Flowering and Seed Production in Seven Hardwood Species

by Ted J. Grisez

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AS FOREST management has grown more intensive in the cherry-maple and oak forests of the Allegheny region, the need for additional knowledge of the seeding habits of important tree species has become apparent. Reproduction of new stands after cutting depends, to a large extent, on an adequate seed supply. And seeds and friuts represent an important source of food for many species of wildlife.

To insure adequate seed supplies for these purposes, forest resource managers need techniques for assessing and predicting seed crops. They need more knowledge of the effects of stand density, tree size, and site factors in order to increase seed production.

In 1963, forest resource managers from various public agencies and private companies in northwestern Pennsylvania[1] joined in establishing a cooperative study of seed production of seven hardwood species: white ash, beech, black cherry, red maple, sugar maple, red oak, and white oak. This is a report of that study.

The study area extended from Crawford County to Potter County, Pennsylvania, and included Allegany State Park in Cattaraugus County, New York.

METHODS

Each cooperator selected and marked trees over 10 inches dbh in even-aged hardwood stands at least 40 years old, where there had been no disturbance during the past 10 years. The trees selected had to meet certain specifications for crown class and proximity to other trees of the same species as sources of pollen.

Dbh, crown width, and point density were recorded for each sample tree. Point density is the basal area of the stand about the sample trees. In this study, it was determined with a 10-factor prism.

The method of seed crop rating developed by Sharp *(1958)* for oaks was used; it was adapted for flower and seed crop rating of other species. Each productivity class was defined as a certain percentage of the assumed maximum number of friuts or fruit

[1] Cooperators were: Hammermill Paper Co.; Larimer and Norton, Inc.; Pennsylvania State University; Cornplanter and Susquehannock Districts of the Pennsylvania Department of Forest and Waters; Allegany (N.Y.) State Park Commission; U.S. Fish and Wildlife Service; and the Bradford and Ridgway Districts of the Allegheny National Forest.

clusters on a specified length of branch or number of branch endings in that species.

Productivity rating	*Percentage of maximum*
Bumper	79 to 100
Good	51 to 75
Fair	26 to 50
Poor	11 to 25
Trace to none	0 to 10

The criteria used to rate flower and seed crops are given in the appendix.

Seed crops were rated by viewing the tree crown through 6x to 8x binoculars when fruits were almost full-grown, but before they ripened and fell or were consumed by wildlife.

We planned to rate the seed crops of each species for 3 consecutive years, or longer if necessary, to get an adequate rating of species that seed infrequently. Flower crops were rated in 1 of the 3 or more years in which seed crops were rated. Red maple and the oaks were not rated for flower production. Red maple was not rated because the seeds ripen in the spring only about a month after flowering. Thus there would be little advantage in being able to predict red maple seed crops from flower crops. The oaks were not included in the flowering phase of the study because pistillate flowers are difficult to see from the ground and, at least for white oaks, Sharp and Chisman *(1961)* found that good crops of male flowers were produced every year and that the periodic scarcity of acorns was not caused by lack of flowering in poor seed years.

RESULTS

Useable data were obtained from 422 trees —40 to 84 per species. Not all of them had their seed crops rated for three or more years and still fewer were rated for both flower and seed crops in the same year.

Records of the seed crops of individual trees whose flower crops had been observed show that the seed crops of white ash and sugar maple can be predicted with reasonable accuracy. The seed crops of black cherry are not closely related to its flower crops. The data for beech were too limited to support firm conclusions.

Chi-square tests of the data for 58 white ash trees and 31 sugar maple trees indicated a close relationship between flower crop and seed crop ratings. Table 1 shows the number of white ash trees with each combination of flower crop and seed crop ratings. For example, out of 49 trees judged to have bumper crops of pistillate flowers in the spring, 35 were found in late summer to have bumper seed crops, 10 had good seed crops, and 4 had fair seed crops. If the flower crops and seed crops were perfectly correlated, all values would fall in the diagonal of the table. Most of the trees had seed crops in the same class as the flower crops or within one class on either side.

Table 2 shows the relation between flower and seed crop ratings for the sugar maple trees. All but seven of the 31 crop ratings were within one rating class of the flower crop ratings. That five seed crop ratings exceeded the flower crop ratings is not surprising; sampling variation can account for the difference—that is, the branches selected

Table 1.—Relationship between flower crop and seed crop ratings in white ash
(Number of trees)

Seed crop rating	Flower crop rating				
	Bumper	Good	Fair	Poor	Trace to none
Bumper	35	0	0	0	0
Good	10	0	0	0	0
Fair	4	1	1	0	0
Poor	0	0	1	0	0
Trace to none	0	0	0	0	0

Table 2.—Relationship between flower crop and seed crop ratings in sugar maple
(Number of trees)

Seed crop rating	Flower crop rating				
	Bumper	Good	Fair	Poor	Trace to none
Bumper	0	2	1	0	0
Good	1	2	0	0	0
Fair	2	1	0	1	1
Poor	0	0	2	0	0
Trace to none	0	1	2	1	14

in rating seed crops may have differed from those used in rating flower crops.

Another factor that may add to the disparity between flower crop and seed crop ratings in sugar maple is its flowering habit. Female flowers may be confined to certain parts of the crown, while other branches, particularly lower branches, may carry only male flowers; or trees may have flowers of both sexes at all crown levels *(Wright 1953; Gabriel 1962)*. Male and female flowers look alike from a distance, so that some clusters of male flowers may be counted in rating flower crops, and the crop overestimated. Even so, the evidence is that flower crops in sugar maple can be used to predict seed crops.

For beech and black cherry, the relationships between flower crops and seed crops were not statistically significant. None of the 31 beech trees used to compare staminate flower crops and seed crops (see appendix) had flower crops in the bumper or good classes. The lower seed-production classes were well correlated with staminate flower production, but there was no test of the better classes.

The absence of a significant relationship between the flower crops and seed crops of 47 black cherry trees was apparently because 17 of the 26 trees with bumper or good flower crops failed to produce any seed crops better than poor. This verifies a common observation: that abundant flowering in black cherry is not necessarily followed by good seed crops. Flowers are usually plentiful, but seed crops are erratic.

Since a late spring frost can destroy a flower crop, it could upset predictions of seed crops. If ratings were made before such a frost, the observer should check to find out whether the flowers were killed on the trees he is observing, so that he can revise the ratings if necessary.

Relationships of Tree Variables to Seed-Producing Capacity

The effects of dbh, crown width, and point density on seed production were studied by regression analysis. Seed-producing capacity, the dependent variable in the regressions, was defined as the highest seed crop rating recorded for each tree during 3 or more years of observation. This rating should reflect the seed-producing capacity of the tree by covering a span of years long enough to include at least 1 year when the seed crop would not be reduced by unfavorable weather or other causes. There were not enough data from beech or white oak to be used in the regressions, but 32 to 52 trees of each of the other five species were used.

Simple regressions of several forms were computed for all combinations of five species and three independent variables. Significant regressions were found for dbh of sugar maple and for point density of white ash, black cherry, red maple, and red oak. Coefficients of determination (R^2) for the significant regressions ranged from .09 to .28.

Some apparent anomalies show up in the signs of the coefficients in the regressions: The smaller sugar maple trees (but all were over 10 inches dbh) and the red maples and red oaks in denser stands had higher seed production *per unit of crown*. For white ash and black cherry, the seed-producing capacity decreased with increasing stand density, as might be expected.

No relationships were found between crown width and seed-producing capacity. Thus differences in *total* seed production among trees of different crown sizes must be due mainly to crown size, and not to the density of seeds on a branch.

Multiple regressions were also computed, but there was very little improvement in the R^2 values. Although the regressions were statistically significant, the R^2 values were low and the standard errors were high, so the equations have little value as predictors of the seed-production capacity of individual trees.

Frequency of Seed Years

The seed crop ratings for each species were averaged for each year for which data were available. The results are shown in table 3. They indicate the consistency of seed production from year to year and the occurrence of seed years during the study, but the study did not run long enough to

Table 3.—Average of seed crop ratings and number of trees observed *(N)* by species and year

Year	White ash		Beech		Black cherry		Red maple		Sugar maple		Red oak		White oak	
	N	Crop	*N*	Crop	*N*	Crop	*N*	Crop	*N*	Crop	*N*	Crop	*N*	Crop
1964	25	Bumper	33	Poor	—	—	—	—	—	—	26	Poor	25	Good
1965	49	None	4	Poor	20	Trace	3	Good	17	Trace	26	Trace	25	None
1966	51	Trace	4	Poor	39	Poor	30	Poor	38	Poor	60	Poor	36	Poor
1967	57	Fair	4	Poor	52	Trace	36	Fair	52	Good	45	Trace	22	Trace
1968	57	Trace	4	None	22	Fair	36	Poor	18	Poor	15	Trace	9	None
1969	25	Poor	8	Trace	5	Fair	—	—	7	None	36	Trace	17	Poor

establish patterns or ratios of good seed years, and the data were not necessarily collected in the same stands throughout the period. These data, when combined with other observations, may help to establish trends.

White Ash.—There was wide variation in white ash seed crops from year to year (table 3) and among stands in the same year. A bumper seed crop in 1964 was followed by 2 years with little or no seed. In 1967 there was a good seed crop in a Warren County stand, and a complete failure in a Potter Couny stand. In the Warren County stands, 2 years out of 5 were seed years during the study. Informal observations in other stands in Warren County and vicinity in the 5 years from 1969 through 1973 also show two seed years in five (1969 and 1971). This agrees with Wright's *(1953)* observation that female white ash trees flowered 2 or 3 years out of 5.

Black Cherry.—No black cherry seed crops better than poor were produced until the fourth year of the study—1968 (table 3). The study results and our experience with seed collection show that there has never been a total failure over a large area in the past 12 years. There are always fair seed crops on a few trees, at least. Sometimes trees in the Allegheny River Valley bear good crops when seeds are scarce on the plateau; this occurred in 1971 and 1972, and the opposite in 1970. Failures are not caused by late spring frosts. Black cherry is virtually frostproof, as far as reproduction is concerned, since the flowers bloom from the last of May through early June in the study area.

Red Maple.—Red maple is reported to have a good seed crop almost every year *(U.S. Forest Service 1948)*, but this is a little optimistic, at least for northwestern Pennsylvania. In some of the stands under observation, immature seeds were killed by late frosts in 1966 and 1968. But this does not explain all of the poor records.

Sugar Maple.—Sugar maple seed crops fluctuated widely, and only one good seed year was recorded during the study (table 3). Thirty-three of the 52 trees observed in 1967 had bumper seed crops. There was another good or bumper seed year in 1972. These two seed years from 1965 to 1973 agree with published information on the frequency of good sugar maple seed crops *(U.S. Forest Service 1948)*.

Red Oak.—No red oak seed years better than poor were encountered during the study (table 3). In the first 4 years of the study, average seed crops ranged from two to five acorns per branch terminal. There was heavy cankerworm defoliation of some study trees in 1967, and this may have reduced seed production for the next 2 years.

White Oak.—There was a very good white oak acorn crop in 1964, but only poor crops to none in subsequent years (table 3). The next good seed year in this area was 1971, making one interval of 7 years between good seed years. Sharp and Sprague *(1967)* did not encounter a good seed year until the sixth year of their study in central Pennsylvania but in the last 6 years they recorded four good acorn seed years.

Consistency of Seed Production

Some species are fairly consistent in seed production from year to year (table 3)—they usually have a few trees that produce fair to good crops or else several trees that produce trace to poor crops. Beech, red maple, and red oak fall in this category. White ash and white oak represent the other extreme. They tend to have either very good or very poor seed crops. Black cherry and sugar maple are intermediate; some stands have no seeds in off years while others have trace to fair crops.

Individual trees were noticeably consistent in seed production from 1 year to another in beech, black cherry, red maple, and white oak. Several black cherry and red maple trees had two or three fair or better seed crops in 3 years, while others never had a seed crop better than a trace. Four beech trees rated for 4 years and seven white oaks rated for 2 years ranked in almost identical order each year. Red oak was variable; some trees had two or even three seed crops in the same rating class in 3 years, while others that had one fair or good crop had little or no seed in other years. There were not enough seed crops in white ash and sugar maple to support conclusions. These and similar records *(Sharp and Sprague 1967)*, the weak relation between phenotypes and seed crops shown in this and other studies *(Down and McQuilkin 1944)*, and the persistence of seed-production characteristics in grafted stock *(Matthews 1963)* indicate that seed-producing capacity is, to a large extent, genetically controlled.

Unfruitfulness

Wright *(1953)*, working in the Philadelphia area, found unfruitfulness common in sugar maple, ashes, and oaks. In our study, unfruitfulness was rare in beech, black cherry, sugar maple, and the oaks. Only 3 out of 39 black cherries, 2 out of 36 sugar maples, 2 out of 59 red oaks, and 4 out of 36 white oaks failed to bear enough seed to earn a "trace" rating in any of the 3 years when they were observed. Sixteen other sugar maples that were observed only 1 or 2 years also bore seed crops. Data on beech are available for only 1 year for most trees, yet all but 5 out of 36 bore seeds. White ash and red maple had somewhat higher proportions of unfruitful trees. Ten out of 54 female white ashes and 10 out of 28 red maples never had more than a trace seed crop in 3 or more years.

Other observations on white ash.—Since white ash trees are dioecious, cooperators were asked to record the sex of the sample trees. It was expected that the ratio of female to male trees would be about 1:1 *(Hunt 1964)*. In this study, the cooperators listed 31 female trees and 22 male trees, a ratio of 1.4:1. This is not significantly different, by chi-square test, from a 1:1 ratio.

The effect of seed crops on diameter growth of trees is also of interest. Holmsgaard *(1972)* wrote that a good [European] beech seed year reduces ring growth to about half that of years without a seed crop. Although our study was not designed to test this, we examined differences in the diameters of male and female white ash trees to see if there was a gross difference in growth rates. We selected 40 trees from the same general area that were believed to be essentially the same age. If seed were produced at the expense of diameter growth, the female trees should have been smaller than the male trees, but there was no difference. The average dbh of the 24 female trees observed was 12.6 inches, while the 16 male trees averaged 12.4 inches. The seven trees that had good or bumper seed crops also averaged 12.6 inches in diameter.

The Seed Crop Rating Method

Visual seed crop ratings proved to be a practical method of assessing the seed crop production of individual trees and stands. This method can be useful (1) in determining the relative seed production of individual trees in stands or in scattered locations, (2) for estimating the total seed crop produced by a tree before it is eaten by wildlife, and (3) in making area-wide surveys of seed crops. This method could be used in combination with others, such as a complete harvest of a sample of trees, to relate seed crop ratings to quantitative measures of seed production.

It may seem difficult to use this visual method in crowded stands where it is not possible to see all parts of the crown of the tree being rated. But it is not necessary to see all of the seeds on a branch, or every branch on a tree; the ratings are derived from averages of samples and high precision is neither possible nor necessary.

CONCLUSIONS

1. Flower crops and seed crops were closely related in white ash and sugar maple, and observation of spring flower crops can be used to predict seed crops of these species. Flower crops of black cherry were not well related to seed crops, and for beech the data were inconclusive.

2. Seed production was related to dbh in sugar maple, and to stand density in white ash, black cherry, red maple, and red oak. But none of these relationships was strong enough to provide an accurate estimate of the seed-producing capacity of a tree.

3. Beech, red maple, and red oak, as species, are fairly consistent in seed production from year to year; white ash and white oak, on the other hand, tend to have either very good or very poor seed crops.

4. Individual trees of beech, black cherry, red maple, and white oak tend to be consistent in seed production. The better producers in one seed year usually produce well in other seed years.

5. Visual seed crop ratings are a practical method of assessing seed crops of individual trees and stands.

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APPENDIX

Seed and Flower Crop Rating Criteria

White ash.—White ash trees are dioecious—male and female flowers are borne on separate trees. The female or pistillate flowers of white ash are large, loose panicles, while the staminate flower clusters are small and dense. Although both sexes were selected as sample trees, sex was identified later by flowers, seeds, or the stems of old seed clusters on the tree or on the ground. Only female trees were used for flower or seed crop ratings.

In white ash, the maximum seed production is likely to be four seed clusters or panicles per single twig. It would be impractical to count the number of seeds per cluster. Therefore the flower or seed crop rating was based on the average number of flower or seed clusters on 10 twigs in the exposed portion of the crown. Several groups of 10 randomly selected twigs in various parts of the exposed crown were counted to estimate the average. Ratings were assigned according to the following table:

Flower or seed crop rating	*Average number of clusters per 10 twigs*
Bumper	31 - 40
Good	21 - 30
Fair	11 - 20
Poor	5 - 10
Trace to none	0 - 4

Beech.—Beech burs are borne on short stalks in the leaf axils of the current year's growth. They appear at or slightly above the level of adjacent leaves and are best viewed from the outside of the crown (not from beneath) after early August when they turn reddish brown. The staminate flowers occur in pendent heads; the pistillate flowers are two to four on a short-stalked spike. Hence the staminate flowers are more conspicuous and so they were used in rating flower crops.

The terminal 24 inches of a branch, including all laterals, were used to rate seed or flower crops. Twenty or 30 branches in the upper half of the crown were randomly selected to determine the average number of burs or staminate flower clusters on the terminal 24 inches. The ratings were assigned as follows:

Flower or seed crop rating	*Average number of burs or clusters per 24-inch branch tip*
Bumper	19 - 24
Good	13 - 18
Fair	7 - 12
Poor	3 - 6
Trace to none	0 - 2

Black Cherry.—The perfect flowers of black cherry occur in long racemes that grow from lateral buds on the shoot of the previous year. There usually are one to three small leaves on the basal part of the flower shoot.

Cherry flower and seed crops are best rated by standing away from the crown to view it from the outside. The unit for rating flower or seed crops is the terminal portion of the branch tip that includes the current and previous year's growth; that is, one terminal or lateral shoot of the previous year, plus all of the current year's growth on it. This is usually about 12 inches on reasonably vigorous twigs.

The average number of clusters (racemes) per 12-inch branch tip was determined by counting those on 20 to 30 randomly selected branches in the upper half of the crown. Also, the average number of flowers or fruits per raceme was determined. These averages were multiplied to obtain an average number of flowers or fruits per 12-inch twig. These numbers were then converted to flower or seed crop ratings as shown in the following table:

Flower or seed crop rating	*Average number of flowers or fruits per 12-inch twig*
Bumper	49 - 64
Good	33 - 48
Fair	17 - 32
Poor	7 - 16
Trace to none	0 - 6

No bumper seed crops and very few good crops were recorded on individual trees during the study, but trees rated fair or even poor had quite a lot of cherries on them. The assumed maximum number of flowers or fruits per twig was 64 but the highest seed crop rating recorded in this study was 45. This is probably because open-grown trees were used in setting the maximum. There can be more than 40 flowers per raceme and more than six racemes per twig, although the combination is not likely to be found—certainly not as an average. Most of the averages for forest-grown trees, and the ratings flowers don't bear fruit. For this species, different scales might be used for flowers and fruit: 80 flowers and 48 fruits are likely maximum should be scaled accordingly.

Red maple.—Although red maple flowers are structurally perfect, they are functionally either male or female. Some trees have only one type of flower; others have both *(Wright 1953)*. Flower crops on red maple were not rated, nor were the trees identifed as to the types of flowers they bore.

The fruit clusters of red maple are derived from lateral buds and, therefore, appear on the shoots of the previous year. The seeds develop before and with the leaves, and the seed crop is easily rated from a short distance away by counting the number of 12-inch branches out of 30 that contain three or more clusters of samaras. The 30 sample branches are randomly selected from exposed parts of the crown. The seed crop ratings are shown in the following table:

Seed crop rating	*Average number of branches with 3 or more clusters (out of 30)*
Bumper	23 - 30
Good	16 - 22
Fair	8 - 15
Poor	4 - 7
Trace to none	0 - 3

Sugar maple. — In a good seed year, most branchlets terminated in fruit clusters of 6 to 12 double samaras *(W. W. Ward, personal communication, 1964).* The seed crops were rated by viewing the crown from a short distance—not from beneath. (Since the flowers are out before the leaves, the position makes little difference when rating flower crops.) Thirty randomly selected terminal branchlets from the exposed part of the crown were used for flower or seed crop rating; short lateral branchlets were not included in the sample. The branchlets that ended in a flower or seed cluster were counted. The ratings were based on the same proportions of the maximum of 30 shown above for red maple seed crops.

Red Oak. — The methods of rating red and white oak acorn crops were developed by Sharp *(1958).* Red oak acorns, which require two years to develop, are found on 1-year old portions of the branch tips. They appear beneath the level of adjacent leaves and are readily observed from under the crown of the tree. All acorns on a 24-inch branch terminal, including all lateral branchlets, were counted. The counts for 20 to 30 randomly chosen branches from the upper half of the crown were averaged and this number was converted to the rating class as follows:

Seed crop rating	*Average number of of acorns per 24-inch branch tip*
Bumper	25 - 32
Good	17 - 24
Fair	9 - 16
Poor	4 - 8
Trace to none	0 - 3

White Oak.—In contrast to those of red oak, white oak acorns mature in one season. At maturity, the acorns are at or above the level of the adjacent leaves. Therefore, white oak acorns are best viewed from outside the crown. As in red oak, the terminal 24 inches (including current growth), and all lateral branchlets were used to rate the seed crop. Acorns were counted on 20 to 30 branches in the upper half of the crown. An average of 24 was considered a maximum, and the table for beech was used to determine the seed crop rating.

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Flowering and seed production of selected trees in northwestern Pennsylvania and southwestern New York were rated visually for several years. The seed crops of white ash and sugar maple were closely related to the amount of flowering, and flowering can be used to predict seed crops in those species. Seed-producing capacity was also related to other measured variables, but not closely enough to make them useful in predicting seed production. Consistency of seed production in species and individuals, and other aspects of seed production are discussed.

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