HERITABILITIES OF SOME FIRST-ORDER BRANCHING TRAITS IN Pinus banksiana LAMB.

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Jack pine *(Pinus banksiana* Lamb.) is considered by many to be an ugly duckling among the world's, pines. One colleague, in personal communication some eighteen years ago, expressed a prevailing attitude when he wrote, "I have never seen a jack pine that I could call a thing of beauty."

The author can subscribe to that statement—almost. Notwithstanding the scarcity of ornamental jack pine trees, however, twelve handsome young phenotypes have emerged variously among ca. twenty thousand trees of the species included in a wide range of plantation experiments near Weldon Spring and Ashland, Missouri. Five of these twelve were found among adaptability, site preparation, and spacing studies; two came from early efforts to study seed-origin effects on performance of the species; and the remaining five arrived more recently through breeding experiments. Three of the five breeding-source trees were members of one 35-tree, full-sibling progeny group.

These superior twelve trees have provided an interesting nucleus for jack pine improvement work; and, to broaden the genetic base, other selections have been (are being) added. These secondary selections are trees that possess in strong measure one or more desirable traits.

Desirability in the present thrust has been interpreted in terms of Christmas tree potential. Important are vigor, a straight and unforking central stem, longer than usual needle retention, symmetry and balance of crown, dense to moderately dense crown, taper (crown width divided by height, expressed as percent) within a range of 30 to 70, and better winter foliage color than is common for the species.

Jack pine is a very variable species, and the variation is largely genetically based. These conclusions are drawn from cumulative evidence, including (a) provenance testing (King, 1964; Schnare, 1969), (b) similarities of trees within clones and contrasts between clones, and (c) selective breeding (as reported below).

Rehfeldt and Lester (1969) have hypothecated that pioneer species such as jack pine, by their very nature, must be sustained through a genetic system that promotes flexibility (population adaptiveness and, hence, high heterozygosity). Jack pine can endure a wide and often impoverished range of site conditions. Even when planted at latitudes far removed from its natural range, as in Missouri, a high survival is easily obtained in planting 1-0 nursery stock. It is not surprising that under such conditions some genotypes will greatly outperform others. Of particular interest to the breeder is the high morphological (and, doubtlessly, physiological) variation that is frequently found among trees growing in proximity (Figure 1).

Figure 1. Coincidental adjacency of two young jack pine, each markedly different from the other in branching habit. Strong heritability of branching traits is indicated by a year-to-year persistency of a distinctive mode of branch development. The two subjects here are members of a 10,000-tree plantation, using nursery stock produced from seed of wild origin.

EXPERIMENTAL METHOD

When one has selected a breeding base of heterozygous individuals from an uncommonly variable population, is there a breeding procedure that can serve to concentrate desirable traits in various family lines and, simultaneously, to give some reliable measure of heritability for those traits? It would seem that an ultimate effort in this direction would be to employ positive assortative mating, a form of non-random mating which crosses like phenotype to like. This breeding method seemed to be particularly applicable in the present study, because the selected trees contained a rather wide assortment of crown types, within which were two or more phenotypes whose crowns looked remarkably like each other. Besides, if a high degree of resemblance between parents and their offspring resulted under such a scheme, more genetic control could probably be obtained in a second cycle of selection and breeding that would seek (a) to modify and combine certain traits under negative assortative matings (complementary crosses) and (b) to further strengthen genetic control of certain characteristics through continued positive assortative matings.

The crosses effected included one or more pairings of the following crown phenotypes: fastigiate to fastigiate; dense and symmetrical to dense and symmetrical; high vigor with symmetrical and moderately dense crown to similar mate; vigorous and open-crowned to like tree. Although these matings included a wide diversity of crown types, they did not include the greatest possible range. Not represented, for example, was a branching type so wide-angled as the more open-branched tree in Figure 1.

Seeds from these matings were sown in April, 1960, in an experimental nursery bed at the University of Missouri-Columbia. Seedlings therefrom (plus 50 nursery-run seedlings to be used as a check) were transferred one year later to No. 7 Cloverset pots (tarpaper) and bedded to prevent overheating of the root systems.

In May, 1962, the 1-1 potted stock (including 25 of the nursery-run check stock) was planted at a 10 x 10-foot spacing on the Ashland Arboretum and Wildlife Area in southern Boone County, central Missouri. Intermingled with 16 progenies representing F_1 generations from the assortative matings were 261 rootstock planting spots. At each such spot three nursery-run seedlings were planted (also in 1962) in triangular arrangement spaced one foot apart. Twenty-nine graft clones were established in April, 1965, through grafting two scions at each of the rootstock locations. Grafting success was 84 percent, and at those spots where two ramets had been obtained, the weaker was removed in April, 1966, as was any extra rootstock, leaving a single tree at each graft location.

Expressed another way, the end result of this establishment effort was to obtain 16 full-sibling progenies and 29 graft clones in a thorough mixture of single trees. Of a 956-tree total on 2.2 acres of ground, 261 trees were grafts (9 each of 29 clones), 25 were nursery-run checks, and the remaining 670 were of control-pollination origin (16 progeny groups). Because of variable and unexpectedly low seed yields obtained in the controlled pollinations, the seedling numbers in the progeny groups ranged from 108 down to several. Regardless of the wide numerical discrepancy in full-sibling lots, all seedlings obtained from the assortative matings were planted.

An objective in the development of this stand was to go from an initial spacing of 10 x 10 feet to 14 x 20 feet by removing alternate trees within each row and with a staggered spacing between rows. This would amount to complete removal of alternate rows along diagonal lines across the plantation. This thinning plan created primary (permanent) and secondary (temporary) sets of spots as to tree location in the planting process. All grafting was done at primary points; and, where a surplus of seedlings was available for primary location of a progeny group, seedling grading was used in an effort to upgrade the family line. This seedling grading was largely unrewarding. In other words, selection within progeny groups was not successful at the seedling stage.

Trees in the plantation were located at random to the following extent: at the outset of the planting, individual trees representing each kind of group (progenies and clones) were randomly located at primary points. Beyond that, trees were located away from other members of their kind. The objective was to get a maximum spread of each progeny group and clone in order to promote outcrossing. This would make possible an evaluation of the general combining ability of any clone or individual tree. Finally, a map was constructed to identify each tree in the stand as to its lineage or clone.

In 1968 the plantation was thinned. For the most part, the thinning to a 14 x 20-foot spacing was accomplished. On a tree-grade basis, however, some trees subject to removal because of location were not removed at that time. The first thinning was timed to maintain an open character in the stand, because primary interest was in crown development and seed production studies, including further controlled pollinations. In this latter respect, the stand has been functioning as a breeding orchard, and additional selected material is being added to the general area from time to time.

On the night of May 10, 1970, these studies received a severe setback. Hurricane-force winds buffetted the already rain-soaked area. Nearby, tornadic funnels ripped swaths through an older plantation and across a mature oak-hickory natural stand. In the subject plantation, fourteen trees were completely uprooted and many others were rootsprung in varying degree. Soon thereafter, through use of a power pull, the most badly leaning trees were hoisted back to a vertical position and guyed. This recovery effort was largely successful. Today only a few of the trees are severely tilted, but the effects of this damage on the subsequent development of the stand cannot be evaluated.

ANALYSIS AND DISCUSSION

It will be recalled that the positive assortative matings, described above, used like crown type to like crown type. How does one quantify a crown type? Perhaps this could be done with taper or some other crown feature, but a fully adequate method cannot be surmised. When one studies the general structural features that give character to a tree crown, it becomes apparent that branching traits are largely controlling. Consider, for example, the importance of the number, size, angle of attachment, curvature, length and seasonal nodality of branches comprising a tree crown; and these are traits that can be quantified. It was decided to record the following branch parameters (Figure 2):

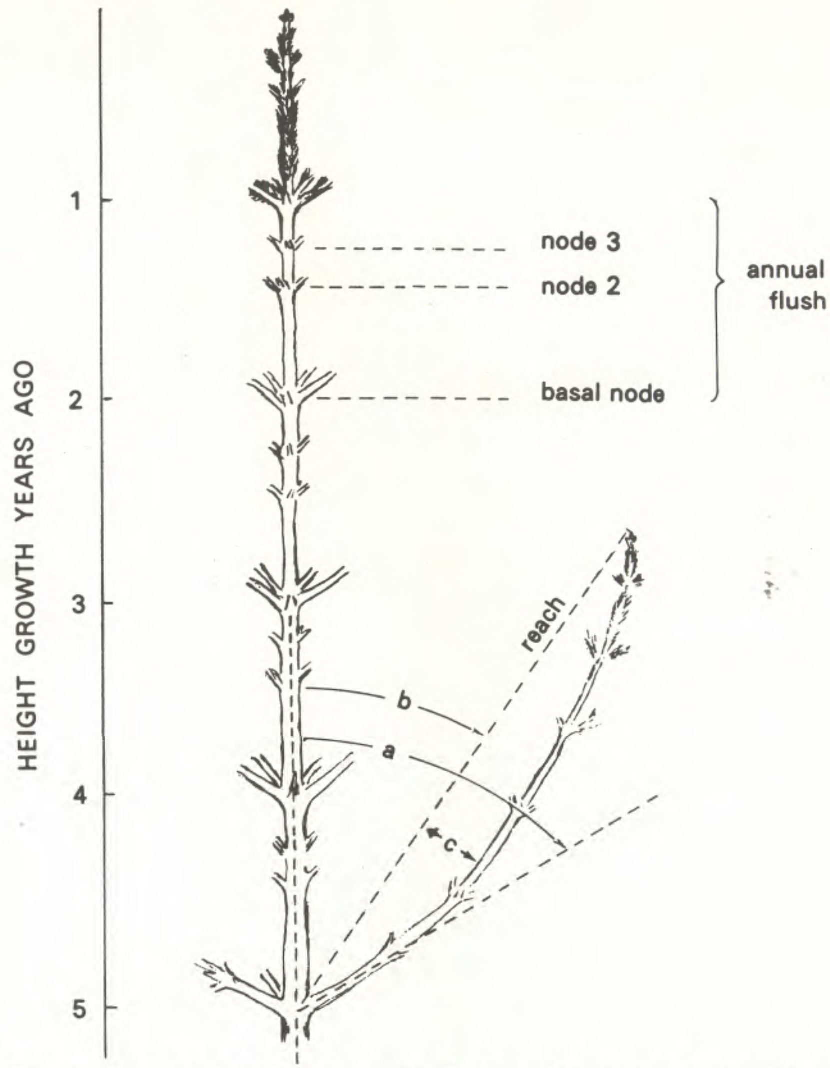

Figure 2. Terms used to describe branching traits: (a) angle of origin, (b) angle of termination, (c) maximum branch curvature. Comparisons were made on the region of height growth that was initiated 5 growing seasons ago.

1. *Angle of origin:* the angle formed by a branch at the point of insertion with the center line along the main stem axis at that point.
2. *Angle of termination:* angle formed by a straight line from a branch tip to its point of origin and the center line along the bole axis.
3. *Reach:* straight-line distance from the point of a branch origin to the tip of that branch.
4. *Maximum branch curvature:* greatest departure in inches of a branch from a straight line extending from the point of origin to the tip of that branch. Upward curvature, true of all branches measured in the present study, would have a positive value; downward curvature, negative.
5. *Branches per node* on the multinodal annual flush of growth. Recorded separately were the number of branches at or near the basal node (lowest and strongest whorl of branches on the annual flush), the second node of the season, and the third.

Moreover, it was decided to obtain the above set of records on the annual flush of growth that had emerged five years (growing seasons) ago. This was a part of the total crown that was accessible on most trees of the progeny groups and graft clones, using a 10-foot step ladder. These 5-year-old branches lent much character to the crowns of the trees at time of measure (summer, 1972), mainly because thinning had kept this portion of the crowns open to sunlight. Additionally, data obtained on the region of height growth initiated five seasons ago was closely representative of adjacent growth. There was only a gradual widening of the disposition of branch whorls from the top downward through the crown.

To an extent tree size was a problem, because some of the trees were well above 25 feet tall at time of measurement. Heights to 48 feet had been attained by the oldest parents and ortets, planted in 1950 at Weldon Spring. Such trees were topped, bringing down to ground level the last five years of height growth in order to facilitate the more difficult measurements of reach, the angle of termination, and maximum curvature.

To measure branch angle, a 90-degree protractor was fashioned from plywood as follows: A vertical arm supporting a 90-degree arc was sawn to dimensions of

12'/a ins. high and 2 ins. wide. A line was drawn 0.2 ins. from the edge of the arm. This was the zero line, from which the 90-degree arc at the top of the arm was scaled into 1-degree units. The lower 31/2 ins. of the vertical arm was attenuated along one side toward the zero line, reducing the arm base to a 0.4-inch width. On the zero line at a point 1/4 ins. from the arm base was affixed a thumb tack, around the shank of which was looped the free end of a nylon fishing line on a spool. This gave the protractor a 12-inch radius.

In use, the tapered lower end of the protractor arm was positioned between branches of the basal whorl to achieve a coincidence of the thumb tack with the convergence of lines sighted along the bole axis and the axis of the branch to be measured. Once thus positioned, the protractor was affixed to the tree trunk by use of two nails fitted through small holes, one bored near the top and the other near the bottom of the protractor vertical arm. The angle of branch origin was obtained by stretching the free-pivoting nylon line along the axis of branch insertion into the tree trunk. The angle of termination was measured accordingly, but a longer distance made it commonly necessary to stretch the line to the branch tip by looping it over the smooth upper end of the shank of a flathead screw set into one end of a wooden rod. The reach of a branch was measured similarly, but the zero point of a metallic tape was held by the flathead screw. On each tree measured, the angle, reach, and curvature records are based on means of the three largest branches in the basal whorl.

Branch number in the 5-year-old (1968) annual flush was recorded separately by nodes and then totalled. Typically, branches of the basal node, termed major whorl by Franklin and Callaham **(1970)**, are more numerous and larger than those at nodes 2 and 3. Among those clones and families having high crown density, the basal flush of branches was commonly comprised of two whorls spaced ca. 2 ins. apart. Branches in such double-whorling were counted and recorded collectively, because together they characterized basal development in such annual flush of growth along the main stem. Double-whorling was not found at nodes 2 and 3.

The measuring process described above proved tedious. Due to the occasional loss of a parent tree or ortet, to scant numbers in several progeny groups, and to the loss of three clones as a result of scion-rootstock incompatibility, complete sets of data were obtained (a) on 12 of 16 parental pairs plus their progenies and (b) on 21 of 29 ortets plus their ramets. Records were obtained at random on five members in each progeny group and on three ramets in each clone.

Statistical methodology and validity of positive assortative mating as a means of determining heritability have been discussed by Reeve (1955) and Falconer (1960). Narrow-sense heritability (additive genetic variance or breeding value) was obtained by regressing offspring means (0) on corresponding mid-parent* values $(\overline{P})$, so that

$$\text{heritability} = h^2 = \text{regression coefficient} = b_{O\overline{P}}$$

Similarly, broad-sense heritability (cloning value) was obtained by the regression of ramet means over corresponding ortet measurements for a trait under study. Results of these analyses are as follows:

Branching trait	*Narrow-sense* h^2	*Broad-sense* h^2
Angle of origin	0.75 ± 0.09	0.83 ± 0.07
Angle of termination	0.83 ± 0.08	0.85 ± 0.06
Reach	0.74 ± 0.05	0.94 ± 0.12
Curvature	0.33 ± 0.06	0.41 ± 0.06
Branch no., basal node(s)	0.93 ± 0.03	0.95 ± 0.05
Branch no., node 2	0.33 ± 0.05	0.48 ± 0.08
Branch no., node 3	0.59 ± 0.07	0.66 ± 0.06
Branch no., all nodes	0.94 ± 0.02	0.97 ± 0.06

All of the heritability values in the above tabulation are significant, and most of them very highly so ($P < 0.001$). The confidence limits placed on each value is at the 95-percent level, based on the standard error of the mean deviation from regression with $n = 5$ for progenies and $n = 3$ for ramets. In general, when field data were plotted, a good fit to the regression line was obtained (e.g., Figure 3).

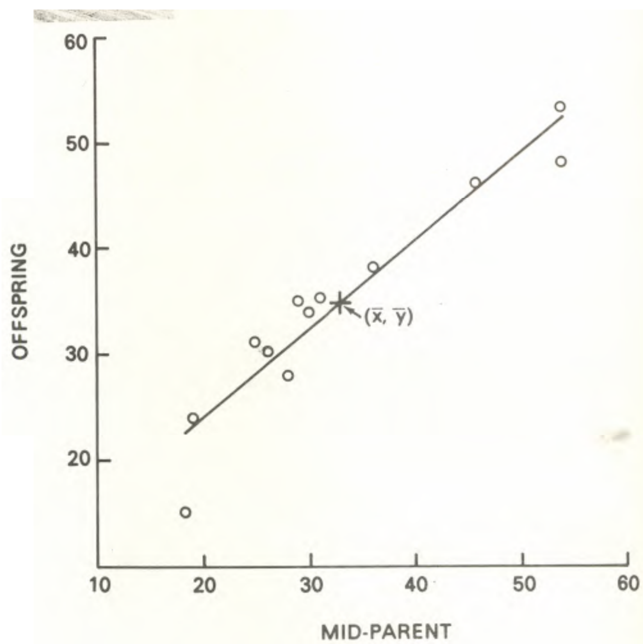

Figure 3. Angle of termination: regression of offspring means on mid-parent values.

It was obvious by age 3 years that strong genetic differences among the progenies had been obtained as a result of assortative mating (Figure 4). When walking through the plantation, with progenies semi-randomly mixed by individual trees (as explained above), one

*A mid-parent value for a trait is the average of the male and female values.

could readily identify members of those families that represented extremes among the crown (branching) types. Fastigiate parents had begotten offspring that were entirely fastigiate. Likewise, parents of spreading and open crown habit had produced young with their branching habit. Such identification of young with their parents was less obvious in the case of intermediate crown types, but even then it was possible ocularly to reduce the prospects to any one of two or three families.

Later, after selected trees had been cloned, equally striking contrasts were noted between the clones.

There is abundant evidence in the literature and among ornamental tree varieties that branching traits can be under strong genetic control. Rehder (1947) documents many woody species within which both pendulous (weeping) and fastigiate varieties are found: to spread a few examples through separate genera—*Ginkgo biloba* L., *Pinus sylvestris* L., *Cedrus atlantica* Manetti, *Picea abies* (L.) Karst, *Pseudotsuga menziesii* (Mirb.) Franco, *Abies alba* Mill., *Thuja occidentalis* L., *Chamaecyparis lawsoniana* (A. Murr.) Parl., *Juniperus virginiana* L., *Taxus bacatta* L., *Fagus sylvatica* L., *Quercus robur* L., *Ulmus americana* L., *Morus alba* L., *Sorbus aucuparia* L., *Robinia pseudoacacia* L., and *Acer saccharinum* L. The point here is that these are contrasting variants that have been selected out of numerous species; and, once selected, they perform faithfully across a wide range of habitats.

Most such varieties are maintained through vegetative propagation, commonly by grafting or, where possible, by rooting cuttings. Larsen (1956) has discussed and illustrated how branching traits far more subtle than fastigiate or weeping habit are perpetuated by asexual means. He stresses the importance of such observations to forest geneticists: "Aided by vegetative propagations, we can have the means at hand for analyzing our already existing material, and we can take a long step forward towards the objective of producing the seed we desire from them."

It is with reference to inherent quality of seed that the present paper makes its greatest contribution. Not only is it seen that genetic variance is high for most of the traits evaluated, but a very high percentage of the total genetic variance is additive. Therefore, one could expect to realize rapid rates of gain in breeding for particular branching traits in jack pine—especially for branch angle, for the number of branches in the basal whorl, or for total branches in an annual flush. This would be less true for the second and third nodes of the multinodal system characterizing annual height development, in considerable part because of the low range of variation found in the second and third nodes (Table 1).

This high degree of identity in performance between parents and their offspring may be less easily obtained if one started with mature or overmature parental stocks. When young progenies are regressed on mature parents, estimates of heritability are sometimes misleading for characteristics subject to environmental alterations (Stonecypher, 1966). Crown traits are strongly altered by weathering, by the random effects of many other environmental factors acting cumulatively through time, and perhaps by phase change. In other words, old trees exhibit inherent branching traits less distinctly than do young trees. In species that are reproductively precocious, however, one can obtain data on progenies and relate them to their parents at the same stage of development. That is the case here. The age of the oldest parents and ortets at time of measurement was 24 years from seed. All trees were in a stage of rapid height growth.

SUMMARY AND CONCLUSION

A jack pine breeding orchard has been developed in central Missouri by progeny testing and cloning selected trees on a common area. The planting procedure used a semi-random mixture by single trees, with the provision that trees of common parentage or of the same clone be spaced away from each other. Positive assortative matings of crown phenotypes produced some strikingly different progenies. A regression of offspring means on mid-parent values indicates high additive genetic variance (i.e., high narrow-sense heritability) for each of several first-order branching traits. Similarly, by regressing ramet means over octet values, somewhat higher broad-sense heritability for any of the same traits was denoted.

Table 1. Ranges in branching traits found among familial and clonal lines that were obtained through selection for improved crown density and symmetry in young jack pine*

Trait	Families		Clones	
	Parent	Offspring	Ortet	Ramet
Angle of origin, degrees	29-66	33-63	23-60	31-63
Angle of termination, degrees	18-58	15-53	13-57	18-57
Reach, feet	5-9	6-9	5-9	5-10
Max. curvature, inches	4-9	3-8	3-10	3-14
Branch no., basal node	6-13	6-12	4-15	5-12
Branch no., node 2	4-5	4-6	3-5	3-8
Branch no., node 3	3-4	3-6	3-5	3-6
Branch no., all nodes	22-14	22-13	24-9	23-12

*These data include the sharpest (most fastigiate) branching found among the subject populations, but they do not include the widest (flattest) angles available.

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