Genotypic Variation in White Ash

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In the past few years attention has been increasingly focused on the importance of seed source in the establishment of forest plantations. The choice of the proper seed demands a knowledge of the genetic variability of the species to be planted. For most of our American trees, especially the hardwoods, these data are lacking. The present study was undertaken to supply basic information on an important group of deciduous trees that might serve as a background for sound planting practice and for future breeding work.

THE present study was undertaken to obtain information on the genetic variability of white ash (*Fraxinus americana* L.). This species was chosen because of its commercial importance, relative ease of handling in the nursery, and wide range (Nova Scotia west to Minnesota, and south to Florida and Texas).

There have been two previous progeny tests of intraspecific genetic variability in *Fraxinus*. The first was by Münch and Dieterich (5), who gathered seeds of *F. excelsior* L. growing on two widely different habitats—dry uplands and swamps—in southern Germany. By making reciprocal plantations on the two sites, they were able to prove the existence of different physiological races, the Kalkesche and Wasseresche. The second was by Meuli and Shirley (4), who grew seedlings of red ash (*F. pennsylvanica* Marsh.) in northern Minnesota from seed collected in 83 localities in the Great Plains. These young trees proved to belong to three genetically different populations, each population being distinct as to geographic range, drought resistance, growth rate, number of leaves per plant, and leaf coloring.

Anderson and Turrill (1) used quite another approach to the problem of genotypic variability within species. They applied special statistical techniques to the analysis of leaf characters in the ashes from the Danube and Mesta deltas of southeastern Europe. The analysis showed that very few of the trees studied were typical of either *F. oxycarpa* Willd. or *F. pallisae* Wilmott, the species native to the region. Rather, the majority showed a combination of characters of both, although tending toward one or the other. This suggests that the two species are descended from a common ancestor through isolation, and that now, with the barriers removed, the two forms are hybridizing.

EXPERIMENTAL PROCEDURE

SEED COLLECTION

In the late summer of 1939, some 150 requests for seeds and herbarium specimens of white ash were sent to men in the Forest Service, Soil Conservation Service, and various forestry schools. The response was gratifying and provided collections[2] from 155 trees representing 28 localities[2] in eastern United States and Canada.

Following is a complete list of the origins of seed used in the study. The capital letters preceding the place names denote the localities into which the individual tree collections (indicated by the numerals in parentheses) were grouped.

Southern Ecotype: A—Ala., Chilton Co. (111-114), Marion Co. (115, 116); B—Ark., Pope Co. (121); C—Ind., Owen Co. (151, 152), Greene Co. (153-156); D—Md., Washington Co. (201-207).

Intermediate Ecotype: E—Ohio, Muskingum Co. (361, 362), Hocking Co. (371-375); F—Ohio, Wayne Co. (381, 382); G—Penn., Westmoreland Co. (391-395); H—Penn., York Co. (401-405), Lancaster Co. (492-495); I—Penn., Berks Co. (430-435), Schuylkill Co. (491); J—W. Va., Marshall Co. (471-475).

Northern Ecotype: K—N. H., Grafton Co. (271-275), Carroll Co. (281-285); L—Vt., Chittenden Co. (451-455); M—Vt., Bennington Co. (461), Windsor Co. (462); N—Mass., Worcester Co. (211-217, 601, 605, 610, 613); P—Conn., Litchfield Co. (131-138); Q—Conn., Tolland Co. (141-145); R—N. Y., Tompkins Co. (313-317), Onondaga Co. (321-325), Schuyler Co. (331-335); S—N. Y., Schoharie Co. (341, 342); T—N. Y. Saratoga Co. (291-295); U—Penn., Indiana Co. (411-414); V—Penn., Warren Co. (421-425); W—Mich., Osceola Co. (231), Wexford Co., (232-235); X—Mich., Ingham Co. (251-255); Y—Ont., Renfrew Co. (501, 511); Z—Ont., Bruce Co. (525); AA—Ont., Norfolk Co. (541, 542, 544, 545); BB—Ont., Dufferin Co. (521), Simcoe Co. (522, 543), Ontario Co. (524); Grey Co. (526), York Co. (531-539).

[2]For simplicity of presentation, the term "collection" is used to denote the progeny of one parent, or the characters or herbarium specimens pertaining to that parent or progeny thereof. The term "locality" is used to denote the collections derived from one limited geographic area.

SEED TREATMENT

The seeds were kept in warm dry storage from the time of collection until December. At that time cutting tests were made, and duplicate lots from each collection were put into cloth bags labelled with aluminum tags. These were packed in moist sphagnum. Following the recommendation of Steinbauer (7), they were given warm moist storage at room temperature for one month, followed by cold moist storage at 3° C. for three months. This treatment induced germination within two to three weeks after sowing.

Considerable pre-germination mortality was caused by an unidentified weevil which emerged during the stratification period. No control measures were attempted, as the presence of the weevil was not discovered until the seeds were sown. This weevil damage is thought to account for the greater part of the variability in the density of the seedbeds the first year.

THE NURSERY

The trees used in the study were grown in the experimental nursery of the Harvard Forest, in Petersham, Mass. The soil is Charleton stony loam, one of the best agricultural soils in the region. Fortunately, most of the stones had been removed. The land is level, and because of a deep clay horizon drains slowly; in the spring it is distinctly muddy. However, there was no standing water during the growing season, even after heavy rains.

In the spring of 1938, the areas occupied by Seedbeds I and II and Plantation I were plowed, given a light application of commercial fertilizer, and planted to cover crops. These were turned over at the end of each season. The sod cover of Plantation II was not plowed under until the fall previous to planting. This area received no fertilizer, and growth was considerably less than in Plantation I. All plowing and cultivation prior to planting was done by means of a power-driven rotary cultivator.

SOWING, TRANSPLANTING, AND CULTIVATION

Half of the stratified seed (one duplicate lot from each parent) was sown in Seedbed I in the middle of May, 1940. Approximately one month later the remainder was sown in Seedbed II. Each lot was sown broadcast in a 20- by 40-inch plot, and the seeds were covered with sand. The young seedlings were given half shade until the middle of the summer.

The original plan was to carry all the trees through two years without transplanting, and to treat Seedbeds I and II as replicates. This proved impossible for two reasons. First, the spacing in the seedbeds (approximately 3 by 3 inches) was not enough to allow completely uninhibited development for even one growing season. Second, considerable difference in height growth was occasioned by the month's differences in planting time.

Therefore in May, 1941, two plantations were established with seedlings grown in Seedbed I. In Plantation I, 2,333 seedlings from 19 localities were set out on a 1 by 1 foot spacing (adequate for one year's growth). Plantation II, with 539 trees from 15 localities, was planted on a 3- by 3-foot spacing, with the intention of allowing the trees to remain for five years. The planting was done on a randomized row arrangement by the slit method, using the Harvard Forest planting tool.

The weed population was kept down by hand pulling in the seedbeds, and by the use of a wheeled cultivator in the plantations. The seedlings were watered only after transplanting.

COLLECTION OF DATA

All measurements were made in September and October of 1941, after cessation of growth for the season. First-year and second-year height, length of 1940 stem killed back by winter cold, and amount of pubescence were recorded for each seedling in the nursery. At the same time, one mature leaf from each tree was collected and pressed; these were used for the determination of leaf shape and stomata size. In addition, notes were taken throughout the first two growing seasons as to the general appearance and habit of the young trees.

RESULTS

VARIATION AND DISTRIBUTION OF ECOTYPES

A preliminary examination of the results of the nursery tests indicated that, within the range studied, the species should be divided into three distinct groups. Each of these is termed an *ecotype*, or "product arising as a result of the genotypical response of an ecospecies to a particular habitat" according to the nomenclature of Turesson (8).

The northern ecotype grows from Michigan to central Pennsylvania and New England, and northward. All the seedlings from this region

showed little winter killing, bushy root systems, and lack of pronounced pubescence or anthocyanin development.

Trees from a narrow belt through southern Pennsylvania, northern West Virginia, and Ohio belonged to the intermediate group characterized by a moderate amount of winter killing, bushy root systems, and a high incidence of pubescence.

The southern ecotype presumably occupies all of eastern United States south of this belt. Trees from this region were very susceptible to damage from winter cold, and had tap roots, reddish petioles, and leaves which were glossy above and pubescent below.

Genotypic variation within these broad areas was minor in most cases.

WINTER KILLING

During the first season, the seedlings grew continuously from the time of germination until late September. They seemed to possess no timing mechanism governing the cessation of growth and the initiation of hardening off, such as is found in the mature trees. This was apparent in several respects. The leaves stayed on the seedlings several weeks longer than on older trees. The young bark remained green until late August for the northern seedlings, and all through the first winter for the southern trees, whereas on mature trees the bark of the young shoots soon became brown. Instead of forming a true winter bud enclosed by simple scales, the growing point was merely enclosed by small undeveloped leaves on which the leaflets were clearly visible. In the southern and intermediate seedlings especially, the buds with which the trees entered the winter were little different from those present during July or August.

The low temperatures during the winter of 1940-41 caused the death of the relatively undifferentiated terminal and uppermost lateral buds of most of the white ash in the nursery. In the spring of 1941, growth was initiated by one or a pair of laterals, the shoots thus formed taking the place of the leader. Apparently the stem tissue itself was undamaged by the cold, for the portion of a stem above the uppermost live lateral bud remained alive for some three or four weeks after the time of leafing out.

The trees of the southern ecotype proved most susceptible to cold damage (Table 1). Many were killed back to or nearly to the ground line. In-

TABLE 1.—LENGTH OF STEM KILLED BACK IN INCHES, WINTER OF 1940-41[1]

Ecotype	Seedbed I	Seedbed II	Plantations I & II
Southern	3.2±0.19[2]	1.5±0.06[2]	2.9±0.08[2]
Intermediate	2.6±0.13	1.2±0.04	2.3±0.06
Northern	1.0±0.04	0.6±0.02	1.2±0.03

[1]Determined in the fall of 1941. The criterion of winter damage was the length of 1940 dead stem above the base of the uppermost live branch.
[2]Standard error of the mean.

deed, on this one character most of the southern trees could be spotted in the nursery.

It is noteworthy that even the northern seedlings (including those from Petersham and points farther north) suffered a moderate amount of winter killing. In general this damage was not evident upon casual examination. It might be supposed that this was due to a particularly severe winter, or to the lack of protection afforded the plants in the nursery, but the repeated killing back of wild seedlings in the vicinity indicates that this is not the case. A more probable explanation is that one of the juvenile characters of white ash is inability to harden off properly even in a climate to which its progenitors were accustomed. Because of this characteristic young ash trees progress very slowly until mature enough to withstand the winters unharmed.

A question arises as to whether the southern and intermediate ecotypes will be able to overcome their susceptibility to cold injury in the same manner as is expected for the northern form. Brief observations made during the third growing season indicate that this is unlikely. Many of the northern trees had passed the second winter entirely unharmed, whereas damage to the southern seedlings was even more severe than it had been the first winter.

With two exceptions there was no evidence of local differentiation of hardy or non-hardy genotypes within ecotypes; trees from New England and Ontario suffered fully as much as did those from northern Pennsylvania. This is substantiated by the evidence offered by the foliage and root systems, and indicates that genic exchange takes place relatively freely within ecotypes, preventing the formation of numerous local races.

The two exceptions were from the southern portion of the range of the intermediate ecotype. Collection 471 (W. Va.) differed significantly in both winter killing and glossiness of leaves from the progenies of four other parent trees

from the same locality. It may be regarded as a northern outlier of the southern ecotype. Collection 495 (Penna.) was intermediate in respect to winter killing, as were progenies of other trees from the same county, but had the foliage characteristics of the Maryland and Alabama trees. It is best considered as a hybrid between the southern and intermediate forms.

Differences in cold damage due to treatment in the nursery were quite noticeable (Table 1). The trees of Seedbed I and Plantations I and II suffered about twice as much winter damage as did those of Seedbed II. This is peculiar, inasmuch as the terminal and uppermost lateral buds of the youngest (Seedbed II) seedlings showed less differentiation (and presumably less hardening off) at the onset of the winter of 1940-41 than did the older trees. Similarly, the differences in amount of winter damage between trees of Seedbed I and those of the plantations are puzzling, since the killing took place before the trees in the plantations were removed from Seedbed I.

The most likely explanation is that sufficient breakage of the dead, brittle stems occurred during the transplanting and subsequent cultivation of the southern and intermediate ecotypes to cause the winter damage to *appear* smaller in the plantations than in the seedbed. The northern trees, having less dead tissue, were not subject much breakage. Another possible explanation is that the differences between the plantation trees and the Seedbed I trees were genetically induced, since the ecotypes were represented by progenies of different parents in the two cases.

ROOT SYSTEMS

Observations made during the planting operations revealed a fundamental difference between the root systems of the northern and intermediate ecotypes on the one hand, and the southern ecotype on the other.

The northern and intermediate seedlings have three to four main roots, each a foot or more in length, as well as an abundance of shorter, much-branched laterals. The result is a fibrous mat offering good anchorage and nutrient supply. Even the smallest of these seedlings suffered little damage from frost heaving during the first winter, and recovered quickly after transplanting.

The southern seedlings developed a pronounced taproot with but few branches, and were therefore especially subject to frost heaving. As a result about half these trees entered

the second growing season with their root collars several inches from the ground, and subsequently died. Damage from this cause was especially severe in the smaller trees of Seedbed II, where only 111 out of approximately 300 southern trees survived the first winter.

Another effect of this taprootedness was to be seen in the death rate of transplanted seedlings during the second summer (Table 2). Because of the heavy clay soil, it was impossible to avoid considerable breakage of the small side roots during the lifting of the trees destined for the plantations. This removal of some of the feeders left a great many of the southern seedlings with nothing but a taproot and some stubs, whereas the northern and intermediate seedlings had a nucleus of several strong lateral roots with which to start the season. As a consequence, there was a significantly higher mortality rate for the southern ecotype than for either the northern or intermediate ecotypes.

HEIGHT GROWTH

On the basis of height growth, also, the seedlings were divided into two groups—northern-intermediate and southern, each group including the ecotypes of the same name. In the plantations the southern trees were significantly smaller at the end of the second summer than were those from Pennsylvania and Ohio northward (Table 3). This difference was probably not due to any great extent to a difference in growth rate. It was more likely caused by differing amounts of damage suffered by the two types of root systems. The southern seedlings, having only the taproot left after lifting, died or recovered so slowly that they barely made up for the previous winter's losses. The differences between the northern and intermediate ecotypes were not significant; neither were the differences between

TABLE 2.—SECOND-YEAR MORTALITY OF TREES IN PLANTATIONS RESULTING FROM DIFFERENTIAL DAMAGE TO LATERAL ROOTS

Ecotype	No. of trees planted	Percent of mortality
	Plantation I	
Southern	329	34
Intermediate	796	11
Northern	1,208	10
	Plantation II	
Southern	84	16
Intermediate	196	9
Northern	259	5

TABLE 3.—TOTAL HEIGHT OF TREES IN PLANTATIONS AT END OF SECOND GROWING SEASON

| | Mean height in inches | |
Ecotype	Plantation I	Plantation II
Southern	7.7±.23[1]	7.2±.29[1]
Intermediate	11.9±.17	9.0±.25
Northern	11.4±.14	9.1±.22

[1]Standard error of the mean.

progeny from different localities within ecotypes.

That the variation in height was due to varying amounts of root damage rather than to inherent differences in growth rate is also indicated by the measurements of seedlings in the seedbeds (Table 4). The difference in total height between the relatively undamaged northern and the frost-heaved and winter-killed southern plants of Seedbed II was highly significant. This difference was negligible for Seedbed I, in which there was little injury from either frost heaving or transplanting.

TABLE 4.—TOTAL HEIGHT OF UNTRANSPLANTED SEEDLINGS AT END OF SECOND GROWING SEASON

| | —Seedbed I— | | —Seedbed II— | |
Ecotype	Mean height inches	No. of trees	Mean height inches	No. of trees
Southern	12.9	110	6.9	111
Northern and intermediate	12.7	1,313	9.8	1,580

Table 4 also shows that the difference of one month in the time of planting caused appreciable differences in total height at the end of the second year. This should be an argument for fall sowing of ash, for fall-sown seed germinates even earlier and produces sturdier seedlings than does that put out at the earliest possible time in the spring.

FOLIAGE CHARACTERS

During both summers, the southern seedlings were easily distinguishable from the others by casual observation. Their leaves were more glossy on the upper surface, and had distinctly reddish petioles and midribs. Clausen, Keck, and Hiesey (3) have also noted an increase in the anthocyanin content of Potentilla glandulosa ssp. nevadensis when grown at high altitudes in California.

For the determination of genotypic differences in leaf shape, length and width measurements were made on one leaflet per tree for the off-spring of a number of parents. The resulting length/width ratios are presented in Table 5.

On the basis of leaflet shape, the progenies may be arbitrarily divided into three groups—broad, normal, and narrow, with respective ratio limits of 1.8-2.0, 2.1-2.3, and 2.4-2.5. Into the first group fall most of the seedlings from Alabama and Maryland, while into the third group fall the progenies of four northern trees (212, 321, 522, 524) from widely separated localities. The remainder, including those not given in the table, may be classed as normal. With the rather limited data available, it seems that genotypic variation in leaf shape is greater within than between ecotypes. No attempt was made to correlate leaflet shape of parent and progeny, as only one leaf from each parent was available.

Because of the conflicting views held by taxonomists as to the value of pubescence in the classification of Fraxinus, it seemed desirable to gather information on the inheritance of this character. Accordingly, at the end of the second growing season, each of the seedlings in the plantations was scored for pubescence of the petiole and lower surface of the leaf, and the percentages of pubescent progeny were com-

TABLE 5.—GENOTYPIC VARIATION IN LEAFLET SHAPE[1]

Parent number	Origin	Mean length width ratio[2]
	Southern ecotype	
111	Ala.	1.8±.05[3]
114	Ala.	1.8±.09
115	Ala.	2.0±.05
116	Ala.	2.0±.05
121	Ark.	2.1±.07
152	Ind.	2.1±.04
153	Ind.	2.2±.04
154	Ind.	2.1±.04
155	Ind.	2.0±.06
156	Ind.	2.1±.06
201	Md.	1.9±.05
202	Md.	1.9±.05
204	Md.	2.0±06
205	Md.	1.9±.03
	Northern ecotype	
212	Mass.	2.4±.08
601	Mass.	2.1±.04
605	Mass.	2.1±.03
321	N. Y.	2.4±.07
322	N. Y.	2.2±.04
323	N. Y.	2.1±.03
522	Ont.	2.5±.06
524	Ont.	2.5±.03
525	Ont.	2.1±.03

[1]Measurements were made on the second leaflet from the base (right-hand side) of the topmost mature leaf of each tree. Seedlings with only simple or trifoliolate leaves were excluded.

[2]Each mean includes all progeny of given mother tree, since in no case were differences due to location in nursery significant.

[3]Standard error of the mean.

puted (Table 6). Two of the parents used in the study were pubescent on the leaf, stem, and twig, and belonged therefore to *F. biltmoreana* Beadle, the rest being true white ash. The percentage of pubescent progeny of these two Biltmore white ash was less than that of the offspring of the glabrous parents from the same locality. In fact, of 25 mother trees of the southern and intermediate ecotypes which were thus tested, 16 gave percentages greater than the 43 percent recorded for collection No. 154.

Thus, *F. biltmoreana*, separated from *F. americana* only by pubescence, is not a good species, as seed of the one may give the other, and vice versa. The correct taxonomic treatment of the Biltmore white ash is discussed more fully in another paper now in the course of preparation. Whereas the genetic factors for pubescence appear to be quite common in the region from central Pennsylvania to southern Indiana southward, they are almost absent in the north. For the northern ecotype, the highest incidence was 11 percent, in collection No. 333. This is in accordance with previous taxonomic work, as Biltmore white ash has never been reported in the northern states.

CHROMOSOME NUMBER

Chromosome counts were made from acetocarmine root-tip smears of seedlings of 24 different parents. For 39 other collections, the approximate chromosome number was found by determination of the mean guard cell length from collodion peels of leaves of the young trees, according to the method used by Babcock and Stebbins (2) in *Crepis*. Preliminary work had shown sufficient correlation between degree of polyploidy and stomata size to make this approximation possible.

Of the 63 trees for which counts or approximations were made, 9 were from the northern ecotype. All these proved to be diploid, with $2n = 46$, confirming the results of Sax and Abbe (6). However, the picture was quite different for the plants of southern and intermediate origin. Of these, 33 were diploids, 8 were tetraploids ($2n = 92$), and 13 were hexaploids ($2n = 138$). Following is the geographic distribution of diploids and polyploids in the southern and intermediate ecotypes:

Diploids—Berks, Lancaster, Schuylkill, Westmoreland, and York Counties, Penn.; Washington Co., Md.; Hocking, Muskingum, and Wayne

TABLE 6.—INCIDENCE OF PUBESCENCE AMONG TRANSPLANTED PROGENY OF SELECTED PARENT TREES

Parent number	Origin	Percentage of trees pubescent	Total no. of trees
Parents pubescent (*F. biltmoreana*)—southern ecotype			
152	Ind.	31	58
154	Ind.	43	40
Parents glabrous (*F. americana*)—southern and intermediate ecotypes			
116	Ala.	13	24
153	Ind.	62	39
155	Ind.	50	28
204	Md.	79	24
393	Penn.	17	59
373	Ohio	26	59
382	Ohio	0	37
Parents glabrous (*F. americana*)—northern ecotype			
605	Mass.	5	84
333	N. Y.	11	46
295	N. Y.	6	68
421	Penn.	0	46
254	Mich.	0	50
525	Ont.	1	121
529	Ont.	2	66

Counties, Ohio; Marshall and Pocahontas Counties, W. Va.

Tetraploids — Lancaster and Westmoreland Counties, Penn.; Washington Co., Md.; Wayne Co., Ohio; Greene Co., Ind.; Chilton and Marion Counties, Ala.

Hexaploids—Lancaster Co., Penn.; Washington Co., Md.; Marshall Co., W. Va.; Greene and Owen Counties, Ind.; Chilton Co., Ala.; Pope Co., Ark.

In some cases, such as Lancaster Co., Penn., all three chromosome numbers were represented within a few miles of each other. Apparently, the polyploidy is of rather recent origin, having arisen since the ecotype differentiation. This is borne out by the fact that there were no apparent differences in growth rate, winter hardiness, or morphological characters which could be associated with the differences in chromosome number. The greater part of the genotypic differentiation appears to have been genic.

SUMMARY AND CONCLUSIONS

Nursery tests with the progeny of 155 white ash trees from 28 localities in the eastern United States and Canada show that the species is composed of at least three ecotypes. The northern ecotype ranges from Pennsylvania to Michigan and northward. Trees from this region were diploid and had glabrous, non-glossy leaves. They developed a bushy root system, and suffered only minor cold damage during their first winter. The southern ecotype, ranging from

Maryland to southern Indiana and southward, was characterized by glossy leaves with reddish petioles and midribs, a tap root, and very severe winter killing. The intermediate ecotype, confined to a narrow belt from southern Pennsylvania to Ohio, is like the northern in type of root system and leaf color, but is similar to the southern in pubescence and chromosome numbers; trees of this ecotype suffered a moderate amount of winter killing. There is considerable local genotypic variation in leaf shape.

Of the many genetically induced differences between ecotypes, variation in the ability to withstand winter cold is most important to foresters. Within rather broad east-west belts, the trees were similar in this respect. Therefore transference of white ash seed within these belts can probably be done with perfect safety to the resulting plantations. However, the use in the north of seed of the intermediate or southern ecotypes is hazardous, since extensive winter-killing will ensue. The effect of the use of northern ash in a southern region is not known, but should be investigated.

Measurements made at the end of the second growing season showed significant differences in total height between the southern and northern-intermediate trees, the latter being much taller. This was due mainly to damage to lateral roots occasioned in lifting the taprooted southern trees. The effects of this injury effectively masked any expression of hereditary differences in growth rate. The question of whether or not trees from the same locality differ sufficiently in their inherent capacities for growth to warrant careful selection of mother trees can only be answered by further study using more refined techniques.

There was a high incidence of pubescence in the progenies of both glabrous and pubescent parents of the southern and intermediate ecotypes. Thus the Biltmore ash (*F. biltmoreana*) and the white ash (*F. americana*), now recognized as distinct species differing only in pubescence, need not be separated, either in taxonomy or in silviculture. This is in accord with the present lumbering practice where no such distinction is made. The chromosome counts and stomata measurements show the species to be variable in the south with regard to chromosome number. Examination of the data showed no evident correlation between the degree of polyploidy and any gross morphological or physiological characters. However, it is known that there is considerable variation in taxonomic characters as well as in wood quality in the very region where the differences in chromosome number are found. Further study of the polyploidy in the species in relation to these characters would be desirable, and might help to explain some seemingly inexplicable differences in strength of wood.

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