

WITHIN-PROVENANCE VARIATION IN YELLOW BIRCH

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Previous work has shown that much variation is present in yellow birch (*Betula alleghaniensis* Britt.). A range-wide study of 55 provenances conducted at the Institute of Forest Genetics, Rhinelander, Wisconsin, demonstrated that variation in growth cessation and growth initiation is clinal (Clausen 1968b, Clausen and Garrett 1969). Height and diameter of two- and three-year-old seedlings, on the other hand, appeared to vary randomly (Clausen and Garrett 1969). The seed lots used for the provenance study were mixtures from an average of 10 trees per stand and thus much of the observed variability in seedling growth could be due to individual tree variation. Because individual trees within stands have been found to vary greatly in catkin and fruit characteristics (Clausen 1968a, Dancik and Barnes 1972) and in bark characteristics (Clausen and Godman 1969, Dancik and Barnes 1971) it seems likely that they could exhibit similar differences in growth rate or other desirable characteristics. The present study was, therefore, undertaken in order to determine how much of the observed provenance variation in yellow birch can be ascribed to differences among the individual parent trees.

METHODS

Ten average or better-than-average trees from each of 20 provenances used in the provenance study and representing a wide geographic range (Table 1) served as seed parents in this study. In addition, 10 trees were selected in a Forest County, Wisconsin, stand (4340).

Open-pollinated seed of each tree was sown without replication in flats containing a 1:1:1 mixture of soil, sand, and peat on March 25-27, 1968. The flats were covered with moist peat, placed in a cooler at 35 F for 4 weeks and then moved to a lathhouse. When germination was complete the seedlings were given supplementary light to provide an 18-hour day until September 1, 1968. The seedlings were transplanted into the Hugo Sauer Nursery at Rhinelander, Wisconsin, during late May-early June 1969 in a compact family block design with 5 replications (Snyder 1966). Due to poor germination of several seed lots, only 198 half-sib families could be transplanted.

Height of 20 seedlings in each family was measured after the first growing season. Height of 10 seedlings in each plot (50 seedlings per family) was measured at the end of the second, third, and fourth growing seasons. Diameter was measured after four years. In order to determine the extent of within-provenance variation in time of growth initiation, ten seedlings or less (1 row) per plot were scored for flushing on a 5-point scale in five families each of 10 provenances during the springs of 1970 and 1971. Similarly, six seedlings per plot (18 per family) of six families each of the same 10 provenances were measured weekly from July 15, 1970, and from July 21, 1971, until shoot elongation had ceased.

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Table 1.--Origin, mean 3-year height, 4-year height, and 4-year diameter of 21 yellow birch provenances and variation among families of each provenance (stand).

Stand No.	State or Prov.	Location		No. of families	3-year height		4-year height		4-year diameter ¹	
		Lat. deg.	Long. deg.		Stand mean	Range of family means ²	Stand mean	Range of family means ²	Stand mean	Range of family means ²
3241	N.S.	46.6	60.5	10	14.7	72-139	55.5	74-149	7.5	84-128
3063	N.S.	44.1	65.8	9	18.8	91-109	66.5	71-112	8.2	82-110
3066	N.B.	47.4	65.2	10	15.5	80-115	47.5	84-112	6.9	93-113
2998	Que.	48.2	70.2	9	16.3	78-119	56.8	77-112	8.4	94-113
3000	Que.	47.5	75.0	10	16.2	89-113	58.0	87-114	7.6	88-117
3004	Ont.	46.7	79.6	9	17.8	77-129	56.2	78-138	7.6	88-129
3309	Ont.	47.5	84.8	10	17.2	80-135	58.5	84-123	7.6	90-111
2977	Me.	44.8	68.6	10	19.0	82-141	67.6	84-141	8.3	88-130
2986	N.H.	43.5	71.4	10	19.4	77-116	58.7	70-122	7.6	74-118
2971	Mass.	42.7	73.2	9	16.3	75-119	59.6	79-129	7.5	82-120
3312	Pa.	41.6	78.7	10	18.5	82-124	72.6	73-122	8.4	81-124
3299	Va.	37.8	79.1	10	18.9	78-112	62.0	84-117	8.0	89-110
2959	N.C.	35.7	82.3	6	20.4	80-115	70.4	78-118	8.4	77-108
2973	Ga.	34.8	83.8	7	16.8	84-110	68.5	88-112	8.2	82-115
2983	Ill.	41.9	89.4	10	15.6	82-130	60.4	79-113	7.8	84-111
2962	Wis.	44.9	87.2	10	19.9	82-116	69.3	75-113	8.3	78-118
4340	Wis.	45.6	88.6	9	18.9	86-114	68.3	88-118	8.2	94-110
2968	Wis.	46.5	92.1	10	18.3	73-120	58.2	74-131	7.6	78-123
2987	Mich.	47.0	88.7	10	17.9	85-137	56.5	84-128	7.4	87-122
2967	Minn.	47.8	90.2	10	15.2	80-131	56.6	81-125	7.6	82-120
2964	Minn.	44.2	94.1	10	18.1	74-120	56.8	84-126	7.4	83-130
Mean					17.6		61.2		7.8	

¹ Measured 2.5 cm above the ground.

² Expressed as percent of stand means.

RESULTS AND DISCUSSION

First-year results not only showed that certain provenances were much more variable in height growth than others, but within-provenance variation was often greater than differences among provenances (Clausen and Garrett 1969). However, because the measurements were taken in unreplicated plots and height growth probably was influenced by the long-day treatment, these results may not be very reliable. Second-year heights may have been affected by the transplanting but the results were generally similar to those in the first year. The tallest family had a 32 percent greater mean height than the shortest family in the most uniform provenance and 158 percent greater mean height in the most variable provenance. For comparison, the best provenance was 106 percent taller than the poorest. Even greater within-provenance variation in 2-year height of yellow birch was noted in a study of 379 Quebec half-sib families.²

The average 3-year height of the provenance was 17.6 cm with a range between extreme provenances of 32 percent of the overall mean (Table 1). If the mean height of the families is expressed as a percentage of their respective provenance means, a southern Nova Scotia provenance (3063) with a difference of only 18 percent was the most uniform. Provenance 3241 from northern Nova Scotia with a difference of 67 percent between the tallest and the shortest families had the most within-provenance variation (Table 1). Only four provenances had less within-provenance variation than the overall difference among the provenances.

By the end of the fourth growing season, the provenances averaged 61.2 cm in height and the range between extreme provenances increased to 41 percent of the overall mean (Table 1). The rank of the provenances also changed from year to year with only two provenances (not the extremes) ranking the same in both years. Provenance 2973 from northern Georgia with a range between families of 24 percent of the provenance mean had the least within-provenance variation, while Nova Scotia provenance 3241 with 75 percent again was the most variable (Table 1). In eleven provenances the within-provenance variation was greater than the variation among provenances.

Four-year stem diameter was less variable than seedling height. The provenances averaged 7.8 mm in diameter 2.5 cm above the ground but the range between extremes was only 19 percent (Table 1). However, within-provenance variation was still large. Only Wisconsin provenance 4340 with a range of 16 percent of its mean had less family variation than the difference among provenances. All other provenances had a greater amount of within-provenance variation -- up to 47 percent of the mean in provenance 2964 from southern Minnesota (Table 1).

² Corriveau, Armand. Forest Research Lab., Canadian Forestry Service, Ste-Foy, Quebec. Personal communication, June 1971.

Variance analyses of plot means included only families present in at least 4 replications and thus were unbalanced due to the unequal number of families per provenance. For 2-year and 3-year height 138 families were used, while 137 families were available for analyses of 4-year height and diameter. Balanced analyses of growth cessation in 1970 and 1971 included 60 families in 3 replications. The following model was used:

Source of variation	Symbols	Expected mean squares
Blocks	R	
Stands (provenances)	S	$\sigma_e^2 + f\sigma_{sr}^2 + r\sigma_{f:s}^2 + fr\sigma_s^2$
Families in stands	F:S	$\sigma_e^2 + r\sigma_{f:s}^2$
Stands x blocks	S x R	$\sigma_e^2 + f\sigma_{sr}^2$
Families in stands x blocks	F:S x R	σ_e^2

In the analyses of 138, 137, and 60 families the coefficient "f" (mean number of families per stand) was 7.235, 7.18, and 6, respectively.

Narrow-sense heritability was calculated as follows:

$$h^2 = \frac{\sigma_{f:s}^2}{\frac{\sigma_e^2}{r} + \sigma_{f:s}^2}$$

In 1969, at age two, the variation in height was greater among provenances (stands) than among families within provenances (Table 2). At age 3, however, the provenance component accounted for only 3.0 percent of the variation while the family component accounted for 34.6 percent. The large difference between these components may in part be due to a serious nitrogen deficiency that developed in the nursery beds during the 1970 growing season. Average annual height growth of all provenances was much less in that year than normal and provenance differences were, therefore, also smaller. The individual families, on the other hand, apparently varied in their response to the nutrient deficiency and thus, the range of variation among them could have increased. The provenance component increased again during the fourth year, but although the family component decreased slightly in size, the greatest amount of variation in height was still due to differences among families (Table 2). Similarly, most of the variation in seedling diameter at age 4 was due to family differences.

Table 2.--Components of variance and heritability estimates
for yellow birch half-sib progenies.

Characteristic	Source of variation			h^2
	σ_s^2	$\sigma_{f:s}^2$	σ_e^2	
	percent	percent	percent	
Height				
1969 ¹	34.6	22.6	42.8	0.679
1970 ¹	3.0	34.6	62.4	0.689
1971 ²	18.5	30.5	51.0	0.705
Diameter				
1971 ²	2.5	23.2	74.3	0.555
Growth Cessation				
1970 ³	45.2	15.4	39.4	0.540
1971 ³	60.9	8.7	30.4	0.461

¹ Based on 40 trees each of 138 families.

² Based on 40 trees each of 137 families.

³ Based on 18 trees each of 60 families.

The heritability estimates are fairly high but are of the same magnitude as results obtained in Germany for comparable material of *B. pendula* Roth (Stern 1962b, Tigerstedt 1966). The fact that the provenances represent a wide geographic range may have led to an overestimate of heritability. The estimates would probably also be lower if they were based on individual plants rather than on plot means. Heritability appears to increase with age of the material, a fact also reported by Stern (1962b), but whether the early growth of these families is a good indicator of their later performance is unknown. If juvenile-mature correlations should be high, early selection for height and diameter growth would be profitable.

The provenances showed the expected clinal variation in phenological characteristics. In 1970, seedlings of the northernmost provenance (2998) had begun to flush on April 14 and were fully leafed out on May 11. Those from the Georgia provenance flushed 2 weeks later. In 1971, the Quebec seedlings had begun growth on April 17 and were in full leaf on May 25, while the Georgia seedlings did not begin to flush until 11 days

later. In both years, the time required by the seedlings to proceed from first bud-break to full leaf was the same in both provenances. Average time of growth initiation of the provenances was closely related to latitude and average April temperature at their origin in both years (Table 3), but there was considerable overlap among families (Fig. 1).

Table 3.--Correlation between growth initiation and growth cessation of 10 yellow birch provenances and environmental variables at their origins.

Characteristic	Latitude	Mean April temperature	Mean January temperature
Flushing			
April 28, 1970	0.935**	-0.841**	-0.712**
May 7, 1971	.965**	-.851**	-.823**
Growth cessation			
1970	-.776**	--	.692**
1971	-.859**	--	.799**

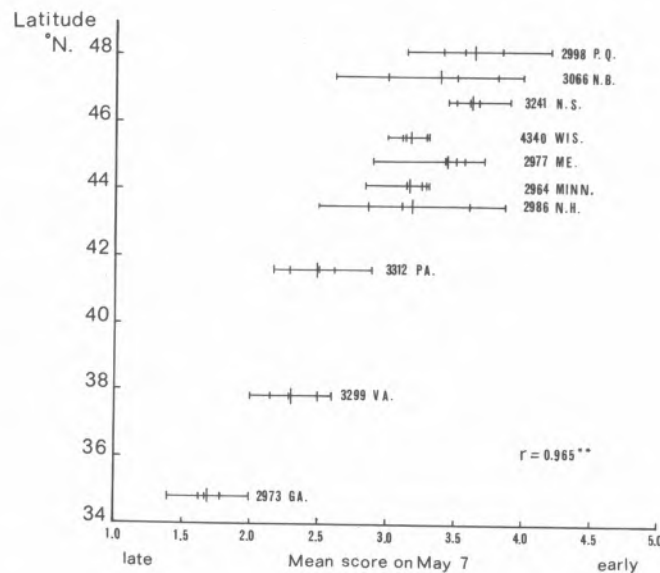


Fig. 1.--Growth initiation of 5 half-sib families each of 10 provenances in 1971. Short and long vertical lines mark family and provenance means, respectively.

Individual seedlings showed even greater variation; some seedlings of the late-flushing Georgia provenances were as far advanced as late seedlings of the earliest provenance in both years. Sharik (1970) reported a similar situation in his test of 23 provenances from the Appalachian Mountains. The amount of within-provenance variation not only differed among provenances (Fig. 1) but also from year-to-year within the same provenance. Thus, the least variable and the most variable provenances in 1970 were not the extreme ones in 1971. Similarly, there was little consistency from year-to-year in relative earliness or lateness of individual families within a provenance.

Growth cessation was correlated with latitude and mean January temperature (Table 3). The provenances differed significantly from each other in average date of growth cessation, but their progenies overlapped considerably (Fig. 2).

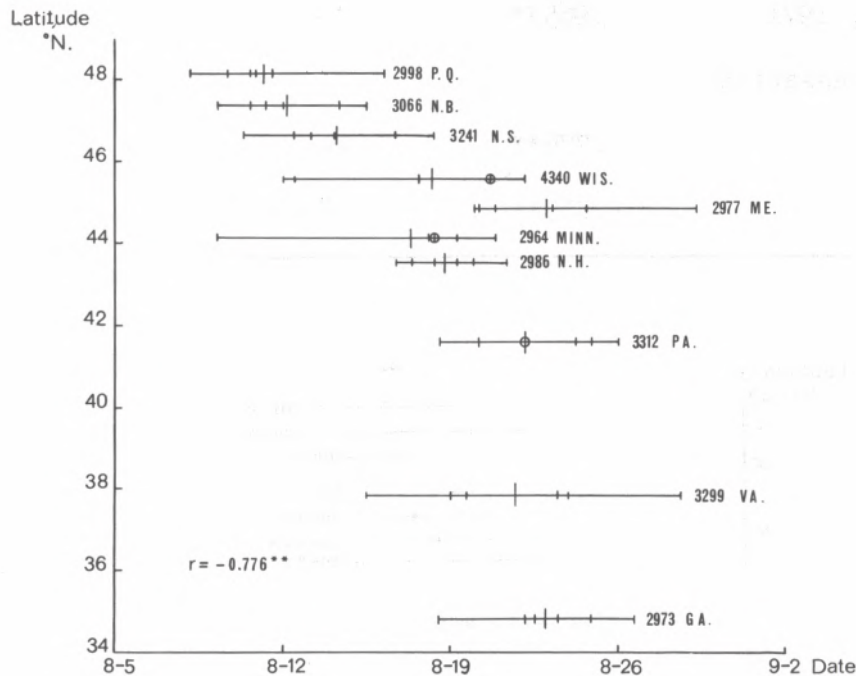


Fig. 2.--Growth cessation of 6 half-sib families each of 10 provenances in 1970. Short and long vertical lines mark family and provenance means, respectively. Circles indicate places where two mean values coincide.

Although there was no overlap between family means of the geographically most widely separated provenances (Quebec and Georgia) individual seedlings of the two provenances showed some overlap. Sharik (1970) reported similar results in his test of 21 Appalachian provenances. Within-provenance variation at Rhinelander differed in magnitude among provenances and with years. In 1970 the earliest family of Virginia provenance 3299 stopped growing 13 days before the latest family -- a difference as great as that between the average dates of growth cessation

for the Quebec and Georgia provenances. In contrast, the range was less than 5 days in New Hampshire provenance 2986 (Fig. 2). The following year the Quebec provenance with a range of 6.5 days was the most uniform and Pennsylvania provenance 3312 with a difference between the earliest and latest families of 13 days was the most variable. The variation among provenances was much larger in 1971 than in 1970, while the within-provenance component decreased in size (Table 2).

That most of the variation in growth cessation was due to differences among provenances is reasonable because time of growth cessation is an adaptation of the trees to their local climate. Apparently, there is also a considerable amount of within-provenance variation in this characteristic. Stern (1962a) has reported similar growth cessation data from tests of *B. japonica* Sieb. and *B. maximowicziana* Reg. The heritability estimates for growth cessation were smaller than for plant height and diameter, but still large enough to indicate fairly strong genetic control of this characteristic, a conclusion also reached by Stern (1962b).

CONCLUSION

The results of this study have shown that within-provenance variation in height of 2, 3 and 4-year-old yellow birch seedlings is often greater than differences among 21 widely separated provenances. Certain provenances are more variable than others, but the amount of variation in a particular provenance frequently differs from year-to-year. Most of the variation in 4-year diameter was due to differences among half-sib families. Considerable within-provenance variation in initiation and cessation of growth was observed, but familial differences were smaller than differences among provenances.

The findings that provenances differ in their genetic variability and that within-provenance variation is large relative to among-provenance variation are difficult to explain. The results could have been influenced by the procedures used in selecting the parent trees. Although a number of different persons provided the seed lots, the same selection criteria were used and the selection intensities were probably about equal. Furthermore, the six provenances in which all the trees were selected by the author differed as much in amount of genetic variation as those selected by several other persons. Introgressive hybridization could be another cause of increased within-stand variability but did not appear to have taken place in most populations. Provenance 2983, which showed evidence of hybridization with paper birch (*B. papyrifera* Marsh.), was less variable than many other provenances, indicating that hybridization apparently was not an important contributor to variation.

The large amount of variation in height and diameter growth of the different families clearly demonstrates how important it is to progeny test all yellow birches to be used in improvement programs. Phenotypic selection appears to be of little value in this species. For example, five of the mother trees in stand 4340 were previously selected superior trees and five were comparison trees. Only one superior tree produced superior progeny, while progenies of the other four had average to very poor performance. On the other hand, because variation in height growth is broad and apparently under fairly strong genetic control, selection for this characteristic should be effective if it is based on the performance of half-sib families in a well-replicated progeny test.

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DISCUSSION

Gerhold - Henry, you referred to the rather large provenance experiment that Peter Krutzsch is involved in. Do you know how many, if any, outplantings there are in North America of this?

Baldwin - The last I heard about that was at the IUFRO meetings in Munich, and I didn't get to the one in Gainesville, so I don't know what the latest report is. I know that Barnard in Denmark is responsible for the seed in this joint effort and they were offering 500 or so. I don't know if anyone in this country offered to take any of those or not. They were getting a rather high price for them, but it was going to include the computer work in Europe. You just give them the measurements and they would feed it in. That was the proposition that they put up in Munich. That was six years ago, or so, and I haven't heard about it except that it is going ahead.

Fowler - I believe that there is only one of this eleven hundred source progeny trial in North America, and that's in New Brunswick.

Gabriel - My question is directed to Tom. With relation to single tree selection with no standards--we have had some experience with this while making selections for superior sap sugar production and it didn't work too well. We sampled sugar bushes to determine a sap sugar average and then selected all trees that exceeded this average by 50 percent. One technician came back with six selections. On investigating I found the six trees to be located on a knoll overlooking the Winooski River. The cool wind blowing off the river and up the hill kept away the flies and consequently the cows that were in the bush used this heavily as seen by the dung that was nearly knee-deep and the trampled roots and compacted soil. I decided not to accept these six selections, even though they met the selection criteria, because of the obvious impact that the environment had on their performance. You could find just the opposite on low wet sites where the environment did not favor high sap sugar content. None of the trees here would even approach the average let alone be 50 percent above and yet you could miss a superior tree using this criteria. I don't quite like the idea of turning down the use of standard trees just yet, even though there is a theory that they could be related to the selected tree.

Ledig - It's getting to be more than theory. We can fly by the seat of our pants as we always have and not pay any attention to genetics. Foresters, all of us including myself, are environmentalists. We really don't buy genetics yet in tree improvement. Our alternative is to act on the basis of genetic considerations.

I agree that you may have to have some environmental yardstick. Van Buijtenen insists that this is necessary, but he nevertheless is abandoning the comparison tree system for Texas, and developing regressions for tree height, diameter, and volume growth based on physical factors of the site. This is good. Also, the approach where you use the entire stand rather than just five, or often even fewer, is another

possibility to make environmental adjustment. Goddard and Brown developed a relationship between crown surface area and diameter increment for a whole stand rather than using five comparison trees to judge a candidate's superiority. The method gives you some handle on the site, but it gets away from the business of using comparison trees.

Remember, the comparison trees that they use in most selection programs are the best trees; in other words, the ones that look most like the candidate tree. You are actually biased toward choosing relatives. If there is any chance of choosing related trees, you're doing your best to get them in usual application of the comparison-tree method.

Gabriel - You may be leading to what a prominent geneticist once recommended. Select trees at random and run progeny tests on them.

Ledig - I don't go that far because you do have, based on 67 progeny tests, five percent gain by wild-tree selection. I am saying that by rejecting the comparison-tree approach, we probably could have gotten more gain; but this is tentative speculation.

The choice of system depends on getting some very good genetic knowledge about relationships among trees, and also learning something about the environmental variation. Foresters are experienced enough now that they report all of their genetic sources of variation, i.e. all the genetic components of variance, but though I have looked through many publications, I haven't been able to find a single one who thought it was worthwhile to report the environmental variation within plots and between plots. Therefore, it is very hard to get a handle on some of these factors.

The method that you use will also depend upon the species involved. I think that in many species, for example the southern pines, we probably haven't been doing any good by comparison-tree selection relative to individual-tree selection.

Another consideration in relation to your comment, is that mass selection is cheap. There is no need to go out and take just any tree to start an improvement program; we might as well choose the best phenotype, and then go to progeny testing if you want.

Gabriel - I would be afraid of going through all the statistical maneuvering involved and then find out that after 20 years you missed the boat when you made your selections. I'm still very leary about giving up on the use of standard trees.

Ledig - All I can say is that the comparison-tree method, in the few cases where it's been tested, has not been of any benefit. In theory, it should result in negative family selection in many cases. The only time it has been compared to individual-tree selection, the results agreed with the theory that I have developed in this paper; i.e., comparison-tree selection is inferior to individual-tree selection in many situations.

Schreiner - If you're only going to use individual tree selection, how effective do you think the dbh--branch-width ratio--would be? That appears to be a fairly valuable constant ratio to estimate growth potential.

Ledig - The constancy of some of these allometric relationships is one of the nice things about them. Maybe I'm thinking about something different, but I would propose one selection criteria would be diameter increment per unit of crown area or crown projection area. This has been proposed by Goddard and Brown and by Rudolf in the past. This is relatively constant for a tree species irrespective of whether it's grown out in the open or grown in a dense stand as shown by Gingrich, by Stout and others. Since this is such a good relationship, I think we could develop a curve for a species and go out and choose those individuals that exceeded the curve by a certain amount.

Schreiner - This was one of the measurements I included in the working plan for the selection of black cherry. The same ratio determinations were to be made for comparison trees.

Ledig - I don't know very much about black cherry. What sort of population structure or breeding system that it might have, but I would be very leary of using the comparison tree-method for any tree species for any trait, without getting some studies first to show that it was justified.

Schreiner - I go along with you on the individual tree selection, but I still want something like the dbh--crown-width--ratio.

Ledig - I have mentioned that relationship in the paper. One section that I've left out in my talk deals with selection criteria. I agree with you.

Schmitt - Listening to you talk now, I happen to think of a possible situation that you might run into in individual tree selection which would bring in both relatives. For example, many times in southern pine when you come to a select tree and as you pointed out before, the comparison trees are almost as good as the select trees. With individual tree selecting, if you were selecting on the basis of a curve, you might pick up four or five of those comparison trees. I suppose it would depend upon the magnitude of the selection program what effect a small number of relatives would have.

Ledig - In the paper that I have prepared for the Proceedings, I summarized right at the very beginning that in any proposed scheme I would select only one tree per stand. I would avoid any case where I might unknowingly include relatives in the same seed orchard.

Schmitt - How would you define stand?

Ledig - This is up to the forester on the ground. Give me a reasonable figure and I will buy it.

Fowler - I have a question on selection in plantations. It is probable that many of the earlier seed collections which gave rise to some of our plantations are from a fairly small number of trees. I suspect that selections from these plantations will contain many half-sibs or full-sibs.

Ledig - Yes, you're probably right, but in many plantations there would be no reason to suspect the nearest trees to your candidate tree would be half-sibs, etc. In wild stands, it's likely that relatives are dispersed non-randomly and adjacent trees might be closely related. It is probable that you could use the comparison-tree method a little more safely in plantations than you could in wild stands for that reason.

Fowler - I agree with that, but I think any way we do it, we're liable to get a fair number of closely related trees.

Ledig - If there was the slightest hint that a plantation was derived from very few parents, then I agree with you that even in this situation, comparison-tree methods should be avoided. Again, I would select one tree per plantation or one tree per stand. I'd be very wary of taking trees that might be related.

Funk - I was surprised by the big differences in seed set for reciprocal crosses that Bill Gabriel described; it didn't fit my preconceived notion. Was this a problem of receptivity or of pollen quality? Do you think that you were able to make what looked like good crosses in both directions?

Gabriel - I wouldn't think it would be a problem of bad pollen, because when crossed to sugar maple we got good seed set from that pollen.

Funk - Were all of your pollinations done on the same day, or approximately?

Gabriel - Very close, If we were using bad pollen, we wouldn't have had the good seed set in the one direction. I suspect there is something else involved here besides this.

Schreiner - They have considerable information on that problem in Europe where they're trying to cross P. deltoides with the European P. nigra. There is high crossability between these species if P. nigra is used as the female parent; I do not like to use the term incompatibility for interspecific crossability. But they have found that many P. deltoides could not be used as female parents.

Larsson - Just to confirm Bill's findings and Ernie's observations. If we cross silver and red maple using the red as the female and silver as the male, they cross quite readily. But if the reciprocal cross is made, we have had very little success. To date we have only one dwarf tree of only 1.5' in height; one large tree of 6' and a medium size tree of 3'. This is the sum total of our success following several hundred crosses.

Dorn - I just wanted to ask Ernie if he found that true within species, too, or is it just between species?

Schreiner - Within species we do have cross incompatibility.

Dorn - I am referring to a tree working as a male but not as a female.

Schreiner - I'm not certain; some of our breeding results seem to indicate that it does happen.

Farmer - I'm interested in the difference in flushing times for the northern and southern provenances. Have you thought about a physiological basis for this? Is it related to spring temperatures or to a difference in dormancy relationship; i.e., incomplete chilling. The relationship is opposite to the one we find in altitudinal studies in the Appalachians or latitudinal studies within the south and central regions.

Clausen - It's also opposite to that in black walnut and several other species, where the southern sources flush earliest and the northern ones flush latest. I think flushing is primarily a temperature controlled phenomenon. I'll bet on heat-sum or perhaps something like that which has to reach a certain accumulated amount. It is not a temperature or degree threshold in that sense. It's probably an accumulation of degree days, or something like that, that is operating. And certainly as far as growth succession is concerned, that seems to be primarily a photoperiodic response. Maybe not entirely, for I'm sure that there are probably some other things involved, but mostly it's a photoperiodic response.

Farmer - If you brought the material into the greenhouse, you wouldn't get the same type of relationship as you do in the nursery then, would you? Assuming that they're all in the state of imposed dormance in March, then would your southern stock that was brought into the greenhouse probably break dormancy a little earlier than the other?

Clausen - I haven't looked at them in the greenhouse, so I wouldn't hazard a guess at how they would react. You may be right, they might in fact behave the other way around because as you suggested, maybe the northern ones would not have had their cold treatment satisfied, whereas the southern ones would. Perhaps if we move them in at that stage, they would behave the way you say.

Zufa - May I refer to Tom's paper and his criteria for selecting on good sites vs. selecting on poor sites. I wonder if we should not select for specific sites. My experience with poplar tests shows, that the clones which grow best on the good sites are often below average on the poor sites. Similarly, the clones which grow best on the poor sites show only average growth under good conditions.

Ledig - I said that the conservative thing to do would be to select on sites similar to those you are going to plant, and I don't know if we can get away from that. There are some people who think you should always select on good sites. Some say that you should select on poor sites. I think the best thing to do is what you suggested. You've got to select from sites of the type you are going to plant.

Gerhold - I also have a comment in relation to Tom's statements on possibilities for juvenile selection. The formula on the blackboard could be used to illustrate a problem that we face in tree improvement. When we're thinking about a decision on whether or not to utilize juvenile selection, we'd like to have values for the regression coefficient and for heritability. But in fact, these can only be obtained after we've gone through a generation. Therefore, we have to act on faith, or good judgment, and start the program. Only after it has been started, can we find out how successful it has been, and can be expected to be in the next generation.

Ledig - We often have to fly by the seat of our pants to get a program going if we are action oriented. However, we've got enough estimates laying around that I think we can start to plug them in and figure out what our range of alternatives might be in new programs. For example, we have Wakeley's correlations over a 30-year period for 4,000-5,000 slash and loblolly pine that he followed through all that time. Those correlations are .4 to .6. So we have an idea that we can at least get that sort of correlation between juvenile and mature growth and might with care, use the estimate for other pines. I admit it is very risky to use this kind of estimate because they are specific to the populations, and furthermore to the southern environments. In fact, they may change from one generation to the next. When you get down to looking for really appropriate estimates, you usually find there are none. So you must commit yourself to an approach before you have the data that really enables you to make the kind of plan that you would like.

Gerhold - In planning experiments that will provide appropriate estimates, you have to commit yourself at least to trying out some approach to improvement before the type of data will become available that you'd really prefer to have before starting.

Schreiner - If we had used juvenile selection in our poplar work, we would have thrown away some of our best hybrids because we had many slow starters; at 15 years these topped many early starters and were among the most disease resistant. The early starters are the types that we need for mini-rotation fiber production, but we also need the slow starters that will outgrow the early starters at twenty years.

Ledig - There are some things that I can see no way to select for, at present, in the juvenile stage, and a disease that hits only mature trees is one of these. Another trait is a tree's seed bearing capacity and its pattern of floral phenology--will it flower in synchrony with the other clones or members of the seed orchard? You can't, with present techniques, select on these characteristics in juveniles. I have been thinking mostly about volume growth. For volume growth, certainly, if your correlation is poor, you're going to get rid of a hell of a lot of your good stuff, but on the average, you're going to be increasing your genetic gain, because you can go through so many more cycles of selection in the same period of time. 11

Schreiner - We should keep in mind that you're thinking in terms of seed varieties and I'm thinking in terms of clonal varieties; these merit different selection procedures.

Ledig - I'm thinking mostly about my experience in the southern pines that are sexually propagated.

Dorn - I'd like to question Tom again; you mentioned that if the correlation was very low it still might be worthwhile to use juvenile selection. If you talk to ten different people, you can find five that say the correlation is positive, and the other five say they think it's negative. In other words, the superseedlings may be the slow growing ones at age 25. Isn't that the danger that we're talking about, not that the correlation is low but that it may be negative instead of positive?

Ledig - I don't think the seedling selection work that's been done is the final answer. If you look at some of the stuff that Nanson's been publishing, you'll find that there are good correlations that last for quite a long while. I don't think the things that were done in "super-seedling" selection are the sort of things that we should do. That work is really not applicable. I'm not talking about selecting an individual and saying that's the individual that's going to turn out well. This is what Ernie is talking about--selecting the best clone. I'm saying select on the basis of progeny average in the first year. The approach doesn't have to be a correlation of growth of that progeny at one year, or size of that progeny at one year, with size at 30 years. Nanson is computing and realizing some quite large gains from the use of flushing data with his material, correlating flushing data in juveniles with volume production at rotation age. The juvenile-mature correlation doesn't have to be something very direct and we don't have to stick with just one trait, either. We don't have to stick with correlations of juvenile size with mature size. The juvenile trait can be a composite one made up of a great many things, which taken together might have some predictive ability for mature volume or growth rate.