BREEDING OF HARDWOODS

by

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INTRODUCTION

The fundamental principles of heredity apply equally well to both hardwoods and softwoods. Yet the hardwood and softwood breeding programs have been very unlike. The main reasons for this are:

1. The general difficulty of planting hardwoods.

2. The uneven-aged and sprout character of most hardwood stands.

3. The presence of reproduction irregularities such as polyploidy and clonal reproduction in many hardwoods.

The fact that hardwoods are so difficult to plant is probably the greatest single reason why relatively little work has been done on them genetically, The tree breeder who produces a better oak or a better ash does not have much of a market for his improved variety. Also, producing a better variety requires a lot of test-planting in the meantime. Getting these test-plantings established is an expensive business.

Perhaps we can counteract this planting difficulty to some extent by doing more of our testing work in the nursery. Two-year-old ash or birch can be quite sizable trees, and they can probably foretell the performance of the mature tree much better than do 2-year-old pine or spruce.

There are a few hardwoods in which planting is not such a bottleneck in the testing program. Examples are high-sugar, sugar Maple, curly-grain clones, black locust, and yellow-poplar.

Another difficulty is the fact that most hardwood stands are mixed, uneven-aged, and have many sprout clumps. This makes selection work difficult and multiplies the amount of testing necessary to determine whether or not there is much hereditary variation in a given character. There is little doubt that red maple is more variable than red pine, yet it is a good deal harder to pick out the really good red maples in a stand of sprout origin than it is to pick out the good red pines in a pure pine stand.

But there are other respects in which the hardwood breeder has an advantage over the pine breeder. Polyploidy promises to be a very useful tool in breeding birch, maple, and ash. And some species such as aspen, black locust, and beech spread by means of root suckers. Here nature has already set out clonal plantings that can be used in statistical studies of inherited characters.

I will confine this discussion to the four hardwood genera (exclusive of poplar) on which the most work has been done: birch, maple, oak, and ash. In general the work has progressed just far enough to show which lines of attack are most promising, but not to give us definite improved varieties.

(A considerable amount of work has been done on the elms and chestnuts, too, but this work is aimed toward shade or nut trees more than toward forest trees. In several other genera smaller amounts of work have been done.)

We now have a fairly satisfactory picture of the general crossabilty pattern in each of these four genera. But there is very little detailed information on the species crossabilities or on the relative growth performances of the hybrids. There is almost no information on variability of races, although this subject has been a favorite one in pine breeding. There are a few fragments of information on the possibilities of selection and polyploidy.

Controlled pollinations and mass-production by seed merit more detailed discussion than vegetative reproduction. This is because vegetative propagation is in general satisfactory for experimental purpose (except in sugar maple and the oaks) but not for the mass-production of clones for forest planting. Most of our improved varieties in these genera will probably have to be progagated by seed.

BIRCH

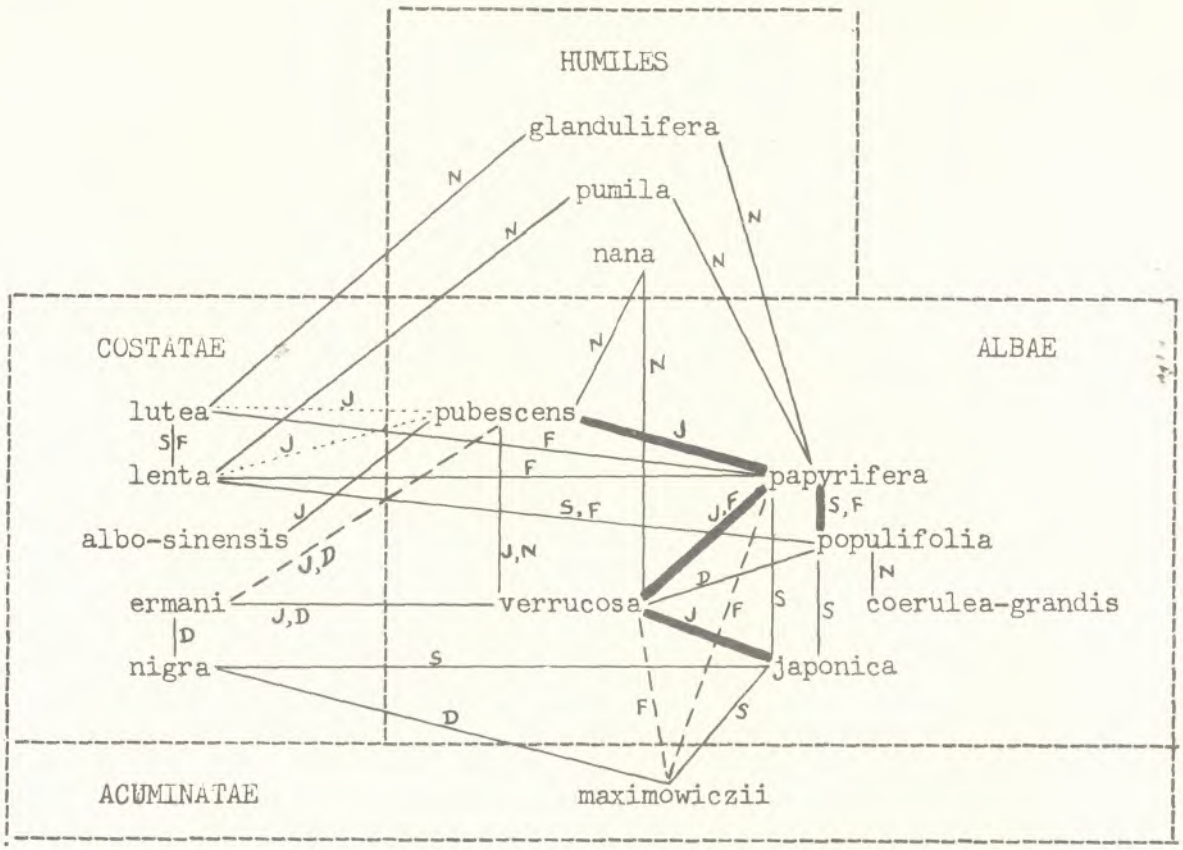
The interspecific crossing picture for birch is shown in figure 1. While some of the hybrids shown there as presumably successful must remain doubtful until carefully checked, there are enough well-authenticated hybrids to show that most crosses within the genus could be made.

Three factors affect the ease with which crosses are made: (1) chromosome number, (2) morphological diversity, (3) geographic range.

Strangely, three of the four most successful crosses involve species with different chromosome numbers. Evidently there's been little need for genic, or chromosomal differentiation where there are differences in chromosome number.

Johnson's (10) results with triploid B. verrucosa show that sterility_ in the triploid keeps the parental types from introgressing even though crosses do occur. However, not all diploid x tetraploid crosses take easily, The closely related B. pubescens and B. verrucosa cross with great difficulty.

There is a well-recognized principle in animal taxonomy that closely related species that are not separated geographically or ecologically do



Legend

- ·········· Cross tried, not successful
- – – – – Cross doubtfully successful
- ——— Cross presumably successful (less than 1% seed set)
- ▬▬▬ Cross successful (more than 5% seed set)

- N Natural, reported by Rehder (22) or Johnson (9)
- S Smith and Nichols (24)
- J Johnsson (9)
- D Delevoy (5)
- F Northeastern Forest Experiment Station, U.S. Forest Service

Figure 1.--Natural and artificial birch species hybrids.

not cross as readily as those which are. Otherwise the species would long ago have lost their identity.

This holds true for the birches. With the exception of gray x paper birch, which involves an isolating difference in chromosome number, the easily made crosses involve species with wholly separate ranges. The hybrids involving species that are riot isolated by geographic or ecological barriers or by differences in chromosome number are either doubtful or very rare. To summarize, birch hybrids are most easily made between species in the same taxonomic section but growing in different regions.

What are the possibilities of interspecific hybridization? The following data are taken from Johnsson (15). The numbers refer to relative heights at 7 years from seed; 100 = 15.4 feet. (For example 98 and 112 refer respectively to B pubescens and to B. papyrifera and 101 refers to the hybrids between the two species.)

98		112		91		—
pubescens	x	papyrifera	x	verrucosa	x	japonica
	101		100		106	

There are similar data for 12-year-old hybrids produced at the North-eastern Forest Experiment Station (100 = 9.3 feet).

97		100		150
lenta	x	papyrifera	x	populifolia
	160		101	

113		100
lutea	x	papyrifera
	108	

In two cases there is probable hybrid vigor; in the rest intermediacy.

No racial studies have been reported. But preliminary evidence from Sweden, and taxonomic and cytological evidence in paper birch, indicate that geographic races are as strongly developed in some birches as in any conifer. Certainly a racial and taxonomic study would be the first step in a paper birch improvement program.

Polyploidy is common in birch. (4). A start has been made in Sweden to produce autotetraploids and thence triploids. The triploid B. verrucosa trees grow much faster than do the diploids (15). Making species hybrids fertile by doubling their chromosome numbers is also a good possibility.

We cannot yet generalize on whether the polyploid types would be superior or inferior to the diploids, and the following tabulation shows:

	Diploid	Polyploid
North America	populifolia	papyrifera
Europe	verrucosa	pubescens

These species are all closely related, belonging to the section Albae. In each continent one species is nearly useless and the other is useful. In America it is the polyploid that is valuable, but in Europe it is the diploid.

To show what selection has to offer I can cite three Swedish experiments. In each case it is fairly certain that the variation has arisen within the species rather than by introgression from another species.

In both major. birch Swedish species there are precocious trees that flower at the age of 2 years. The character is hereditary, and the early flowering seems to be controlled by a single dominant gene (13).

Figured grain is found only in B. verrucosa. The character can usually be recognized from the bark. The character is apparently under the control of just a few genes, as 1 to 52 percent of the open-pollinated progeny and 44 to 62 percent of the control-pollinated progeny possess the figured grain (16).

Thus there is already a cheap source of seed of this valuable type. However, a little further selection may be considered desirable, as the grain pattern does vary and the figured progeny grows 0 to 20 percent slower than does normal progeny from the same parents. It should be perfectly possible to transfer these Swedish strains to the Northeast and avoid doing our own selection and development work.

Johnsson (15) presents decisive evidence in the inheritance of form and vigor differences in birch species. In one experiment there was an 8:5 ratio in height and 7:2 ratio in stem volume between the best and poorest families from different parents at 6 years from seed. And even at this early age differences in stem form were noticeable.

A few words on breeding technique. The birches are parthenocarpic, maturing catkins whether pollinated or not. Premature fruit drop is no problem. Seed sets to intraspecific pollinations are usually so high that one bagged branch usually natures ample seed for a progeny test. Either sausage casings or paper bags are satisfactory.

The female flowers are at least partially receptive as soon as they emerge from the bud. Therefore bagging before flower emergence or before pollen-shedding is necessary. Some of the reported hybrids are suspected to have resulted from contamination resulting from too-late bagging. There is a possibility that some suspected hybrids have also arisen through apomixis, but this is not definitely proved.

MAPLE

The following represent our successful maple species crosses (31).

Section	Female parent	Male parent	Hybrid vigor
Platanoidea	platanoides	mayrii	No
Platanoidea	platanoides	cappadocicum	Yes?
Saccharina	saccharum	nigrum	No
Rubra	rubrum	saccharinum	No
Negundo	negundo	henryi	Yes?

Most of the possible intersectional crosses involving these and 3 other species were also tried repeatedly, but failed--with one possible exception (A. platanoides x saccharum). The above species, together with A. campestre (section Campestria) and A. macrophyllum and A. pseudoplatanus (section Spicata), and a few sugar maple relatives are all that need to be considered even remotely for this country at present. Nearly all the rest of the maples are small trees or shrubs.

Since the intersectional crosses have failed, it is a good bet that future maple improvement must come from within sections. Moreover, within a section the work can be centered around one species, as each section has one outstanding species.

It should be mentioned that natural intersectional hybrids are reported by Rehder (22) and artificial intersectional hybrids by Al'Benski (2). The natural hybrids are presumably rare, and with the present international situation, the authenticity of Al'Benski's hybrids cannot be confirmed. Al'Benski reports hybrid vigor in certain of his hybrids.

Mass-production of these F1 hybrids will be a tricky problem. Seed sets are relatively high--10 to 50 percent. But, except in the red and silver maples, the number of flowers per bag and the number of bags that may be worked per man-day are low and would make mass-production by hand pollination expensive.

Mass-production by interplanting of selected clones also hits a snag. For the maples are primarily honeybee pollinated. Any one honeybee confines itself pretty much to one species, so that the percentage of hybrid seeds obtained from a mixed planting is unexpectedly low (17). The use of F_2 and backcross progeny and of amphidiploids produced by colochicine probably represent the best ways of utilizing these hybrids.

There have been no formal racial tests in any of the maple species. Taxonomically, though, red maple is quite variable, and has two different chromosome numbers (7). We have tried a few crosses between red maple trees of different geographic origins. Replicated nursery tests show probable hybrid vigor, New Jersey x Philadelphia trees outgrowing Philadelphia trees, which in turn outgrow Philadelphia x Massachusetts trees.

There are just a few clues to the amount of individual tree variation in the maples. Snow (25) found differences in rooting ability among various red maples from the same locality. Boxelder furnishes an example of the way in which we shall need to combine selection and interspecific hybridization work. So far all the hybrids of boxelder with the Japanese A. henryi have been obtained from one female parent. The hybrids grow faster than nonhybrid progeny from this same parent. But they do not grow as fast as do npnhybrid progeny from another female. In this case selection and interspecific hybridization practiced together can accomplish more than either alone.

Considerable work has been done on sugar maple but this work has not panned out well. For one thing, only a small percentage of the large trees flower well in any one year, and we must often wait 10 years or more before making a desired cross. Too, sugar maplehas proved very difficult to root and graft.

Several starts ite been made toward selecting strains with high sugar contents in their saps, but none of these programs has gone beyond the sap-testing stage. However, several farmers are convinced that this selection is a good thing, and they practice selection on their own trees with a sap hydrometer and cull the low yielders.

There is one exotic maple that is especially promising. The Norway maple has established itself in parts of Pennsylvania where it reproduces readily and shows good log form in the forest. So far it is most common in localities without sugar maple. Since it is about equal to sugar maple in wood density (1) and seems to be a better tree than red maple, it would make a useful addition to the native forest.

OAK

In the oaks most American genetic thought to date has been directed toward interspecific hybridization. There is a general feeling that our American oak species really represent no more than a series of well defined races that hybridize at every opportunity, and that introgression between these races is the major source of variation.

This picture does seem to apply to some complexes of western species (26). But I think another picture is more applicable to the majority of the oak species common to the deciduous forests of the East:

1. There as a large number of relatively stable species.

2. These species are not well differentiated from each other genetically, and the majority of them could cross with each other. However, the number of hybrids actually produced is a small fraction of the number possible.

3. When hybrid swarms are formed they persist only for a few generations and do not generally lead to introgression.

Palmer's list (20) is the best source of information on the relative commonness of natural oak hybrids in the East. As a result of 30 years' search he has found "not more than a few hundred trees of unquestionable hybrid origin" in 72 different species combinations. Most of these he regards as F_1 hybrids. This list, large as it is, includes but a small fraction of the combinations that could occur if all possible hybridizations were to take place.

There are two recent papers bearing on introgression or the lack of it. Stebbins, Matzke, and Epling, (27) found that, in New Jersey, hybrid swarms involving blackjack and scrub oak are small and restricted in area, and that there has been little or no introgression despite the fact that similar crosses must have occurred repeatedly in the last 25,000 years.

Muller (19) studied hybrid swarms involving several different species combinations in Texas. In all but one case these swarms are practically confined to the boundary between the two parents. The parents had quite different soil preferences and the hybrids were not able to compete except on areas of intermediate soils. One hybrid swarm is located several hundred miles inside the range of one of the parent species, and seems to represent an ancient hybridization followed by limited introgression.

Now to pass on to the artificial species hybrids (23, 8, 21, 31). The complete list includes 44 different combinations, 5 produced in the United States and 39 in Russia. (Several of the Russian hybrid combinations are purely maternal and therefore open to doubt.)

The most famous are the Ness Hybrids, Q virginiana x stellata, originally produced in 1909 and 1910, and F2 generation was raised in the late 30's. The F_1's show considerable hybrid vigor, as well as otter characters making them desirable as ornamentals. Several of the Russian F_1's also show hybrid vigor.

Most of the work on the natural hybrids has been done by taxonomists not particularly interested in the forestry possibilities of the trees. Many of these hybrids and hybrid swarms should be reinvestigated by foresters. It is quite likely that in a short time we could get as much data on the forestry possibilities of the F_2's and backcrosses as we could from several years breeding and testing work. However, it will probably be necessary to establish special F1 test-plantings, as most F_1's in nature are not certainly identifiable as such and are not growing under the best conditions for determining their potential value.

There's very little to report on geographic races in oak. Also very little on polyploidy. All species have the same chromosome number (4). The only polyploids reported are a few triploids of unknown value found in twin seedlings (11).

Over a period of centuries the Dutch have sown what may be done by conscious selection in the sessile oak. In their roadside plantings they have left only the straightest trees. The end result is a strain known as "Dutch oak" which is generally acknowledged in northern Europe to be superior to the wild type in form. However, this improvement was at the expense of growth rate, as the Dutch oak is slower growing than normal.

Johnsson (15) reported on a replicated 81-parent progeny test of Q. robur, Q. petraea, and their hybrids. At the end of the 7th year the poorest progenies from each origin had 21 to 50 percent of the stem volume per tree of the best progenies from the same origin. Some of this variation was due to differences between species and hybrids (Q. robur was the fastest growing). A great deal of the variation occurred within species.

Downs (6) has given us almost our only data on hereditary variability in form in an American species. He studied twin stems arising from the same sprout clump. Where the larger stem was forked the smaller. stem was apt to be forked too; the smaller stem was usually unforked if the larger stem was unforked. This indicates that there is a common hereditary influence. on both stems of a sprout clump. In view of the technical difficulties encountered in crossing and rooting oaks, this method of Downs' should be more widely used to get preliminary estimates of the, amount of heritable variability.

The technique problems are more serious in the oaks than in almost any other genus. In fact they are so serious that they will affect our future oak breeding plans just as much as will the genetic facts. The principal difficulties are:

1. Oaks are nearly impossible to root. Of 10 different groups of investigators who have attempted to root oaks (8, 28), only one group has reported successful rooting from trees more than 20 years old.

2. Oaks are difficult to graft. Little successful grafting work has been done by either nurserymen or tree breeders.

3. Oaks are difficult to control-pollinate. Using the correct type of bag (vegetable parchment)and working fruitful trees helps. But even with the best technique, seed sets to controlled pollinations have been somewhat below those to open pollination on the same tree. Seed sets to open pollination commonly run from 0 to 5 percent, rarely up to 50 percent. One man working for a season can expect about 200 acorns (occasionally 0 or 500 acorns) if making all crosses within species, and fewer if trying to produce hybrids. (These figures apply only to the better tree species; higher yields could be expected for some very fruitful shrubs such as bear oak.)

The Swedes recognize these difficulties and are apparently bypassing controlled-pollination work. Instead they contemplate establishing test-plantings consisting of 30 selected clones--selected on the basis of phenotype (14). When the trees come into fruit each clone will be progeny-tested and the planting will be thinned to leave only the best parents as a seed orchard. The small number of clones tested is the biggest flaw in the scheme. The number should be increased to 300 or 400, as many of the clones will be unfruitful, and our present ability to pick good genotypes in the woods is very low.

We can also make use of open-pollinated progenies in studying F1 species hybrids, collecting seeds from isolated trees subject to pollination by related species. At the worst such studies will give data on the incidence of natural hybridization.

ASH

In the eastern United States there are two major ash species--white ash and green ash. Both are widespread and racially variable; both have close relatives in Mexico and the Southwest.

Our crossing results from the ashes a meager. They indicate that these two closely related species do not cross with each other, nor with other unrelated species such as blue, black, or European ash (31). The one cross that has been successful is between green ash and its Arizona counterpart--Arizona ash. The only natural hybrid swarm reported also involved two close relatives that might be regarded as geographic replacements for each other (3).

In Philadelphia either the green or the white ash grows more than twice as fast--and has generally better form--than the nearest competitor among about 10 other species. We could test the other 30 species in the genus. But in view of the poor performance of the exotics already tried and the probable lack of crossability of the exotics with the best natives, this does not seem too important. For the time being we can safely concentrate our ash improvement program on white and green ash and possibly on hybrids between them and a few western species as yet untried.

There is a more complete picture of racial variability in white and green ash than in any other hardwoods (18, 29, 30). In both species the northern and southern races differ sufficiently from each other that individual trees in a nursery may be identified as to approximate origin.

The races differ from each other in drought-resistance, frost-hardiness, winter-hardiness, growth rate, type of root system, leaf shape, and color. In white ash there is polyploidy in the southern race, but the polyploids are indistinguishable from diploids except under a micro-scope.

There's a very good chance, however, that the polyploids and diploids differ in wood qualitiy. (Tests are now being conducted at the Forest Products Laboratory.) If so, we shall be able to work out methods for quickly improving the genetic duality of natural stands without planting by favoring either the diploids or polyploids. This would not be so difficult as it sounds, as they are probably grouped in nature.

In green ash racial tests there were a few progenies that did considerably better than others from the same locality, indicating that in some areas considerable progress can be made by merely selecting and progeny-testing female parents.

In control-pollinating ash there are two big difficulties, neither insurmountable with proper planning. One is that even over a period of 3 or 4 years a relatively small percentage of even large trees bloom. The other is that nearly half of the female trees that do bloom mature few or no seeds. To counteract these difficulties it is necessary to have more trees available for breeding work--at least 15 or 20 trees of each different type--in order that 1 or 2 will fruit when wanted. But they will fruit when relatively small, and on a close spacing. In view of the large numbers of trees needed, it will be more satisfactory to use test-plantations as breeding arboreta rather than to set up special breeding arboreta.

TRIFLOIDS

Some attention has already been given to polyploidy. But I would like to point out one special type of polyploid—the triploid-- as worthy of special mention in the hardwoods. The triploid condition is known to be a very favorable one in apples, and so it would seem to be in other trees, as shown in the following tabulation (9, 12, 14, 15).

Species	Relative dry weight of young trees		Relative specific gravity of wood	
	Diploid	Triploid	Diploid	Triploid
Alnus glutinosa	100	148	100	94
Populus tremula	100	130	100	91
Betula verrucosa	100	More than 100	No data	

The ultimate value of these triploids can be determined only by carefully balancing the advantages and disadvantages of the greatly increased growth rate and the slightly decreased specific gravity. From the information available the balance seems definitely in favor of the triploids, especially inasmuch as the triploid alder and aspen can be easily mass—produced by seed.

CONCLUSION

This review has hit the high spots in four genera. In a few isolated instances there is enough information now to enable us to get improved, new varieties into the forest.

But for the most part we have only fragments of information showing that certain lines of attack are promising. It will take a good many more of these fragments to get our hardwood breeding program into high gear.

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