EVIDENCE FOR AND AGAINST THE EFFECTIVENESS OF FIELD SELECTION IN NORTHERN CONIFERS[1]

Carl A. Mohn[2]

Abstract--Cost, factors which influence response and reported results of field selection of northern conifers were reviewed. Despite a long history of field selection, published data relative to its effectiveness are limited and inconclusive. Reports deal almost exclusively with height growth and provide an indication that plus-tree selection has generally been ineffective for four northern conifers.

Additional Keywords -- plus-tree, Picea glauca, Picea mariana, Pin us banksiana, Abies balsamea

Plus-tree selection in the northern United States and eastern Canada apparently was initiated with white pine prior to world War II and, at least on a small scale, with several other northern conifers in the early 1950's. It is mentioned in reports contained in the proceedings of the 1953 and 1955 conferences sponsored by the Lake States Tree Improvement Committee, was a part of the early tree improvement work in Canada (Heinberger 1953, Heinberger 1954, Hoist 1955) and played a role in the early work in the northeastern United States (Gabriel 1958).

Such selection is an early phase of almost every tree improvement program and we might well expect it to have been completed for many of our species. Indeed, the need to address this topic at a 1988 tree improvement conference can be questioned. After all, activities like biochemical evaluation (Yeh, 1985), *in vitro* screening (Ettinger et. al. 1985, Belanger and Manion 1985) and measurements made at the molecular level (Bongarten et. al. 1985) are currently the "hot" topics in the selection arena.

Justification for this review is really quite simple. For a number of reasons plus-tree selection is still a major activity in our part of North America and one on which we are spending substantial sums of money. This is evidenced by reports in recent proceedings, particularity those of the Canadian Tree Improvement Association. Given the status of most budgets, what we are receiving for those dollars is important to everyone in the tree improvement "trenches".

Ideally we would examine effectiveness of field selection by reviewing analyses of the economic efficiency of improvement programs and the impact of selection alternatives. This approach for northern conifers would result in a very short discussion. We would be limited to the work with black spruce reported by Cornellius and Morgenstern in 1986.

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[2] Professor, Dept. of Forest Resources, College of Natural Resources, Univ. of MN.

In the absence of suitable body of economic evaluations, a more general approach to plus-tree selection in northern conifers will be utilized in this review. It will briefly examine the reported costs of field selection, list some of the factors which influence response and then examine published data indicting the returns from field selection of northern conifers.

FIELD SELECTION COSTS

Costs of plus-tree selection are strongly influenced by species, improvement strategy, program size, discount rates and the accounting time frame. As a result, reported values only give us a sense of "order of magnitude". In northern conifers costs per plus-tree selected have been reported to range from $75 to $1,118 (early 80's dollars) (Morgenstern 1983, Morgenstern and Mullen 1987). Predictably, highest cost are reported for programs based on mass selection and grafted seed orchards. For example, in eastern Canada mean selection cost per plus-tree of $558 for grafted seed orchard programs (white spruce, red spruce and tamarack) and $255 for seedling seed orchard programs (black spruce and jack pine) were cited by Morgenstern and Mullen (1987).

When plus-tree selection costs are reported relative to total program costs, they range from approximately 8% of the total costs in a typical southern pine improvement program (Porterfield et. al., 1975) to as high as 36% for a Pinus caribaea program in Queensland (Reilly and Nikles 1977). In this region the field selection costs for a typical black spruce improvement program were examined by Cornellius and Morgenstern (1986). Given a 4.5% discount rate, the selection cost in a program to establish a 5.2 hectare seedling seed orchard using 221 open-pollinated families was about $76 per plus-tree. (selection expenditure were reduced by allocating them to several seed orchards) and equalled approximately 14.8% of the orchard's total cost (Morgenstern and Mullen 1987). While the costs for field selection in programs utilizing grafted seed orchards are higher than those for seedling programs, the percentage is probably about the same because of the differences in total costs.

A "best guess" is that about 15 percent of dollars expended in a typical first generation improvement program in our region go to field selection. This guess is suspect because of the lack of "good" cost data but it does provide a point of reference.

FACTORS INFLUENCING RESPONSE

The process for which field selection dollars are spent seems simple enough: we identify trees in natural stands or plantations which are observably superior in one or more characteristic. Scoinwood, cuttings or seed from these plus-trees are then used in seed orchards and/or breeding programs to produce improved planting stock. The underlying principle is straight forward: good parents produce good progeny. Field selection is the way we identify good parents.

Obviously, this is oversimplification. The process of plus-tree selection and its theory have been described in considerable detail elsewhere (Morgenstern et. al. 1975, Wright 1976, Zobel and Talbert 1984 and others) and will not be detailed here. It is enough to note that predicted genetic gain from plus-tree selection isthe product of: 1) narrow-sense heritability or h^2 - an estimate of the extent to which the observed superiority of our plus-trees is predictably transmitted to progeny, 2) selection intensity or "S" - the difference between the average of our population of plus-trees and the average of population they were selected from and 3) a coefficient reflecting the method used to transfer the genes of our selections into production and breeding populations.

All of these components can be influenced by the techniques used in field selection and seed orchard development. In general, techniques which are expected to result in a greater return add to the costs of plus-tree selection. As a result, the effectiveness of plus-tree selection must be examined in the context of the traits evaluated, selection method, the improvement scheme and costs. Factors to be considered when evaluating reports of response to to field selection of northern conifers include:

1. Traits

Heritabilities varies with the traits evaluated in the field. Experience suggests that we can expect fairly high heritabilities for traits related to adaptability and wood quality; intermediate values for stem and branching characteristics and low values for characteristics related to growth (Shelborne 1969). What we select for will strongly influence the level of the response. Significantly, most field selection with northern conifers has involved growth traits.

It is also critical that evaluations of the biological response to field selection be based on measurements of characteristics related to those actually selected for in the field. While this seems obvious, there are reports in which the traits selected for and the traits for which the response was observed have no apparent connection.

2. Populations

Age, composition, site qualities etc. of the stands in which selection takes place can influence the environmental contribution to phenotypic variation and thus heritability. (Wright 1976). In general, the more uniform the population we select in the greater the response and the greater the selection costs. How the source population are defined in plus-tree selection is therefore critical to our assessment of actual or potential effectiveness.

The other side of this coin is the population used as a basis for measuring responses to selection. In order to evaluate the selection process fairly, control populations should be representative of the population in which selection was carried out and be large enough to permit the detection of differences. These conditions are not always met.

3. Selection Method

The use of plus-tree selection systems in which candidate trees are compared to other trees growing in a similar environment may provide a means of controlling environmental effects. A careful definition of the methods used in selection is important to interpretation of its effectiveness.

4. Selection Intensity

Estimating selection differential for plus-tree selection can be difficult. It is complicated by the fact that almost all plus-tree selection involves several traits and the actual selection intensity for each trait is unique and substantially lower than that associated with selecting the same proportion of a population for a single trait. These "effective" selection differentials should be used in evaluating field selection. Valid measures of the intensity achieved are not always available, "Ocular" selection systems which do not involve measurements or ratings (Morgenstern et. al. 1975) leave us in the dark. Base-line selection systems can provide a basis for estimating selection intensities (van Buijtenen 1969) and estimates for comparison tree systems can be developed with some supplementary measurements (Porterfield et. al. 1975). In many published reports selection intensities are omitted or given in a form which precludes generalization.

5. Propagation method

While there are other alternatives, in this region we normally use grafting or open-pollinated seed to transfer genes from plus-tree into breeding and production populations. The use of open-pollinated seedling reduces the potential for genetic gain from plus-tree selection by half, a major consideration in evaluating selection effectiveness. In addition, in northern conifers the use of open-pollinated seed collected from selections in situ for testing has been almost universal which impacts the measurement of responses.

RESPONSES TO FIELD SELECTION

Most of the recent studies utilizing materials developed from field selections of other northern conifers have involved comparisons among progeny of selected trees and have not included controls. The result is a scarcity of data with value for judging the effectiveness of plus-tree selection.

The oldest useful reports from our region relate to selection for blister rust resistance in white pine. The evidence supports the conclusion that field selection, even under favorable conditions, has not been effective for the improvement of this trait (Heimberger 1972, Ricker et. al. 1943).

Table 1 summarizes the published reports for four other northern conifers and gives insight into the performance of populations developed using plus-tree selection. With the exception of the observations related to selection for branch characteristics in balsam fir (DeHayes et. al. 1983), the studies all relate to selection for height growth. The results are an indication that field selection was not effective in three of the four species.

In the case of white spruce field selection may have resulted in an increase in the rate of height growth. The lack of response reported by Khalil 1975, 1978) can be discounted because of test age. Holst and Tiech (1969) reported a positive response to field selection. However, a subsequent evaluation of the same materials by Ying and Morgenstern (1979) raises doubts. Data from a Maine-New Hampshire study (Carter 1985) indicate an unreasonably high response. These results were reported in an abstract and details of the study are lacking making evaluation difficult.

Table 1. Summary of reports of response to field selection of northern conifers.

CITATION	FIELD SELECTION SUMMARY				RESPONSE MEASUREMENT SUMMARY			
	TRAITS	POPULATION	METHOD	INTENSITY	TRAITS	TYPE MATERIAL	CONTROL	RESPONSE
				******WHITE SPRUCE******				
CARTER 1987	not reported	natural stands ME. & NH	not stated	not stated	ht. age 14	O.P. progeny	nursery run	+23%
KHALIL 1975, 1978	height; age 25-50	2 stands Nfld.	ocular	> 1 std. dev.	ht. & dia age 2 - 4	O.P. progeny	avg. trees same stands	none
HOLST & TIECH 1969	crown width & height; age not stated	Petawawa area 9 stands	ocular	i = .75 (?)	ht. age 11	O.P. progeny	random trees same stand	+ 1 %
YING & MORGENSTERN 1979	crown width & height; age not stated	Petawawa area 9 stands	ocular	i = .75 (?)	ht. age 8-22	O.P. progeny	random trees same stand	none
				******BLACK SPRUCE******				
MORGENSTERN 1974	mean annual increment; age 30-50	Petawawa area 4 stand	n.a.	n.a.	ht. ages 4 & 9	O.P. progeny	n.a.	no parent progeny correlation
VAN DAMME & PARKER 1986	2 growth-crown ratios, ht./age; ca. 50 yrs.	1 stand Ontario	baseline	10/398 (i= 2.317)	growth & crown traits at ages 1 & 2	O.P. progeny	random trees same stand	selections inferior

(continued next page)

Table 1(continued). Summary of reports of response to field selection of northern conifers.

CITATION	FIELD SELECTION SUMMARY				RESPONSE MEASUREMENT SUMMARY			
	TRAITS	POPULATION	METHOD	INTENSITY	TRAITS	TYPE MATERIAL	CONTROL	RESPONSE
				******JACK PINE******				
CANAVERA 1975	growth, stem straightness; age unstated, avg. ht. 60'	L.P. Mich. 60 stands	comparison	2 or more std. dev.	ht. age 2	O.P. progeny	average or "minus" trees same stands	not significant (0.4%)
MEIER & MURPHY 1985 MILLER & MURPHY 1975	growth, form & disease resistance; age unstated	Lake States 8 National Forests	comparison	not reported	ht. age 10 4 locations	O.P. progeny	bulked seed lots from same forests	most controls equal to or taller than counter parts
				******BALSAM FIR******				
DeHAYES et. al. 1983	ht. & radial growth age unstated	New England	comparison	+25-30%	hts, terminal shoot length age 9 & 11	O.P. progeny	random selections & comparison trees	none
DeHAYES et. al. 1983	Christmas tree traits: form, color etc. age unstated	New England	ocular	not stated	nr. branches, nr. buds age 9 & 11	O.P. progeny	random selections	none

CONCLUSIONS

The data currently available points to little or no response to field selection for height growth of northern conifers. For other traits there is no basis for even tentative conclusions.

Even for growth the jury is really still out. It seems safe to conclude that we should not expect large gains for any of the species considered. However, the possibility of small but economically significant gains in any of the species can't be discounted on the basis of the information available. For several reports questions can be raised about.the relationship between growth traits evaluated in the field and those measured in subsequent tests. Does height growth to age two or four or even ten have any real relationship to height or height growth in 50-year-old natural stands?

In other cases selection intensity was low or not satisfactorily quantified and selection methods were not always clearly described. As a result, the sensitivity of tests may be a major factor. Morgenstern and Mullen (1987) pointed out that heritabilities for height growth in natural forests are probably very low and that even with selection differential of between 2 and 3 standard deviations the expected gains from plus-tree selection for growth are very small. Test may not have been of adequate size to detect small differences. In addition, all of the tests reviewed used open-pollinated progeny from *in situ* mother trees which reduces the chances for detecting a response to selection.

My assignment was to review the evidence for and against the effectiveness of field selection in northern conifers. Despite a long history of field selection in this region, very little evidence as to its effectiveness was found. Such evidence may already exists in your files or it could be generated in conjunction with ongoing work. Given the costs of field selection, there is clearly a need for all of us to more clearly document our experiences with northern conifers.

LITERATURE CITED

Belanger, P.R. and P. D. Manion. 1985. Testing of a method for screening aspen for hypoxylon canker resistance. Proc. 12th Meeting of the Canadian Tree Improvement Association, Part 2. pp. 91.

Bongarten, B.C., N.C. Wheeler and K.S. Jech. 1985. Isozyme heterozygosity as a selection criterion for yield improvement in Douglas-fir. Proc. 12th Meeting of the Canadian Tree Improvement Association, Part 2. pp. 121-128.

Canavara, D. S. 1975. Variation among the offspring of selected lower Michigan jack pines. Silvae Genetica 24:1:12-15.

Carter, K. 1985. Progeny test of plus-tree selection in white spruce. Abstract of Poster in Proc. of the 20th Meeting of the Canadian Tree Improvement Association. Part 1. pp 23.

Cornellius, J. P. and E.K. Morgenstern. 1986. An economic analysis of black spruce breeding in New Brunswick. Canadian Journal of Forest Research. 16:3:476-483.

Dehayes, D.H., D.S. Canavera and K.K. Carter. 1983. Variation among progeny of mass selected balsam fir. Proc. 28th. Northeastern Tree Improvement Conference. pp. 163-174.

Ettinger, T.L., P.E. Read, W.P. Hackett, M.E. Ostry and D.D. Skilling. 1985. Development of resistance in Populus to Septoria musiva utilizing somaclonal variation. Proc. 12th Meeting of the Canadian Tree Improvement Association, Part 2. pp. 83-90.

Gabriel, William J. 1957. Summary of forest tree improvement work in the northeast. Proceedings 5th Northeastern For. Tree. Imp. Conf. pp 3-5.

Heimberger, C. 1953. The present status of forest tree breeding in Canada. Proc. Lake States Forest Genetics Conference. Lakes States Forest Exp. Sta. Misc. Rpt. No. 22: 33-41.

Heimberger, C. 1954. Forest tree breeding in Canada. Jour. of For. 52(9):682-684.

Heimberger, C. 1972. Relative blister rust resistance of native and introduced white pine in eastern North America. in Biology of Rust Resistance in Forest Trees. USDA For.Serv. Misc. Pub. No. 1221 pp. 257-269.

Holst, M. J. 1955. Forest tree breeding in Canada. Proc. Lake States Forest Tree Improvement Conf. Lake States Forest Exp. Sta. Misc. Rpt. No. 40: 41-42.

Holst, M. J. and A. J. Tiech. 1969. Heritability estimates in Ontario white spruce. Silvae Genetica 18-2:23-27.

Khalil, M. A. K. 1975. Early growth of progenies from some phenotypically superior white spruce provenances in central Newfoundland. Silvae Genetica 24:5-6:160-163.

Khalil, M. A. K. 1978. Early growth of some progenies from two phenotypically superior white spruce provenances in central Newfoundland. II. heritability and genetic gain. Silvae Genetica 27:5:193-196.

Meier, R. J. and J. D. Murphy. 1985 Results of a 10-year-old jack pine progeny test at four Lake States locations. Proc. of the 4th North Central Tree Improvement Conf. pp. 82-91.

Miller, R. G. and J. D. Murphy. 1975. Forest tree improvement program for the National Forests in the Lake States. Proc. of the 12th Lakes States Forest Tree Improvement Conf. pp. 1-9.

Morgenstern, K. E. 1974. Selection of black spruce progenies for the genetic improvement of height growth. Forestry Chronicle 50:4:160-162.

Morgenstern, K. E. 1983. Tree selection techniques in the northeast: some problems and questions. Proc. 28th. Northeastern Tree Improvement Conference. pp. 145-157.

Morgenstern, K. E., M. J. Holst, A. H. Teich and C.W Yeatman. 1975. Plus-tree selection: review and outlook. Dept. Environment, Can. For. Ser. Pub. No. 1347. 72pp.

Morgenstern, K. E., and T. J. Mullin. 1987. Plus-tree selection: controlling its cost. Proc. 21st Meeting of the Canadian Tree Improvement Association., Part 2. pp. 108-113.

Porterfield,, R. L. B. J. Zobel and F. T. Ledig. 1975. Evaluating the efficiency of tree improvement programs. Silvae Genetica 24:(2-3):43.

Reilly, J. J. and D. G. Nikles, 1977. Benefits and costs of tree improvement: Pinus caribae. Proc. Third World Consultation on Forest Tree Breeding (Volume 2). F0-FTB-77-5/3:1099-l124.

Riker, A. J., T. F. Kouba, W. H. Brener and L. E. Byam. 1943. White pine selections tested for resistance to blister rust. Jour. Forestry. 41:10:753-760.

Shelborne, C. J. A. 1969. Tree breeding methods. Forest Res. Institute, New Zealand For. Serv. Tech. Pap. No. 55. 43pp.

Van Buijtenen, J. P. 1969. Progress and problems in forest tree selection. Proc. of the Tenth So. Conf. on For. Tree Improvment. pp. 17-26.

Van Damme, L., and W. H. Parker. 1987. Selection of Picea mariana for growing space efficiency. Can. Jour. For. Res. 17:5:421-427.

Wright, J. W. 1976. Introduction to forest genetics. Academic Press, New York. 463pp.

Yeh, F.C. 1985. Recent advances in the application of biochemical methods to tree improvement. Proc. 12th Meeting of the Canadian Tree Improvement Association, Part 2. pp. 29-39.

Ying, C. C. and E. K. Morgenstern. Correlations of height growth and heritabilities at different ages in white spruce. Silvae Genetica 28:5-6:181-184.

Zobel, B. and J. Talbert, 1984. Applied Forest Tree Improvement. John Wiley and Sons. N.Y., N.Y.