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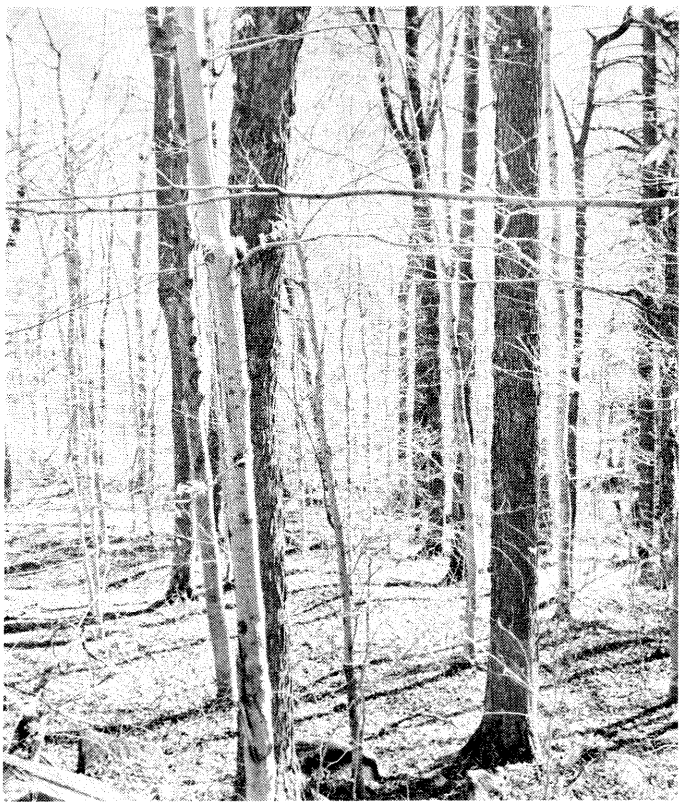
SEEDS IN THE ORGANIC LAYERS AND SOIL OF FOUR BEECH-BIRCH-MAPLE STANDS



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Abstract

Forest floor samples were collected in northern hardwood stands 5, 38, 95, and 200+ years old. The seeds contained in these samples were germinated in a greenhouse. Thirty-five species of herbs, shrubs, and trees were identified. The largest number of species, 23, were from the 5-year-old stand. The oldest stand had the fewest species, 17. *Rubus* and pin cherry (*Prunus pensylvanica* L.f.) were the most numerous of the buried seeds. Their total numbers were highest in the 5- and 38-year-old stands and much lower in the older stands. The current practice of timber harvesting at rotations of 100 years or more results in moderate densities of these plants. If short rotations are used, the increased densities of these species may require intensive silviculture practices to ensure adequate stocking of the high-value timber species.

INTRODUCTION

THE BEECH-BIRCH-MAPLE forest of the White Mountains of New Hampshire is a plant community with numerous checks and balances that help retain its natural stability. When the mature forest is harvested or destroyed, a secondary succession of shrubs and short-lived trees starts the process that will culminate in a high forest once again (Marks 1974). The typical regeneration sequence after the removal or destruction of a beech-birch-maple forest includes the early establishment of most of the species found in the mature forest. Woody shrubs such as *Rubus*[1] quickly dominate many sites, reaching a peak development in 2 to 5 years. Pin cherry ordinarily overtakes *Rubus*, and is in turn dominated by paper and yellow birch within 20 to 30 years after the disturbance. From this point, the mid- and late-successional species—red maple, white ash, sugar maple, and beech—become more important with each passing decade.

The rapid replacement of the harvested or destroyed forest by a secondary succession of short-lived woody species serves the important functions of conserving the soil and plant nutrients and stabilizing the soil until the more slowly developing high forest species again dominate the site.

The seed of some species that dominate New England forests in the first years after disturbance are present in the litter and soil before the overstory is removed (Frank and Safford 1970, Livingston and Allessio 1968, Marks 1974, Olmsted and Curtis 1947). Marquis (1975) has found a relationship between numbers of buried seed and stand age in Pennsylvania. But we know very little about the numbers and species of buried seeds in the beech-birch-maple forest, and especially about how this seed population changes over long periods of time. The purpose of this study was to determine the numbers and species of buried seeds in forest stands of widely differing ages.

[1] Common and scientific names are listed in Table 2.

METHODS AND MATERIALS

Four stands in the White Mountain National Forest were selected for this study:

(1) A 5-year-old northern hardwood stand that developed following the clearcutting of a mature beech-birch-maple stand in 1967 (Fig. 1).

(2) A 38-year-old northern hardwood stand that developed following the clearcutting of an old-growth beech-birch-maple stand in 1934 (Fig. 2).

(3) A mature beech-birch-maple stand 95 years old (Fig. 3). There was heavy cutting in this area in the early 1870s when red spruce and better quality hardwoods were removed.

(4) An undisturbed climax beech-birch-maple stand (Fig. 4). This virgin stand has had no major natural disturbance in more than 200 years.

Species composition was measured in the four stands. Basal area data were collected in the three older stands (Table 1a). Fresh-weight biomass data were used to measure composition in the 5-year-old stand (Table 1b).

In each stand, at 20 points selected at random, samples of the forest floor were collected. The material was dug from pits 22.36 cm^2 (8.8 in^2) and carefully divided into three groups: combined litter and fermented layers (L-F); the humus layer (H); and the upper 5 cm (2 in) of mineral soil (M). The material in each group from each stand was spread out in separate 30 cm^2 (11.8 in^2) flats (Fig. 5). The flats were placed in a greenhouse and irrigated with a misting system to provide conditions favorable for germination. Each seed that germinated was marked, grown until it could be identified, and then discarded. The greenhouse was screened so that no local seed could fall into the flats. The experiment was maintained in the

Figure 1.—Five years after the old-growth beech-birch-maple was clearcut, samples were taken from the forest floor under this young stand dominated by pin cherry. Little remains of the dense *Rubus* of earlier years.

Figure 2.—This stand, dominated by paper birch, developed after clearcutting 38 years ago. Most of the pin cherry (the dark stems in the foreground) are dead or dying.

Figure 3.—There was very heavy cutting in this stand 95 years ago. The major species now are beech, red maple, white ash, and yellow birch. The paper birch is decadent and will die out completely during the next 10 to 20 years.

Figure 4.—This virgin forest has been undisturbed for over 200 years. The only tree species present are sugar maple, beech, yellow birch, and an occasional striped maple.

Table 1a.—Species composition as a percentage of total stand basal area (150 mm dbh and larger)

Stand age	Species										Total basal area
	Large-tooth aspen	Pin cherry	Striped maple	Paper birch	Red maple	White ash	Beech	Sugar maple	Yellow birch	Eastern hemlock	
Years	*Percent*										m^2/ha
38	8.6	7.8	0.8	47.6	1.6	0.8	10.9	8.6	13.3		23.4
95				6.1	20.1	15.3	42.8	4.8	9.6	1.3	35.7
200+							40.0	50.5	9.5		50.6

4.356 × m^2/ha = $ft.^2/acre$.

Table 1b.—Species composition as a percentage of above-ground biomass (fresh weight)

Stand age	Species										
	Pin cherry	Striped maple	Paper birch	Yellow birch	Sugar maple	Beech	*Rubus*[a]	Red-berried elder	Hobble-bush	Yew	Misc.
Years	*Percent*										
5	41.9	9.9	9.4	5.6	3.6	2.9	14.8	6.1	3.5	1.3	1.0

[a] In this paper, *Rubus* includes *R. idaeus* and *R. allegheniensis*.

Figure 5.—A 30 cm² greenhouse flat containing the litter and fermented layer from the 200+ year-old stand. Seedlings of yellow birch and an unidentified grass predominate.

unheated greenhouse through three growing seasons and two winters.

Analysis of variance was used to evaluate the data after transformation to fit normality assumptions. A separate analysis was done for each major species. Among species, comparisons of numbers of germinating seeds were made using Duncan's new multiple range test.

RESULTS AND DISCUSSION

Seeds of 35 species germinated and grew in the forest floor samples (Table 2). The greatest number of species germinated in samples from the 5-year-old stand, with 23 identified plus several unidentified grasses, sedges, and a rush. In the 38-year-old stand, there were 20 species identified

Table 2.—Germinating seeds per m^2 in forest floor samples from four beech-birch-maple stands

Species		Stand age (years)				Total
		5	38	95	200+	
Herbs						
Shining club-moss	*Lycopodium lucidulum* Michx.	—	1	1	1	3
Grass[a]	Gramineae	53	—	7	5	65
Sedge[a]	*Carex* L.	117	1	—	2	120
Rush[a]	*Juncus* L.	1	—	—	—	1
Wild-oats	*Uvularia sessilifolia* L.	—	—	—	1	1
Sweet white violet	*Viola blanda* Willd.	7	2	2	2	13
Round-leaved violet	*Viola rotundifolia* Michx.	—	—	—	78	78
Purple-leaved willow-herb	*Epilobium coloratum* Biehler	3	—	—	—	3
Northern willow-herb	*Epilobium glandulosum* Lehm.	90	—	2	—	92
Narrow-leaved willow-herb	*Epilobium leptophyllum* Raf.	1	—	—	—	1
Small enchanter's night shade	*Circaea alpina* L.	5	—	—	—	5
Rough-stemmed goldenrod	*Solidago rugosa* Ait.	15	—	—	—	15
Canada goldenrod	*Solidago canadensis* L.	73	—	—	—	73
Narrow-leaved goldenrod	*Solidago graminifolia* (L.) Sabisb.	35	1	—	—	36
Whorled wood aster	*Aster acuminatus* Michx.	4	1	—	—	5
Pilewort	*Erechtites hieracifolia* (L.) Raf.	1	—	—	—	1
Spikenard	*Aralia racemosa* L.	1	7	—	1	9
Birstly sarsaparilla	*Aralia hispida* Vent.	—	2	—	—	2
Wild sarsaparilla	*Aralia nudicaulis* L.	1	—	1	—	2
Total		407	15	13	90	525
Number of species		12	6	4	5	
Shrubs						
Long-beaked willow	*Salix bebbiana* Sarg.	—	2	2	1	5
Meadow-sweet	*Spiraea latifolia* (Ait.) Borkh	13	2	5	—	20
Raspberry	*Rubus idaeus* L.	1016	286	68	12	1382
Blackberry	*Rubus allegheniensis* Porter	31	166	21	—	218
Bush-honeysuckle	*Diervilla lonicera* Mill.	1	1	8	1	11
Red-berried elder	*Sambucus pubens* Michx.	42	25	3	69	139
Total		1103	482	107	83	1775
Number of species		5	6	6	4	
Trees						
Balsam fir	*Abies balsamea* (L.) Mill.	—	—	1	—	1
Eastern hemlock	*Tsuga canadensis* (L.) Carr.	—	—	1	—	1
Quaking aspen	*Populus tremuloides* Michx.	1	124	—	2	127
Large-toothed aspen	*Populus grandidentata* Michx.	13	174	8	5	200
Yellow birch	*Betula alleghaniensis* Britt.	181	144	961	1460	2746
Paper birch	*Betula papyrifera* Marsh.	87	1340	445	20	1892
Mountain paper birch	*Betula cordifolia* Regel	—	—	—	18	18
American beech	*Fagus grandifolia* Ehrh.	—	—	—	4	4
Pin cherry	*Prunus pensylvanica* L. f.	2	111	52	1	166
Striped maple	*Acer pensylvanicum* L.	3	1	—	—	4
Sugar maple	*Acer saccharum* Marsh.	—	2	4	123	129
Red maple	*Acer rubrum* L.	—	—	10	—	10
White ash	*Fraxinus americana* L.	—	7	10	—	17
Total		287	1903	1492	1633	5315
Number of species		6	8	9	8	
Unknown		32	9	3	2	46

[a] Species not identified for this group and not counted in totals for number of species.
Seeds/m^2 $\div$ 10.76 = Seeds/$ft.^2$

and a single unidentified sedge. The 95-year-old stand had 19 species, and the 200+ year-old stand had 17 species; both stands had unidentified grasses. In addition, unknown plants germinated in the litter and soil from the four stands. These unknowns died before they were mature enough to be identified. Total germination in the samples ranged from 16 million to over 24 million per hectare in the four stands (Table 3).

Delayed germination

The samples were maintained 3 years in the greenhouse so that dormant seeds would have an extended opportunity to germinate. Most of the germination (92.7 percent) took place the first summer. Germination was 99.6 percent complete at the end of the second growing season. *Rubus* from the 5-year-old stand and pin cherry from the 38- and 95-year-old stands accounted for almost all of the second- and third-year germination (Table 4).

During the first summer, more than 90 percent of the *Rubus* seeds germinated in samples from the 38-, 95-, and 200+ year-old stands, while only two thirds of *Rubus* from the 5-year-old stand germinated. Apparently some of the seeds from the 5-year-old stand were dormant and required an extended period for germination. These seeds had been produced and deposited beneath the parent *Rubus* since the clearcut 5 years earlier. *Rubus* seeds stored for longer periods (e.g., in the 38- and 95-year-old stands) exhibited very little delayed germination. The proportion of dormant *Rubus* seeds may be time-dependent, with most of the seeds ready to germinate at a stand age between 5 and 38 years.

Pin cherry germination reached 73.9 percent in samples from the 38-year-old stand and 71.1 percent in samples from the 95-year-old stand during the first summer. Germination was completed the second summer. Too few pin cherry seeds germinated in samples from the 5-year-old and 200+ year-old stands to indicate any trends.

Table 3.—Total number of seedlings germinating per hectare in the organic layers and soil collected in the beech-birch-maple stands

Stand age (years)	Seedlings
5	18,290,000
38	24,090,000
95	16,150,000
200+	18,080,000

Seedlings/ha ÷ 2.471 = seedlings/acre.

Table 4.—Cumulative germination of *Rubus*, pin cherry, and all other species, as a percentage of total germination

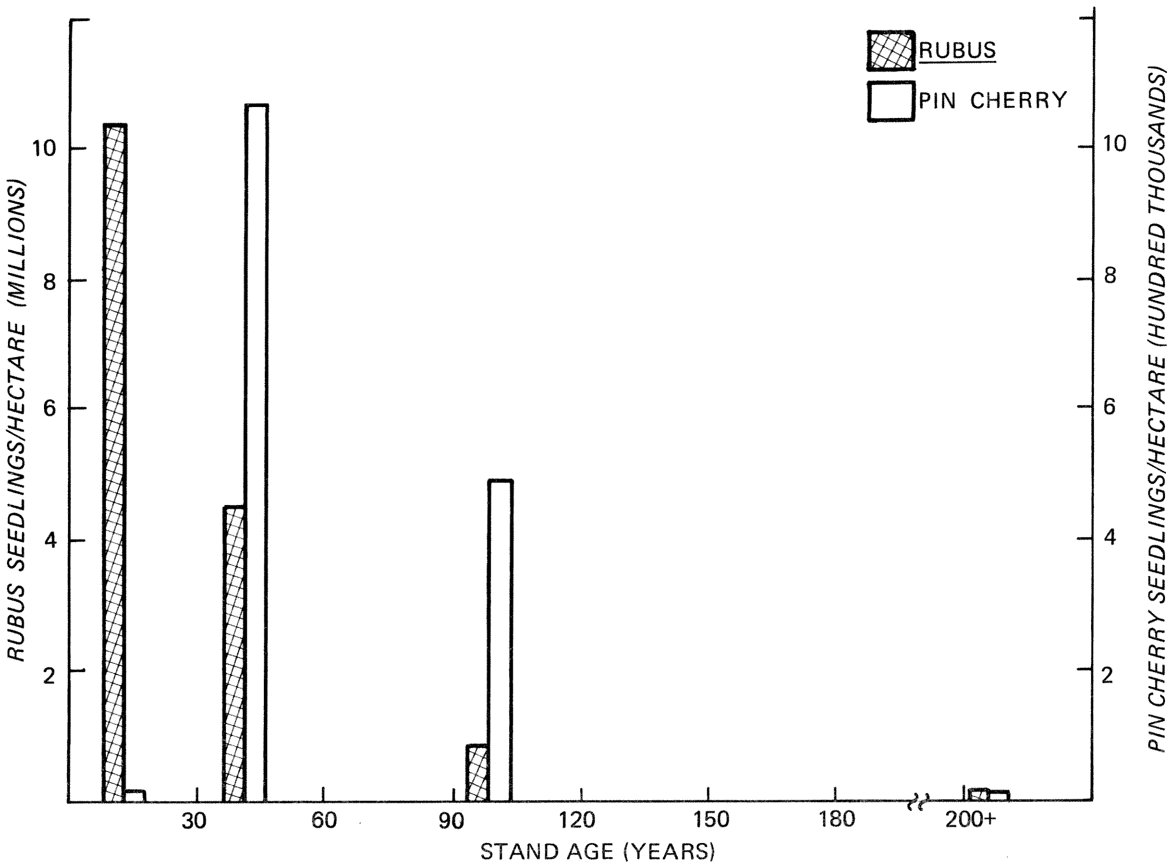
Year of germination	Stand age (years)			
	5	38	95	200+
		Rubus		
First	66.5	98.0	96.6	91.7
Second	98.5	100.0	100.0	91.7
Third	100.0	100.0	100.0	100.0
		Pin cherry		
First	0	73.9	71.7	100.0
Second	100.0	100.0	100.0	100.0
Third	100.0	100.0	100.0	100.0
		All others		
First	97.8	97.7	95.8	98.8
Second	99.3	100.0	100.0	100.0
Third	100.0	100.0	100.0	100.0

Stand age

The four stands were growing on fairly typical northern hardwood sites. The chief difference among the stands was length of time since a major disturbance. The number of germinating *Rubus* and pin cheery seeds differed significantly ($p < 0.05$) among the four stands (Fig. 6). Seeds of *Rubus* were present in very large quantities in the youngest stand but the number dropped rapidly in the old stands, falling from more than 10 million per ha in the 5-year-old stand to 120,000 per ha in the 200+ year-old stand. Three basic causes of this dramatic reduction in viable *Rubus* seeds are: (1) the natural time-dependent degeneration that culminates in seed death, (2) losses due to bacteria, fungi, and predation by birds, small mammals, and insects, and (3) the annual germination of some of the buried seeds. To further complicate the situation, birds transport additional seeds annually. Seed-fall data (collected for another study on these same plots) indicated these annual deposits to be 6,000 to 7,000 viable *Rubus* seeds per hectare. We believe that the few germinating *Rubus* seeds from the 200+ year-old stand were deposited by birds and were not an artifact of the early succession. We estimate the maximum age of viable *Rubus* seed to be 50 to 100 years.

The pin cherry seed supply peaked at a later age. Pin cherry matures rapidly, dying off at 20 to 40 years of age, and it is logical that there would be the maximum buried seed supply as the tree

Figure 6.—Germinating pin cherry and *Rubus* seeds stored in the forest floor.



reached maturity. The causes of pin cherry seed depletion are the same as for *Rubus*. The number of pin cherry seeds found in the 95-year-old stand was high, indicating a long life for this species.

We have evidence that very few pin cherry seeds are deposited by birds in the 95- and 200+ year-old stands. In 6 years of monitoring seed fall, not a single pin cherry seed has been found. Our estimate of maximum longevity for pin cherry seeds is 75 to 150 years.

Seed depth

Much of the germination took place in the upper organic layer of the forest floor (Fig. 7). Germination of the L-F layer ranged from 57.7 percent in the youngest stand sampled to 88.0 percent in the 95-year-old stand. The seeds germinating in this layer were representative of the overstory. They were primarily the wind-disseminated birch, aspen, and maple seeds, with one exception. In the 5-year-old stand, tree seed production was just beginning (e.g., pin cherry), and most of the germination in the L-F layer samples was *Rubus* and various herbs typical of the early successional plant cover. The birch seeds present were blown in from trees on the perimeter of the 5-year-old clear-cut.

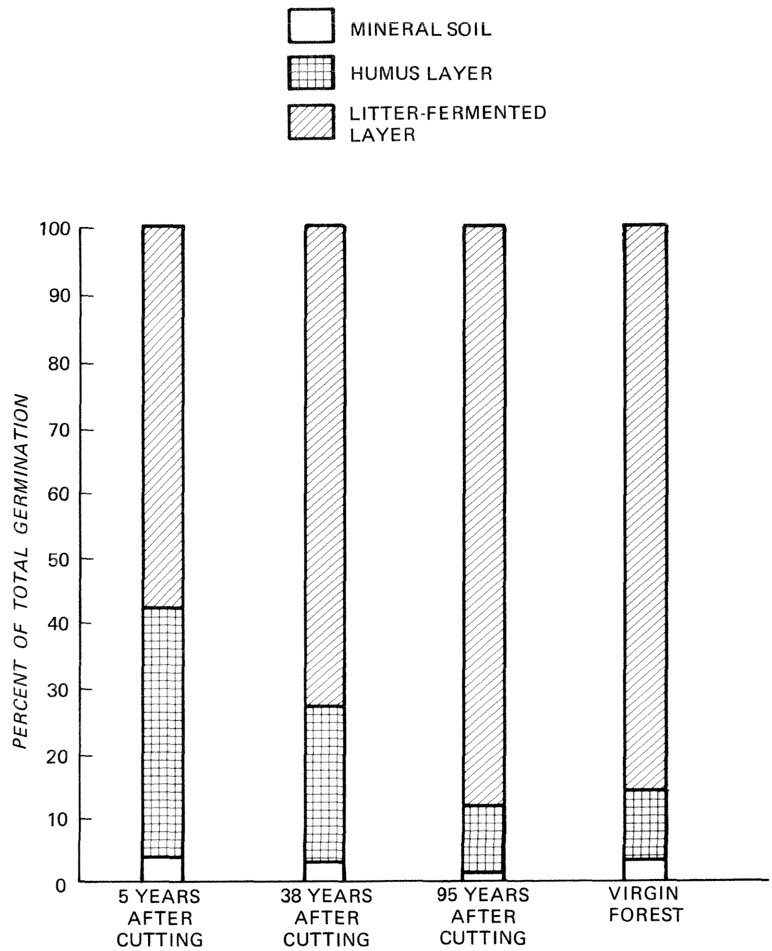
The proportion of total germination in the H layer samples declined from 37.9 percent in the 5-year-old stand to 10.3 percent in the 200+ year-old stand. Since most of the long-lived buried seeds are in this layer, a change in viable seed numbers here would influence species composition and density in any secondary succession triggered by clearcutting or natural calamity.

Germination in the mineral soil samples also appeared to be related to stand age. There was a reduction in the percentage of germination from the 5- to 95-year-old stand. However, this trend was reversed in the 200+ year-old stand. At least 75 percent of the seed germinating in the soil from the three younger stands was pin cherry and *Rubus*. In the 200+ year-old-stand samples, there was no pin cherry and less than 8 percent *Rubus*. The most numerous species in the mineral soil of this very old stand were round-leaved violet (57 percent) and red-berried elder (26 percent).

Round-leaved violet plants were common in the 200+ year-old stand and absent in the other three stands. This violet blooms early in the spring before the trees leaf out, and produces some fresh seed each year. The seed has a hard coat and may survive for years in the forest floor.

The presence of red-berried elder seed is more difficult to explain. Our data (Table 2) show the equivalent of 420,000 red-berried elder seeds per ha germinating in the 5-year-old stand, and a decline to only 30,000 in the 95-year-old stand. The equivalent of 690,000/ha germinated in the samples from the 200+ year-old stand. A number of stunted red-berried elder plants of low vigor were noted in the understory of this stand. None of these understory plants has flowered or fruited in the past 5 years. In 1970 and 1971, there was a severe defoliation by the saddled prominent (*Heterocampa guttivitta* (Wlkr.)), and flowering and some seed production by red-berried elder was observed in adjacent areas. However, no visit was made to the collection site during that period, and we do not know if seed was produced there. We suspect that viable red-berried elder seeds are stored in the forest floor for one or more decades. Birds are voracious consumers of red-berried elder fruit and probably distribute the seed widely, but in small quantities. We have never collected, in

Figure 7.—Depth of germinating seeds in organic layers and soil from the four northern hardwood stands.



seed traps, a single-red berried elder seed that could be attributed to dispersal by birds. The saddled prominent causes large-scale defoliation at about 30-year intervals. This periodic defoliation may be sufficient to ensure fruiting and survival of some red-berried elder seeds in the forest floor.

CONCLUSIONS

Seed numbers and species differed in important ways among the four stands. The greatest number of species germinated in samples from the 5-year-old stands. Delayed germination was also most common in this young stand, largely due to the natural dormancy of the newly deposited *Rubus* seeds. The number of seeds germinating in the humus and soil of the 95-year-old and 200+ year-old stands was only one-third of that in the two younger stands. This reduced germination is a reflection of the decline in all seeds, but especially in *Rubus* and pin cherry seeds.

This pattern of viable seed survival could have an important bearing on future even-age management practices. Currently, many northern hardwood stands in New England are harvested at ages of 100 years or more, when the stored supplies of *Rubus* and pin cherry seeds are relatively low. As resource managers attempt to extract greater yields from our forests, they may of necessity resort to shorter rotations. When stands are harvested at lower ages, the dense populations of pin cherry and *Rubus* are likely to cause intense competition for growing space.

Competition for light, moisture, and nutrients may limit the stocking and development of commercial species, particularly paper birch, yellow birch, and white ash. Wilson and Jensen (1954) reported poor stocking after a 60-year-old northern hardwood stand on the Bartlett Experimental Forest was clearcut. They concluded that the timber species could not compete with the rank growth of *Rubus* and pin cherry that followed the harvest.

It is likely, then, that short rotations in the beech-birch-maple forest will require intensive silvicultural practices on some sites to control *Rubus* and pin cherry to retain adequate stocking of the high-value timber species.

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