A PLAN FOR ADVANCED-GENERATION BREEDING OF JACK PINE

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ABSTRACT

A plan is described for a third generation of a jack pine breeding program that serves a planting program of about 2 million trees / year, requiring a modest level of resource use. Based on multiple-trait breeding values at 20–21 years from planting, 198 trees were selected in 100 of 209 open-pollinated progenies of wild parent trees for use as parents of third-generation full-sib families. Another 4 selections were added from a provenance test plantation. Families resulting primarily from single-pair mating of the selected trees will constitute the third-generation breeding population. First-stage selection at about 10 years in the third-generation breeding population will be based on multiple-trait breeding value scores estimated from family and within-family effects. Second-stage selection will depend primarily on mean performance of progenies, most likely from single-pair mating, of trees selected at the first stage, along with 20-year performance of the same trees. Seed orchards will be established with grafts of third-generation trees having high multiple-trait breeding value scores at 10 years, and re-selected using information from second-stage selection.

Key words: breeding strategy, jack pine, *Pinus banksiana*, mating design

INTRODUCTION

Tree breeders have presented results of simulation modelling on genetic gains from alternative breeding strategies (COTTERILL 1986; COTTERILL & JACKSON 1989; LINDGREN 1977; SHELBOURNE 1969; VAN BUIJTENEN 1976; VAN BUIJTENEN & BURDON 1990) or have presented narrative discussions on strategy choices for breeding programs (BURDON *et al.* 1977; BURDON & SHELBOURNE 1971; COTTERILL 1984; JOHNSON & KING 1989; LOWE & VAN BUIJTENEN 1981; TALBERT 1979; WHITE *et al.* 1993). Both kinds of papers have value for other programs facing decisions on population organization, mating designs, and selection procedure. Most of the narrative discussion papers have dealt with programs operating on a relatively large scale. The choices made in these programs and described in their public documentation are not necessarily equally appropriate to breeding programs motivated by smaller planting programs. An account of the strategy choices for the third generation of a relatively small-scale breeding program may be of interest to some tree breeding practitioners.

This paper describes a plan for selecting parents of the third generation population for a jack pine (*Pinus banksiana* Lamb.) breeding program in southeastern Manitoba in interior western Canada, for producing the third generation breeding population from the selected parents, and for selecting in the third generation population to capture genetic gain incremental to the gain achieved in the first two generations. This plan was designed to provide a satisfactory amount of incremental gain in the shortest feasible time period, at a cost appropriate for a planting program of about 2 million trees per year, and without impairing the capacity of the breeding population to provide further gains in future generations of breeding.

First Breeding Cycle

Breeding programs were initiated to improve yield at maturity and stem quality of jack pine for three areas in interior western Canada (KLEIN 1982). The program for one of these areas, in southeastern Manitoba, serves a planting program of about 2 million trees per year. Climate of this area is sub-humid cool continental, with mean January and July temperatures of $-17\,^{\circ}$C and $19\,^{\circ}$C, and mean annual and growing-season precipitation of 530 and 330 mm. Because little wood has been harvested from plantations in this area, the yield from fully-stocked plantations at maturity is open to conjecture. Yield expectations in the range of 2–5 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ on a rotation of 50–80 years appear reasonable. Harvested wood is processed into construction lumber or bleached kraft pulp.

During the first breeding cycle (Figure 1), measure-

ESTABLISH AND MEASURE
FAMILY TEST

SELECT AND PROPAGATE

SEED ORCHARD AND
BREEDING GARDEN

Year

Assemble open-pollinated
progenies from 209 selected
wild founder parents

1970

Plant first-generation family test

Continuation

Transfer of
materials

Transfer of
information

LEGEND

1975

Measure year 5

1980

Measure year 10

Select 200 trees in 40
families

1985

Measure year 15

Control-pollinate 20
family pairs

Rear 20 first-cousin
progenies

Plant 18 progenies in
seed orchard

Select 56 trees +
spares in 56 families

1990

Measure year 20

Control-pollinate 28
select-tree pairs

Assess secondary
traits year 21

Plant 18 full-sib
progenies in added
seed orchard area

1995

Select 198 trees in 100
families + 4 provenance test
trees as parents of third-
generation progenies

Graft selected trees
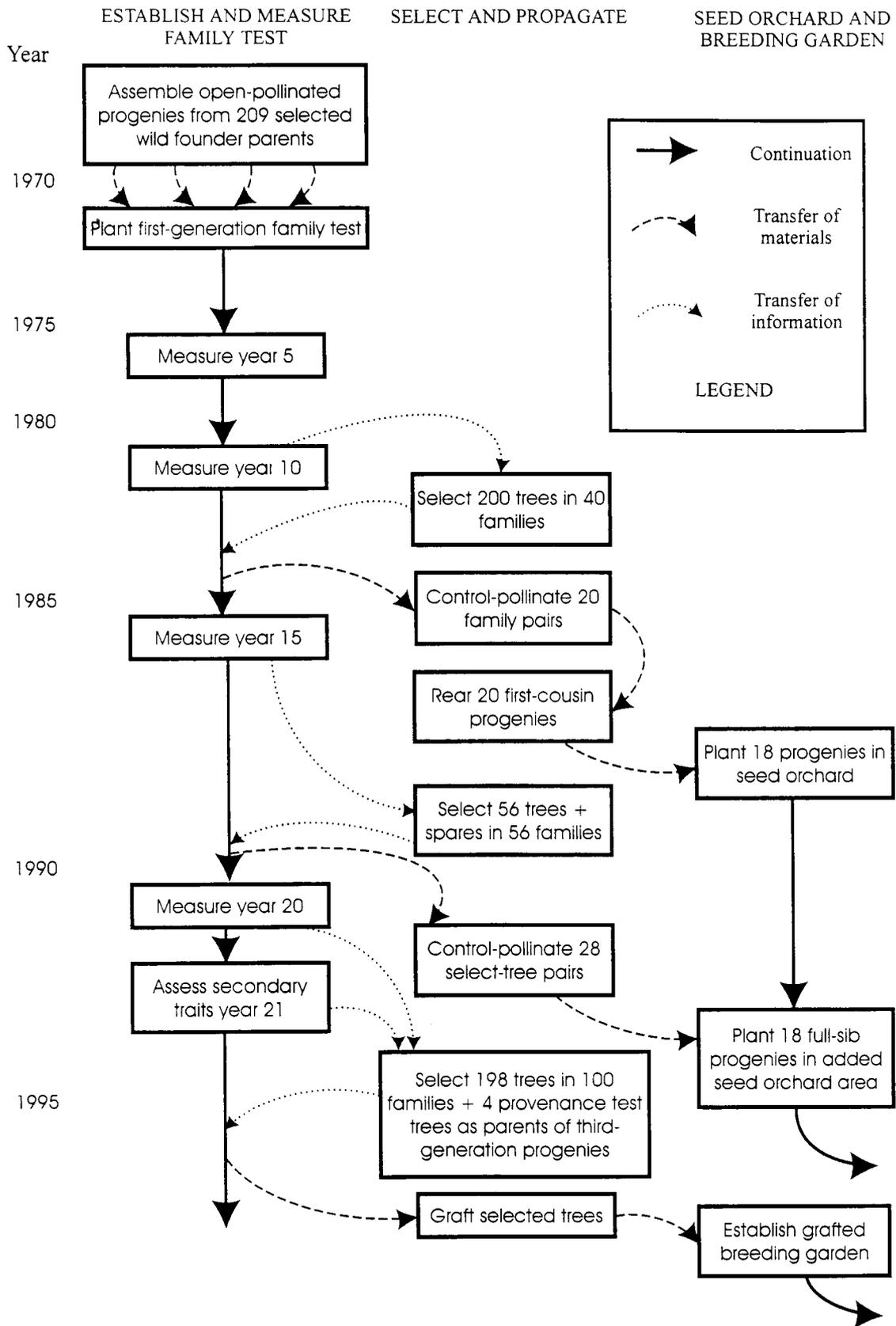
Establish grafted
breeding garden

Figure 1. Procedure used for the first two generations of a jack pine breeding program in southeastern Manitoba, Canada.

ment data from four family-test plantations planted in 1972, containing open-pollinated progenies of 209 parent trees selected in wild stands in southeastern Manitoba, were used to assess genetic merit of trees in these plantations. Results of measurements at 10 years and 15 years were used to select genetically superior progeny trees in the family test that were then used as parents of control-pollinated families (KLEIN 1986; KLEIN 1992) which were planted in a seed orchard in 1988 and 1994. The selected wild parents and grafted ramets of those parents of the program's first generation, and the second-generation progeny trees which grew in the family-test plantations, jointly constituted the first breeding cycle.

Measurement data at 20–21 years from planting, along with variance and covariance components calculated from these data were used to calculate trait breeding values by Best Linear Prediction (BLP) (WHITE & HODGE 1989). BLP breeding values were calculated for height and diameter adjusted for neighbourhood environment effects, stem quality (a composite of stem straightness and branch angle), resistance to western gall rust, and wood density (from Pilodyn determinations) for 2410 individual trees in 191 families growing in the family-test plantations. Eighteen families from one source area were excluded from calculation of breeding values, owing to a disproportionate contribution to source area effect. About half of the trees in other families were excluded from assessment of stem quality, rust resistance and wood density, and from calculation of breeding values, owing to below-average height and diameter. A total score was calculated for individual scored trees as the weighted sum of the trait breeding values. The desired weight vector, derived subjectively by adjusting weights after inspection of trait gains resulting from trial weight vectors, was 0.1, 0.2, 2.8, 1.2, and 0.4 for height in cm, diameter in mm, stem quality in score units (on a scale of 1–6), proportionate rank of rust gall counts × 10, and wood density in $g \cdot ml^{-1} \times 100$. Families produced by mating the best 64 unrelated trees, according to the chosen weight vector, would be genetically improved by 18, 10, and 10% for stem dry weight (volume × wood density), stem quality, and resistance to western gall rust, in relation to the family test mean. Details of the measurements, calculation of breeding values, and calculation of total scores have been published elsewhere (KLEIN 1995).

Breeding values were calculated for the wild parent genotypes, of which about half survive in a clone archive. There was no instance of a parent clone having a clearly higher total score than its best progeny tree, and only a few families in which the parent clone had close to the best total score (unpublished data).

SELECTION OF PARENTS OF THIRD-GENERATION FAMILIES

Selection of parents for the third-generation population, after calculation of predicted trait breeding values and total scores, was largely a matter of deciding how many of the 2410 scored trees to use as parents, and how to spread that number among the 191 families to which the scored trees belong. Satisfactory gain in the third generation could be achieved at low cost by pair-mating 18 unrelated trees with the highest total scores to produce 9 unrelated full-sib families, then selecting scion donors for a systematic seed orchard (VAN BUIJTENEN & LOWE 1979; MCKEAND & BEINEKE 1980) within these 9 families. The potential for gain in later generations would be severely impaired by choosing such a small breeding population size. Conservation of the potential for gain in later generations requires maintenance of a population size in the third generation, larger than required for satisfactory gain in the current generation. Consequently it was necessary, in planning for the current generation, to postulate a plausible design for future breeding generations. A future breeder will be at liberty to use another design, but will be more likely to have sufficient genetic resources at hand, if an effort is made now to accommodate future needs.

The population size chosen for the third generation breeding population is intended to provide for advanced-generation open-pollinated seed orchards producing fewer than 10% of selfed matings. This goal can be achieved by maintaining a recurrent breeding population structured into nine sublines, each descended from no fewer than eight founder parents and eight second-generation families. More than one tree would need to be selected for seed orchard use from each subline in each generation. For example, in a seed orchard with two clones from each of nine sublines, and equal numbers of effective gametes from each clone, about 5.5% of the pollinations in the seed orchard would be self-pollination. With unequal but reasonably balanced gamete frequencies, selfing would be higher than 5.5%, but might be less than 10%. To avoid replacement of selfed trees with other highly inbred seed orchard offspring, the selected trees from the same subline would need to be related not closer than as second or third cousins.

Realization of this hypothesized long-term population structure requires inclusion of a minimum of 72 founder parents among trees selected as parents of third-generation families. This structure would allow use of open-pollinated seed orchards in systematic arrangement, with blocks containing one tree from each of the nine sublines. Each subline would be regenerated
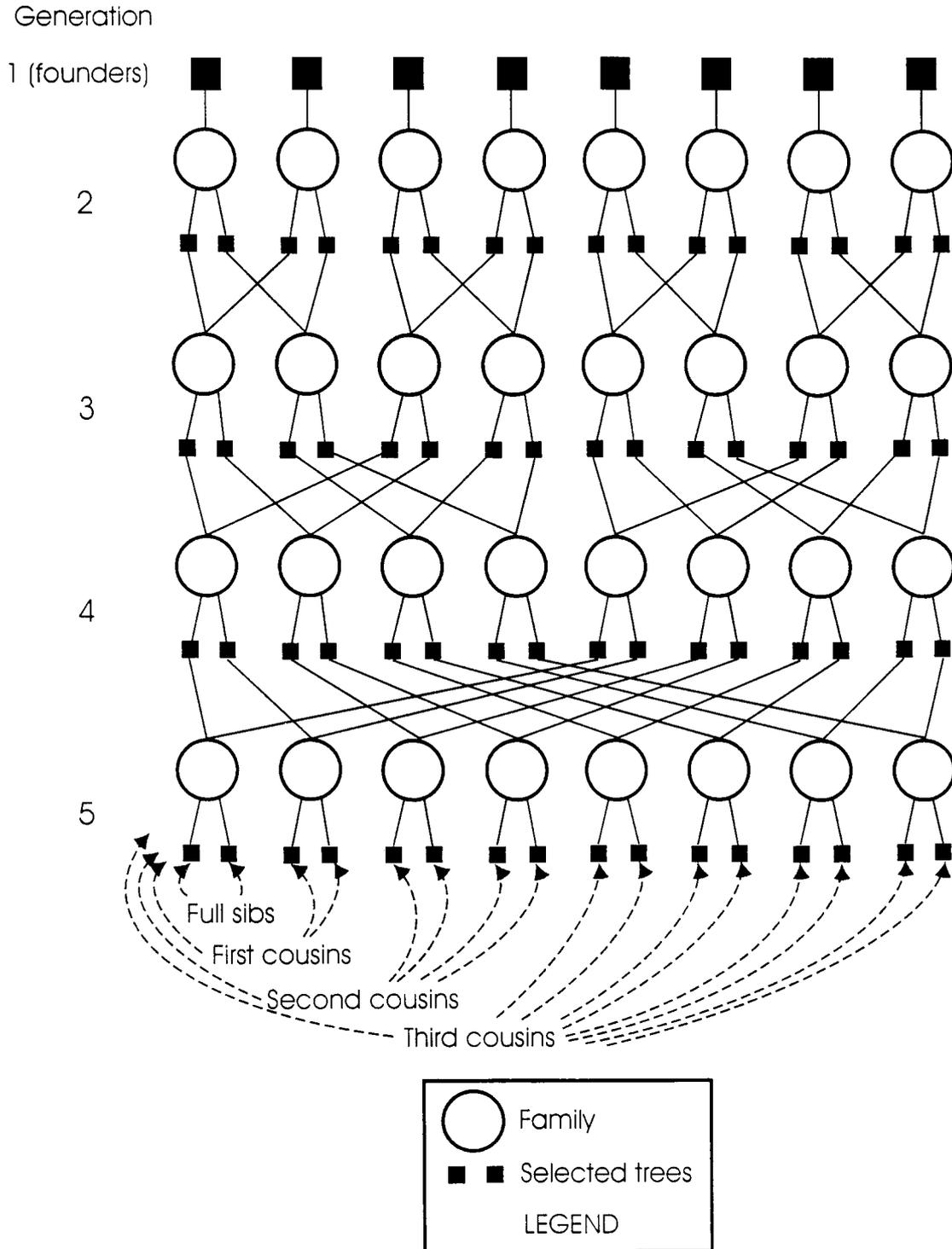
Generation

Figure 2. Development of co-ancestry in a subline descended from eight founder parents over three generations of unrelated matings.

by selecting two trees from each of eight or more families, then using complete pedigree records to ensure matings between selected trees of the least-related (usually third-cousin) families to regenerate the breeding population (Figure 2). Within sublines, effective population size would be not less than 31 (2
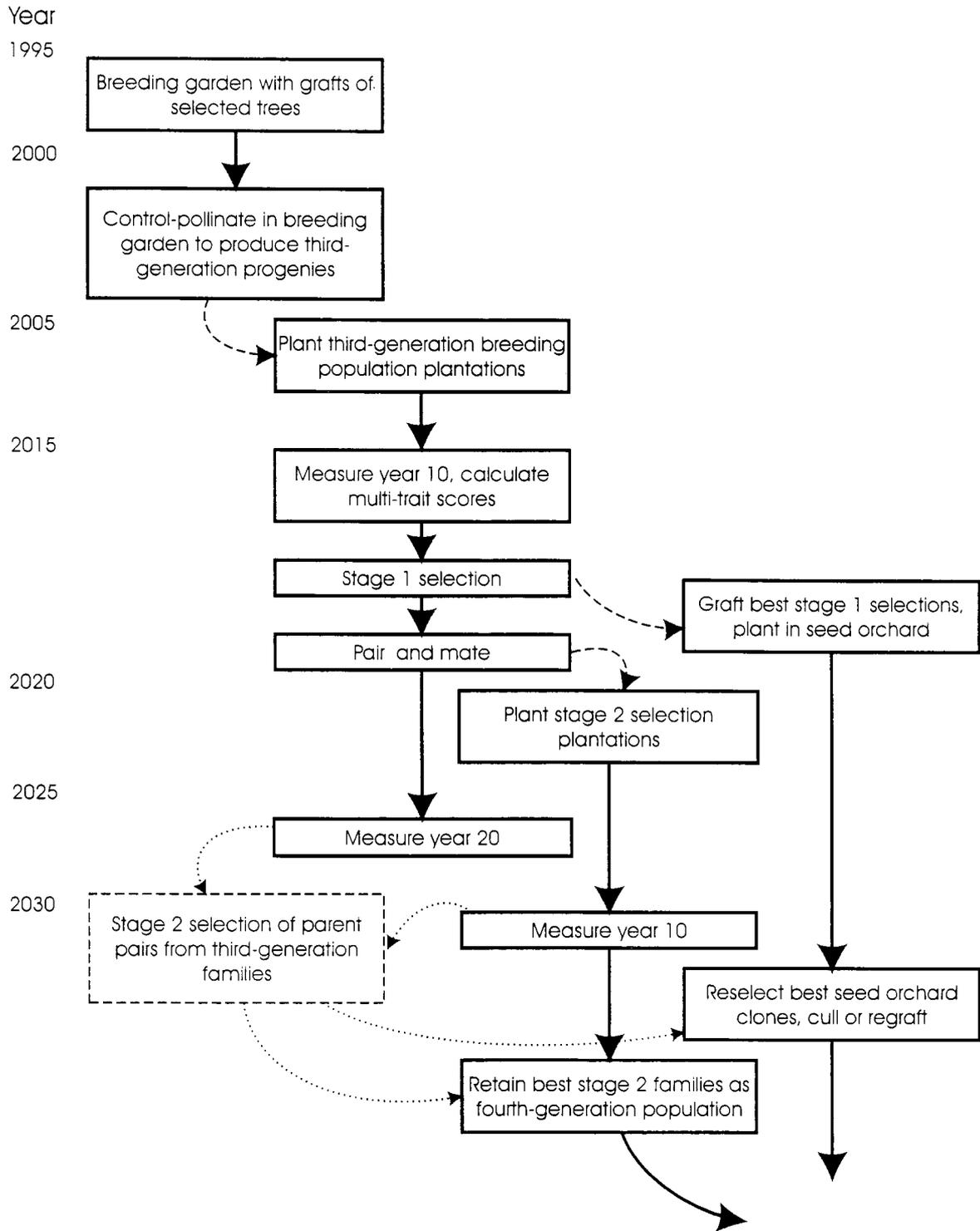
76

Year

1995

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┌─────────────────────────────┐
│ Breeding garden with grafts of │
│      selected trees         │
└─────────────────────────────┘
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2000

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┌─────────────────────────────┐
│ Control-pollinate in breeding │
│   garden to produce third-   │
│   generation progenies       │
└─────────────────────────────┘
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2005

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┌─────────────────────────────┐
│ Plant third-generation breeding │
│   population plantations     │
└─────────────────────────────┘
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2015

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┌─────────────────────────────┐
│  Measure year 10, calculate  │
│     multi-trait scores       │
└─────────────────────────────┘
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┌─────────────────────────────┐
│       Stage 1 selection      │
└─────────────────────────────┘
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┌─────────────────────────────┐          ┌─────────────────────────────┐
│       Pair  and mate        │          │ Graft best stage 1 selections, │
└─────────────────────────────┘          │    plant in seed orchard     │
                                         └─────────────────────────────┘
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2020

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┌─────────────────────────────┐
│   Plant stage 2 selection    │
│       plantations            │
└─────────────────────────────┘
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2025

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┌─────────────────────────────┐
│       Measure year 20        │
└─────────────────────────────┘
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2030

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┌─────────────────────────────┐          ┌─────────────────────────────┐
│  Stage 2 selection of parent │          │      Measure year 10         │
│  pairs from third-generation │          └─────────────────────────────┘
│         families             │
└─────────────────────────────┘          ┌─────────────────────────────┐
                                         │ Reselect best seed orchard   │
                                         │   clones, cull or regraft    │
                                         └─────────────────────────────┘
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┌─────────────────────────────┐
│ Retain best stage 2 families as │
│  fourth-generation population │
└─────────────────────────────┘
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Figure 3. Plan for the third generation of the southeastern Manitoba jack pine breeding program.

× 16–1) (FALCONER 1989), and the inbreeding coefficient in each generation would be no greater than 0.0235.

This proposed breeding population size and struc-

ture, requiring retention of no fewer than 144 family-test trees descended from 72 founder parents, appears to be a reasonable and prudent strategy to preserve options for advanced-generation breeding, although it

can not easily be proven superior to alternative configu-
rations. Long-term gain would likely be lower for
sublines of this size than for larger sublines (BAKER &
CURNOW 1969), and the number of sublines proposed
is about half or less of the minimum number required
for permutated neighbourhood seed orchard layouts.
Increasing the proportion of founder parents retained so
as to remove either one of these constraints, would
increase program cost and virtually eliminate any
opportunity for excluding low-ranking families from
the breeding population. On the other hand, substantial
reduction in the number of founder parents retained
would require acceptance of a level of inbreeding
within sublines higher than third cousin, or exclude the
possibility of predominantly unrelated seed orchard
matings by open pollination.

Because the total scores from BLP breeding value
estimates are not free of error, the size of the second-
generation selected population (that is, the number of
second-generation trees used as parents) was aug-
mented from the minimum requirement of 144 trees
from 72 families to a target of 200 trees from 100
families. Additional information on the genetic worth
of the parents and their descendants will become
available from assessments in the third and subsequent
generations. By delaying for one or more generations
the final selection of founder parents to be retained,
that selection can be made more accurate.

Distribution among 100 families of the 198 trees
actually selected attempted to balance considerations of
effective population size and genetic gain by including
more selections from families with the highest-scoring
trees (LINDGREN 1986). Parallel breeding using multi-
ple selections within third-generation families, will
avoid inbreeding until generation six in sublines with at
least eight founders, when it will occur at the third-
cousin rate (Figure 2). For each third-generation family
providing a single parent, one additional founder will
need to be included in that subline to avoid earlier or
closer inbreeding.

There were 37, 42, 13, 2, and 6 families with 1, 2,
3, 4, and 5 selected trees. Mean predicted breeding
values for the 198 trees selected in the family test
provide predicted gains of 17, 9, and 10% for dry
weight, stem quality, and rust resistance. Computer
selections were confirmed by field inspection. An
additional four trees were phenotypically selected for
use as parents of third-generation families, from plots
of Minnesota, U.S.A., origin which grew better than all
other sources in a provenance test plantation adjacent
to one of the family test plantations (KLEIN 1990).
Parents of third-generation families thus comprise 104
unrelated trees, plus one or more sibs of most of these
trees, amounting to an additional 98 trees.

PAIRING OF SELECTED PARENTS

Assortative single-pair mating based on multiple-trait
total scores will be used for most of the matings to
produce families for the third-generation breeding
population. Use of assortative mating will allow higher
gains in third-generation seed orchards than random
mating of third-generation selections.

Less-superior parents will likely be paired with
other less-superior parents under assortative mating.
Progeny from these matings would provide seed
orchard selections in advanced generations only if their
genetic worth were incremented more than average by
recurrent selection, or if they provided some uniquely
advantageous trait. If less-superior parents were mated
with higher-ranked parents (e.g., WHITE et al. 1993),
their genetic material could be included in a seed
orchard without having gained any improvement of
their own genetic material. In the latter case, the inclu-
sion of genetic material from less-superior parents
would result in dilution of genetic gain without a
compensating gain in diversity.

Matings have been explicitly designated, although
the breeding has not yet been done. Families including
more than one selected tree were paired with other
families having the same number of selected trees with
similar total scores. Two selected trees were not paired
(in effect, removed from the select list) because there
were no remaining families with the same number of
selected trees. Within family pairs, paired trees usually
had the same within-family score rank. Trait breeding
value was used along with multiple-trait total score in
some instances, in pairing families or individual trees.
A tree or family having a low breeding value score for
one trait was paired with the tree or family of similar
score providing correction of its weakness, rather than
with the tree or family closest to it in total score but
sharing the same trait weakness.

Some second-generation families have a single
individual with a score of medium to high rank, but
having their next lower-ranked member being near or
below the minimum score for select rank. There is
greater uncertainty as to the true breeding value of these
trees, because the predicted values seem to depend
more upon observations on the individual tree itself.
Some trees in this category may have true breeding
values close to their predicted values. The likelihood of
favourable environmental effects influencing predicted
breeding values seems higher for these trees than for
the previous group. Any trees in this group having true
breeding values as high as their predicted values are
likely to be paired with a less valuable mate if single-
pair mating is used.

Such trees were formed into groups of four for half-

diallel mating, to reduce the likelihood of wasting accurately scored trees by mating them with trees having scores summed from inflated breeding value predictions. Six matings will be required for each group of four trees. Third-generation selections will be retained in the best of the six families and possibly in the family that is unrelated to the best family. Selection within any of the four families having one parent in common with the best family, offers no apparent benefit.

Breeding and assessment of four or five redundant families to ensure improved pairing for the one or two retained families would be an inefficient use of the program's limited resources, except for an additional benefit expected from the diallel matings. A rough estimate of specific combining ability (SCA) could be obtained by appropriate analysis of the half-diallel families (YEH & HEAMAN 1987). This estimate will be useful in assessing the efficiency of alternative methods for the second stage of third-generation selection, to be described later in this paper.

Selected trees of relatively low rank with no selected sibs were paired by similarity of total score, with due consideration of mid-parent trait breeding values. The four provenance test trees will be paired with one another.

ESTABLISHMENT OF THE THIRD-GENERATION BREEDING POPULATION

Mating will be performed on grafts of the 202 selected parent trees, grown under conventional soil culture. Grafting of scions from all selected parent trees was done in February 1996 or in earlier years. Planting of third-generation families may occur about 2005.

Layout of the third-generation families will be in single-tree plots. The margin of preference for this layout is narrow, in relation to a combination of single-tree plots for family means with family-block plots for within-family effects. Family block design has been advocated for within-family selection where family breeding value is inferred from parent breeding values (JOHNSON & KING 1989; WHITE et al. 1993). Neighbourhood environment effects on height and diameter can be estimated and removed effectively in a small-plot layout by averaging within-family deviations of neighbouring trees (LAMBETH 1986; LOO-DINKINS 1992), as occurred in the analysis of the family test which led to the scoring of the parent trees of these third-generation families (KLEIN 1995). The advantage, if any, in estimating within-family effects as deviations from a mean of a large single-family plot, is judged likely to be small.

Trees planted in block plots would have limited

value for estimation of family contributions to breeding values of third-generation trees, whereas trees grown in single-tree plots will be efficient in estimating family means. Accurate estimates of family means will be important, but not in selecting parents for the next-generation breeding population, because only a small proportion of third-generation families will be excluded from that function. Their importance will be in selecting scion donors for seed orchards, for which fewer than half of the founder parents need to be retained, and for pairing to produce families for the fourth generation.

More accurate family means would also contribute to accuracy in estimating the magnitude of SCA by analysis of the diallel groups.

Family size will be about 100–200 trees, distributed over 2 sites to reduce the likelihood of complete destruction of the population. A spacing of 3.0 m, which is wider than the customary plantation spacing for jack pine, will avoid crowding effects on growth and stem quality for the planned assessment duration of 20 years, promote flowering and scion production, and expedite access for controlled breeding.

SELECTION IN THE THIRD-GENERATION POPULATION

A two-stage selection process, similar to strategy (4) of COTTERILL & JACKSON (1989), will be applied to the third-generation breeding population to select seed orchard donors and parents for the fourth-generation breeding population (Figure 3). The first selection stage will rely on phenotypic assessment to screen out trees in the third-generation breeding population plantations that are unlikely to have the genetic characteristics desired for seed orchard use and further breeding. Trees passing the first-stage screening will be assessed more accurately by use of progenies in the second stage of selection.

First Selection Stage

Measurement of the breeding population plantations for first-stage selection will be at 10 years from planting. At that age, jack pine trees in carefully tended plantations in eastern Manitoba are expected to have a mean height of about 3.5 m and breast-height diameter outside bark of about 40 mm. Stem quality, branch quality, presence of rust galls, and juvenile wood traits can be scored conveniently at that size. Tree size as well is easily measured, but may not be as heritable for this breeding population as tree size after a longer test duration (KLEIN 1995). Total scores for individual trees will be calculated by applying a weight vector to trait

breeding values calculated by Index Selection or Best Linear Prediction. Trees will be ranked by their scores in relation to other trees in their own family and to trees in other families.

It is intended that most third-generation families will contribute two sibs to be parents of the following generation. In order to allow a selection proportion of one in four at the second stage, so that a reasonable return can be expected from the cost of assessing progenies, it will be necessary to select eight trees in most families at the first stage. Fewer than eight trees may be selected in families that share founder parents with better families, or in families with low scores, that are surplus to the population size target set for the breeding population. The distribution of selections among families must ensure retention of a sufficient number of unrelated lines of descent to provide for nine unrelated sublines having no fewer than eight founders and capable of regeneration entirely by matings no closer than third-cousin. Gains from first-stage selection will be marginally greater than for phenotypic within-family selection (COTTERILL 1986; COTTERILL & JACKSON 1989), because of the reduced presence or elimination of families having mean scores lower than expected from the scores of their parents.

Second Selection Stage

In the second stage of selection, individual trees selected within most third-generation families will be re-selected, mainly on performance of their progeny and secondarily on their own performance at 20 years from planting. Trees will be selected at the second stage by designation of their progenies with unrelated mates for retention in the fourth-generation breeding population.

Single-pair mating appears to be the most appropriate mating system for second-stage selection in this program, primarily on grounds of economy. This system requires the smallest number of test progenies (one progeny for two first-stage selections), and all families for the next-generation breeding population are provided with no additional work.

Pairing of first-stage selections for single-pair mating would begin with pairing of their families. Each third-generation family including one or more first-stage selections would be paired with an unrelated family that included, preferably, the same number of first-stage selections with similar total scores. Pairing of individual trees within family pairs would use within-family rank of total scores along with trait breeding values.

Families sharing founder parents would need mate families that also shared founder parents (Figure 2), for

testing of their first-stage selected trees. Maintenance of parallel pedigrees for descendants of the same founder parents in the third generation as well as in subsequent generations, will simplify control of inbreeding within sublines, while avoiding relatedness between sublines. Mismatches of number of first-stage selections between paired families will be resolved by dropping or adding selections, but not by pairing trees from one family with trees from more than one other family.

Progenies from single-pair mating of third-generation first-stage selections, would be measured and scored for progeny mean total multiple-trait score at 10 years from planting. These scores would be used as part of the selection criterion to select pairs of parents, typically two pairs from among the eight mated, from each pair of third-generation families. The remainder of the selection criterion would be the separate breeding value estimates on the parent trees, including the first-stage selection scores, and scores obtained by remeasurement of the third-generation breeding population plantations at 20 years from planting. Tree size data are expected to be better correlated with harvest-age size, at 20 years than at 10 years from planting. Data on mature wood traits, if desired, would also be available. Trees would then be likely to average about 7 m in height and 120 mm in diameter, and would be producing merchantable volume. In the first-generation family test, heritability of total height increased from 0.12 at 10 years from planting (KLEIN 1989) to 0.43 at 20 years from planting (KLEIN 1995). This selection of pairs of parents based on mean total score of their joint progenies, together with breeding value estimates of 10-year and 20-year performance traits, would constitute second-stage selection for the single-pair mating strategy.

Alternative procedures for second-stage selection include polycrossing and half-diallel mating. Polycrossing offers higher efficiency than single-pair mating for selection of parents. The additional gain expected by use of polycrossing was estimated at, for example, about 23% at SCA of 0 and heritability of 0.1, and about 55% with SCA equal to ½ of general combining ability and heritability of 0.5 (BURDON & VAN BUIJTE-NEN 1990, Figure 1). Polycrossing requires producing and assessing twice the number of progenies as pair-mating. Because the strategy for this program requires full pedigrees for control of relatedness in later generations, the progenies produced by polycrossing are not usable to constitute the next-generation breeding population.

A disconnected half-diallel design with 5 parents in each set, would require 2 matings per parent for a total of perhaps 1160 matings (580 parents in 116 sets), or

four times the number required for single-pair mating. The half-diallel design would likely be more efficient than single-pair mating for second-stage selection (BURDON & VAN BUIJTENEN 1990), and the same families would be more efficient for selection in the fourth generation if SCA variance were present at medium to high levels (VAN BUIJTENEN & BURDON 1990). This design would also allow estimation of SCA variance, which would not be available from single-pair mating or polycross designs. As no applicable estimate of SCA variance in jack pine is now available, it is not possible to quantify the probable increase of genetic gain from use of polycross or half-diallel mating. Marginal costs of these alternative strategies could be quantified at the time of first-stage selection, if there were interest in an alternative strategy at that time.

Resistance to western gall rust was one of the traits used in selecting parents for the third-generation families, and could be used in selection within those families. Scoring of response to western gall rust can be accomplished efficiently by artificial inoculation of seedlings in addition to observation of galls on test plantation trees (KLEIN et al. 1991). If there is sufficient interest in scoring of rust resistance in third-generation trees and families, test progenies for assessment of response to artificial inoculation will be produced from trees selected at the first stage.

Third-generation Seed Orchard

Individual trees in the third-generation breeding population plantations will be selected as seed orchard donors based on the same multiple-trait breeding value scores used for first-stage selection of parents for the next-generation breeding population. Because the purpose of the seed orchard differs from that of the breeding population in not requiring maintenance of a large effective population size for multiple-generation gains, the distribution of seed orchard selections among families will differ from the distribution of breeding population selections. Both sets of selected trees will be likely to include the best tree from each of the best 20 pairs of founder parents. Additional trees selected as seed orchard donors will include a high proportion of trees descended from the same founder parents, plus a smaller number of trees with high multiple-trait scores from additional families. There will be little motivation to include in the seed orchard select group, trees with relatively low scores that are the best descendants of their founder parents. Some of those trees must be included as parents of the next-generation breeding population. Genetic gain from selection of seed orchard donors in the third-generation population should be higher than that for breeding population selection,

because family selection can be used to a greater extent for the seed orchard.

Grafting will be used to produce seed orchard trees from selected donors, despite the earlier and more abundant cone production on seed-grown trees of jack pine. Production of seed orchard trees by controlled pollination would require two unrelated breeding-population families for each group of inter-related seed orchard trees, reducing the opportunity for genetic gains from family selection in constituting the seed orchard.

Seed orchard donors will be 10 years of age from planting when selected. They will need to be maintained in a state suitable for performance assessment for another 10 years following first-stage selection, in addition to the requirement to use some of the same trees for controlled breeding for second-stage selection. To avoid impairing ability of the scion donors to fulfill these other functions, scion collection from the selected breeding population trees themselves, the ortets, must be constrained. It is estimated that 5–10 scions can be removed each year from selected trees without undue risk of impairing subsequent performance.

Development rate for a seed orchard can be accelerated with little impact on gain by selecting related seed orchard ortets. If only the 20 unrelated trees with the highest multiple-trait scores were selected as seed orchard ortets, establishment of a seed orchard of adequate size would extend over an excessive number of years, mitigated to some extent by use of the first-grafted ramets as scion donors. The rate of seed orchard establishment can be increased by using more trees from the third-generation breeding population as ortets. Selection of more than two trees as third-generation parents in some of the best second-generation families will increase the number of potential seed orchard ortets capable of providing near-maximum gains.

Details of seed orchard design do not need to be decided prior to completion of first stage selection, expected to occur about 2015. The amount of inbreeding in the seed orchard will depend upon the proportion of successful pollen originating from trees having ancestors in common with the pollinated tree; and the proportion of selfing will depend upon the proportion of successful pollen originating from the pollinated tree or other ramets of the same clone. Details of the interspersion of related and unrelated trees in the immediate neighbourhood of a pollinated tree appears to have little influence on mating patterns (HODGE & WHITE 1993). In the third-generation seed orchard, the lowest degree of relationship will be first-cousin, which may be close enough to risk substantial loss of expected genetic gain, but not close enough to allow visual culling of affected plants. Consequently it would be prudent to assume that

the proportion of inbred seed will be about equal to the proportion of the total number of trees contributed by each of the best founder pairs, and to limit the maximum proportion of trees from any founder pair to the amount of inbred seed that can be tolerated.

Following completion of second-stage selection, breeding value of the trees in the third-generation breeding population plantation will be known more accurately. More accurate scores will support selection of seed orchard clones using a higher selection intensity. An increase in selection intensity could be realized in the seed orchard by producing new grafts using a smaller number of clones having a higher mean breeding value, or by culling out grafts having lower second-stage scores than their neighbours. The latter option will provide immediate improvement in the genetic quality of seed orchard seed.

A third-generation seed orchard could be configured for production of control-pollinated seed, allowing greater gain by means of a higher selection intensity and complete avoidance of inbreeding. Capture of genetic gain by controlled pollination can be expedited by vegetative propagation to increase the supply of improved stock (CHAPERON 1991). Progress to date in development of vegetative propagation technology for jack pine (BROWNE & CAMPBELL 1995; CAMPBELL & BROWNE 1995; KLEIN et al. 1995) indicates that vegetative multiplication can be an option for producing planting stock from control-pollinated seed orchards. The flexibility of control-pollinated seed orchards with vegetative multiplication will become increasingly attractive in later generations as the number of unrelated groups of families is reduced to the minimum number of entries required for open-pollinated seed orchards.

ACKNOWLEDGEMENTS

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