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SEEDBANKS IN SEVERAL RECENTLY CLEAR-CUT AND MATURE HARDWOOD FORESTS IN NOVA SCOTIA

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Forest floor organic layers from three 75-year-old hardwood stands were examined for the occurrence of early successional species in the seedbanks prior to disturbance. In addition, two 5-year-old hardwood clear-cuts were examined in order to compare the seedbanks of immature and mature stands. One clear-cut had a total number of germinants that was intermediate to those of the mature stands. The other clear-cut had a much larger seedbank. Species composition of the seedbanks varied considerably among the stands. However, each mature stand had several species in the seedbanks that were not present as adult plants e.g., *Aster* spp., *Rubus* spp., *Prunus pensylvanica,* and *Sambucus pubens. Prunus pensylvanica* was found to be a relatively minor component of the seedbanks, whereas *Rubus idaeus* was found to be relatively abundant in the seedbanks of the mature stands. Regeneration strategies are discussed for the more important species present in the seedbanks.

Les couches organiques du sol de trois associations de bois dur agées de 75 ans ont été examinées dans le but de détecter la présence, parmi l'ensemble des graines présentes des espèces appartenant aux premiers stades de succession et ce, avant perturbation. De plus, deux coupes claires de bois dur, agrées de 5 ans, ont été examinées dans le but de comparer l'ensemble des graines présentes dans des associations matures et immatures. Un coupe claire avait un nombre total de graines germées intermédiaire de ceux des associations matures, tandis que l'autre avait un nombre plus grand. La composition spécifique que l'ensemble des graines variait considérablement parmi les differentes associations. Cependant, chaque association mature possédait plusieurs espéces de graines qui n'étaient pas représentées parmi les plantes adultes e.g., *Aster* spp., *Rubus,* spp., *Prunus pennsylvanica,* et *Sambucus pubens.* Il a été noté que *Prunus pennsylvanica* représentait une composantes mineuse de l'ensemble des graines tandis que *Rubus idaeus* etait relativement abondant dans les associations matures. Les stratigées de régéneration sont discutées pour les espèces les plus abondamment représentées dans l'ensembles des graines.

Introduction

Succession in a forest is disrupted by major disturbances, such as harvesting or fire. The initial response of the vegetation includes a proliferation of ruderal plant species, usually mixed with some surviving later-successional species. For example, seedlings of some species that occurred prior to the disturbance appear with seedlings of species that are only associated with early series. These seedlings, along with vegetative survivors of the disturbance, serve to re-colonize the site.

Seedbanks, which have developed from the accumulation of viable seeds over the stand's history, are partially responsible for the regeneration by sexual propagules (Oostings & Humphreys 1940; Olmstead & Curtis 1947; Marks 1974; Johnson 1975; Marquis 1975; Moore & Wein 1977; Bormann & Likens 1979). Seed inputs leading to the development of these seedbanks occur from the following sources: (i) exogenous seed dispersed by wind and animals from surrounding sites, and (ii) endogenous seed produced *in situ* over the course of time. The longevity of seed viability varies among plant species which, in combination with annual seed production, will affect the contribution to the seedbank.

Grime (1979) divided the seedbank into two components: (i) transient-seed viability lasting for one year, and (ii) persistent-most seed remaining viable for more than one year. Livingston and Allessio (1968) found that most species exhibiting a buried seed strategy were herbaceous. Although Harper (1977) stated that tree seeds were rarely present in seedbanks, Marks (1974) found pin cherry (*Prunus pensylvanica* L.) seeds to be an exception.

From a silvicultural point of view, the post-disturbance establishment of a vigorous and competitive plant community from the seedbank may be a problem, since the successful regeneration of desired tree species may be impeded by this vegetation (Olmstead & Curtis 1947; Graber & Thompson 1978). Ecologically, however, the rapid establishment of vegetation on a disturbed site may contribute to the recovery of site stability by minimizing soil erosion and nutrient loss (Marks 1974; Bormann & Likens 1979). For example, Bormann & Likens (1979) measured significant nutrient losses from a clear-felled watershed that had been subjected to three years of herbicide treatments to retard revegetation.

The purpose of this study is to investigate the size and species composition of the seedbanks of a hardwood forest in Nova Scotia. By identifying the relative proportion of early and late successional species in two age-classes of hardwood stands, it will be possible to determine whether ruderal species exist in the seedbanks of mature stands prior to disturbance. In addition, the regeneration strategies adopted by the more important species present will be discussed.

Study sites

The five stands used in this study were located in a hardwood forest in central Nova Scotia (44°55′N, 65°44′W) in an area mapped by Loucks (1962) within the Sugar maple-Hemlock-Pine Zone. The three mature stands originated approximately 75 years ago following a fire (Freedman *et al.*, 1981). Site A was dominated by sugar maple (*Acer saccharum* Marsh) and red maple (*A. rubrum* L.), with lesser amounts of yellow birch (*Betula allegheniensis* Britt.) and white birch (*B. papyrifera* Marsh) (Table I). The total stem density was 1835/ha, and the total basal area was 32.1 m^2/ha. Shrub density (i.e., <5 cm diameter at breast height) was low in this stand, with only 300 stems/ha, mostly sugar maple.

Site B had 1580 trees/ha and a total basal area of 27.2 m^2/ha. It had an even distribution of hardwood species (Table I). Shrubs (total stem density of 2360/ha) consisted mostly of sugar maple, with smaller quantities of red maple and striped maple (*Acer pensylvanicum* L.) also present.

Site C consisted mainly of red maple and white birch (Table I). The total stem density was 1300 trees/ha, with a basal area of 18.9 m^2/ha. Shrubs were diverse and abundant (7320 stems/ha) with alder (*Alnus* app.), witherod (*Viburnum cassinoides* L.), red maple, and beech (*Fagus grandifolia* Ehrh.) being the most common.

The remaining two sites were clearcut 5 years previously and were dominated by (i) stump sprouts of hardwood trees and shrub species, and (ii) a dense ground vegetation consisting of a diverse mixture of ruderal plant species. The shrub-sized vegetation of Site D was mainly red maple and alder, with smaller quantities of beech and pin cherry. The total stem density was 23,600/ha. Red maple and white birch were most abundant in Site E, with lesser amounts of pin cherry, white ash (*Fraxinus americana* L.), sugar maple, and raspberries (*Rubus* spp.). Total shrub stem density was 36,800/ha.

Methods

In November, 1981, samples were collected from six 50 cm x 50 cm quadrats at each 75-year-old stand, and three quadrats in each 5-year-old stand. All organic forest floor material down to the mineral soil was collected and taken to the laboratory. Following 1 1/2 months of storage at below-freezing temperatures, each sample was mixed and spread to a depth of ca. 2 cm in plastic trays. These

Table I Density and dominance of tree species in the three uncut hardwood stands[1,2]. Values expressed as percentages.

Species	Stand A		Stand B		Stand C	
	Relative Density	Relative Dominance	Relative Density	Relative Dominance	Relative Density	Relative Dominance
Acer rubrum	37.9	41.8	26.9	32.4	48.8	45.4
Betula papyrifera	11.7	19.5	33.5	33.9	35.8	44.8
B. alleghaniensis	14.7	12.2	21.5	12.4	6.5	4.6
Picea rubens	0.5	0.1	2.2	4.1	0.8	0.1
Amelanchier spp.	a	a	a	a	0.4	0.3
Pinus strobus	a	a	a	a	6.1	3.8
Fagus grandifolia	2.2	0.5	1.0	0.5	0.8	0.3
Alnus spp.	a	a	a	a	0.4	0.1
Picea glauca	a	a	a	a	0.4	0.6
Acer saccharum	33.0	25.9	14.6	16.6	a	a
Acer pensylvanicum	a	a	0.3	0.1	a	a
Total	1835 trees/ha	32.09 m^2/ha	1580 trees/ha	27.21 m^2/ha	1300 trees/ha	18.86 m^2/ha

[1]a = absent from stand
[2]Data collected in five 20 m x 20 m plots per stand.

trays were kept in a greenhouse, where they received daily waterings and a 16h artificial light regime which supplemented the mid-winter natural sunlight. All seedlings in the trays were harvested after 75 d. Then the soils were mixed again and placed back in the greenhouse to extract more germinants. After a further 30 d, the germination trials were terminated. Since the soil samples were collected in November, both buried seed and the current season's input of viable seed would be included in the seedbank. The germinated seeds were allowed to develop to facilitate identification, which follows the nomenclature of Roland & Smith (1969).

Stand descriptions of the trees and shrubs found in the sites are summarized in Tables I and II. In addition, observations of the various ground species in each site were made, but these data are not presented here. However, seedlings that appeared in the soil samples which were present in the vegetation of the sites are marked in Table III.

Results and Discussion

Germinated seeds from the five sites represented at least 37 genera of vascular plants, with seedbank composition varying considerably among the sites (Table III). The major difference between the mature and clear-cut sites was the higher proportion of ground vegetation species (mainly herbs) found in the latter (78 and 75% of all species in the clear-cuts, compared with 61% in the mature stands). Much of the ground vegetation was comprised of early successional species having a ruderal life history strategy (Grime 1979). Their short life cycle and high seed output ensure their rapid establishment and early prominence in disturbed environments.

Total seed germination ranged from ca. 700 to 4750/m^2. The largest seedbank was found in the clear-cut Site D, but the other clear-cut had a seedbank that was intermediate in size to that of the three uncut stands (Table III). The difference between the two clear-cuts can be attributed to the large quantities of *Rumex acetosella* and unidentified grasses at Site D, which accounted for 84% of the total number of germinated seeds at that site.

Harper (1977) generalized that early successional species tend to make a greater contribution to seedbanks than late successional species. In the 5-year-old stands (Sites D and E) and one 75-year-old stand (Site A), herb species that we consider to be early successional in nature contributed a high proportion of the total number of germinants (96,87, and 69% respectively). On the other hand, these species only contributed 28 and 20% of the total number of germinants in the other two 75-year-old stands (Sites B and C), where tree seeds dominated the seedbanks (Table III).

White birch was the most abundant tree species in the seedbank of all sites, accounting for 98% of all tree seeds that germinated. Frank and Safford (1970) found that birch seed remained viable in the soil for two years. Thus, its contribution to the seedbank would be transient since the amount of viable white birch seed found in any year is dependent upon a constant production of seed from mature plants. The fugitive strategy, as exhibited for trees by white birch, is common among early successional species (Marks 1974; Grime 1979). The lower density of white birch seed in the clear-cuts (71 and 79 seeds/m^2) compared with the mature stands (290, and 486 seeds/m^2) may be due to the lack of mature trees in the 5-year-old stands. Thus, exogenous seed input from surrounding uncut stands is necessary to maintain white birch in the clear-cut seedbanks.

Early successional species that were present in the seedbank, but not in the established vegetation, totalled 5, 10, and 7 species for the mature sites A, B, and

Table II Relative Shrub Density (As Percentages)

Species	Site A	Site B	Site C	Site D	Site E
Fagus grandifolia	3.3	3.4	13.1	6.4	4.4
Acer rubrum	1.7	22.0	19.1	46.6	30.5
Fraxinus americana	a	1.7	a	0.7	10.3
Acer saccharum	72.0	35.6	0.5	0.8	8.5
Betula papyrifera	1.7	1.7	3.3	a	19.9
Acer pensylvanicum	1.7	15.2	a	a	3.0
Amelanchier spp.	a	a	2.7	0.8	0.6
Hammenalis virginiana	1.7	a	2.2	a	a
Rhododedron spp.	a	a	7.6	a	a
Viburnum cassinoides	a	a	21.9	a	1.1
Pinus strobus	a	a	1.6	a	a
Abies balsamea	a	a	0.5	1.0	a
Alnus spp.	a	a	25.1	40.7	a
Betula alleghaniensis	10.0	11.9	1.1	a	a
Picea rubens	8.3	8.5	1.1	0.3	a
Populus tremuloides	a	a	a	0.2	2.0
Prunus pensylvanica	a	a	a	2.2	10.5
Rubus allegheniensis	a	a	a	a	2.9
Rubus idaeus	a	a	a	0.2	4.9
Salix spp.	a	a	a	a	1.3
Total (stems/ha)	300	2360	7320	23600	36840

[1]Density of shrubs (DBH <5 cm) in the five stands studied.
[2]a = absent from stand.
[3]Data were collected using ten 5 m x 5 m plots per stand.

Table III Seedbank Germinants ($\bar{x} \pm$ S.E., Values In Seeds/m^2).

Species	Site A	Site B	Site C	Site D	Site E
TREES					
Acer pensylvanicum L.	0.8 ± 0.8(P)[1]	— (P)	—	—	— (P)
Acer rubrum L.	2.8 ± 0.8(P)	2.0 ± 1.2(P)	0.8 ± 0.8(P)	— (P)	1.2 ± 1.2(P)
Betula alleghaniensis Britt.	1.2 ± 1.2(P)	— (P)	—	1.2 ± 1.2	—
Betula papyrifera Marsh.	290.0 ± 80.8(P)	460.0 ± 48.4(P)	486.0 ± 90.4(P)	70.8 ± 44.8(P)	78.8 ± 18.0(P)
Populus tremuloides Michx.	—	—	—	—	1.2 ± 1.2
Prunus pensylvanica L.f.	—	2.0 ± 1.2	2.0 ± 2.0	2.8 ± 2.8(P)	— (P)
SHRUBS					
Ribes spp.	—	1.2 ± 1.2	—	—	—
Rubus hispidus L.	—	0.8 ± 0.8	5.2 ± 4.0	— (P)	— (P)
Rubus idaeus L.	45.2 ± 34.4	112.8 ± 46.0	29.2 ± 17.6	117.2 ± 30.0(P)	26.8 ± 24.8(P)
Sambucus pubens Michx.	0.8 ± 0.8	8.0 ± 5.2	16.8 ± 14.4	— (P)	— (P)
Vaccinium myrtilloides Michx.	1.2 ± 0.8(P)	31.2 ± 30.4(P)	22.8 ± 7.2(P)	2.8 ± 1.2(P)	9.2 ± 9.2(P)
Viburnum cassinoides L.	—	0.8 ± 0.8(P)	— (P)	— (P)	— (P)
GROUND VEGETATION					
Anaphalis margaritacea (L.) C.B. Clarke	2.0 ± 1.2	7.2 ± 2.0	—	2.8 ± 1.2(P)	37.2 ± 37.2(P)
Aralia nudicaulis L.	0.8 ± 0.8	— (P)	1.2 ± 1.2(P)	1.2 ± 1.2(P)	— (P)
Aralia racemosa L.	—	—	—	—	2.8 ± 2.8
Aralia hispida Vent.	—	—	—	4.0 ± 4.0	—
Aster spp.	2.0 ± 1.2	2.0 ± 0.8	0.8 ± 0.8	70.8 ± 68.8(P)	53.2 ± 27.6(P)
Carex spp.	566.8 ± 449.6	89.2 ± 30.0	86.0 ± 38.8	273.2 ± 271.2(P)	21.2 ± 21.2(P)
Cornus canadensis L.	— (P)	— (P)	— (P)	4.0 ± 4.0(P)	1.2 ± 1.2(P)
Corydalis sempervirens (L.) Bernh.	—	—	—	—	1.2 ± 1.2
Epilobium angustifolium L.	—	6.8 ± 4.4	—	1.2 ± 1.2(P)	17.2 ± 17.2(P)
Fragaria virginiana Duchesne	—	—	—	—	100.0 ± 79.2(P)
Gramineae spp.	58.0 ± 54.0(P)	37.2 ± 18.0(P)	0.8 ± 0.8(P)	1838.8 ± 919.6(P)	380.0 ± 183.6(P)
Hieracium spp.	1.2 ± 0.8(P)	0.8 ± 0.8	—	1.2 ± 1.2(P)	45.2 ± 30.8(P)
Linnaea borealis L., var. *americana* (Forbes) Rehd.	—	—	—	4.0 ± 4.0	—
Lycopodium spp.	— (P)	0.8 ± 0.4(P)	— (P)	—	—

Maianthemum canadense Desf.	7.2 ± 4.0(P)	13.2 ± 6.4(P)	— (P)	21.2 ± 11.6(P)	22.8 ± 22.8(P)
Oxalis montana Raf.	34.0 ± 34.0(P)	1.2 ± 1.2	0.8 ± 0.8	—	—
Potentilla spp.	—	—	3.2 ± 1.6	—	—
Prenanthes spp.	— (P)	—	—	5.2 ± 5.2	—
Rumex Acetosella L.	—	—	—	2133.2 ± 1951.2(P)	1.2 ± 1.2(P)
Solidago rugosa Ait.	— (P)	17.2 ± 4.4(P)	18.8 ± 13.2(P)	161.2 ± 50.8(P)	76.0 ± 24.4(P)
Solidago spp.	—	0.8 ± 0.8	—	12.0 ± 12.0(P)	— (P)
Sonchus spp.	3.2 ± 3.2	4.0 ± 1.6	—	2.8 ± 1.2	—
Trientalis borealis Raf.	14.0 ± 9.2(P)	— (P)	12.8 ± 4.0(P)	1.2 ± 1.2	—
Veronica officinalis L.	—	—	4.8 ± 3.2	—	—
Viola spp.	64.8 ± 30.0(P)	59.2 ± 30.0(P)	13.2 ± 9.6(P)	16.0 ± 14.0(P)	14.8 ± 9.2(P)
Unknown	—	0.8 ± 0.4	0.8 ± 0.8	—	2.8 ± 1.2
TOTAL GERMINANTS	1096.0 ± 376.8	859.2 ± 127.6	706.0 ± 148.0	4748.8 ± 2230.0	894.0 ± 74.0
TOTAL TREE	294.8 ± 80.4	464.0 ± 48.4	488.8 ± 90.8	74.8 ± 48.8	81.2 ± 18.8
TOTAL SHRUB	47.2 ± 34.8	154.8 ± 62.4	74.0 ± 23.6	120.0 ± 30.4	36.0 ± 34.0
TOTAL GROUND VEGETATION	754.0 ± 422.0	240.4 ± 69.2	143.2 ± 63.2	4554.0 ± 2030.4	776.8 ± 75.2
TOTAL SPECIES	18	23	18	23	20
TOTAL TREES	4	3	3	3	3
TOTAL SHRUBS	3	6	4	2	2
TOTAL GROUND VEGETATION	11	14	11	18	15

[1]p = present in site vegetation.

C, respectively. These accounted for 28, 43, and 39% of the total number of species and 7, 16, and 9% of the total number of germinants in these respective sites. Harper (1977) predicted a difference between seedbank composition and the composition of the vegetation of the site. A life history that includes the buried seed and/or fugitive strategy helps promote this difference (Marks 1974; Grime 1979). In this study, examples of the buried seed strategy include the raspberries, pin cherry, and elders (*Sambucus* spp.), with asters (*Aster* spp.) exemplifying the fugitive strategy.

The asters and goldenrods (*Solidago* spp.), although not present on site, contributed 2.0 (Site A), 20.0 (Site B), and 19.6 (Site C) seeds/m^2 to the seedbanks of the mature stands. Many Asteraceae have a pappus and light seed which increase their dispersal range. However, in these cases, mobility has been favored over seed longevity (Harper 1977), which means that the contribution to the seedbank will be relatively transient. Therefore, species exhibiting the wind-dispersed fugitive strategy such as many Asteraceae, must rely upon large seed outputs in order to ensure successful establishment on disturbed sites within their dispersal range (Grime 1979).

Pin cherry is a well-documented example of a tree species that exhibits a buried seed strategy (Marks 1974). In a study in Pennsylvania, Marquis (1975) found 490 pin cherry seeds/m^2 in a stand, even though the species no longer occurred as mature trees. He suggested that the number of viable pin cherry seeds decreased as the time since pin cherry existed in the overstory increased. Marquis (1975) found that a sharp decrease in viability would be experienced once stand age increased beyond 70 years. In our study, two 75-year-old stands each had only 2 viable pin cherry seeds/m^2 and one 5-year-old site had 3 seeds/m^2. The values for the 75-year-old stands were lower than those found in other studies in northern hardwood stands (Marks 1974; Marquis 1975; Graber & Thompson 1978), although a similar value for a 5-year-old stand was reported by Graber and Thompson (1978). Lees (unpub. data 1980) also found pin cherry to be a minor component in the seedbanks of other hardwood stands in this area.

The low values for pin cherry may be related to the history of disturbance in the area. Mark's (1974) study of the life cycle of pin cherry showed that frequent disturbances were needed to promote a high density and, thus build large seedbanks. With few disturbances, the number of viable seeds decrease and avian dispersal of fruit becomes more important (Marks 1974). In the area we studied, disturbances have been infrequent, with harvesting only becoming important within the last decade, following the construction of a hardwood fibreboard mill nearby. Historically, fire would have been the major mode of disturbance. Cann *et al.*, (1965) stated that past fires were very intense, and that they destroyed much of the soil organic matter. This would also have destroyed most of the seedbank since many studies have shown that organic horizons contain many more seeds than the mineral soil (Leavitt 1963; Kellman 1970; Moore & Wein 1977; Graber & Thompson 1978).

In northern hardwoods, *Rubus* spp. will commonly dominate sites for the first few years following disturbances (Olmstead & Curtis 1947; Marks 1974; Moore & Wein 1977; Graber & Thompson 1978; Bormann & Likens 1979). We found *Rubus idaeus* to be abundant in the seedbanks of all sites. The site age classes did not exhibit any differences, with 117 and 27 seeds/m^2 in the 5-year-old sites, compared with 45, 113, and 29 viable seeds/m^2 in the mature stands. The high density in the uncut stands may be attributed to the ability of *Rubus* to persist for long periods in the seedbank (Graber & Thompson 1978), as well as to dispersal by birds and mammals (Olmstead & Curtis 1947; Martin *et al.*, 1951; Graber & Thompson 1978).

For example, Graber and Thompson (1978) estimated an annual deposition rate of ca. 0.7 *Rubus* seeds/m^2 in a study in New Hampshire. They also calculated that *Rubus* seeds remained viable in the soil for 50-100 years.

Although mature plants were not present in the uncut stands, *Sambucus pubens* was found in the seedbanks at a relatively high density, with 0.8, 8.0, and 16.8 viable seeds/m^2. *Sambucus* fruits are a preferred food for some birds, and these may have been important as agents of seed dispersal from nearby younger stands (Olmstead & Curtis 1947; Graber & Thompson 1978). *Sambucus* has been estimated to remain viable in the soil for up to 10-20 years (Graber & Thompson 1978).

In summary, the three mature stands had seedbanks similar in size to 5-year-old clear-cut (Site E). The other clear-cut had a much larger seedbank. In the seedbanks of the mature stands, early successional species were found in association with later successional species. Since some species were not present as mature plants, the presence of these early successional species in the seedbanks of the mature stands suggest their existence prior to disturbance. Some of the ruderal species are very persistent in the seedbank (e.g., *Prunus pensylvanica),* while others (e.g., *Betula,* Asteraceae) may be relatively ephemeral due to differences in seed longevity.

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