spp.		
*Parthenocissus quinquefolia**	*Geranium maculatum*		
Prunus avium	*Geranium* spp.		
Prunus serotina	*Geum canadensis*		
Prunus virginiana	*Geum* spp.*		
Quercus alba	*Impatiens capensis*		
Quercus bicolor	*Lysimachia quadrifolia*		
Quercus rubra	*Maianthemum canadense*		
Quercus velutina	*Oxalis* spp.		
Rhamnus frangula	*Polygonatum biflorum*		
Rosa multiflora	*Polygonum virginianum**		
Rubus allegheniensis	*Smilacena racemosa*		
Rubus spp.*	*Solidago caesia*		
Sassafras albidum	*Solidago* spp.*		
Sambucus canadensis	*Symplocarpus foetidus*		
Smilax herbacea	*Viola* spp.*		
Toxicodendron radicans			
*Ulmus americana**			
Vaccinium spp.			
Viburnum acerifolium			
Viburnum dentatum			
Viburnum prunifolium			
Vitis spp.			

Note: Not all graminoids and herbs in the seed bank samples were identified to genus or species. Some identifications from the seed bank were tentative and so are not included. Ferns were removed at the gametophyte stage and no further identifications were attempted.

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