Breeding of *Picea mariana* (Mill.) B.S.P.: seed orchard and clonal approaches

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Introduction

Black spruce, *Picea mariana* (Mill.) B.S.P., is one of the most widely distributed species of North American cool-temperate and boreal forests, ranging from the Atlantic Coast in Newfoundland to the Pacific Coast in Alaska (Heinselman 1957). It is relatively resistant to insects and diseases, possesses great reproductive capacity by seed and layering, regenerates well after fire, and is adapted to various soils and local climates. It grows in association with many other species, and pure stands are often found on shallow, poorly drained and cold soils where competitors are lacking. As a result of its favourable wood density and fiber characteristics and the availability of large volumes, it is an important species for the pulp and paper industry.

Increased utilization of forest resources in Canada has led to the development of large reforestation programs. Black spruce is the species most frequently planted in Canada east of Manitoba (Smyth and Brownright 1984). Significant silvicultural programs for this species also exist in the Lake States of the U.S.A. Along with these programs, selection and breeding were begun in some provinces and states as early as about 1960, first on a small scale, and since about 1975 on a large scale in all areas where the species is important. The purposes of this paper are to review progress in research and breeding during the last 20 years and to propose alternative breeding strategies for advanced generations.

Characteristics influencing selection and breeding

Range-wide variation and population structure

The distribution and population size of black spruce across its range are important factors in the development of genetic variation. Large populations exist throughout much of the Boreal and Acadian Forest Regions of Canada (Rowe 1972) and in the cool-temperate regions of the Lake States (Heinselman 1957). In these regions, it is found on both moist lowland and dry upland sites. Natural selection by day length and temperature is seen as the dominant genetic process that created a clinal variation pattern. There is also strong gene flow by pollen and seed, particularly after fire. There is no evidence of soil ecotypes (Dietrichson 1969, Morgenstern 1969, 1978; Fowler and Mullin 1977, Khalil 1986, O'Reilly et al. 1985, Park and Fowler 1988, Morgenstern and Mullin 1990). The mating system in these large populations as inferred from allozyme data is marked by high outcrossing rates and the population structure shows a large within-population component of variation and within any region relatively little variation among populations (Boyle and Morgenstern 1986; 1987).

Smaller populations near the edge of the range have a different mating system and population structure. Where the species is restricted to bogs or swamps, as in southern Ontario, the New England states, and the Cape Breton Highlands of Nova Scotia, there is some evidence of inbreeding. As shown by controlled crosses, this reduces seed set and vigor (Park and Fowler 1984). Values of the inbreeding coefficient, F, found in experiments in Alberta, Ontario and Nova Scotia have ranged from 0.08 to 0.23 (Morgenstern 1972, Sproule 1988, McCurdy 1990). The poor performance of native Cape Breton Island provenances when grown in Cape Breton is an illustration of the silvicultural effect of inbreeding (Park and Fowler 1988).

From Pennsylvania north to New England, the Maritime Provinces, and southeastern Ontario and Quebec, black spruce is sympatric with red spruce (*Picea rubens* Sarg.) and introgressive hybridization of the two species has been demonstrated (Morgenstern and Farrar 1964, Manley 1972). This has increased the variability of the two species but they still remain essentially distinct, although identification of the species may sometimes be difficult during inventory and silvicultural operations (Gordon 1976).

Physiology: growth, flowering, regeneration

Black spruce is a pioneer species but at the same time long-lived and shade-tolerant. Natural regeneration often takes place after fire from semi-serotinous cones, where seed is stored for several years after maturity, or vegetatively from buried branches of old trees (layering). Plantations on open areas are fast growing. Flowering begins at the age of 6 years (Morgenstern and Fowler 1969). This capacity for early flowering influences breeding strategy and the choice of seed orchard type.

Morphology: stem and crown form

There is minimal variation in stem and crown form. Black spruce trees are very uniform across the range and are very easily identified by their straight stems, narrow crowns, and short branches. With so little variation, selection to improve these characteristics is not important. Consequently, the tree characteristics chosen for selection include primarily height growth and perhaps wood density.

The development of breeding strategy

At the time when the improvement of black spruce was first considered (about 1958–1960), genetic information on black spruce was practically non-existent and foresters were not familiar with breeding methods. The development of breeding strategy was therefore a gradual process, beginning with the discussion of plus-tree selection methods (Carmichael 1960) and culminating in the publication of a detailed plan based on much research information which had become available in the interim period (Fowler 1986).

Methods of selection

Two methods of selection were used in the first generation of breeding: (1) individual-tree (or mass) selection combined with the establishment of grafted clonal seed orchards, and (2) open-pollinated family selection based on individual phenotype followed by planting of seedling seed orchards.

The first method is the traditional one practised for many species world-wide. The utility of this method was questioned; it is expensive and requires specialized skills and facilities that take years to develop. Furthermore, black spruce scions from mature trees are often so small that grafting success has been low. For these reasons, only a few organizations have used this method, primarily during the earliest period of black spruce breeding.

The second method, open-pollinated family selection, i.e., collection of open-pollinated seeds from selected trees, is simpler and cheaper than the first method. Thus, it was adopted by most organizations. It was realized that plus-tree selection could be done rapidly because lengthy tree comparisons and rating of individual traits were not required; variation in stem and crown form is minimal while rate of height growth could be much more effectively evaluated in the family tests than in wild stands. The early flowering habit of black spruce was also a reason for the adoption of this method. The method has been thoroughly discussed, economically evaluated, and early results indicate reasonable genetic gains (Morgenstern 1978, Morgenstern et al. 1975, Cornelius and Morgenstern 1986, Carter 1988, Nelson and Mohn 1991).

Orchard types

The timing and cost of seed production are important factors in the realization of benefits from breeding. Although we are concerned here only with first-generation breeding, cost efficiency is desirable.

The first option, clonal seed orchards, is problematic because of the high cost of development, for example, expenditures for stump and rock removal, levelling, drainage, for grafting and graft maintenance before outplanting. The method may be more acceptable if successive orchards can all be developed in the same area. Also, seed production may begin slightly later than in seedling orchards, i.e., about 8 years after grafting (McPherson et al. 1982).

The second option is the seedling seed orchard. These can be established quickly on ordinary cut-over areas without special measures, except control of competitors and provision for fire protection. After roguing, the number of producing trees is similar to that in clonal orchards, and seed production is probably comparable.

Advanced-generation breeding

Several provincial breeding programs have now reached the end of the first generation, and plans for the next generations of recurrent selection have been made. One of the most comprehensive breeding plans is that prepared for New Brunswick (Fowler 1986). A total of 1,200 plus trees was initially selected, and these have given rise to the same number of open-pollinated families in tests, from which the best 400 will be identified. Second-generation breeding will use polycrossing and pair-mating to develop 20 20-tree-sublines for the third generation breeding population. At that stage, polycrossing will be used for progeny testing, while a partial-diallel mating system will be used for next generation breeding. In each generation, a new clonal orchard is established which is subsequently rogued on the basis of the test results. The use of sublines minimizes inbreeding. In this way successively better seeds are produced.

Alternative breeding strategies for clonal forestry

As an alternative to conventional seed orchard procedures, tree improvement strategies using "breeding-cloning" procedures to produce improved planting stock, i.e., clonal forestry, have been explored for advanced generation. There are many advantages of clonal forestry (Libby and Rauter 1984, Libby 1990), including the opportunity to capture both additive and non-additive genetic variances. Thus, genetic gains from breeding-cloning strategies are expected to be larger than those from conventional programs.

Although it has advantages, clonal forestry to date is limited by several factors. Perhaps the most important one is our ability to propagate true-to-type individuals at a reasonable production rate. This results from the maturation state of donor plants. Currently, in black spruce, true-to-type propagation via rooted cuttings is possible only with young seedlings, and, thus, an operational clonal program requires several cycles of propagation to meet stock requirements.

Since 1985, rapid progress has been made in the development of somatic embryogenesis using seed embryos for several northern conifers including black spruce. Although this technology is still labor intensive, it is expected to replace conventional micropropagation techniques based on rooting adventitious or axillary shoots (Park and Bonga 1990). Research on refinement of somatic embryogenesis techniques in black spruce is being carried out in the Maritimes Region of Canada to bring this technology to an operational level.

In advanced generation breeding, we propose alternative breeding-cloning strategies in conjunction with breeding hall technology (Greenwood et al. 1991), in lieu of managing conventional seed orchards. While the production of clonal populations expedites the deployment of improved material and permits additional genetic gain (Burdon 1982), the management of the breeding population, such as using breeding-groups or sublines (van Buijtenen and Lowe 1979), continues to be the main source of progressive improvement.

The implementation of an effective clonal strategy requires accurate genetic information at different levels, i.e., the population, family, and individual tree. Also, this information is necessary to obtain estimates of both additive and non-additive genetic variances, including dominance and epistatic variances, to predict genetic gains. To provide a means of obtaining such genetic information, the conventional genetic testing procedure should be modified by the use of clonal replicates (Shaw and Hood 1985, Park and Fowler 1987, Mullin and Park 1991).

We consider three possible options incorporating vegetative multiplication for advanced generation breeding, namely, "backward general combining ability (GCA) selection and polycrossing", "backward specific combining ability (SCA) selection and repeat crossing", and "forward clonal selection" (Mullin and Park 1991). A simplified illustration of "backward selection" is presented in Fig. 1. The second generation breeding-cloning strategy can begin by selecting the best individuals of the best families in the first generation family test. The selected trees may be sublined, e.g., 20 20-tree-sublines, and will be control-pollinated to produce material for progeny testing. At the same time, the selections will be grafted in clone banks or breeding halls. Depending on the breeding-cloning strategy adopted, different mating designs may be used. For "backward GCA selection and polycrossing", for example, a simple polycross can be used; however, to utilize non-additive variance as in "backward SCA selection and repeat crossing", it is necessary to use a full-sib mating design. Furthermore, using clonal replicates in the test with any mating design is likely to increase the efficiency of estimating genetic parameters and selection (Shaw and Hood 1985).

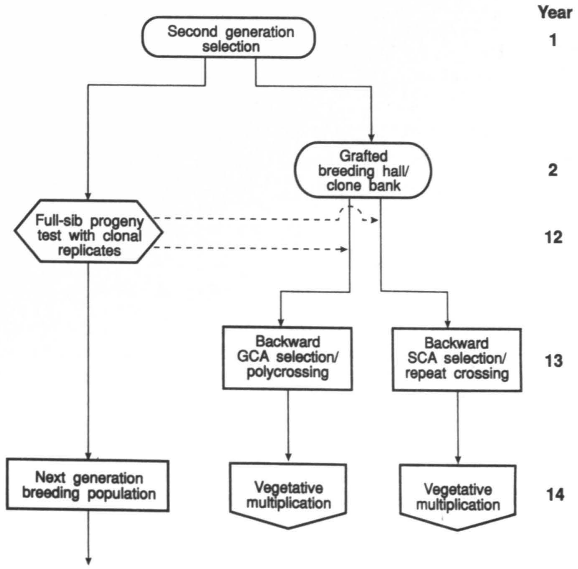

Fig. 1. Breeding-cloning strategy using "backward GCA" and "backward SCA" selection schemes. It is assumed that field testing requires 10 years. Dotted lines indicate information flow.

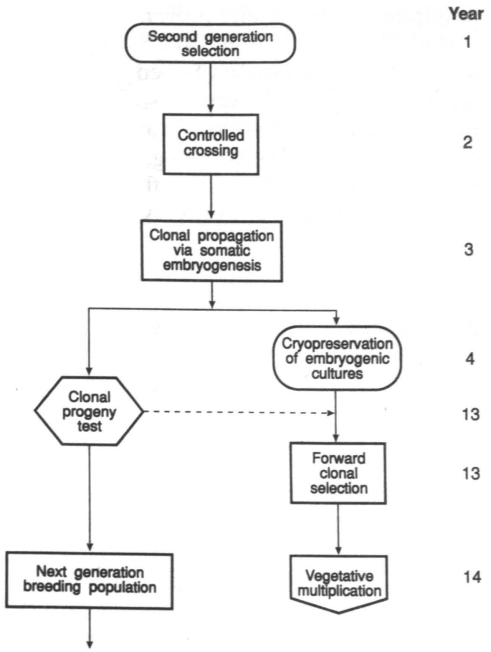

Fig. 2. Breeding-cloning strategy using "forward clonal selection" scheme. It is assumed that field testing requires 10 years. Dotted line indicates information flow.

Backward GCA selection and polycrossing

The best GCA parents identified by the progeny test may be crossed in the breeding halls or clone banks with a polymix of other best GCA parents of different sublines. Limited quantities of seeds from the crosses could be vegetatively multiplied using serially rooted cuttings of juvenile seedlings, and steckling stock is deployed to plantations (Mullin and Park 1991). The theoretical genetic gain in this scheme is the same as in a rogued seed orchard; however, some important assumptions apply to this gain estimate. Mating in the orchard is assumed to be random, without inbreeding or pollen contamination. In practice, these assumptions are violated to some degree by most, if not all, seed orchards. These assumptions are likely to be met if the seeds are produced by controlled pollination in breeding halls or clone banks.

Backward SCA selection and repeat crossing

The best full-sib families or crosses identified by the progeny test may be obtained by repeated controlled crossing in the breeding hall or clone banks. This scheme can utilize the SCA of pairs of parents in addition to their individual GCA (Mullin and Park 1991). Thus, expected additional gain is dependent on the magnitude of SCA variance. Similar to the previous scheme, small quantities of seeds may be vegetatively multiplied using serially rooted cuttings.

Both "backward GCA" and "backward SCA" selections can be practised using serially rooted cuttings from juvenile seedlings, albeit at a higher production cost. However, it is likely that the efficiencies gained by using small breeding halls instead of large conventional seed orchards, the elimination of seed extraction plants, as well as the additional genetic gain and flexibility, will offset the higher cost of stock production. Obviously, when somatic embryogenesis techniques become operational, the efficiency of vegetative multiplication will be increased.

Forward clonal selection

In this scheme, the best tested clones are vegetatively multiplied and deployed in the production plantations. As in "backward selection" schemes, the selection, breeding and testing follow the same procedure (Mullin and Park 1991). However, after 5 or more years of genetic testing, vegetative propagation of superior clones in true-to-type fashion may not be possible. Thus, the main obstacle in this scheme is the maintenance of juvenility during the test period. As illustrated in Fig. 2, this scheme relies on the cryopreservation of embryogenic cultures in liquid nitrogen during the test period and subsequent repropagation of proven clones using somatic embryogenesis.

Conclusion

During the past 30 years, genetics research has accumulated much information on black spruce. The adoption of less intensive and faster plus-tree selection, establishment of seedling seed orchards and family selection significantly increased the rate of progress in improvement of the species. In New Brunswick this approach made it possible to obtain substantial quantities of seeds 10 years after the initiation of the program, and now all the seeds used in reforestation are derived from seed orchards.

Fourteen years after beginning the black spruce breeding program, second generation breeding is underway. The possibility of implementing alternative breeding strategies using "breeding - cloning" procedures are explored for the advanced generations. Until somatic embryogenesis techniques become fully operational, "backward selection" schemes and crossing in breeding halls followed by vegetative multiplication using serial rooted cuttings can be adopted. Larger genetic gains than those from conventional breeding are expected not only from the utilization of both additive and non-additive variances, but also from the elimination of inefficiencies of large conventional seed orchards.

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Review of manuscripts in 1991
Käsikirjoitusten tarkastus vuonna 1991

The editorial board of the Society of Forestry in Finland has received invaluable assistance from a large number of experts who have kindly provided assessments of the scientific level of the manuscripts submitted for Acta Forestalia Fennica and Silva Fennica. For review of manuscripts in 1991, the Board would like to express its sincere thanks to the following experts.

Suomen Metsätieteellisen Seuran julkaisusarjojen Acta Forestalia Fennica ja Silva Fennica toimituskunta on saanut arvokasta apua lukuisilta asiantuntijoilta, jotka ovat hyväntahtoisesti arvioineet painettavaksi tarjottujen käsikirjoitusten tieteellistä tasoa. Vuonna 1991 tehdystä tarkastustyöstä toimituskunta esittää parhaat kiitoksensa seuraaville asiantuntijoille.

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