FUTURE BREEDING STRATEGIES AND THE NEED FOR EARLY TESTING IN BLACK SPRUCE

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Abstract. Operational improvement programs for black spruce must be efficiently designed, genetically and economically. Recent results suggest that there may be benefit in the use of selected non-local material, and also breeding zones may need to be re-designed. Specific combining ability may contribute significantly to height growth genetic variance at later ages, in which case the seedling seed orchard approach may be sub-optimal.

Additional keywords: Combining ability, seed orchards, genecology, breeding zones, heritability.

The ultimate aim of commercial forestry operations is to maximize the economic return per unit area of afforested land. Thus, the objective of tree improvement is to enhance this net economic return, either through an increase in net yield of marketable products, or a reduction in economic rotation ages, or both. Research in forest genetics and tree improvement must, therefore, be designed to provide information to maximize genetic gain of these marketable products at rotation age, through suitable breeding strategies.

This immediately introduces the problem of time. Although individuals of a particular species tend to exhibit similarly shaped growth curves (Assmann 1970: pp. 46-47), the relative growth rate at different stages of development can differ substantially among individual genotypes and families. In the extreme case, genotypes or families may be classified into different ideotypes, either "isolation", "crop", or "competition" ideotypes, depending on their performance under various competitive conditions (Donald 1968). Cannell (1982) demonstrated for Sitka spruce (*Picea sitchensis* [Bong.] Carr.) that the relative performance of 10 open-pollinated families differed radically under different conditions of crowding. At regular spacing, isolation ideotypes will be the best performers in the early years of a field trial, before competition effects become significant. As root and crown competition develops, either crop or competition ideotypes will perform better, depending on the particular experimental design and assessment unit. Single-tree or non-contiguous plots will favour competition ideotypes when individual tree productivity is assessed, whereas large, contiguous plots in which production per unit area is assessed will favour crop ideotypes. Therefore, under normal testing conditions, rank correlations between early assessments of individuals or families and rotation age assessments are likely to be low.

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One experimental approach which can help alleviate this problem of low age-to-age rank correlations is the establishment of closely-spaced nursery or field trials in which root and crown competition develop at a much earlier age than in normal field trials. To some degree, stand development may therefore simulate development in a much older, regularly-spaced trial allowing, for example, accurate selection at an early age of crop or competition ideotypes, rather than isolation ideotypes. Such an approach is particularly useful for species such as jack pine (*Pinus banksiana* Lamb.), which aggressively occupy a site in the first few years after planting or regeneration (Magnussen and Yeatman 1986). Black spruce (*Picea mariana* [Mill.] B.S.P.) however, grows much more slowly in the early years after planting, with crown closure not occurring on most sites until at least 15 years from planting at regular spacing. This implies that, in order to make use of close-spacing trials, black spruce would either have to be planted at extremely close spacing (30 cm or less), which becomes practically very difficult; or utilizable results would be delayed for several years, reducing the usefulness of the trials.

Over the last five to eight years, large-scale operational improvement programs for black spruce have been initiated in Ontario and the Maritime Provinces of Canada and similar programs are currently being developed in Maine and Quebec. The improvement strategies being adopted for the operational programs are, in the absence of detailed information specifically on black spruce, making use of assumed parallels with other species. This is only reasonable and is the best that can be done in such a situation. However, in view of the large amounts of money being dedicated to such programs, it is clearly vital that whatever information is available that specifically relates to black spruce should be incorporated into the program as soon as possible.

In Ontario, for example, establishment costs for seedling seed orchards are typically around $17,000/ha (1983 figures - J. Hood, pers. comm.). Planting programs in individual administrative regions may require 200 ha or more of such seed orchards. The breeding strategies adopted for such programs must, therefore, be confirmed as being adequate at as early a stage as possible, before large amounts of money are fully committed to less efficient approaches.

In Ontario, research into the genecology and population genetics of black spruce was strongly developed in the late 1960's (Morgenstern 1969a,b 1972 1973 1974 1975). Many field trials are now approximately 15 years old. The latest information from such trials is very useful in confirming or rejecting the suitability of existing strategies. In summarizing the latest information, this paper will consider the implications for the selection of genetic material and the design of breeding zones and seed orchards.

SELECTION OF GENETIC MATERIAL

Commencing in 1967, over 200 seed collections were made from populations across the entire range of black spruce (Selkirk 1974) and 33 field tests were subsequently established using subsamples of the complete collection. These field tests are located throughout Canada and the northern United States, from Newfoundland to Alaska. In Ontario five field tests were established in 1974 (Morgenstern and Kokocinski 1976) and currently the trees are 16 years old from seed.

Early results from this and similar material suggested that variation of height growth in black spruce is basically clinal and strongly related to latitude of origin (Morgenstern 1969b 1978). By 15 years of age, however, the pattern is not as clearly defined. At this stage, root competition has certainly commenced and on the more fertile sites, crown competition is also becoming significant. Results from the Ontario series of tests (Boyle 1985) demonstrate that certain provenances, notably one from just north of North Bay, Ontario (Lat. 46° 51'N Long. 79° 42'W), are outstanding, even though neighbouring provenances may be no more than average. Similarly, many provenances from northwestern Ontario are ranked in the upper quartile even when planted at more southerly latitudes in eastern Ontario. In the test planted at Dryden, in the north west, eight of the top 10 provenances were from that region and all but two of the 23 provenances from that region exceeded the plantation mean by at least 10%. Conversely, at Petawawa in the east, four of the top 10 were from the north west and only two from eastern Ontario. All other eastern Ontario provenances were shorter than the plantation mean.

Currently, operational improvement programs in black spruce utilize only local material from the region in question. It seems likely, however, that although such an approach may be valid in some regions, such as northwestern Ontario, in others more valuable breeding material could be assembled by including selections from other regions.

DESIGN OF BREEDING ZONES

The existence of genotype-environment interactions within an administrative region necessitates the establishment of distinct breeding zones, each providing genetically improved material for use in different environments in the region. Two sites should be considered to be in the same breeding zone based on similar ranking of genetic entries, rather than similar productivities (Burdon 1977). Without the benefit of existing information, breeding zones must be set up based either on information from other species or on non-genetic information. In such a situation, it is genetically prudent to take a conservative approach by designing small breeding zones. It is far simpler at a later stage in the improvement process to amalgamate material into a larger unit than to manage a single seed orchard in which material from two or more breeding zones may have inadvertently been mixed.

In both the Maritime Provinces and Ontario, eco-climatic information has been used in the design of breeding zones tempered, on occasion, by administrative considerations such as the lack of suitable seed orchard sites. Site region 3E in Ontario, which lies almost entirely in a single administrative region, has been divided on this basis into four breeding zones (see Figure 1). Zone 4, in contrast to the other three zones, is predominantly latitudinal in orientation, reflecting the presumed influence of the Great Lakes just to the south.

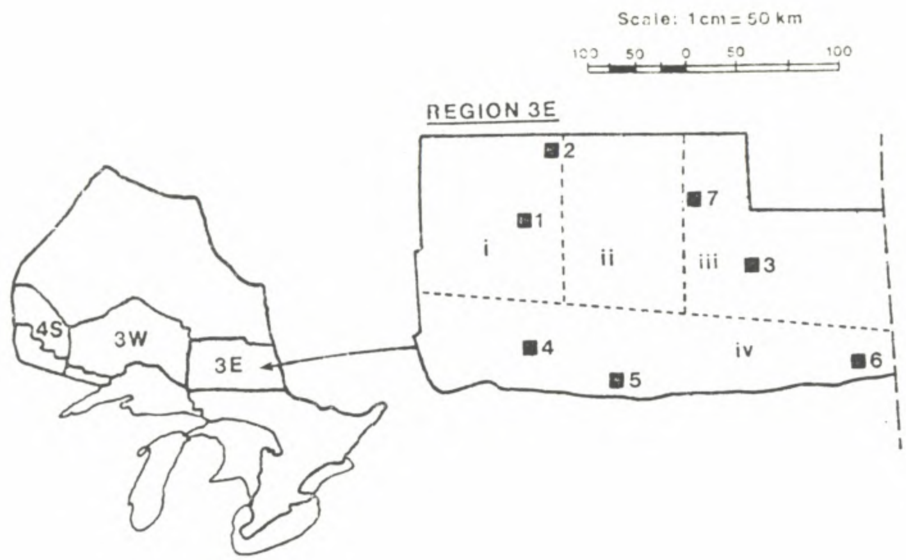

Figure 1. Administrative breeding zones in site region 3E of Ontario.

A series of seven open-pollinated family tests of largely local black spruce material was established in this site region in 1974-75. Family rankings for 10-year height growth were used by Boyle (1986) in an overlapping cluster analysis to identify those planting sites which ranked families similarly. On this basis, five "genetic" breeding zones were delineated. The more northerly three zones approximated closely with the administrative breeding zones, but the fourth zone was divided in half longitudinally according to the genetic analysis. More recent data, based on 15-year height growth rankings produced a similar picture, except that the southern-most zone is now divided into three (Figure 2). This suggests firstly that the influence of the Great Lakes on genetic variation in height growth is not as great as would be predicted from their influence on climate, and secondly that the eco-climatic zones themselves may not be sufficiently sensitive to predict patterns of genetic variation. On the other hand, a question that still needs to be answered is whether the additional genetic gain to be realized by more finely adjusting the improvement program is worth the additional administrative costs.

DESIGN OF SEED ORCHARDS

Because black spruce exhibits little variation in the highly heritable form characters such as branch angle and stem straightness, selection criteria are based on height and volume growth, which generally have substantially lower single-tree and family heritabilities. For this reason, and assuming that what genetic variation exists in such growth characters predominantly consists of general combining ability, a seedling seed orchard approach is usually adopted. Family selection is then carried out based on results from field trials. Due to the low individual-tree heritabilities, individual phenotypic selection is not a major component of such a strategy.

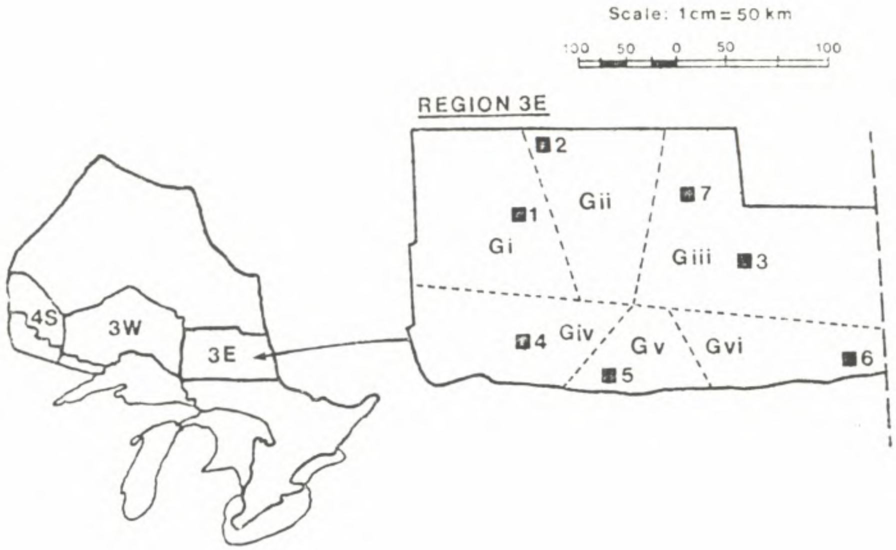

Figure 2. Genetic breeding zones for the site region 3E based on family height growth rankings at age 15 years on seven planting sites.

Various open- and control-pollinated progeny tests have tended to confirm most assumptions on which this strategy is based. For example, the open-pollinated family tests in site region 3E provided estimates of family and individual-tree heritabilities of 0.10 and 0.55 respectively at 15 years of age for height growth (unpublished data).

Evidence from a 7 x 7 complete diallel planted in three locations at the Petawawa National Forestry Institute, however, suggests that a substantial proportion of the genetic variation in height growth of black spruce at rotation age may consist of specific combining ability (Boyle 1986, in preparation). The three plantations have been measured at various ages from six to 14 years. In all three plantations at all ages, general combining ability comprised the majority of the among-family genetic variance. After about 10 years from seed, however, the proportion of the family variance accounted for by general combining ability decreased at all sites (Figure 3). If these trends continue through to rotation age, any improvement strategy designed to exploit only general combining ability would result in significantly smaller genetic gains than an alternative strategy capable of exploiting both general and specific combining ability. The significance of age 10 in the apparently consistent inflection of curves in Figure 3 may be due to the onset of inter-tree competition. Only at age 15 does crown closure occur, but in view of the limited rooting depth at all three sites, root competition is likely to have begun much earlier.

A seedling seed orchard, in which members of open-pollinated families selected as a result of field-planted family tests are allowed to freely intermate, is designed exclusively for general combining ability. An open-pollinated family, unless effective population sizes are very large, will actually consist of a limited number of full-sib family groups. If the superiority of a full-sib group is, to a large extent, the result of specific

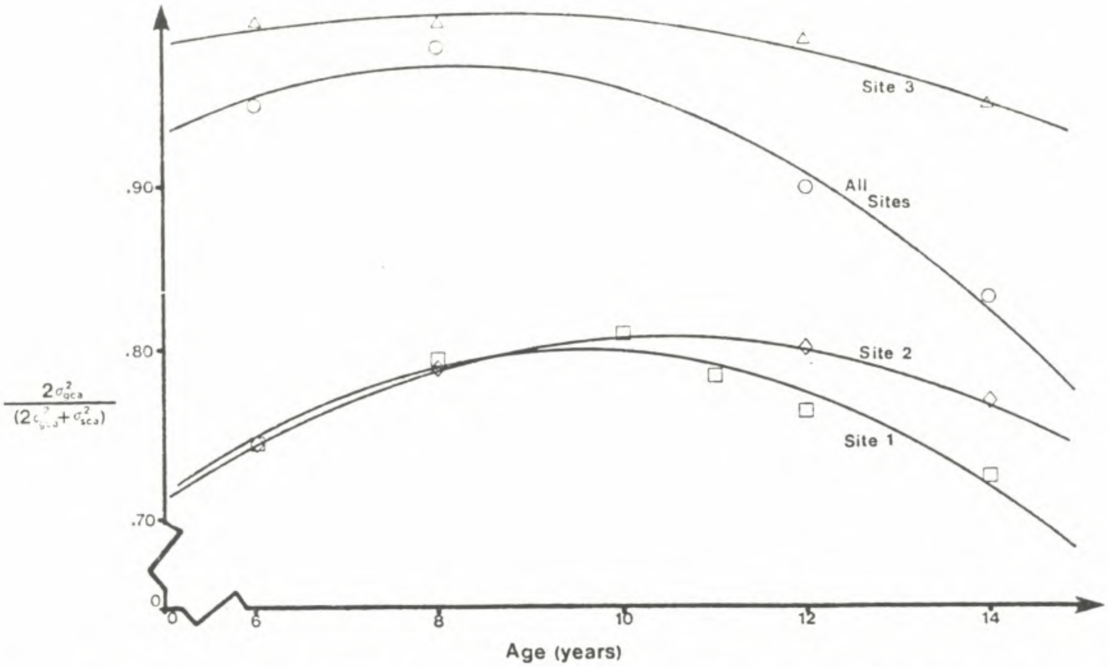

Figure 3. The proportion of among-family genetic variance height growth accounted for by general combining ability at different ages for a 7 x 7 black spruce diallel planted at three locations.

combining ability and, by random chance the open-pollinated family is disproportionately represented by such a group in the family test, then it may be selected for retention in the seed orchard. The individuals of this family planted in the orchard however, may be under-represented by the superior full-sib group. Furthermore, as soon as open-pollination occurs in the seed orchard, specific combining ability superiority will be lost anyway.

CONCLUSIONS

Current improvement strategies for black spruce tend to be consistent in the predominant use of local material, breeding zones based on eco-climatic data and administrative considerations, and the adoption of a seedling seed orchard approach with subsequent family selection based on field-planted family tests. Such a strategy is reasonable, given the amount of information on black spruce available at the time and taking advantage of assumed parallels with other species. However, the most recent information available from a variety of experimental tests suggests that some redesign of the strategy is required.

The question always remains as to how far these experimental results apply generally to the species, and this is where closely-spaced trials have a role to play. As noted earlier, by imposing conditions of competition at an abnormally early stage in the development of a plantation, it is possible to simulate conditions that may apply at a much later stage in a normally-spaced plantation. Thus, if the objective of a test is to select correct families or genotypes for rotation age performance, i.e. to select crop or competition ideotypes rather than isolation ideotypes, then closely-spaced tests can be most useful. Such short-term tests are, therefore, required both in existing and developing programs in order to confirm or deny the superiority of local material.

Similarly, in the design of genetic breeding zones, where the requirement is to identify those sites that rank genetic entries similarly at rotation age, or at least following crown closure, closely-spaced tests can be used to provide the required information. In fact, the two objectives of identifying superior material and delineating breeding zones can easily be combined in a series of small-scale, short-term tests.

When it comes to investigating the design of the strategy itself, however, because closely-spaced tests can only simulate conditions in a normal plantation and do not reproduce them, they cannot be used for the accurate estimation of genetic parameters that is required for such an investigation. In this instance, it is necessary to rely on the traditional, normally-spaced, replicated field trial. It would be difficult to justify adjusting an improvement strategy based solely on a single series of field tests from a 7 x 7 diallel, but results from this experiment suggest that further similar research is required as a matter of urgency. If it appears that a high level of specific combining ability is, in fact, the general situation for height growth of black spruce, then improvement strategies will indeed need to be radically altered. Rather than extensive areas of seedling seed orchard, containing large numbers of open-pollinated and open-pollinating families, far greater gains could be expected from identifying a small number of clones for each breeding zone which exhibit high specific combining ability when crossed with each other. Controlled pollination, in breeding halls, followed by vegetative propagation of the resulting seed would provide the required high genetic value propagules for operational reforestation.

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