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Seed Fall in an Old-growth Northern Hardwood Forest

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Abstract

Seed fall was measured for 11 years in a 200-year-old stand of sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), and beech (*Fagus grandifolia* Ehrh.) in New Hampshire. These species accounted for 98 percent of the seed fall. Yellow birch had 5 good seed years, sugar maple had 3, and beech had none. Time of seed fall varied among species and years. Viable seed fall of yellow birch in good seed years began in August and continued through autumn and winter. Most of the viable sugar maple seed fell during a short period in October, just before and after leaf fall. Beech seed fall was similar, but occurred slightly later than sugar maple. Seed losses caused by pollination or fertilization failure, abortion, incomplete development, insects, small mammals, and birds varied widely among years, but averaged about 2/3 of the potential seed crop. Losses often were proportionally greater during poor seed years.

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Introduction

The production of seed by forest trees is a fundamental step in stand replacement. Most harvested stands in the northern hardwood forest are replaced through natural regeneration. Foresters try to time harvest cuts to coincide with good seed crops. To do this effectively, they need accurate and detailed information on the frequency, timing, size, and viability of seed crops.

Seed crops also are of concern to wildlife managers interested in seed as food for birds and mammals. The abundance of seed from year to year has a major bearing on feeding habits and population levels of certain species.

There are many gaps in our knowledge of seed production in the northern hardwood forest, particularly in New England. Much of the past research is subjective, short-term, lacking in detail on seed viability or stand conditions, or derives from other regions where soils and climate differ from those in New England (Curtis 1959, Eyre and Zillgitt 1953, Benzie 1959, Godman and Mattson 1975, Marquis 1969, Grisez 1975, and Bjorkbom 1979). To fill some of these informational gaps, this study was designed to measure total seed production over an 11-year period, annual variations in seed crops, seed viability and seed losses in an old-growth sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), beech (*Fagus grandifolia* Ehrh.) stand in New Hampshire.

Study Area

The study was conducted in the Bowl Research Natural Area, White Mountain National Forest, New Hampshire. The stand consisted of mature sugar maple, beech, and yellow birch (Eyre 1980) that had been undisturbed for more than 200 years (Fig. 1). It contained a relatively small number of tree species: an overstory of mature sugar maple, yellow birch and beech, and a well-developed understory of beech with a few red spruce (*Picea rubens* Sarg.) and striped maple (*Acer pensylvanicum* L.).

A uniform stand of 1 ha was selected as the study plot. The aspect was southeasterly with an average slope of 27 percent and an elevation of 630 m. The soil was a fine sandy loam till (Leak 1980) derived from granitic bedrock. Northern hardwoods grow well in this type of habitat (Leak and Riddle 1979). The plot had a basal area (trees >5 cm d.b.h.) of 44.5 m/ha and a seed tree (>25 cm d.b.h.) basal area of 34.4 m/ha (Table 1). Mean d.b.h. and height of dominant seed trees were: sugar maple, 52.1 cm and 24.7 m; beech, 41.9 cm and 22.2 m; yellow birch, 46 cm and 23.8 m.

Methods

Twenty seed traps were distributed systematically in the study plot, from a random start, for the May-November observation periods. A modified version (Fig. 2) of Bjorkbom's (1971) cylinder trap was used. The trap was a metal cylinder 15.3 cm diameter and 17.7 cm tall, open at the top with drainage holes in the bottom. A cloth liner was placed in the trap to ensure the capture of very small seeds. During windy periods, this type of trap produces an air stream deflection that reduces the seed catch. To correct this problem, a strip of metal screening was attached to the top of each trap. To eliminate small mammal depredation, a no. 2 mesh hardware cloth cover was placed across the top of the metal cylinder.

Figure 1.—This old-growth sugar maple-yellow birch-beech stand has been undisturbed for more than 200 years.

Table 1.—Stand composition (percent of basal area) by species and d.b.h. in the Bowl plot

D.b.h.	Sugar maple	Beech	Yellow birch	Red spruce
	percent basal area			
All trees (>5 cm)	58.1	30.1	11.1	0.7
Seed trees (>25 cm)	69.4	17.2	13.4	0.0

Figure 2.—Cylindrical seed trap as used during the growing season. The screen top reduced wind deflection during windy periods, increasing trap reliability.

During winter, the trap construction and layout were modified. The number of traps was reduced to 10, placed at intermediate points between the locations of the summer traps. Instead of drainholes in the bottom, a single drain was drilled in the side of the cylinder, 6.4 cm above the bottom. A plastic spout with gauze across the inlet was friction-fitted into the hole. The hardwood cloth mesh cover and the cloth bags were removed from the cylinder. Six hundred ml of antifreeze (ethylene glycol) were poured into the trap. The trap was mounted on a pole at a height above the maximum snow pack. In operation, the snow melted as it came into contact with the antifreeze. Excess liquid drained out through the plastic spout. The gauze prevented loss of seed. These traps remained operational without maintenance for at least 8 weeks under conditions in the White Mountains.

Seeds were collected at 2-week intervals during snow-free periods, and at 6- to 8-week intervals during winter. In the laboratory, the seeds were identified, counted, and tested for viability. Viability was determined by cutting and testing for germination during the growing season. Winter seeds were tested only by cutting due to the toxic effects of ethylene glycol. Nonviable seeds were examined carefully to determine the cause. Bird, mammal, and insect injury was recognized by the unique damage. Empty seed denoted pollination-fertilization failure. Early seed fall of green, immature seeds occurred with some species. Other seeds were partially filled, indicating incomplete development due to environmental causes.

The final measure of the effectiveness of a seed crop is the number of seedlings produced. Seedling emergence was observed on 10 randomly located circular plots (1 m^2) from 1972 through 1980. The plots were checked for emergence at 2-week intervals during the growing season, when the seed traps were emptied.

Results and Discussion

Annual Seed Fall

Yellow birch. Seed fall varied greatly during the 11 years of observation (Table 2). An excellent crop of 64 million seeds/ha occurred in 1974. The amount of viable seed was substantially lower, about 33 million (Fig. 3). Good viable crops of 6 to 15 million were produced in 1971, 1972, 1977, and 1979. Medium crops of about 2 million were produced in 1976 and 1981. In the remaining 4 years, the crops were poor, such that they don't show on the chart, a fraction of a million viable seeds.

Table 2.—Total seed fall (millions/ha) by species and year[a]

Year	Yellow birch	Sugar maple	Beech
1971	16.37±1.48	11.86±1.08	0.30±0.06
1972	32.08±2.89	1.38±0.21	0.03±0.002
1973	0.35±0.07	0.00±0.00	0.14±0.02
1974	64.02±7.98	6.73±0.78	0.19±0.03
1975	1.17±0.23	0.16±0.03	0.05±0.01
1976	6.19±0.50	6.13±0.66	0.05±0.005
1977	32.78±2.92	0.03±0.002	0.00±0.00
1978	1.17±0.19	3.12±0.40	0.43±0.10
1979	18.05±1.00	7.08±0.76	0.27±0.07
1980	2.74±0.40	1.06±0.22	0.22±0.03
1981	11.53±0.94	7.63±0.68	0.24±0.05

[a]Mean ± confidence limit, P=0.95.

Seed viability of yellow birch ranged from 4 percent in the poor 1980 seed year to 51 percent in the excellent 1974 year. Viability increased as the size of the seed crop increased (Fig. 4). In the 5 good or better years, viability never fell below 25 percent; in the 4 poor years, it never exceeded 10 percent.

Sugar maple. Total annual seed fall ranged from 0 to 12 million seeds/ha (Table 2). Good viable crops of approximately 3 million seeds/ha were produced each year in 1971, 1974, and 1981 (Fig. 3). Medium crops of 1-2 million seeds/ha occurred in 1976, 1978, and 1979. Poor

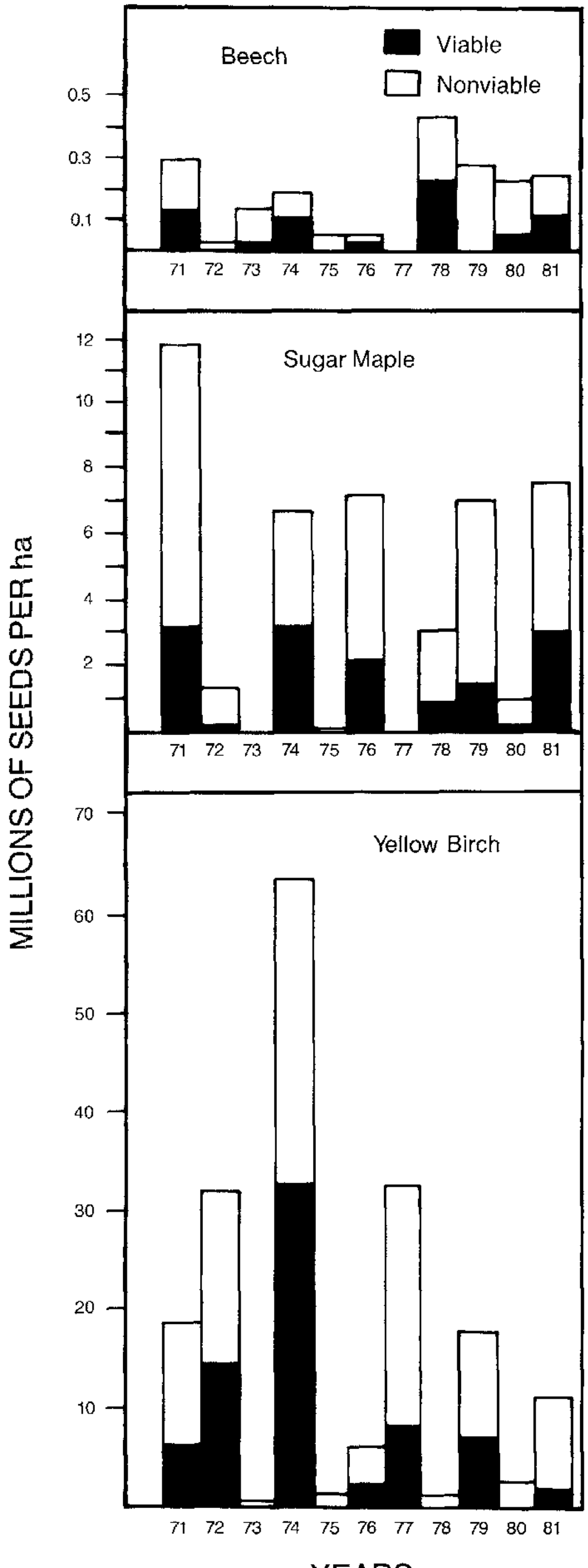

Figure 3.—Total (viable and nonviable) seed production by species and years.

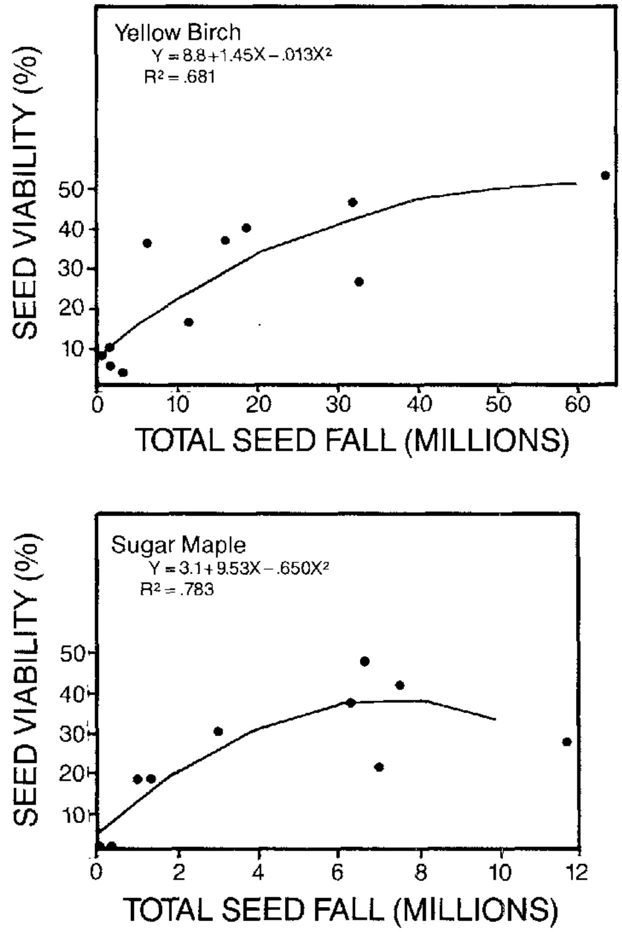

Figure 4.—Percent viable seed over total seed fall for yellow birch and sugar maple.

crops of approximately 0.2 million seeds were recorded in 1972 and 1980. Only nonviable seeds fell in 1975 and 1977 and no seed was found in 1973.

Viability was related to size of the seed crop (Fig. 4) and ranged from 0 to 48 percent. An exception was the largest seed crop (1971), which had the relatively low viability of 26 percent. This low viability was the result of a severe outbreak of the saddled prominent (*Heterocampa guttivitta* Wikr.), a general foliage eater that consumed the seed pedicels and occasionally part of the samara, causing lethal injury to immature seeds.

Six years of the 11-year period produced good or medium crops of viable sugar maple seed and 5 years produced little or no seed. This is not a serious limitation since most successful sugar maple regeneration originates from advanced growth present in the understory at the time of harvest. This advanced growth is replenished periodically during good seed years (Forcier 1975).

Beech. Total seed fall ranged from 0 to 0.43 million seeds per ha (Table 2). The largest crop, 0.22 million viable seeds per ha in 1978 (Fig. 3), was considered a medium crop. Medium amounts of seed also were produced in

Table 3.—Species shedding minor amounts of seed on the study plot in seeds per ha during the entire 11-year period

Species	Seed fall		No. of years	Nearest plant	
	Total	Viable		Elevation	Distance
				--------meters--------	
Red maple *Acer rubrum*	570,000	0	3	587	151
Striped maple *Acer pensylvanicum*	489,000	190,000	7	632	29
Mountain paper birch *Betula cordifolia*	678,000	244,000	5	794	451
Paper birch *Betula papyrifera*	6,378,000	3,497,000	11	587	172
Red spruce *Picea rubens*	326,000	81,000	6	617	53
Eastern hemlock *Tsuga canadensis*	163,000	27,000	2	611	37
Balsam fir *Abies balsamea*	54,000	0	1	616	41
Goldenrod *Solidago* Spp.	380,000	353,000	1	Unknown	Unknown
Round-leaved violet *Viola rotundifolia*	27,000	27,000	1	632	On plot
Shining club-moss *Lycopodium lucidulum*	163,000	27,000	2	632	On plot

1971, 1974, and 1981. Poor seed crops occurred in 1973, 1976, and 1980; and there was no viable seed in 1972, 1975, 1977, and 1979. Seed viability, ranging from 0 to 57 percent, was unrelated to size of crop.

The frequency of beech seed years—4 with no seed, 3 with poor crops, and 4 with medium crops—may be low for this species. There are reports of good seed years every 2-5 years (USDA 1974). This low production may be due to poor tree vigor since many of the largest beech appeared to have large dead branches in the crown. The cause of this condition could be the beech scale *Nectria* complex, which was present in the stand. Senescence could be a factor; but beech is a long-lived species that may survive 300-400 years (Deen 1937). Another reason for the poor seed production might be the relatively high elevation of the plot (630 m). Beech seldom grows above 760 m in this area (Leak and Graber 1974).

Minor Species. The viable seeds of the species listed in Table 3 represent less than 3 percent of the total viable seed fall (all species) during the 11-year study. Only two species, shining club-moss and round-leaved violet, had mature plants present on the study plot. Seed from the other species came from beyond the plot boundaries. Possibly, one reason for the low seed viability of some minor species—balsam fir and red maple, for example—was that empty or partially-filled seed is more likely to travel farther than filled seed.

Seasonal Pattern of Seed Fall

Yellow Birch. Some seed fell in every month of the year. A small amount of new seed fell as early as June, but no viable seed of the current crop fell until August. In the 5 best seed years, viable seeds fell by mid-August. During the 3 medium seed years, the first viable seed fell in late August or early September. Seed fall in poor years occurred later: the first viable seed was noted in early September (1975), early October (1973), or as late as mid-November (1978 and 1980). Thus, the smaller the seed crop, the later the dispersal of viable seed.

Three yellow birch seed years are illustrated in Fig. 5 to show the year-to-year variation in pattern. In 1974, approximately three-fourths of the viable yellow birch seed fell in October; in 1972 and 1977, only one-third or less fell by this date. At the end of November, 1974, most of the viable seed had been shed. The comparable figure was 88 percent in 1972 and 57 percent in 1977. The 1977 seed crop was unusually late: approximately two-fifths of the seed fell in December and January. In good seed years, viability usually remained above one-third of the total through early winter, and then declined.

Sugar Maple. Nearly all of the seed fell between June and late November regardless of crop size. This pattern was basically the same in a good year (1974), a medium year (1978), and a poor year (1972)(Fig. 5). Very little of the seed fall from May through August was viable. There were two peaks in the annual seed fall. The first occurred in mid-June and was caused by seed abortion and insect attack. The June seed fall usually was much smaller than the October peak. A single exception was in 1979 when

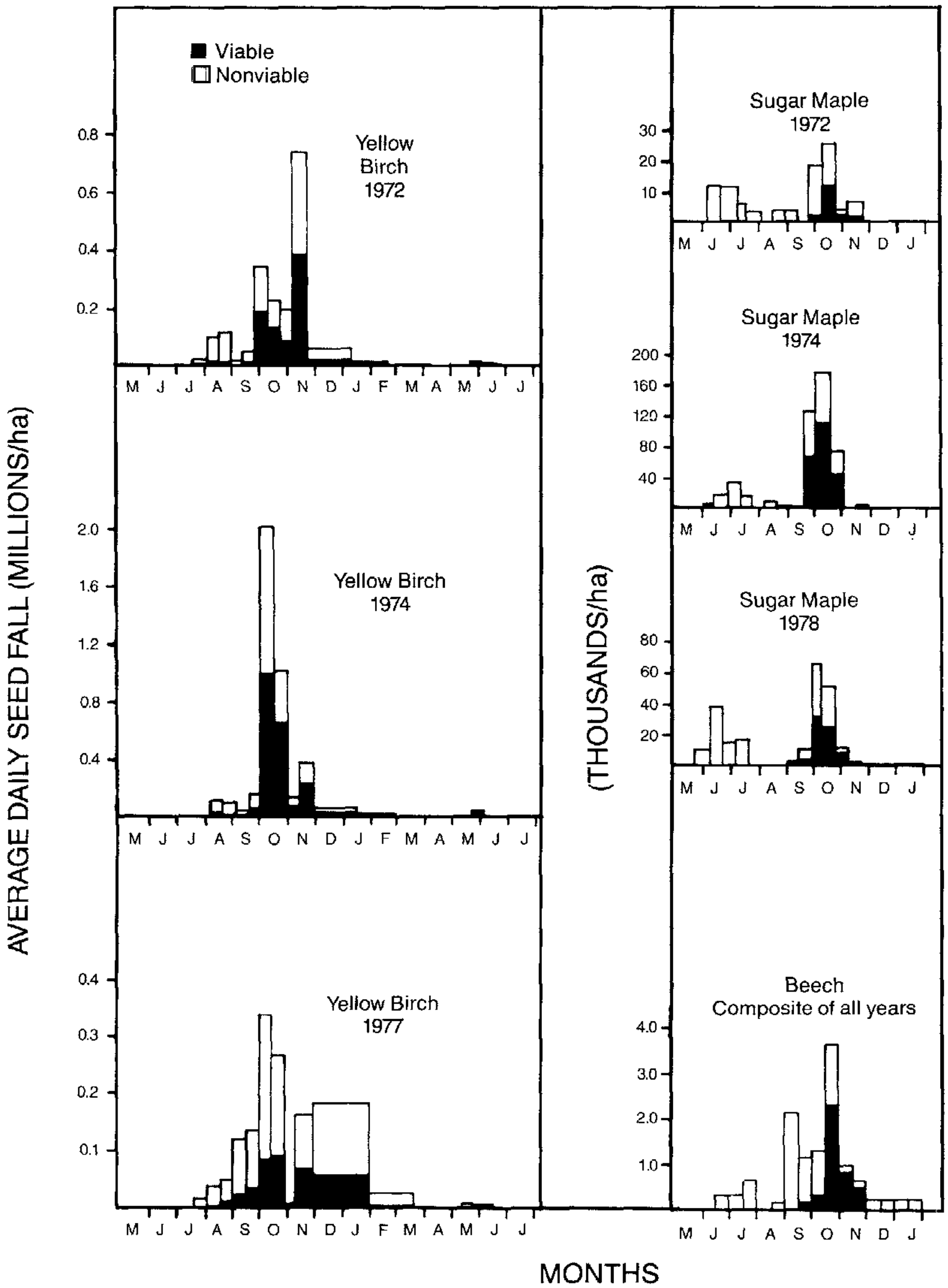

Figure 5.—Average daily seed fall (viable and nonviable) by time periods, species, and selected years.

the June seed fall was 3.71 million per ha and the October seed fall was 2.47.

Generally, much of the viable sugar maple seed fell in October. Seed fall was particularly heavy during and just after leaf fall. In some years, most of the viable seed fell in a single 2-week period in early October: 77 and 89 percent of the viable crop fell during this period in 1976 and 1979, respectively. Few seeds fell in November, and viable seeds fell in December only in 1977 and 1979.

Seed viability of sugar maple changed in a predictable way as the season advanced. Seed fall during June, July, and most of August was nonviable. Beginning in September or October, viability rose sharply, signaling the start of rapid seed fall. In good and medium seed years, viability averaged approximately 50 percent during this period. Peak viability remained for 2-4 weeks, and then dropped abruptly.

Beech. The observations on this species are limited since there were no really good seed years, and only 3 medium years during the study. A composite graph of all seed years illustrates the sequence (Fig. 5). The seeds were shed in a pattern similar to that of sugar maple. There were two periods of seed fall in most years, a small amount in early summer (about 10 percent) and the remainder from late summer into early winter. The summer seed fall was nonviable because nearly all the seeds were insect infested. The first viable seeds fell in later September. Peak viable seed fall took place in mid-October to early November. The percentage of viable seeds increased from 14 percent in September to 83 percent in early November, then declined. The year-to-year variation in dates of seed fall was minor and did not seem related to size of the seed crop.

Losses to Birds and Small Mammals

Birds. The study provided estimates of bird consumption from feeding in the trees; there was no measure of consumption from ground feeding. However, little ground feeding was noted in the course of the study, and the data should represent a fairly good measure of the impact of birds on the seed supply. The species of birds observed consuming seed are listed in Table 4.

During the 11-year period, birds consumed an average of 1.1 percent of the sugar maple seed, 3.5 percent of the beech seed, and 16.3 percent of the yellow birch seed. The impact of birds on sugar maple and beech was minor, but the impact on yellow birch was substantial, ranging from none to 24.2 percent of the total seed crop. Bird consumption as a percentage of filled seed was as high as 39.8 percent. The amount of seed eaten was correlated with the total yellow birch crop (Fig. 6). Birds consumed the highest percentage of seeds during good and excellent seed years. In only 1 of the 4 poor years was a measurable amount of seed consumed by birds.

Table 4.—Birds observed eating tree seed in the study area.

	Species consumed		
Bird species	Yellow birch	Sugar maple	Beech
Blue jay *Cyanocitta cristata*		X	X
Black-capped chickadee *Parus atricapillus*	X		
White-breasted nuthatch *Sitta carolinensis*			X
Evening grosbeak *Coccothraustes vespertina*		X	X
Purple finch *Carpodacus purpureus*		X	
Common redpoll *Carduelis flammea*	X		
Pine siskin *Carduelis pinus*	X		
American goldfinch *Carduelis tristis*	X		
Slate-colored junco *Junco hyemalis*	X		

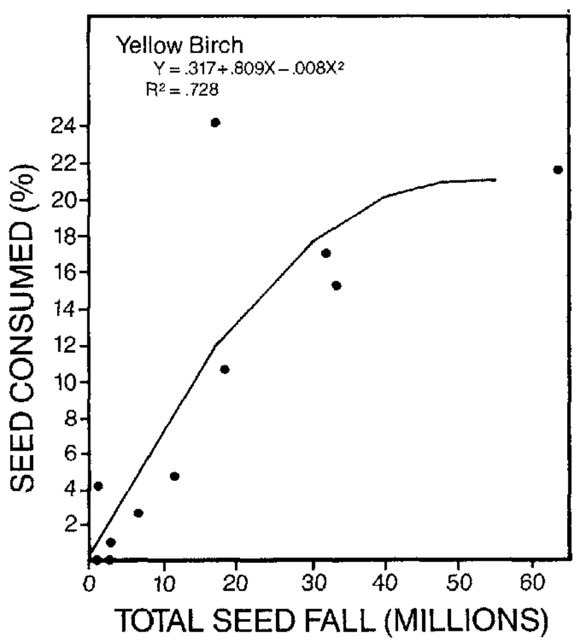

Figure 6.—Percent of yellow birch seed consumed by birds over total seed fall.

Table 5.—Small mammals eating tree seed on the study area

	Species consumed		
Mammal species	Yellow birch	Sugar maple	Beech
Red-backed vole *Clethrionomys gapperi*	X	X	
Deer mouse *Peromyscus maniculatus*	X	X	X
Woodland jumping mouse *Napaeozapus insignis*	X	X	
Eastern chipmunk *Tamias striatus*		X	X
Red squirrel *Tamiasciurus hudsonicus*	X	X	X

Small Mammals. Five species of small mammals known to be seed predators were observed on the study plot (Table 5). Deer mice, chipmunks, and red squirrels were the most numerous and the most voracious consumers of seed.

Seed losses were attributed to small mammals only when the seeds were eaten in the trees and characteristic fragments with tooth marks fell into a trap. No yellow birch seed fragments were found in the traps. The percentage of total seed fall destroyed was 0.5 for sugar maple and 4.7 for beech. This arboreal feeding was done primarily by red squirrels and chipmunks in late summer and autumn. In contrast to losses to birds, the bulk of seed losses to small mammals, no doubt, occurs after seed fall.

Losses to Insects

Yellow Birch. The average annual seed loss to insects was 15.1 percent of the total yellow birch seed fall. The amount of seed consumed by insects ranged from 4.2 percent in 1974, the best seed year, to 44.6 percent in 1980, a poor seed year. While the actual number of seeds consumed was positively related to seed crop size, there was a trend (nonsignificant) toward greater percentages of consumed seed with smaller seed crop (Fig. 7). This trend may reflect the inability of insects to rapidly increase in population size to take advantage of good seed crops—especially when preceded by a poor crop.

Three species of insects are known to damage yellow birch seed (Baker 1972; Shigo and Yelenosky 1963; Shigo, personal communication). The birch seed midge (*Oligotrophus betulae* Winn.) caused only minor seed losses. Far more important were the seed weevil (*Apion washii* Smith) and the birch catkin moth (*Epinotia transmissana* Wik.). The larvae of these two species tunneled into the developing yellow birch strobili, causing 98 percent of all losses of yellow birch seeds due to insects.

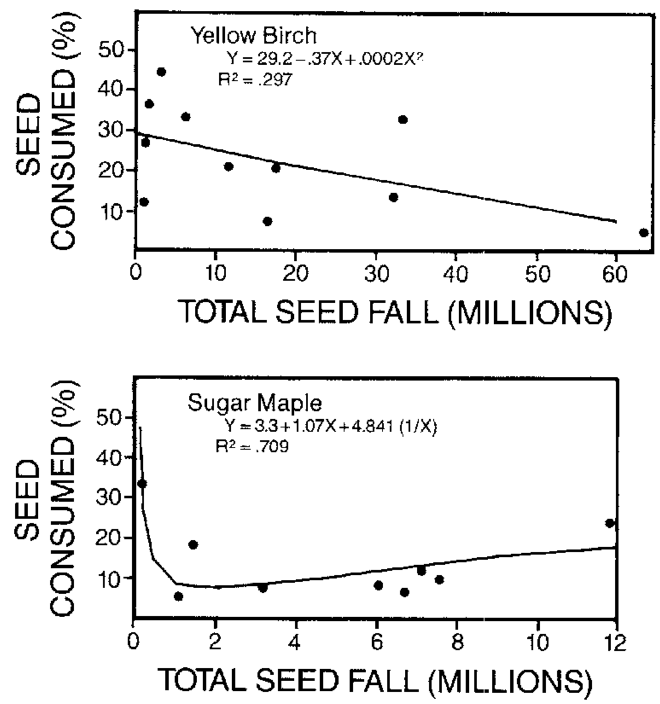

Figure 7.—Percent of seed consumed by insects over total seed fall for yellow birch and sugar maple.

Sugar Maple. As with yellow birch, there was some suggestion of a negative correlation—a sharp drop preceding a plateau—between percent insect damage and crop size (Fig. 7). Annual losses averaged 12.4 percent. Most of the damage was caused by unidentified lepidopterous larvae, which burrowed into the seeds and consumed their contents.

Beech. Insect-damaged seeds were not recorded separately for this species before 1977. From 1977-1981, 34.9 percent of all beech seeds were destroyed by insects, ranging from 11.1 percent in 1981 to 90 percent in 1979. Most of the insect-infested seed fell during the summer. Larvae of the filbert worm (*Melissopus latiferreanus* Wlsm.) were identified; these bored into the seed and mined the interior.

Other Causes of Nonviable Seeds

Many seeds were not viable due to pollination or fertilization failures, abortion, or incomplete development. These nonviable seeds represented 28.1 percent, 53.8 percent, and 27.9 percent of all yellow birch, sugar maple, and beech seed, respectively.

Eighteen percent of the yellow birch seeds were empty; the paired ovules in the individual seeds had not developed. This was primarily the result of pollination or fertilization failure (W. Gabriel, personal communication). The primary cause of this failure probably was poor quality or sparse pollen. In years characterized by sparse flowering, seed production was poor and the proportion of empty seeds was high (Fig. 8). In the poor seed year of 1973, over half

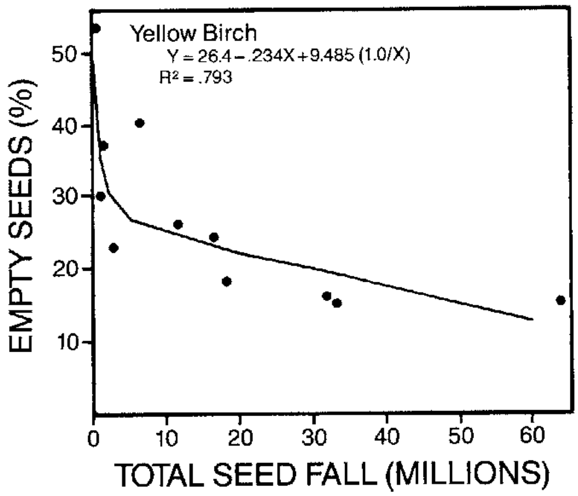

Figure 8.—Percent of empty yellow birch seed, resulting from pollination or fertilization failure.

the seeds were empty; in the excellent year of 1974, only 14.9 percent of the crop was nonviable due to empty seeds.

The other important cause of nonviable yellow birch seed was incompletely developed or partially filled seed, which accounted for 10.1 percent of the total catch. The percentage of partially filled seed tended to be higher in poor seed years, averaging 22.2 percent, and lower in good-to-excellent years, averaging 8.9 percent.

Sugar maple had the highest proportion of empty seeds (46.2 percent); the percentage did not seem related to size of crop. The high percent of empty seed was due primarily to post-zygotic abortion, which occurred in the spring soon after fertilization (Gabriel 1967). As a result, one seed in each double samara usually was empty in both good and poor seed years. Abortion of the remaining seed in June and subsequent abscission of the double samara was far less common, accounting for an average of only 3.5 percent of the sugar maple seed crop. The highest June losses were in 1979, when 15.7 percent of the seed crop dropped. This loss probably was related to unusually dry conditions. June rainfall in 1979 was less than half that of normal, primarily occurring late in the month. By mid-June of that year, newly-fallen double samaras littered the ground.

For sugar maple, incomplete development or partially filled seed was relatively unimportant, accounting for only 4.0 percent of the seeds. The percentage of partially filled seed ranged from 1.1 percent in the excellent seed year of 1974 to 8.7 percent in the moderate year of 1978.

Nearly all of the empty beech seed, 26.7 percent of the total crop, was caused by pollination or fertilization failure. The amount of empty beech seed was unrelated to size of seed crop.

Seed Loss After Dissemination

On the average, about one-third of the total seed fall reached the ground in a viable condition (Fig. 9). Only general observations were made on the fate of seeds after seed fall. No ground feeding was observed on yellow birch,

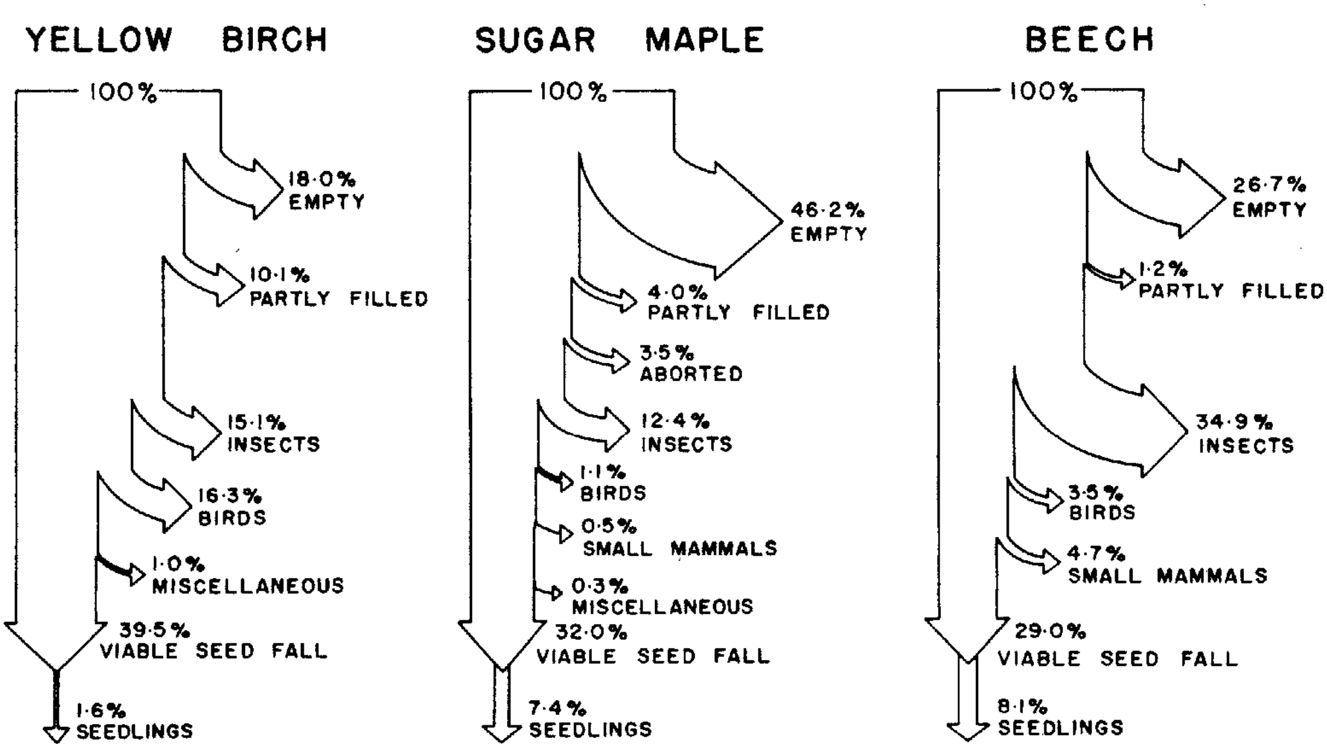

Figure 9.—Seed losses by cause, and final seedling production in percent of total seed fall by species.

though some small amount probably occurred. Why, then, was there such a low percentage of emergence (1.6 percent) for this species? In most years, when seedling emergence took place, large numbers of newly germinated yellow birch seeds were found buried in the leaf litter, too deep to emerge successfully. Perhaps the main factor limiting emergence and initial survival of yellow birch was not predation, but lack of favorable microsites or niches for initial seedling establishment.

With both beech and sugar maple, seed predation on the ground undoubtedly was significant. During the period of rapid seed fall in medium and good years, much viable seed could be seen on the forest floor. But within a week or two, most of the viable seed exposed on the surface of the forest floor had been consumed or removed by small mammals and, to a lesser extent, by birds. Seeds that escaped this feeding activity almost always were buried deep in the litter or humus.

Viable Seed Biomass

Dry weights of viable seed collected in the seed traps were determined for yellow birch, sugar maple, and beech. Sixteen seed lots were weighed for each species. The seeds were collected during periods of maximum seed fall from 1976 to 1981. Yellow birch averaged 734,888 viable seeds per kg. Based on this weight, the annual seed biomass for yellow birch ranged from 0.03 to 44.71 kg per ha, and averaged 9.10 kg. The average number of viable sugar maple seeds per kg was 12,333. Sugar maple seed crops ranged from zero to 257.58 kg per ha, averaging 106.80 kg. The average number of beech seeds per kg was 3,728. The annual beech crop ranged from zero to 57.30 kg per ha, and averaged 16.54 kg. The three species combined produced an average of 132.44 kg of viable seed per ha.

In the best seed year, 1974, total seed fall of viable seeds was 44.71 kg for yellow birch, 259.60 for sugar maple, and 28.65 for beech—a combined total of 332.96 kg per ha. In the poorest year, 1975, neither sugar maple nor beech produced viable seed and the yellow birch crop was only 0.15 kg per ha. The extreme year-to-year fluctuation in seed biomass undoubtedly has a major impact on wildlife food supplies and population levels in the old-growth northern hardwood forest.

Viable seed biomass is a measure of the resources a species allocates to regeneration and serves as a guide to its reproductive strategy. It is apparent from these data that seed production represents a substantial investment in reproductive energy that varies with species. The annual seedfall biomass per 10 m^2 of seed-tree basal area averaged 19.7 kg for yellow birch, 44.7 kg for sugar maple, and 27.9 kg for beech. The dry weight seedfall of sugar maple was 60 percent greater than that of beech and 127 percent greater than yellow birch. A possible reason for these differences is that sugar maple is mostly dependent for its maintenance on seed with sufficient reserves to assure root penetration and survival in the undisturbed litter and low light levels characteristic of northern hardwood understory conditions. Beech, on the other hand, has less need for a major expenditure of energy on seed, since its characteristic ability to root sucker provides an alternative means of reproduction. Yellow birch becomes established on disturbed mineral soil (windthrow mounds, for example) and rotten logs or stumps within canopy gaps. In this case, the strategy appears to be the production of many seeds, with low food reserves, to maximize the chance that seeds will find a suitable regeneration niche.

Seedling Emergence

The emergence of newly germinated seedlings is the crucial test of the effectiveness of a seed crop. The proportion of the seed fall actually resulting in a seedling was low (Fig. 9). The number of yellow birch seeds required to produce a single seedling ranged from 22.5 to 319.9 and averaged 62.5 over the 11-year study period. A major factor affecting the required number of seeds was viability of the seed crop. But even more important was the moisture condition during the growing season, which favored germination and root penetration into the seedbed. In years when precipitation was inadequate, emergence was very low and the seed-to-seedling ratio was very high. The number of emerging seedlings was not closely correlated with total seed fall (r^2=.20) due to this sensitivity to seedbed moisture.

The mean number of sugar maple seeds per emerged seedling was 13.4, ranging from 8.5 to 84.2. In years of abundant seed fall, sugar maple produced a lower ratio of seeds to seedlings than in poorer seed years. In such abundant years, there was sufficient seed to satiate ground feeders, and still produce many seedlings. As a result, seedling emergence was positively correlated with total seed fall (r^2=0.75). Seedbed moisture was not an important factor because most sugar maple emergence took place early in the spring when moisture was not limiting.

The number of beech seeds per seedling was similar to that of sugar maple: an average of 12.3, ranging from 4.5 to 17.4. Seed viability, ranging from 0 to 57 percent, was an important factor influencing the seed-to-seedling ratio. Although seed fall and viability were not closely related, total seed fall did correlate with numbers of emerging seedlings (r^2=0.45), but viable seed fall correlated much better (r^2=0.84). Beech seed was subject to heavy ground feeding, primarily by small mammals. Most of the seed that escaped the predators germinated in May and June. These seeds were deeply buried in the litter and humus and were little affected by the occasional mild spring droughts that occur in northern New England.

Conclusions

Results of this study show that seed production in an old-growth northern hardwood forest varies by species. Yellow birch produces more abundant seed crops at more frequent intervals than sugar maple or beech. For an equal amount of basal area, yellow birch was 26 times as prolific as sugar maple and 169 times as prolific as beech. Medium or better seed years occurred in 2 of 3 years for yellow birch, 1 of 2 years for sugar maple, and 1 of 4 years for beech. Seedling emergence as a percentage of total seed fall was much lower for yellow birch than for beech and sugar maple. These seed fall and emergence figures reflect different reproductive strategies. Yellow birch, especially in a closed stand, has specific seedbed requirements in terms of moisture and seedbed conditions, due in part to the small size of seed. To contact an appropriate seedbed, large numbers of widely distributed seeds are needed. Sugar maple and beech have large seeds that can tolerate a wide range of seedbed conditions. And, because of its ability to root sucker, seed production in beech is not as critical as for sugar maple.

Timing of seed fall differed by species. Yellow birch seed was distributed over an extended period, especially when seed was abundant, from August through the following May. Most of the viable seed fell in September, October, and November; but, there were exceptional years when up to 43 percent of the viable seed fell in December and later. While both sugar maple and beech seed fell throughout the summer and autumn, the viable seedfall was mostly confined to September through October for sugar maple and October through November for beech. No viable beech seed fell after November, and less than 1 percent of the viable sugar maple seed fell in December or later.

Approximately one-third of the total seed crop reached the ground in a viable condition. Birds, mammals, and insects destroyed 14 percent of the sugar maple crop, 31 percent of the yellow birch crop, and 43 percent of the beech crop (Fig. 9). Additional predation took place after seed fall, especially on beech and sugar maple. The annual seed crop constituted a major but highly variable wildlife food resource. The total annual dry weight of the viable seed fall averaged 132 kg per ha, and ranged from less than 1 to more than 300 kg during the 11-year period.

Empty seed was the major nonviable category for all three species. This condition was usually caused by pollination or fertilization failure in yellow birch and beech. Sugar maple differed in that post-zygotic abortion consistently caused one-half of the seeds to be empty. Incompletely developed or partially filled seed was prevalent in yellow birch (10 percent), but not in sugar maple (4 percent) or beech (1 percent). Sugar maple was the only species with a significant seed fall in June (abortion). This loss coincided with periods of environmental stress.

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Seed fall was measured for 11 years in a 200-year-old stand of sugar maple, yellow birch, and beech in New Hampshire. Yellow birch had 5 good seed years, sugar maple had 3, and beech had none. Viable seed fall of yellow birch began in August and continued through autumn and winter. Most of the viable sugar maple seed fell during a short period in October. Beech seed fall occurred slightly later than sugar maple. Seed losses caused by pollination or fertilization failure, abortion, incomplete development, insects, small mammals, and birds averaged about 2/3 of the total seed fall, but varied widely among years.

Keywords: beech-birch-maple, seed production, seed viability

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