REALIZED AND ESTIMATED EFFICIENCY OF EARLY SELECTION IN HYBRID POPLAR CLONAL TESTS

Ronald C. Wilkinson[1]

At the 20th Northeastern Forest Tree Improvement Conference held in 1972, I reported on the inheritance and correlation of juvenile (1-, 4-, and 9-year) and mature (15-year) growth characters of hybrid poplar clones, but at that time I only speculated on the effectiveness of early selection (Wilkinson, 1973).

The response of a mature character to selection for a juvenile character can be predicted if the genetic correlation and the heritabilities of the two characters are known. The predicted effectiveness of early selection is given by the formula:

$$\frac{CR_m}{R_m} = r_G \frac{i_j}{i_m} \frac{H_j}{H_m}$$

adapted from (Falconer, 1960)

[1]Research Geneticist, Forest Service, U. S. Department of Agriculture, Northeastern Forest Experiment Station, Durham, New Hampshire.

CR is the correlated response of the mature characters resulting from selection applied to the juvenile character. Rm is the direct response following selection for the mature character.

r_c is the genetic correlation between the juvenile and mature characters. i_i, i_m and H_i, H_m are the standardized selection intensities and the square roots of the heritabilities for the juvenile and mature characters.

If we are to obtain values for the genetic correlation and heritabilities a generation of testing is required; 15 years with our hybrid poplars. If the necessary early measurements are made, we have another method for determining the effectiveness of early selection; that is, conducting a simulated early selection program and following the progress of the selected clones through maturity. The ratio of the gain attained by early selection to those made by selecting at maturity is the realized effectiveness or efficiency of early selection.

The purpose of this study was to evaluate the effectiveness of early selection for mature (15 year) height of hybrid poplar clones and to compare predicted and observed mature responses to early selection.

All data are from hybrid poplars in 15-year clonal tests on the former Lawrence Hopkins Memorial Experimental Forest in Williamstown, Massachusetts. Each clone was represented by a square plot containing 16 ramets (unrooted cuttings) spaced four feet apart. In each year, two replicates were located on an upland terrace site at an elevation of 790-820 feet, and two more replicates on a sloped site at an elevation of 900-1000 feet (Schreiner 1972). One clone-plot was randomly located within each of the four replicates for each clone under study for that year. Fifty different clones were established each year from 1949 to 1952. Thirty hybrid poplar clones were planted in 1953 together with 20 *Populus deltoides* clones. The *Populus deltoides* clones are not included in the analyses. Thus, 230 clones are each represented by 16 ramets in 4 separate replicates. The height of each ramet at 1, 4, 9, and 15 years after planting was measured, along with mean mature (15 year) heights of clones selected after 1, 4, 9, and 15 growing seasons.

Following analysis of variance, the clone and error variance components were estimated from the expected mean squares and ratios of genetic to phenotypic variance (broad-sense heritability) and their confidence limits were calculated (Becker 1967). Genetic correlations were estimated from cross-product analysis for the most recent growth measurements (15-year height) and earlier measurements (Falconer 1960).

Genetic correlations, estimates of genetic variance, and broad sense heritability were calculated separately for each planting year but combined between sites. All calculations were made on a plot-mean basis.

For the purposes of simulated early selection the 7 tallest clones in each planting year (only 5 in the 1953 planting) at each age 1, 4, and 9 years were evaluated for 15-'year performance. The mean 15-year heights of the selected clones at each age were compared to the plantation mean height to establish the selection differential and to the 7 tallest clones at 15 years to determine the realized efficiency of early selection.

The selection of 7 clones from each planting corresponded closely to the number of final selections made by Schreiner (1972) and also to the number of clones that were two standard deviations above the plantation means.

Table l.--Mean 15-year heights and selection differentials of clones selected for superior height growth at fifteen years and earlier ages.a

Planting year	Selection age (years)	Mean mature height (feet)	Mean mature height of selected clones (feet)	Selection differential (feet)	Selection differential as % of mature mean height
1949	1	40.3	35.7	-4.6	-11.4
	4		31.9	-8.4	-20.8
	9		47.0	6.7	16.6
	15		52.9	12.6	31.3
1950	1	40.7	45.3	4.6	11.3
	4		48.5	7.8	19.2
	9		51.8	11.1	27.3
	15		53.7	13.0	31.9
1951	1	32.3	37.8	5.5	17.0
	4		37.1	4.8	14.9
	9		41.4	9.1	28.2
	15		44.6	12.3	38.1
1952	1	37.8	46.1	8.3	22.0
	4		46.7	8.9	23.5
	9		47.7	9.9	26.2
	15		48.9	11.1	29.4
1953	1	45.8	53.5	7.8	17.0
	4		52.2	6.5	14.2
	9		55.1	9.4	20.5
	15		56.0	10.2	22.3

aSelected clones were the seven tallest in each planting year at each age except the 1953 planting year in which only the tallest five were considered.

RESULTS AND DISCUSSION

Two criteria, aside from the economic benefits obtained by compressing a number of generations into a clonal testing program, are important in evaluations of the efficiency of early selection. They are the genetic gain, as measured by the selection differential, resulting from early selection for mature performance; and the number of superior genotypes that would be lost if the test clones not selected were rogued subsequent to early selection.

In all five test plantings of hybrid poplar, the 15-year selection differentials increased with increase in selection age, corresponding to the pattern for phenotypic and genotypic correlations between early and mature heights (Wilkinson 1973). Selection differentials resulting from the selection of the 7 tallest clones at 15 years were quite uniform, ranging from 10 to 13 feet (table 1). On the other hand, selection differentials resulting from simulated selection at earlier ages varied from one planting year to another.

Selection of the 7 tallest of 50 clones after 1 or 4 years of testing in the 1949 plantation resulted in a negative selection differential. Most of the tallest clones at the earlier ages were below average height by the fifteenth year. In the 1949 planting, selection even as late as 9 years would result in little more than one-half of the gain obtainable by selection at 15 years.

However, this tendency for the fast-starting clones to lose their superiority by the fifteenth year was not evident in all five planting years. Gains from selection after 1 or 4 years in the 1952 and 1953 plantations would be 60 to 80 percent of those obtained from selection at 15 years. In these two planting years even selection at 1 year would result in appreciable gains at maturity. Genetic differences in the growth patterns of the various clonal mixtures in each planting year probably account for the differences in correlations between early height growth and 15-year heights, and therefore, in the wide differences in gain to be expected from early selection (Wilkinson 1973).

The efficiency of early selection based on mathematical prediction $\left(\frac{r_G\, i_j\, H_j}{i_m\, H_m}\right)$ agreed closely with the observed efficiency (ratio of juvenile to mature selection differentials) obtained by simulated early selection (table 2). Predicted efficiency was in some instances higher and in other instances lower than the efficiences actually observed with no apparent trends. Only in the 1953 planting did the predicted efficiency of early selection severely underestimate the efficiency which was possible. Over-estimates were generally small, suggesting that the use of broad-sense heritabilities and genetic correlations would be reliable in estimating gain from a program utilizing early selection of clonal material. Moreover, if the errors in the estimates of heritability and the genetic correlation are taken into account the predicted efficiencies would bracket those that were observed. However, the differences in heritability and correlation between planting years would restrict their use to a limited range of sites and genotypes, and they would not have genus-wide application.

Table 2.--Broad-sense heritabilities, genotypic correlations, and efficiency of selection for fifteen-year height based on heights at earlier ages.

Planting	Selection	Broad-sense heritability H^2 $(\sigma^2_c/\sigma^2_c + \sigma^2_e)$	95-percent confidence limits for H^2	Genotypic correlation r_G	Predicted efficiency $\left(r_G \frac{i_j}{i_m} \frac{H_j}{H_m}\right)$	Observed efficiency
					Percent[a]	
1949	1	.264	.147 - .413	-.555	-27.4	-36.5
	4	.372	.252 - .517	-.861	- 7.5	-66.7
	9	.420	.294 - .569	.646	37.3	53.0
	15	.623	.450 - .773	____	____	____
1950	1	.530	.410 - .661	.404	57.6	35.5
	4	.554	.436 - .681	.670	68.4	60.3
	9	.757	.672 - .838	.814	89.8	85.7
	15	.684	.541 - .804	____	____	____
1951	1	.244	.128 - .392	.580	33.2	44.6
	4	.292	.144 - .441	.485	49.2	39.0
	9	.623	.452 - .771	.624	99.0	73.4
	15	.450	.235 - .662	____	____	____
1952	1	.495	.377 - .626	.741	63.3	74.8
	4	.532	.416 - .658	.770	66.0	80.5
	9	.538	.416 - .669	.848	84.4	89.1
	15	.487	.309 - .662	____	____	____
1953	1	.676	.517 - .809	.667	33.1	75.8
	4	.428	.240 - .626	.699	31.5	63.3
	9	.682	.523 - .814	.864	60.8	91.6
	15	.523	.312 - .727	____	____	____

[a] Percent of gain attained by direct selection at fifteen years.

Table 3.--Selection intensities required to retain the seven tallest clones at fifteen years by selection at earlier ages.

Planting year	Selection age (years)	Number of tallest clones not selected[a]	Number of selections required	Number of surviving clones	Percent of clones required
1949	1	6	44	50	88
	4	6	33	50	66
	9	4	24	48	50
1950	1	5	28	46	61
	4	5	26	46	56
	9	3	17	46	37
1951	1	5	26	50	52
	4	5	22	50	52
	9	3	18	49	37
1952	1	3	22	50	44
	4	2	25	50	50
	9	3	14	48	29
1953	1	3	24	30	80
	4	3	19	30	63
	9	1	11	30	37

[a] Selected clones were the seven tallest in each planting year at each age except the 1953 planting year in which only the tallest five were considered.

Juvenile or early selection for mature characters cannot be expected to be as efficient as mature selection unless the juvenile character has a substantially higher heritability than the mature character and the genetic correlation between the two is high. In the 1952 planting the heritabilities for height at 1 and 4 years were greater than the heritability for height at 15-years (table 2). These higher heritabilities coupled with the high genotypic juvenile-mature correlation in this planting account for the high efficiencies of early selection were considerably lower, heritabilities increased with age and were the highest in the ninth or fifteenth year. The high heritabilities at 9 years of age and the strong correlations between 9-year and 15-year heights also account for the high efficiency of selection at 9 years in all five plantations.

Equally as important as the genetic gain from early selection is the loss of superior genotypes by early roguing. Selection of the 7 tallest clones at 1, 4, or 9 years in any one of the five plantings would result in the loss of at least one of the best performing clones at 15 years (table 3). In the 1949 planting 6 of the best 7 performing clones at 15 years would not be selected as among the best 7 clones at 1 or 4 years. Consequently, the selection intensities required to retain the 7 tallest clones at 15 years would have to be considerably reduced at earlier ages. Selection intensities for 1-year selection range from 44 percent to 88'percent of the population. Even after 9 years the range would be 29 to 50 percent of the population.

If preservation of the best performing clones at 15 years is imperative, the reduced selection intensities required at early ages would result in a further reduction in gains from early selection unless a multi-stage selection program is used.

SUMMARY

Selection of hybrid poplar clones for total height at 1 or 4 years in clonal tests may result in negative selection differentials at 15 years. Genetic gains in total 15-year height increased with increases in the ages at which selections are made, but were quite variable from one year and set of clones to another. Broad-sense heritabilities and genetic correlations are reliable for predicting the mature response to early selection, but they are applicable only to a limited range of sites and genotypes. When genetic correlations between early and mature performance are low, selection intensities utilized in an early selection program may have to be reduced considerably in order to preserve the best performing clones at 15 years.

LITERATURE CITED

Becker, W. A. 1967. Manual of procedures in quantitative genetics ed. 2. Wash. State Univ. Press, Pullman. 130 p.

Falconer, D. S. 1960. Introduction to quantitative genetics. Ronald Press Co., New York. 365 p.

Schreiner, E. J. 1972. Procedure for selection of hybrid poplar clones for commercial trials in the northeastern region. NE. Forest Tree Improve, Conf. Proc. 19(1971):108-116.

Wilkinson, R. C. 1973. Inheritance and correlation of growth characters in hybrid poplar clones. NE. Forest Tree Improve. Conf. Proc. 20 (1972):121-130.

DISCUSSION

Ledig - Why does there seem to be a trend in correlations from 1949-1953? Juvenile valuation seems to improve from year to year.

Wilkinson - That would be mainly because of the clonal make-up. The 1949-1950 plantings included a number of fast-starting *Populus maximowiczii* clones which were among the shortest clones at 15 years.

Kriebel - Are you saying then that the efficiency of early selection might vary with the species?

Wilkinson - Yes, the clonal make-up of the test.

Klein - I am wondering whether at the stage you are on now, if you had a new set of clones whether you could try a correction factor for certain taxonomic groups knowing their overall pattern of growth and thus get better prediction for individual clones, whether they are apt to slow down or speed up.

Wilkinson - It should be possible.

Long - Do you know if there have been any correlations between growth and root traits that would be useful for early selection?

Wilkinson - Yes, they have been. Santamour conducted studies on root-bark diameter and showed an 80% negative correlation at one year with nine-year growth performance. My study was strictly juvenile height versus mature height.

Zsuffa - Would the selection at either four or seven years be more efficient than the selection at the end of the first year?

Wilkinson - Yes, as the age increases, the efficiency of selection increases. One year is the least efficient.

Zsuffa - Would the selection at 2 or 4 years be satisfactory then?

Wilkinson - Well, that would depend on your criteria and what you would accept for gain.

Larsson - Did you have any history on the seedlings from which the clone material originated? Did it come from mature trees that already proved themselves to be highly superior in growth or was it clonal material from fast-growing seedlings?

Wilkinson - I don't know if you are familiar with the history of the NE hybridization program, but these clones were all part of this program starting out with 13,000 progenies and finally selecting 250, which were clonally tested in the plantation at Williamstown. So I would say that these were unproven.

Garrett - I don't think the initial trees used in the breeding program were selected for growth; they were whatever was available in the New York Botanical Garden where the crosses were made, but then they were selected in the nursery on the basis of growth and rootability.

Klein - I was wondering if you are keeping records of sap volume on the trees selected for sugar content and sugar content on trees selected for sap volume so you could find, in the first generation selection population, trees that are above-average for both traits.

Gabriel - At this time, we aren't keeping any records like that. It probably would be a good idea to start doing this.

Zsuffa - If we go back to my first question, it would seem to me that the height of the trees at the end of the first year reflected mainly the size of planting stock in that plantation, so if you didn't get good correlations comparing the height at first year with the height at the end of the 4, 7, etc., to me it didn't mean that the early selection in poplar was not efficient.

Wilkinson - I would agree that probably is partially true, except I would like to point out that these cuttings were very carefully graded as to size before they were planted.

Zsuffa - Were these unrooted or rooted cuttings?

Wilkinson - Unrooted cuttings.

Kriebel - Were your correlation calculations based on plot means or on individual trees?

Wilkinson - Plot means.

Hunt - Bill, I was just wondering about your selection technique. It's a little obscure to me and I see you didn't have time to explain it. You start in the morning to begin sampling your trees and after you have gone through 100 trees, which takes at least 1½ hours or so, the sun comes up, they begin to run faster, and you probably take time out for lunch and then the sun goes down and it begins to cool down, and at the end of the day they are slower still. Now, how do you compare a tree in the middle of the day when it's nice and warm and sunny with a tree in the early part of the day or one sampled at the end of the day. You said you were not measuring sugar contents, so what if your tree is pushing out pure water at gallons per minute?

Gabriel - Why didn't you ask me something easy? Well, we have training sessions for all of our field men, and we make it a point to impress upon our men that they have about two or three hours at the most to complete their samples--get their 100 trees in so as not co ennround time of testing with sap volume produced. There is another reason why we like to use the old standard select-tree system. We can reduce a lot of variation due to environment by working in small areas. As far as the sugar content is related to sap volume, we are not too concerned with this at present. Did I answer your question?

Hunt - Well, what mechanical sleigh-of-hand do you use to say that this is your plus-tree? Is there actually that much difference between one tree and its neighbor?

Gabriel - Yes, there is. We showed that on the selection forms, where we had readings for the standards taken at the same time as the select trees, and the variability between the select trees and the average of the standards is quite large. We have a comparison on an individual tree basis as well as on a stand average basis. We do require that the field men collect their data within a given time period because we do recognize that there are changes in flow rate associated with time of day.

Hunt - Do you find that you can check yourself by going from the 100th tree and go back to the first tree on another day and get the same results?

Gabriel - We don't check the same tree in the same day twice. We get an average sap volume production for the stand and try to get as wide a field coverage as possible by restricting the testing to the 100-tree sample. But I would expect that during the time that the sampling would take, the repeat test on the first tree in the sample might be different than the initial reading on that tree.

Cech - Looking at your sampling form, I see first 3, 4, 20, 26, 18, etc., and later on we run into 68, 69, 54, etc. It seems that this is a time of day response because there is a gradual increase and at the end it drops off a little bit. How do you make your selection from the preliminary screening in spite of this response.

Gabriel - Some of the changes in sap flow rate from one tree to another you saw reflects the change in the environment along the transect. Although I am not familiar with this particular bush in Michigan, the different values could very well reflect these changes in the environment rather than a change due to the time of day.

Kriebel - Bill, your assumption is that there is 100% correlation between flow rate and sap volume yield, but is it also possible that some trees will have a longer period of flow than others? If so, this would introduce another variable in total sap volume which you have not considered.

Gabriel - We find that there is some difference with respect to length of flow. But most of this extended flow period would come near the end of the sap season, in the last week of April or the last ten days of April. Normally, the sugaring season comes to an end several weeks before this. Perhaps in the first week of April. During the latter half of the month the quality of the sap is usually poor, and it is not very desirable to select a tree that produces most of its sap at the end of the season.

Kriebel - I was referring to variation of trees in the duration of flow within runs, not at the end of the season.