Making Choices -- Seedling and Clonal Options for Breeding and Reforestation in New Brunswick

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Executive summary

Over the past few years, refinement of rooted cutting procedures and major advances in micropropagation through cell culture have stimulated considerable interest in the potential of clonal propagation to enhance returns from breeding and reforestation programs in New Brunswick. The question facing forest managers in the light of this advancing technology is "Does clonal propagation offer potential gains and management benefits which might justify the higher cost anticipated for planting stock production?" This study was initiated under the Canada/New Brunswick Cooperation Agreement on Forest Development to investigate factors that should be considered in the evaluation of clonal propagation as a breeding tool and deployment method for reforestation.

Interviews were conducted with personnel from government and industrial members of the New Brunswick Tree Improvement Council to gather information on their current plans for advance-generation breeding and to elicit their ideas on the role of clonal propagation. Most cooperators are encouraged by the progress made in the first generation, but most have not committed to a definite plan for the second generations. To date, clonal forestry has received little attention, although some cooperators have gained experience in the production of stecklings from juvenile spruce cuttings. A computerized literature search was used to assemble background literature on the use of clonal propagation in forest tree breeding programs. Over 180 items were reviewed and developed into an annotated bibliography.

Conventional approaches to breeding were reviewed. Wind-pollinated seed orchards currently form the source of all improved stock in New Brunswick. Pollen contamination is well recognized as a problem in such orchards, since half of the genetic gain is attributable to the male parent. In addition to contamination problems, trees in the orchard will not produce equal quantities of seed or pollen, and mating is rarely random. Although the combined impact of contamination and non-panmictic mating on genetic gain and diversity is difficult to predict, it is virtually certain that actual gains and diversity will be substantially lower than would be predicted under assumptions of "ideal" pollination. The only way to overcome this problem is to physically control the source of pollen delivered to each tree in the orchard.

New approaches to breeding and reforestation which use utilize clones must satisfy stringent requirements for *(i)* technical and logistical feasibility, *(ii)* biodiversity and risk of failure, and *(iii)* benefits and costs. The impact of each of these requirements is reviewed and reference made to previously published studies.

The question of genetic gains was approached by simulating the results over time of various seedling and clonal strategies. A computer program was written which allows the user to define genetic and environmental parameters in an initial breeding population. This population is then subjected to selection and testing schemes which generate tested parents for seed orchard parents and clonal deployment. The simulator was used to estimate gains under a variety of genetic variance scenarios for eight breeding strategies. A consistent 28-year breeding cycle was used in all cases and the testing effort fixed. All of the strategies used sublining (breeding groups) to control inbreeding and positive assortative mating to generate selection material was based on polycross results for each parent. The results were

plotted over a time line and average genetic gain calculated for a 140-year period (5 breeding cycles).

Cost estimates from the literature and personal communications are reviewed for tree breeding, production of control-pollinated orchard seed, and various types of clonal propagation. The project also developed a financial analysis procedure which extends standard discounted present value techniques to incorporate allowable-cut effects and changes in stumpage value resulting from genetic improvement. The calculations are performed within a computer spreadsheet which allows the user to conduct the analysis for any scenario of site quality, genetic gain, and economic parameters. The effect of these factors is illustrated by a series of graphs showing the present value of expected gains, compared with the extra cost of nursery stock resulting from seedling- and clone-based improvement programs.

The simulations demonstrated that *clonal replication* of genotypes in genetic tests can have a major impact on the efficiency of breeding programs, even when clones are not actually used for deployment of operational planting stock. Clonal replication will increase test efficiency over a broad range of genetic variance scenarios, but is particularly effective when most of the genetic variance is additive and/or heritability is moderately low, i.e., ≤ 0.3. In these situations, the extra gain resulting over time from the use of clonal replicates should be 7 to 11% higher than that achieved when tests are established as seedlings.

Vegetative multiplication may be used to amplify the number plantable trees from control-pollinated orchards and selected full-sib crosses when insufficient seed is available to fill the planting requirement. Seed produced in control-pollinated orchards will produce average gains which are 20 to 30% higher than those predicted for an "ideal" wind-pollinated orchard. Because wind pollination is frequently far from ideal, controlled pollination should achieve gains which are at least 50% higher, perhaps even *double* those actually achieved in conventional wind-pollinated orchards. Although other approaches may be used to deploy control-pollinated materials, the economic analysis suggests that cloning is an economically viable method when allowable-cut effects are available, even at high rates of interest. Without allowable-cut effects, vegetative multiplication will be worthwhile at low to moderate real interest rates. The uncertainty regarding the gain and economic assumptions used in the analysis is perhaps the greatest deterrent to selecting vegetative multiplication as a deployment option.

The simulations demonstrate that true *clonal forestry* (deployment of tested clones) will only be attractive when there is a substantial component of nonadditive genetic variance. Data from young genetic tests in spruce and jack pine suggest that most of the genetic variance is additive, although limited data now available from older tests and the few existing clonal tests suggest that the nonadditive component may account for as much as one third of the total genetic variance. Under this scenario, the economic analysis suggests that clonal forestry will be worthwhile pursuing if allowable-cut effects are available. Even in the absence of allowable-cut effects, clonal forestry should be viable at low to moderate effective rates of real interest. The high degree of uncertainty with respect to actual genetic gains and costs of propagation makes it unlikely that clonal forestry will be attractive until additional data are available to confirm assumptions made in the analysis.

The study identified several areas where further work is required, including: *(i)* development of practical field experience with clonal material; *(ii)* incorporation of clonal replication in genetic testing; *(iii)* testing of critical assumptions regarding clonal performance; *(iv)* storage protocols for clonal materials during the time required for field testing; *(v)* enhancements to the simulation technique and application to other breeding problems; and, *(vi)* quantitative tools for optimized strategic planning of silviculture.

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Introduction

Until very recently, propagation technology for important New Brunswick conifers was restricted to cultivation of new plants from seeds. However, refinement of rooted-cutting procedures and recent advances in micropropagation through cell culture have stimulated considerable interest in the potential of clonal propagation to enhance the returns from breeding and reforestation programs in the Province.

Several conifer species are used in reforestation programs conducted on both Crown and freehold lands. In 1988, a total of more than 43.7 million seedlings were shipped from government and private nurseries in New Brunswick for reforestation purposes (Hallett *et al.* 1990). Over the past 15 years, the New Brunswick Tree Improvement Council (NBTIC) has concentrated its efforts on producing genetically improved material for the three most important reforestation species: black spruce (*Picea mariana* [Mill.] B.S.P.), jack pine (*Pinus banksiana* Lamb.), and white spruce (*Picea glauca* [Moench] Voss), as well as tamarack (*Larix laricina* [Du Roi] K.Koch). In all cases, breeding work and deployment of improved stock has relied totally on planting materials grown from seed. A difficult question now faces breeders and reforestation planners alike: "Does clonal propagation offer potential gains and management benefits which might justify the higher cost anticipated for planting stock production?".

Study objectives

This study was initiated under the Canada/New Brunswick Cooperation Agreement on Forest Development to investigate factors that should be considered in the evaluation of clonal propagation as a breeding tool and deployment method for reforestation. Specifically, the project focused on three objectives:

(a) to identify operational activities, costs and comparable time schedules for conventional seed orchards and clonal forestry;

(b) to determine key genetic and operational decision factors for comparison of advance-generation breeding and deployment strategies; and,

(c) to assess the genetic gains, management benefits and costs associated with seedling and clonal reforestation strategies under various scenarios in order to evaluate the relative importance of these key decision factors.

Gathering of background material

Interviews with NBTIC cooperators

A series of interviews was conducted at the beginning of the study, which included personnel from Forestry Canada, the New Brunswick Department of Natural Resources and Energy (NBDNRE), and three of the larger NBTIC industrial cooperators: Fraser Inc., J.D. Irving Limited, and NBIP Forest Products Inc. Personnel were asked to review their experience with seed orchards currently in use and to speculate on seed-orchard management and production expectations in second-generation orchards. The interviewees were also questioned about their ideas on the role of clonal propagation as a breeding tool and method for planting stock deployment.

The role of tree breeding and orchard programs as part of a larger silvicultural strategy is rarely stated in terms of its expected contribution to future harvest flows. Rather, reforestation programs which already exist are seen as creating an opportunity for worthwhile investment in tree improvement. The additional costs of a breeding program are generally weighed against the value of additional yield from plantations, and the investment seen as worthwhile if the net present value is positive. This rationale takes a somewhat narrow view of forestry investment and fails to identify the optimal place of tree improvement activities in the management strategy. Tree improvement is not unique in this respect, and in its defense, any activity which generates a positive return can contribute to diversification of the silvicultural investment portfolio, which, in turn, will help to minimize the overall risk associated with forest management investment.

NBTIC cooperators have been encouraged by the results achieved over the last 15 years. Experience with first-generation seed orchards of black spruce and jack pine demonstrate that early estimates of seed production were very conservative. Many cooperators now feel that these species can produce 5 million seeds per hectare or more, and that second-generation orchards can be much smaller. Understandably, gain expectations are uncertain, but estimates of 8-15% are thought possible from rogued, first-generation seedling seed orchards. Some cooperators can now supply most of their seed requirements from seedling seed orchards and have already begun to establish second-generation clonal orchards. The importance of pollen distribution is well understood and most NBTIC orchard managers have carried out monitoring studies to evaluate the impact of outside-orchard sources. Induction treatments are also being investigated by some cooperators as a means to increase the contribution of clones which are reluctant to flower. Techniques for growth acceleration and indoor orchard management techniques are under development, but are generally viewed as a means to expedite breeding, rather than operational seed production.

The interviews with key personnel indicated that consideration of the role of clonal propagation in breeding and reforestation programs has been superficial, although there is much interest in developing operational techniques for large-scale clonal deployment. Some cooperators have gained experience in the production of stecklings from juvenile spruce cuttings, but most feel that labour demands are expensive and impractical for large-scale production.

High-tech cloning methods such as asexual embryogenesis combined with cryopreservation of somatic embryos are generally regarded as the most promising techniques for operational deployment of clones.

Assembly of literature

A computerized literature search was used to assemble background literature relevant to the objectives of this project. The search was conducted on the Agricola (1970 - 03/91), AGRIS (1986 - 90) and CAB Abstracts (1984 - 06/91) databases. Topics addressed by the search included the use of vegetative propagation in forestry, economic aspects of tree improvement and seed-orchard management, commercialization and economic aspects of micropropagation, and the integration of clonal propagation with tree breeding strategy. References selected from the computer search were obtained and reviewed. An annotated bibliography covering more than 180 of these references was prepared using the PAPYRUS™ bibliographic system (Goldman 1989), and is reproduced in Appendix I.

Additional information from other sources

Throughout the course of this project, contact was made with many individuals and agencies with expertise and practical experience in all aspects of clonal forestry, breeding strategy, and economic analysis. Contact took a variety of forms, from written correspondence, to telephone conversations, to face-to-face discussions. Although information provided by some of these sources is referenced in the text, all contributed insight and are acknowledged towards the end of this report.

Overview of tree breeding and reforestation options

Conventional approaches to tree improvement

Conventional breeding and reforestation programs are designed to ship planting stock grown from seed. Superior phenotypes are selected to form a breeding population which is managed to produce genetic improvement through recurrent selection. Parents in the breeding population are inter-mated and their progeny established in test plantations. The plantations provide information to assess the genetic value of each parent and the best progeny are selected to form the next generation of the breeding population. In each generation, the best parents are established in wind-pollinated seed orchards and the seed produced is used for production of operational planting stock.

In the "ideal" seed orchard, no contamination would occur from pollen sources outside the orchard, all of the orchard parents will produce equal numbers of gametes, will mate randomly with all other parents, and will refrain from self fertilization. Of course, all orchards will fall short of this ideal, and in some cases, orchards will only produce a fraction of the genetic improvement possible from the selected orchard parents. Pollen contamination in seed orchards is well-recognized as a problem in many wind-pollinated seed orchards, with 40 to 50% or more of the pollen cloud originating from sources outside the orchard (Di-Giovanni and Kevan 1991; Lindgren 1991). Since half of the genetic component of orchard progeny is contributed by the male parent, the potential impact on genetic gain is quite serious. If all of the pollen were to originate from surrounding "average" stands, the genetic gain from the orchard would be cut in half. The impact would be even greater if the source of contaminating pollen were poorer than average, or adapted to entirely different site conditions; a situation which might be expected if the orchard has been located "off-site" in order to enhance seed production. In addition to the impact of pollen contamination on gain, the resulting increase in effective population size will likely increase the genetic diversity of orchard seed. Koski (1987) claimed that the only way to avoid contamination is to locate orchards where species composition and/or flowering times of surrounding stands differ from those in the orchard.

The impact on gain and diversity from unequal gamete production and non-random mating in wind-pollinated orchards is more difficult to predict. Determining the effect of nonsynchronized flowering times and differences in reproductive output requires elaborate monitoring procedures and will vary from year to year (Askew 1988; Copes and Sniezko 1991; El-Kassaby and Askew 1991). Of those species planted in New Brunswick, imbalance in orchard gamete production has been documented for both white and black spruce (O'Reilly *et al.* 1982; Schoen *et al.* 1986). Observations such as these have given rise to the rule-of-thumb which states that 80% of the gametes are often produced by only 30% of the clones in the orchard.

Even if all of the parents in the orchard are unrelated, inbreeding due to selfing can have an impact on gain and diversity of orchard seed. Reports in the literature generally indicate that selfing rates in seed orchards are not much different from those of natural stands, around 10% (J. Loo-Dinkins, pers. comm.). Barrett *et al.* (1987) reported selfing rates in the range of 6 to 16% for a black spruce orchard near Thunder Bay, Ontario.

Only a few studies have generated the data required to document the impact of contamination and non-panmictic mating on genetic gain and diversity of actual orchard crops (e.g. Szmidt 1987). Although careful location and management can mitigate contamination and non-panmictic mating in wind-pollinated seed orchards, the only way to completely eliminate the potential negative effects is to fully control the source of pollen. This is commonly done when performing controlled pollination for the purposes of breeding, but is more difficult to accomplish on a large scale for operational seed production. Isolation barriers are effective, but difficult to install. It may be possible to manipulate flowering times of trees in indoor orchards, and even in small "meadow" orchards, to eliminate most contaminating pollen, while using manual application of pollen to control parentage.

Non-conventional approaches using clones

The term *clonal forestry* is often applied rather loosely to refer to any use of cloning technologies in breeding and reforestation operations. There are, however, three contrasting ways that clones may be utilized:

1. *clonal replication* of genotypes in test plantations may be used to enhance testing efficiency;

2. *vegetative multiplication* of planting stock may be used to amplify the number of plantable trees from a limited quantity of seed; and finally,

3. *clonal selection* may be combined with vegetative multiplication to deploy operational planting stock originating from tested individual clones or clonal mixtures.

In this report, the term *clonal deployment* refers to any use of clones in breeding or reforestation, whereas *clonal forestry* is used in the narrower sense where selection at the clonal level is carried out. It is important to realize that while clonal forestry is often promoted as a means to maximize genetic gain, it is not itself a breeding method (Burdon 1989). Continued genetic gain over successive generations still requires the inter-mating of parents in a base population, followed by recurrent selection to produce progressively higher numbers of alleles with favourable additive effects.

Although clonal selection may result in gain from the entire range of additive and nonadditive effects expressed in a population of genotypes, vegetative multiplication can only increase the extent to which gains from polycross or full-sib family selection are realized. If sufficient numbers of seed from selected families are available to supply the entire reforestation requirement, vegetative multiplication will not contribute to additional genetic gain, although it is generally recognized that the best seed material will always be in short supply (Schooley and Mullin 1988). Even in cases where sufficient numbers of seeds can be produced, differences in performance between vegetative propagules and seedlings may offer other opportunities for yield or quality improvement and reductions in silvicultural costs (Arnold 1990; Arnold and Gleed 1985; Klomp 1988).

Clones may also be used to replicate test material in the field and thus enhance the effectiveness of ranking based on clonal means, rather than individual values (Libby 1964; Shaw and Hood 1985). When family relationships exist among the clones in the test, it may also be possible to partition nonadditive sources of genetic variance which would otherwise be confounded with the error variance (Mullin and Park 1992). Clonal replication may be advantageous, even if operational planting stock is to be grown from seed. In this case, it is not necessary for the growth of the test propagules to resemble that of seedlings, provided that rankings between clones and seedlings are highly correlated.

Overview of General Decision Factors

Technical and logistical feasibility

Obviously, any consideration of opportunities for integration of cloning into breeding and reforestation strategies is largely academic unless clonal propagation is technically possible and can be readily accomplished in an operational setting. To say that clonal propagation of important New Brunswick conifers has not been without problems would be to understate the situation. Nevertheless, the persistent efforts of propagation specialists have been rewarded with considerable success.

The only cloning system which has been used on an operational scale for these species is based on the rooting of cuttings from very young seedlings, producing *stecklings*. Maturation of donor plants has long been recognized as a major hinderance to vegetative propagation (Bonga 1987; Greenwood 1987). As donor plants age, cuttings become more difficult to root and often display poor form and a decline in growth rate. However, cuttings from very young donor plants of spruce and larch species are relatively easy to root and, for the most part, appear indistinguishable from seedlings once planted in the field. Jack pine has proven to be much more difficult and attempts to produce steckling stock have not had much success. Large quantities (i.e., 1 million or more trees per year) of vigorous steckling stock have been produced vegetatively from young donor plants of spruce species in operational settings (Rogers 1990; Brian White, Michel Villeneuve, Bengt Bentzer, pers. comm.). Although technically feasible, the labour-intensive nature of striking and setting operations creates logistical problems when annual production levels rise to more than a few million. Larger production levels will require a high quality nursery labour pool, careful production scheduling, and improvements in mechanized handling. These factors will have a major impact on the achievable production level and the ultimate cost of clonal planting stock.

New technology for vegetative propagation could have a profound impact on the feasibility of producing large quantities of clonal planting stock. Tissue culture methods for micropropagation of forest trees have attracted much attention and several approaches have been pursued by laboratory scientists (Thorpe *et al.* 1991). Organogenesis, the production of differentiated plant parts in culture for subsequent rooting, has shown much promise for some species such as radiata pine in New Zealand with potential for mechanization (Aitken-Christie 1991; Aitken-Christie and Jones 1987). Up to now, New Brunswick conifers have not responded as well to organogenic procedures (Dr. Jan Bonga, pers. comm.).

Most recently, the production of plantlets by means of asexual embryogenesis has renewed interest in tissue culture propagation of New Brunswick conifers, particularly in spruce and larch (Attree *et al.* 1990; Hakman and von Arnold 1988; Hakman and Fowke 1987; Klimaszewska 1989a, 1989b; Lelu *et al.* 1990; Lu and Thorpe 1987; Tremblay 1990; von Arnold 1987; Webster *et al.* 1990). Many authors have speculated that somatic embryogenic systems should reduce the cost of cloning, although there are as yet few operational demonstrations to substantiate this claim. Certainly, many of the laboratory procedures show promise for mechanization (Harrell and Simonton 1986) and many of the workers in this field are hopeful that encapsulation of somatic embryos to form artificial seeds (Janick *et al.* 1989; Redenbaugh *et al.* 1988) will have a major impact on the viability of embryogenic systems. Other automated systems are also under development to deliver embryos suspended in liquid media directly to growing containers; for example, a group of alfalfa breeders in Ottawa have modified a Japanese paper-pot seeding line to deliver embryo suspension into paper-pots filled with sterilized peat and covered with a thin layer of agar (A.R. McElroy, pers. comm.).

Beyond the actual production of high-quality clonal planting stock, the integration of cloning into breeding and reforestation problems poses other logistical problems. The pursuit of additional gain through clonal selection will require additional testing of individual clones to capture nonadditive genetic variance. Such gains represent a genetic dead end which cannot be carried forward to the next generation. Furthermore, effort which is expended in the pursuit of these gains must come at the expense of efforts to advance additive gain through recurrent selection. A trade-off must be recognized between clonal testing and advancement of the breeding population (Burdon 1986, 1989).

Additional logistical problems are introduced when operational deployment of clones is required to achieve a given level of diversity or a particular spatial arrangement of clones. There may be a requirement to deploy clones in particular mixtures or in mosaics of individual clonal blocks. Maintaining the identity of many clones in the nursery and producing particular clonal mixtures will pose a challenge to nursery managers and will certainly add to the cost of production.

Biodiversity and risk of failure

For many people, the phrase "clonal forestry" conjures up disturbing images of widespread plantations composed of a single, super-yielding clone. No one would argue that such a scenario would be anything short of foolish. Diversity is widely regarded as an important strategy to decrease susceptibility to all manner of injurious agents and to lower the risk of failure. Nevertheless, there remains a great temptation to select only the very best genetic material for operational deployment; and this is true regardless of the deployment method used.

All of our important reforestation species are outbreeders and have evolved to maintain genetically diverse populations in nature. Genetic diversity in a breeding population will minimize the risk that adverse sampling during sexual recombination will render progeny susceptible to a particular pest or environmental stress factor. Diversity is also known to inhibit the spread of a pathogen through a population, even if some genotypes are highly susceptible, but interspersed among other resistant genotypes (Burdon 1989; Carson, S.D. and Carson 1991).

If deployment of only one genotype is hazardous, how do we know when a planting mixture has a sufficient level of diversity to be regarded as "safe"? The question is legitimate but difficult to answer since diversity, particularly at the allelic level, is difficult to observe directly. The problem is not unique to clonal mixtures; seed-orchard populations must also represent an adequate level of genetic diversity to ensure that seedling progeny will not be at risk. Unfortunately, the only means to characterize diversity at the genetic level is to study isozyme loci with electrophoretic techniques. Such studies form a large body of scientific literature and describe frequencies of alleles, the number of alleles per locus, and the level of heterozygosity in many types of forest stands and seed orchards. By screening a large number of isozyme loci, the allelic diversity of an orchard crop can be related to the levels normally found in natural populations, and that expected in an efficient seed orchard. The diversity of clonal mixtures can be controlled rather more easily, provided that identification of clones and their proportional contribution to the mixture is known.

Several authors have considered the problem of ensuring adequate diversity while maximizing genetic gain from mixtures (e.g. Hühn 1986, 1987; Kleinschmit 1979; Libby 1982; Lindgren *et al.* 1989; Roberds *et al.* 1990). Although the optimal number remains open to debate, and will in any event vary according to the species and location, the required number of clones is probably in the order of 20 to 40. Similar required numbers of parents in seed orchards also seem appropriate, although non-panmictic pollination conditions in orchards may require greater numbers to achieve the same effective population size (J. Loo-Dinkins, pers. comm.).

Although the number of parents in a seed orchard is normally determined on the basis of local expert advice, the numbers of clones required for planting mixtures has been the subject of legislation in Sweden and Germany (Muhs 1988). Clones used in both countries must be tested and are then approved for deployment in mixtures. Although some adjustments have been made recently (J. Hood, pers. comm.), Germany approves clones for a 10-year period and generally requires mixtures of 100 to 500 clones, depending on the size of the planting project; larger areas require larger number of clones. Sweden classifies approved clones, based on the extent of testing in space and time. The minimum test requirement is 2 sites over 6 years, for mixtures of at least 120 clones. As few as 30 clones can be used in a mixture, when testing over 6 sites has been replicated in time over 12 years. Sweden also limits the total number of ramets which can be deployed from an approved clone; the highest level of testing permits a maximum of 1.5 million ramets to be deployed. Vegetative multiplication of seeds is not permitted in Germany and is limited to 100 ramets per genotype in Sweden. Legislation restricting the deployment of clones of local genetic material does not exist in North America, although Ontario has adopted a policy on subject which may be revised by its Ministry of Natural Resources as new information becomes available.

The decision to use clones does not require acceptance of decreased diversity. In fact, the effective population size of clone mixtures can be controlled with some precision, and this could be used effectively to maintain or even increase diversity over that found in natural stands. The main challenge here is to implement clone identification and sorting procedures at the nursery, to ensure quality control over the make-up of clonal mixtures deployed to the field. Such control over diversity of seed crops might also be desirable, but effective implementation might be difficult in wind-pollinated orchards. Loo-Dinkins (Undated) estimated that the effective number of parents in a conventional seed orchard might be only 40% of the actual number. Although one could control the contribution of female gametes by collecting seed on a clonal basis, the orchard manager has little control over panmixis and contamination which will affect effective size of the male population. The usual strategy would be to sacrifice some genetic gain by increasing the number of clones in the orchard, in the hopes that the effective population size represented by orchard crops will be adequate. Modifications of the conventional seed orchard which utilize controlled pollination offer more precise control over diversity and panmixia, and should greatly decrease the number of parents required to achieve a given effective population size, which, in turn, will increase genetic gain.

Benefits and costs

Once the prerequisites of technical feasibility and biological safety are satisfied, the decision to use clones comes down to a weighing of expected advantages and costs. The objectives of forest management will dictate how the assessment is performed and how the results are compared with other silvicultural options. The evaluation of forest management options is an ongoing process as much of the information used is associated with a degree of uncertainty. The information base available to the decision-maker can undergo rapid change as technology develops and markets respond to socioeconomic forces.

Economic comparisons of benefits and costs often concentrate on financial aspects, and commonly employ investment analysis techniques such as net present value (NPV) and rate of return. These analyses have the appeal of quantifiable comparisons and the appearance of precision. However, investment analysis techniques typically employ data such as discount rates and future stumpage values which are characterized by a high degree of uncertainty. Moreover, they focus the attention of the decision-maker to returns at the stand level, rather than the impact of management to output from the forest as a whole (Reed and Baskerville 1991). Nevertheless, investment analysis is well accepted as a means to compare individual components of the silvicultural investment portfolio. A level of investment capital will be allocated based on the requirement to increase or stabilize harvest flows. These resources will then be divided among the silvicultural components based, not only on their NPV, but also on the degree of uncertainty, length of exposure to risk, and impact on investment diversification.

The potential advantages of using clones in breeding and reforestation programs go well beyond the ability to exploit the nonadditive portion of genetic variance (see Carson, M.J. 1986; Libby 1990; Libby and Rauter 1984). These advantages include genetic aspects such as increasing selection gain and diversity, and non-genetic possibilities such as control of juvenile traits and reproductive activity, and benefits from propagation effects. It is difficult to assign a dollar value to many of these benefits, and for many New Brunswick species, some benefits remain speculation in the absence of supporting data. For example, observations made in non-native spruce and pine species suggest that growth and form of cuttings taken at certain ages is superior to that of seedlings, resulting in higher yield and lower silvicultural costs, even when no genetic gain is realized (Arnold and Gleed 1985; Gemmel *et al.* 1991).

Most economic analyses have been cautiously optimistic about the financial viability of clonal forestry options, assuming that significant genetic improvement will be achieved (Hasnain *et al.* 1986; Smith 1986; Timmis 1985; Wilhelmsson 1991). Invariably, economic assessments of particular situations conclude that the viability of clonal strategies is highly sensitive to the cost of propagation (Gill 1983; Lundkvist and Gullberg 1981; McKenney *et al.* 1988; Smith 1991; Wilhelmsson 1991). Some of these analyses illustrate the limitations of investment analysis techniques to adequately describe many of the benefits that may accrue from silvicultural investment. For example, an analysis conducted for black spruce in Ontario concluded that gains from clonal forestry over those attainable from seed orchards do not warrant the higher cost of planting stock. Unfortunately, these authors used simple discounting and valued the extra volume increment at regular stumpage rates; an approach which fails to recognize the overall effect on harvest flows, cost reductions resulting from closer wood supply, and gains from quality and value enhancement (Reed 1989).

The current study did not attempt any definitive analysis of decision factors in the context of an optimal silvicultural regime for New Brunswick. Such an analysis would have to be limited to a specific management scenario on a given forest, and would not be appropriate to all forest owners. Furthermore, any analysis carried out today must incorporate estimates of costs and benefits which are highly uncertain and likely to change in response to new scientific data and development of technology. Rather, the study focused on the development of decision-support tools to assist in the evaluation of genetic gain from alternative tree improvement strategies and in the determination of marginal costs that might be justified for the production of clonal planting stock.

Evaluating genetic gain from alternative strategies

Genetic gain calculations reported in the literature are often no more than extensions of heritability estimates made in test populations and are typically expressed as gain achieved from one round of selection at an arbitrary selection intensity. Actual breeding strategies tend to be much more complex, involving multiple-stage selection over several breeding cycles in populations where restrictions on coancestry and selection intensity are enforced. When comparing strategies, it is important to avoid comparing apples with oranges. Gain estimates must be calculated on an equal-effort basis and should be considered in terms of gain achieved over time. This study demonstrates the use of simulation techniques to predict gains from alternative seedling and clonal strategies over several breeding cycles, and comparison of gains achieved over time. The simulation is far more flexible than standard gain equations and can accommodate complex modifications to selection strategies.

Simulation of breeding strategies

A Monte Carlo computer simulation approach was used to estimate genetic gains from several comparable breeding strategies, under different population structure scenarios. The simulation used the familiar model which defines a tree's phenotypic value as the sum of independent, normally distributed genetic and environmental effects:

$$P = G + E$$

Genetic effects are further partitioned into components which reflect different modes of gene action that affect the way a trait is passed on to offspring: (1) Additive effects (A)

represent the average effect of substituting one allele at a locus for another; (2) Dominance effects (*D*) are the within-locus allele effects which remain after subtracting additive effects, i.e., the intra-locus interaction between alleles; and (3) Epistasis effects (*I*) which arise from interactions among all loci which affect expression of the trait. The total phenotypic variation is therefore the sum of independent variances for each of these effects:

$$\sigma_P^2 = \sigma_A^2 + \sigma_D^2 + \sigma_I^2 + \sigma_E^2$$

The simulation began with the generation of genetic and environmental effects for each tree in a normal, random-mating population of a given size. Each effect was generated from a set of randomly distributed effects with a given mean and variance, such that:

$$x_i = \bar{X} + r\sqrt{\sigma_X^2}$$

where x_i is a normal variate effect for the i^{th} tree, with mean of $\bar{X}$ and variance σ_X^2, and r is a normal random variable with mean of 0 and variance 1. The phenotype of a given tree is the sum of independently generated additive, dominance, epistasis and environmental effects.

A standard pollen mix for polycross testing was simulated by generating a given number of male genotypes, using the same genetic variance structure specified for the original breeding population. The same pollen mix was used for testing of subsequent breeding cycles. Polycross progeny were produced by random mating of males in the pollen mix with the selected tree being tested.

Genetic effects for individual progeny were generated as a function of among-family and within-family inheritance. The among-family additive effect was calculated as the average additive effect of the two parents, i.e., the mid-parent value, and progeny were generated around this mean with a variance equivalent to the within-family portion of additive variance, i.e., $\frac{1}{2}\sigma_A^2$. The among-family dominance effect for a given female-male combination was generated randomly from a normal distribution with a mean equivalent to the dominance effect of the original population, and a variance of $\frac{1}{4}\sigma_D^2$. Within-family dominance effects were generated with a mean equal to the among-family dominance effect and a variance of $\frac{3}{4}\sigma_D^2$. All epistasis effects were considered to be within-family, with a mean and variance equal to that of the original population. Environmental effects for all test propagules were generated with the environmental mean and variance associated with trees in the original population.

The results of the polycross simulation were used to select a production population from GCA-tested trees, and to rank trees for positive assortative mating (PAM) schemes used to generate progeny for selection plantations. For the purposes of this study, the simulation used an "unequal" PAM scheme, where each parent ranking in the top 40% was crossed with three other top-ranking trees, the middle 40% each crossed twice, and the bottom 20% excluded from the mating scheme. The simulator also provided the option to generate clonal replicates of test progeny established in selection plantations. The genetic effects within clones remained constant but independent environmental effects were generated for each ramet.

Inbreeding was controlled by a combination of sublining and coancestry controls. Trees in the original breeding population were assigned to sublines (breeding groups) after polycross testing so that the mean breeding value of each subline was approximately equal. From then on, all crossing for advanced-generation selection was performed among trees within the same subline. Using this technique, an out-crossing production population can be assembled at any time since trees selected from different sublines are not related, regardless of the level of inbreeding which may have accumulated within the subline. The simulator imposed a level of coancestry control to minimize the accumulation of inbreeding within the sublines. Phenotypic selection within the test plantations was restricted to a limited number of trees (or clones) from each of the best families in each subline. Coancestry restrictions were as suggested by Fowler (1986): 4 trees were selected from each of the top-ranking families while excluding families which share a half-sib relationship with a previously selected family. These selected trees formed the next breeding population. The best clones tested in the selection plantations may be used for clonal forestry, or they may be used as seed-producing parents in a seed orchard.

Important assumptions

Use of this simulation to compare breeding strategies requires several important assumptions:

1. parents in the initial breeding population are from a large, random-mating population, of regular Mendelian behaviour, and in near linkage equilibrium;
2. all model effects are uncorrelated and normally distributed;
3. selection is based on a single quantitative trait, measured without error;
4. when present, epistasis is due primarily to interactions involving more than two or three loci, otherwise, additive and dominance effects would be seriously contaminated by a fraction of epistasis, leading to overestimation of genetic gain (Mullin and Park 1992); and,
5. C effects, defined by Lerner (1958) as non-random environmental variances common to members of sub-groups within a population, are negligible or absent.

Tested strategies

A hypothetical population of 400 trees was simulated under eight breeding and selection strategies representing a wide array of options utilizing both seedling and clonal testing and deployment techniques. The initial population is the same for all strategies and consists of selections made in family tests. The starting point for the first simulated breeding cycle is therefore analogous to the time of second-generation selection in the NBTIC black spruce or jack pine family tests. The strategies incorporate similar time schedules for activities such as orchard establishment, progeny testing, etc., and all require similar levels of effort. In each case, polycross testing of parents in the breeding population is based on 50 test progeny per parent, for a total testing effort of 20,000 trees in each breeding cycle. The parent trees are ranked for positive assortative mating when the polycross progeny are 4 years old, although in actual practice the field tests would likely be maintained to provide additional information for later roguing of seed orchards and confirmation of parent GCA values.

The pair-mating conducted under the unequal positive assortative mating scheme produces 400 full-sib test families which are established in selection plantations to test a total of 80,000 trees in each breeding cycle. When these plantations are established with seedling material, 200 genotypes are tested for each full-sib family; when the plantations are established with clonal replicates, 40 genotypes from each family are tested with 5 ramets per genotype. The breeding population for the next cycle is formed by selecting the best 4 individual trees or clones from the top-ranking, unrelated full-sib families in each breeding group.

1. Conventional wind-pollinated seed orchard with selection plantations deployed as seedlings

This strategy is analogous to that described by Fowler (1986) for black spruce, with adjustments made in timing to reflect shortened periods for breeding anticipating the use of breeding hall and flower stimulation technology. As a result, the timing given for realization of genetic gain is relatively optimistic. Mating in the orchard is assumed to be random and there is negligible pollen contamination from outside the orchard. Gamete production in the orchard will vary among clones such that the effective population size is half the actual number of clones in the orchard; the minimum effective population size is set at 20, so that 40 selections are required. In order to minimize inbreeding in the orchard, the breeding population will be divided into 20 sublines, and two trees from different families will be selected from each subline for orchard use.

Year	
0	Phenotypic selection of 400 unrelated trees from family tests, one from each of the top 400 families. First cycle only: grafts from each of the best 40 trees are used to establish a clonal seed orchard.
4	Seed production begins on the grafted trees and mating with a 20-tree polymix is carried out as soon as female strobili are available.
8	Polycrossing of 400 trees completed and short-term tests established in nursery with 50 test seedlings per cross.
12	Trees are ranked based on polycross test results and assigned uniformly to 20 sublines (breeding groups). Double-pair mating of 400 trees using unequal positive assortment. Begin establishment of grafted orchard with best 40 polycross-tested parents.
14	Untested clonal seed orchard now in full production and all planting stock now originates from orchard seed. Selection plantations established in field using seedling test stock with 200 test trees per full-sib family.

16 Polycross-tested orchard begins production.

26 Polycross-tested orchard at full production.

28 Selection of 400 trees from the selection plantations (15 years from seed), consisting of top 4 trees from each of the top 5 unrelated full-sib families in each breeding group.

The cycle is then repeated while maintaining the integrity of the original sublines. Establishment of a seed orchard in subsequent breeding cycles will likely be delayed until polycross test results are available for confirmation of best GCA parents. This seed orchard will consist of top polycross-tested tree from each of two unrelated families in each of the 20 sublines, for a total of 40 trees.

2. *Conventional wind-pollinated seed orchard with clonally replicated selection plantations*

This strategy is identical to the previous scheme, with the exception that selection plantations are established with vegetative propagules, using 5 ramets from each of 40 genotypes resulting from each pair mating. Selection of trees for the next breeding population will be based on clone means, and should be more effective than phenotypic selection of individuals used in the previous strategy. This encourages the early establishment of a production orchard before polycross test results are available, opting for early gain rather than the marginal improvement which may result from polycross testing.

3. *Control-pollinated seed orchard with selection plantations deployed as seedlings*

From a breeding standpoint, this strategy is similar to the conventional seed orchard, however, all pollination among parents in the orchard is controlled so that only 20 parents are required to produce the specified effective population size of 20. The original phenotypic selections used for seed production during the first simulated breeding cycle will be replaced on the basis of polycross test results. In subsequent cycles, only polycross tested parents will be used in the orchard. Sublines are again used to control inbreeding, but since pollination is manual, only 2 groups of 200 trees are required to produce unrelated matings in the orchard; pollen from trees in one group will be used to pollinate parents in the other group. Intensive orchard management or vegetative multiplication, or a combination of the two, will reduce the time for control-pollinated orchards to reach full production to 4 years (compared to 10 in conventional orchards).

Year

0 Phenotypic selection of 400 unrelated trees from family tests, one from each of the top 400 families. First cycle only: grafts from each of the top 20 trees are established in a control-pollinated seed orchard; seed production begins.

4 Seed production begins in first-cycle orchard. Mating with a 20-tree polymix is

carried out as soon as female strobili are available.

8 Polycrossing of 400 trees completed and short-term tests established in nursery with 50 test seedlings per cross. Control-pollinated orchards reach full output.

12 Trees are ranked based on polycross test results and assigned uniformly to 2 sublines. Pair mating of 400 trees using unequal positive assortment. Begin replacement of seed-orchard parents based on polycross rankings.

14 Selection plantations established in field (200 test trees per full-sib family).

16 Seed production begins on grafts from polycross-tested parents.

20 All seed production in control-pollinated orchard now originates from polycross-tested parents.

28 Selection of 400 trees from the selection plantations (15 years from seed), consisting of top 4 trees from each of the top 50 unrelated full-sib families in each breeding group.

The cycle is repeated while maintaining the integrity of the sublines. The seed orchard in each subsequent breeding cycle will consist of the top, polycross-tested tree from each of the top 10 full-sib families from each of the 2 sublines, for a total of 20 trees.

4. Control-pollinated seed orchard with clonally replicated selection plantations

Again, this is identical to the previous scheme, with the exception that selection plantations are established with clonal replicates, using 5 ramets from each of the 40 genotypes per full-sib family. Selections based on clone mean performance are more efficient than selection of individual phenotypes so that selections will improve orchard quality even before polycross testing. Further improvement may be expected once polycross evaluations are available.

5. "Family" forestry with selection plantations deployed as seedlings

This scheme attempts to capture some of the dominance effect which is expressed by superior parent combinations. Management of the breeding population is identical to that used for control-pollinated orchards, however, the selection plantations are used to identify superior pair-matings which are then repeated and vegetative multiplication used to produce the required numbers of trees for reforestation.

Year

0 Phenotypic selection of 400 unrelated trees from family tests, one from each of the top 400 families. First cycle only: grafts from each of the top 20 trees are

established in a control-pollinated seed orchard; seed production begins.

4 Seed production begins in first-cycle orchard. Mating with a 20-tree polymix is carried out as soon as female strobili are available.

8 Polycrossing of 400 trees completed and tests established in nursery with 50 test seedlings per cross. Control-pollinated orchards reach full output.

12 Trees are ranked based on polycross test results and assigned uniformly to 2 sublines. Double-pair mating of 400 trees using unequal positive assortment. Begin replacement of seed-orchard parents based on polycross rankings.

14 Selection plantations established in field (200 test trees per full-sib family).

16 Seed production begins on polycross-tested parents.

20 All seed production in control-pollinated orchard originates from polycross-tested parents.

24 Selection of 10 best unrelated full-sib families in each subline (for a total of 20); begin seed production from best families by repeat pair-mating.

28 All planting stock now produced from selected full-sib families. Selection of 400 trees from the selection plantations (15 years from seed), consisting of top 4 trees from each of the top 50 unrelated full-sib families in each breeding group.

Since pair matings occur among trees in the same subline, inbreeding is not under complete control in the production population. The use of coancestry restrictions and large subline size will help to reduce the accumulation of inbreeding effects, and selection within sublines will also tend to favour outcrossed genotypes. The subline structure will be maintained to guarantee outcrossing at any time in the future.

6. "Family" forestry with clonally replicated selection plantations

This scheme is identical to the previous strategy, with the exception that genotypes in selection plantations are replicated clonally. Higher selection efficiency will affect gain from family selection, and will increase the efficiency of phenotypic selection of parent trees for the next breeding population.

7. "Clonal" forestry strategy with mixtures of 20 or 40 clones

Deployment of selected clones in operational plantations will capture gain from both additive and nonadditive genetic effects. Rather than install an additional series of clonal tests, evaluation of candidate clones is based on mean performance of clonally replicated genotypes established in selection plantations. The assumption is made that minimum requirements for diversity of clonal mixtures will require 20 to 40 weakly related clones. It is further assumed that juvenile material will still be available for clonal propagation after completion of field testing; most likely this will require cryopreservation of somatic embryos during the testing period.

Year	
0	Phenotypic selection of 400 unrelated trees from family tests, one from each of the top 400 families. First cycle only: grafts from each of the top 20 trees are established in a control-pollinated seed orchard; seed production begins.
4	Seed production begins in first-cycle orchard. Mating with a 20-tree polymix is carried out as soon as female strobili are available.
8	Polycrossing of 400 trees completed and tests established in nursery with 50 test seedlings per cross. Control-pollinated orchards reach full output.
12	Trees are ranked based on polycross test results and assigned uniformly to 2 sublines. Double-pair mating of 400 trees using unequal positive assortment. Begin replacement of seed-orchard parents based on polycross rankings.
14	Emblings from pair-matings are established in selection plantations (5 ramets from each of 40 genotypes per full-sib family) and somatic embryos of these genotypes placed in cryo-storage.
16	Seed production begins on polycross-tested parents.
20	All seed production in control-pollinated orchard originates from polycross-tested parents.
24	Selection of the best clone in each of the 10 or 20 best unrelated full-sib families in each subline (for a total mixture of 20 or 40 clones). Retrieve somatic embryos of selected clones from cryo-storage and begin clonal propagation.
28	All planting stock now produced from selected clones. Selection of 400 trees from the selection plantations (15 years from seed), consisting of top 4 clones from each of the top 50 unrelated full-sib families in each breeding group.

All deployment in subsequent breeding cycles will be restricted to tested clones. The clone mixture can be adjusted as additional data are collected from the selection plantations, and of course when new tested clones become available from the next breeding cycle. As with the family forestry strategy, the accumulation of inbreeding could degrade performance and coancestry controls are necessary to minimize this. Maintenance of the subline structure provides assurance of the ability to outcross the breeding population as necessary.

TABLE 1. Summary of simulation parameters

Parameter	Fixed or varied	Value(s)
Number of trees in breeding population	Fixed	400
Trees per subline	Strategy dependent	20 for wind-pollinated orchards, 200 for all others
Genetic variances:		
Additive	Fixed	1.0
Dominance	Varied	0, 0.25, 0.5
Epistasis	Varied	0, 0.25, 0.5
Narrow-sense heritability (h^2)	Varied	0.1, 0.2, 0.3, 0.4, 0.5
Polycross pollen mix	Fixed	20 individuals, equal amounts
Polycross test progeny	Fixed	50 per parent, 20,000 total
Selection plantation	Fixed	400 FS families with 200 test plants per family, 80,000 total
Number ramets per genotype	Strategy dependent	1 for seedling strategies, 5 for clonal testing
Number trees selected per family	Fixed	4 from each of best 5 FS families per subline

Comparison of breeding strategies

The simulation was performed for each strategy and for populations exhibiting one of four contrasting patterns of genetic structure. In the first scenario, all genetic variance was assumed to be additive and was set to 1 in the initial population. The other scenarios also assumed additive variance equal to 1, but included additional nonadditive genetic variance. In the first nonadditive case, dominance and epistatic variance in the initial population were each set to 0.25; in the second case, all of the nonadditive variance was composed of epistatic variance and was set to 0.5; and in the final scenario, all of the nonadditive variance was dominance variance and also set to 0.5. The simulation was repeated with different levels of environmental variance, such that narrow-sense heritability varied from 0.1 to 0.5, in increments of 0.1. The variables varied through the test simulations are summarized in Table 1.

The simulation was carried through five breeding cycles. Based on experience with sample test runs, the simulation was repeated 20 times to provide average results which were repeatable. The simulation was programmed using Microsoft FORTRAN 4.1, and generation of random numbers and normal deviates used the RAN2 and GASDEV algorithms, respectively, given by Press *et al.* (1986). The complete source code for the program is reproduced in Appendix II. The program accepts input parameters interactively and generates a summary of the simulation parameters and average results for each breeding cycle, illustrated in Figure 1.

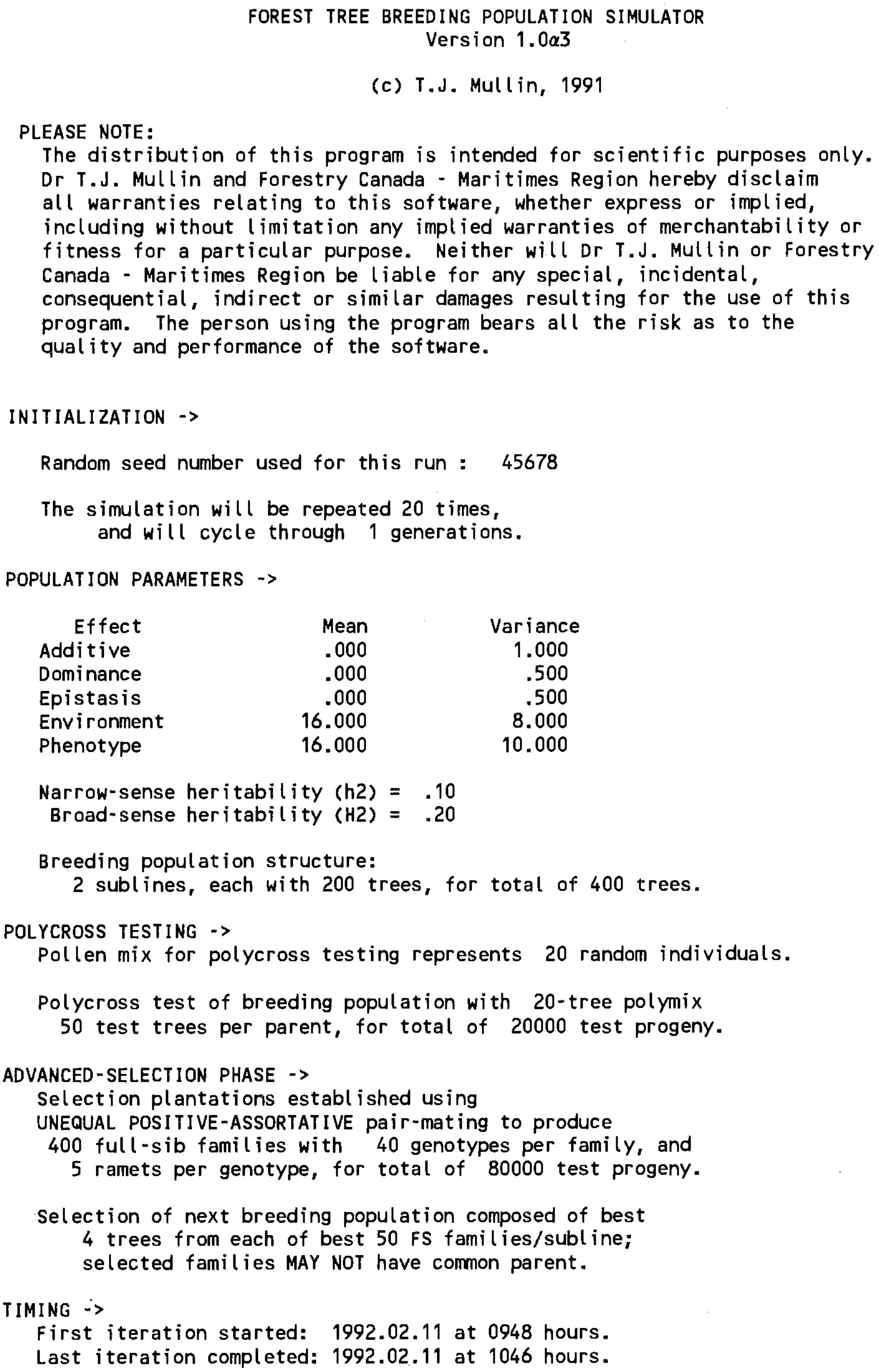
All simulation runs were carried out on an Intel-based 386 personal computer with an 80387 math co-processor. Changes in estimated gain were plotted for each strategy against a 140-year time-line, equivalent to five complete breeding cycles, using a spreadsheet template prepared using Microsoft Excel 3.0. Although gain differences among strategies varied at different points in time, the spreadsheet was used to compare the strategies on the basis of average genetic gain achieved over the 140-year period.

Results

Comparisons of average genetic gain for each strategy are given for each of the genetic variance scenarios in Tables 2A through 2D, respectively. Regardless of genetic variance structure, the genetic potential of material deployed under the control-pollinated orchard strategy was higher than that achievable under ideal pollination conditions in the wind-pollinated orchard. Gain in control-pollinated orchards was 15-19% higher than wind-pollinated orchards when h^2 was 0.1, and this difference rose to 28-29% as h^2 was increased to 0.5. Different patterns of development of these gains over the 140-year period are illustrated in Figure 2 for each genetic variance scenario when h^2 is set at 0.3. It is important to note that deviations from ideal pollination and contamination in wind-pollinated orchards would lead to larger differences in gain.

Under the all-genetic-variance-is-additive scenario described in Table 2A, there is no advantage to repeat-crossing of best families over production of polycross progeny by controlled pollination. Since all of the variance is additive, all of the genetic gain from tested full-sib families will be derived from GCA, and information on this is available directly from the polycross test. The only way to increase gain in this case is to increase selection intensity which, in turn, will decrease the genetic diversity of material deployed to plantations. Clonal selection of the best 40 clones will produce no more gain (generally less) than is available from the control-pollinated orchard strategy using the best 20 parents. Reducing the number of clones to 20 will produce more gain, although the difference is more pronounced at low heritabilities. Using the best 20 clones produces 9% greater gain than the control-pollinated orchard with clonally replicated tests when h^2 is 0.1, but only 5% more gain when h^2 increases to 0.5. Clonal replication of material in test plantations was clearly advantageous under this scenario, producing 7-11% more gain for the wind-pollinated orchard strategy, and 4-9% more gain for the control-pollinated orchard. One would expect that the optimum number of ramets at different heritabilities would involve a different trade-off between numbers of tested genotypes and selection efficiency. In this case, 5 ramets per genotype resulted in the largest gain difference when h^2 was 0.2.

A somewhat different pattern emerged when nonadditive variance was introduced (Tables 2B through 2D). The control-pollinated orchard again gave a dramatic improvement over the gain achieved by an ideal wind-pollinated orchard; however, the use of clonal replicates



```
                     FOREST TREE BREEDING POPULATION SIMULATOR
                                 Version 1.0α3

                              (c) T.J. Mullin, 1991

   PLEASE NOTE:
     The distribution of this program is intended for scientific purposes only.
     Dr T.J. Mullin and Forestry Canada - Maritimes Region hereby disclaim
     all warranties relating to this software, whether express or implied,
     including without limitation any implied warranties of merchantability or
     fitness for a particular purpose.  Neither will Dr T.J. Mullin or Forestry
     Canada - Maritimes Region be liable for any special, incidental,
     consequential, indirect or similar damages resulting for the use of this
     program.  The person using the program bears all the risk as to the
     quality and performance of the software.


  INITIALIZATION ->

     Random seed number used for this run :   45678

     The simulation will be repeated 20 times,
          and will cycle through  1 generations.

  POPULATION PARAMETERS ->

        Effect                 Mean            Variance
     Additive                  .000              1.000
     Dominance                 .000               .500
     Epistasis                 .000               .500
     Environment             16.000              8.000
     Phenotype               16.000             10.000

     Narrow-sense heritability (h2) =  .10
      Broad-sense heritability (H2) =  .20

     Breeding population structure:
        2 sublines, each with 200 trees, for total of 400 trees.

  POLYCROSS TESTING ->
     Pollen mix for polycross testing represents  20 random individuals.

     Polycross test of breeding population with  20-tree polymix
       50 test trees per parent, for total of  20000 test progeny.

  ADVANCED-SELECTION PHASE ->
     Selection plantations established using
     UNEQUAL POSITIVE-ASSORTATIVE pair-mating to produce
      400 full-sib families with   40 genotypes per family, and
        5 ramets per genotype, for total of  80000 test progeny.

     Selection of next breeding population composed of best
         4 trees from each of best 50 FS families/subline;
         selected families MAY NOT have common parent.

  TIMING ->
     First iteration started:  1992.02.11 at 0948 hours.
     Last iteration completed: 1992.02.11 at 1046 hours.
```

FIGURE 1. Sample output generated from Forest Tree Breeding Population Simulator. The first page summarizes the input parameter supplied by the user to control the simulation. The next two pages summarize effects and variances, averaged over 20 iterations, found in the breeding and production populations after one generation.

```
AVERAGE SIMULATION RESULT (with 1 SD in parentheses) FOR 20 ITERATIONS

GENERATION #1

    Breeding population of  400 trees:

     Effect            Mean          Variance        Maximum         Minimum
    Additive         .011( .047)   1.007( .077)    3.003( .368)   -2.886( .310)
    Dominance       -.005( .029)    .488( .039)    2.035( .251)   -2.074( .311)
    Epistasis        .000( .032)    .493( .023)    2.063( .201)   -2.097( .289)
    Environment    15.990( .195)   8.049( .441)   24.532( .845)    7.547(1.062)
    Phenotype      15.996( .198)   9.964( .664)   25.047(1.223)    6.454(1.412)

UNTESTED Production Population ->

    Seed orchard or clone mixture composed of   20 best untested phenotypes:

     Effect            Mean          Variance        Maximum         Minimum
    Additive         .565( .246)   1.001( .317)    2.326( .480)   -1.344( .460)
    Dominance        .326( .135)    .458( .137)    1.669( .352)    -.902( .352)
    Epistasis        .277( .143)    .492( .149)    1.580( .297)   -1.060( .384)
    Environment    21.212( .426)   2.640( .760)   24.526( .862)   18.241( .687)
    Phenotype      22.380( .392)   1.273( .588)   25.047(1.223)   21.161( .324)

    Seed orchard or clone mixture composed of   40 best untested phenotypes:

     Effect            Mean          Variance        Maximum         Minimum
    Additive         .512( .155)    .960( .207)    2.670( .458)   -1.561( .406)
    Dominance        .248( .107)    .481( .098)    1.757( .340)   -1.208( .311)
    Epistasis        .270( .105)    .463( .115)    1.701( .238)   -1.237( .390)
    Environment    20.437( .302)   2.794( .673)   24.532( .845)   17.207( .477)
    Phenotype      21.466( .329)   1.547( .507)   25.047(1.223)   20.083( .306)

POLYCROSS-TESTED Production Population ->

    Seed orchard or clone mixture composed of   20 best polycross-tested trees:

     Effect            Mean          Variance        Maximum         Minimum
    Additive        1.552( .190)    .488( .202)    2.896( .450)     .254( .462)
    Dominance       -.094( .132)    .439( .169)    1.248( .505)   -1.349( .405)
    Epistasis        .040( .153)    .530( .162)    1.330( .255)   -1.267( .396)
    Environment    16.004( .607)   6.886(2.485)   20.725(1.571)   10.584(1.261)
    Phenotype      17.502( .636)   8.466(3.149)   22.746(1.482)   11.546(1.430)

    Seed orchard or clone mixture composed of   40 best polycross-tested trees:

     Effect            Mean          Variance        Maximum         Minimum
    Additive        1.310( .146)    .558( .111)    2.993( .374)    -.212( .321)
    Dominance       -.076( .093)    .468( .124)    1.452( .387)   -1.562( .380)
    Epistasis        .012( .124)    .498( .123)    1.459( .280)   -1.535( .280)
    Environment    16.116( .457)   7.646(1.448)   22.080(1.228)    9.781(1.277)
    Phenotype      17.362( .494)   9.063(1.826)   23.501(1.290)   10.474( .950)
```

FIGURE 1. *continued*

```
Deployment of TESTED FAMILIES ->

    Full-sib family mixture composed of   20 best families:

      Effect              Mean          Variance        Maximum         Minimum
    Additive         1.612( .102)    .455( .116)   3.786( .430)   -.371( .251)
    Dominance        -.042( .100)    .469( .130)   2.144( .329)  -2.192( .423)
    Epistasis         .049( .129)    .501( .125)   2.230( .399)  -2.141( .405)
    Environment     16.124( .050)   1.595( .076)  20.052( .541)  12.129( .415)
    Phenotype       17.743( .196)   2.900( .267)  23.134( .707)  12.329( .594)

    Full-sib family mixture composed of   40 best families:

      Effect              Mean          Variance        Maximum         Minimum
    Additive         1.284( .082)    .503( .113)   3.786( .430)   -.942( .371)
    Dominance        -.046( .093)    .470( .130)   2.305( .492)  -2.332( .393)
    Epistasis         .053( .133)    .497( .129)   2.422( .461)  -2.300( .346)
    Environment     16.118( .032)   1.606( .055)  20.448( .469)  11.883( .434)
    Phenotype       17.409( .171)   2.947( .202)  23.134( .707)  11.547( .672)


Deployment of TESTED CLONES ->

    Clone mixture composed of best clone from each of   20 best families:

      Effect              Mean          Variance        Maximum         Minimum
    Additive         2.016( .204)    .471( .161)   3.330( .350)    .799( .280)
    Dominance         .547( .242)    .401( .124)   1.763( .405)   -.652( .357)
    Epistasis         .673( .243)    .417( .176)   1.853( .428)   -.450( .260)
    Environment     18.090( .221)    .857( .280)  19.785( .632)  16.335( .604)
    Phenotype       21.327( .256)    .743( .327)  23.134( .707)  20.056( .325)

    Clone mixture composed of best clone from each of   40 best families:

      Effect              Mean          Variance        Maximum         Minimum
    Additive         1.676( .168)    .500( .127)   3.330( .350)    .315( .244)
    Dominance         .541( .221)    .397( .123)   1.950( .446)   -.785( .336)
    Epistasis         .646( .246)    .417( .120)   2.049( .413)   -.758( .334)
    Environment     18.161( .180)    .845( .183)  20.204( .547)  16.217( .515)
    Phenotype       21.024( .250)    .721( .184)  23.134( .707)  19.453( .293)
```

FIGURE 1. *continued*

TABLE 2A. Comparisons of average genetic gain over 140 years achieved by various breeding strategies when all genetic variance is additive and σ^2_A in the initial population is equal to 1

Heritability		Breeding strategy							
		Wind-pollinated orchard		Control-pollinated orchard		Family forestry		Clonal forestry	
h^2	H^2	Seedling test	Clonal replicates	Seedling test	Clonal replicates	Seedling test	Clonal replicates	Best 20 clones	Best 40 clones
0.1	0.1	1.85	1.97 (+7%)	2.17 (+18%)	2.34 (+27%)	2.28 (+24%)	2.36 (+28%)	2.56 (+38%)	2.35 (+27%)
0.2	0.2	1.97	2.18 (+11%)	2.37 (+20%)	2.58 (+31%)	2.42 (+23%)	2.53 (+29%)	2.75 (+40%)	2.52 (+28%)
0.3	0.3	2.06	2.20 (+7%)	2.54 (+23%)	2.67 (+30%)	2.54 (+24%)	2.58 (+26%)	2.83 (+37%)	2.59 (+26%)
0.4	0.4	2.11	2.25 (+7%)	2.63 (+25%)	2.76 (+31%)	2.61 (+24%)	2.65 (+26%)	2.91 (+38%)	2.68 (+27%)
0.5	0.5	2.14	2.33 (+9%)	2.74 (+28%)	2.86 (+34%)	2.68 (+25%)	2.73 (+28%)	3.00 (+41%)	2.77 (+30%)

NOTE: Gain figures are given in variance units with percent difference compared to the wind-pollinated orchard with seedling tests given in parentheses.

TABLE 2B. Comparisons of average genetic gain over 140 years achieved by various breeding strategies when the genetic variance in the initial population has both additive and nonadditive components, such that $\sigma^2_A = 1$, $\sigma^2_D = 0.25$, and $\sigma^2_I = 0.25$

Heritability		Breeding strategy							
		Wind-pollinated orchard		Control-pollinated orchard		Family forestry		Clonal forestry	
h^2	H^2	Seedling test	Clonal replicates	Seedling test	Clonal replicates	Seedling test	Clonal replicates	Best 20 clones	Best 40 clones
0.1	0.15	1.86	1.90 (+2%)	2.13 (+15%)	2.24 (+21%)	2.49 (+34%)	2.53 (+36%)	3.50 (+88%)	3.30 (+78%)
0.2	0.30	1.93	2.02 (+5%)	2.36 (+22%)	2.53 (+31%)	2.74 (+42%)	2.77 (+43%)	3.94 (+104%)	3.70 (+91%)
0.3	0.45	2.03	2.08 (+3%)	2.54 (+25%)	2.52 (+24%)	2.94 (+45%)	2.81 (+38%)	4.16 (+105%)	3.92 (+93%)
0.4	0.60	2.09	2.10 (+0%)	2.63 (+26%)	2.62 (+25%)	3.06 (+46%)	2.93 (+40%)	4.37 (+109%)	4.13 (+97%)
0.5	0.75	2.16	2.12 (-2%)	2.77 (+28%)	2.75 (+27%)	3.21 (+48%)	2.03 (+40%)	4.56 (+111%)	4.31 (+99%)

NOTE: Gain figures are given in variance units with percent difference compared to the wind-pollinated orchard with seedling tests given in parentheses.

TABLE 2C. Comparisons of average genetic gain over 140 years achieved by various breeding strategies when the genetic variance in the initial population has both additive and nonadditive components, such that $\sigma^2_A = 1$ and all of the nonadditive variance is epistatic variance where $\sigma^2_I = 0.5$

Heritability		Breeding strategy							
		Wind-pollinated orchard		Control-pollinated orchard		Family forestry		Clonal forestry	
h^2	H^2	Seedling test	Clonal replicates	Seedling test	Clonal replicates	Seedling test	Clonal replicates	Best 20 clones	Best 40 clones
0.1	0.15	1.86	1.94 (+4%)	2.20 (+19%)	2.26 (+22%)	2.31 (+24%)	2.32 (+25%)	3.51 (+89%)	3.27 (+76%)
0.2	0.30	1.96	2.09 (+6%)	2.34 (+19%)	2.49 (+27%)	2.41 (+23%)	2.46 (+26%)	3.91 (+99%)	3.66 (+87%)
0.3	0.45	2.02	2.12 (+5%)	2.56 (+27%)	2.57 (+27%)	2.57 (+27%)	2.51 (+24%)	4.04 (+100%)	3.81 (+89%)
0.4	0.60	2.15	2.16 (+0%)	2.66 (+24%)	2.63 (+22%)	2.62 (+22%)	2.55 (+19%)	4.12 (+92%)	3.88 (+81%)
0.5	0.75	2.19	2.18 (-0%)	2.81 (+29%)	2.74 (+25%)	2.73 (+25%)	2.64 (+21%)	4.24 (+94%)	4.01 (+83%)

NOTE: Gain figures are given in variance units with percent difference compared to the wind-pollinated orchard with seedling tests given in parentheses.

TABLE 2D. Comparisons of average genetic gain over 140 years achieved by various breeding strategies when the genetic variance in the initial population has both additive and nonadditive components, such that $\sigma^2_A = 1$ and all of the nonadditive variance is dominance variance where $\sigma^2_D = 0.5$

Heritability		Breeding strategy							
		Wind-pollinated orchard		Control-pollinated orchard		Family forestry		Clonal forestry	
h^2	H^2	Seedling test	Clonal replicates	Seedling test	Clonal replicates	Seedling test	Clonal replicates	Best 20 clones	Best 40 clones
0.1	0.15	1.80	1.93 (+7%)	2.13 (+18%)	2.28 (+26%)	2.72 (+51%)	2.79 (+55%)	3.48 (+93%)	3.27 (+81%)
0.2	0.30	2.03	2.15 (+6%)	2.17 (+7%)	2.34 (+15%)	2.77 (+36%)	2.89 (+42%)	3.68 (+81%)	3.51 (+73%)
0.3	0.45	2.05	2.14 (+4%)	2.50 (+22%)	2.58 (+26%)	3.25 (+58%)	3.20 (+56%)	4.05 (+97%)	3.82 (+86%)
0.4	0.60	2.09	2.12 (+2%)	2.64 (+26%)	2.68 (+28%)	3.51 (+68%)	3.31 (+58%)	4.22 (+102%)	3.98 (+90%)
0.5	0.75	2.20	2.17 (-1%)	2.75 (+25%)	2.77 (+26%)	3.64 (+66%)	3.39 (+54%)	4.32 (+96%)	4.08 (+85%)

NOTE: Gain figures are given in variance units with percent difference compared to the wind-pollinated orchard with seedling tests given in parentheses.

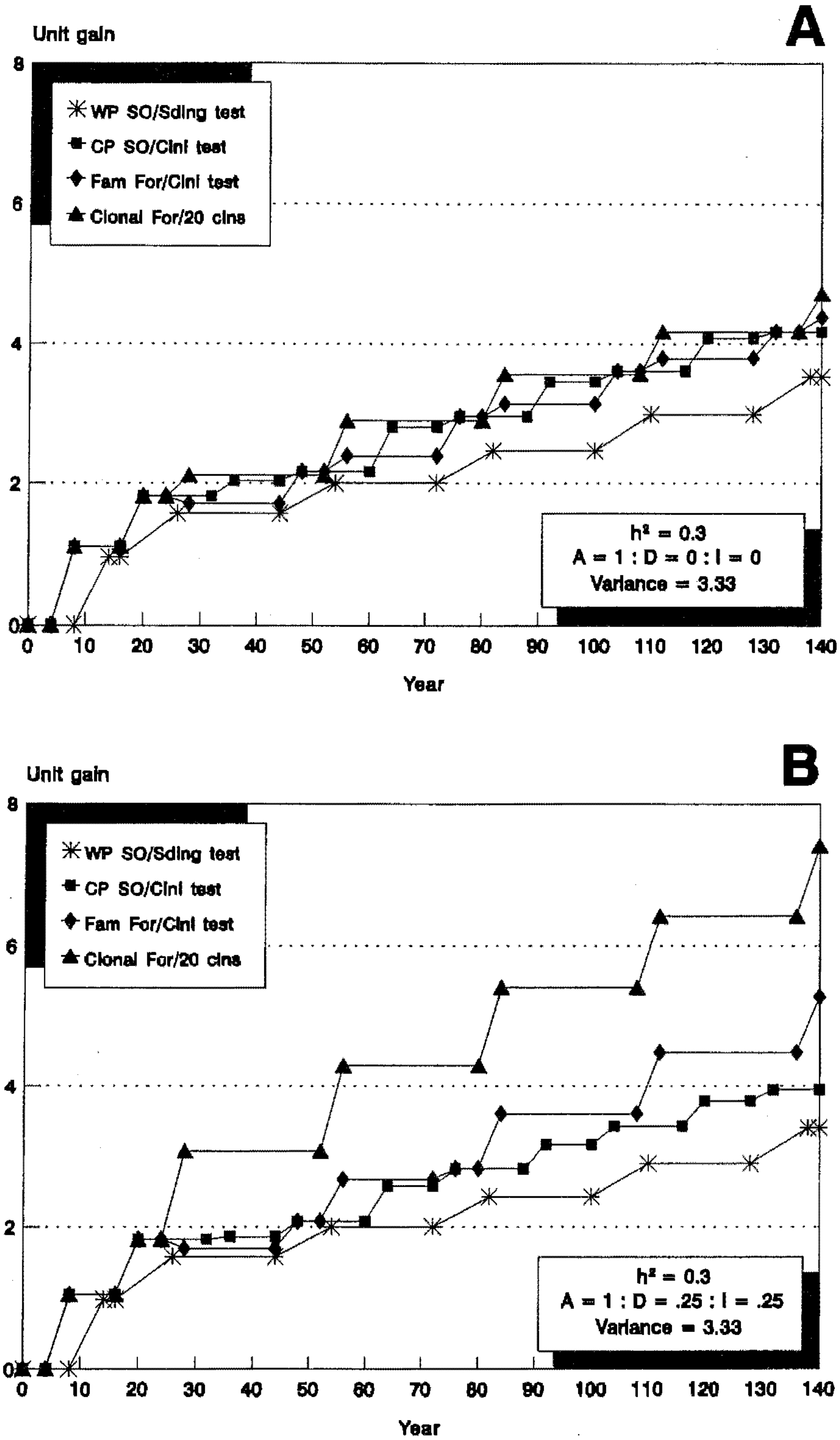
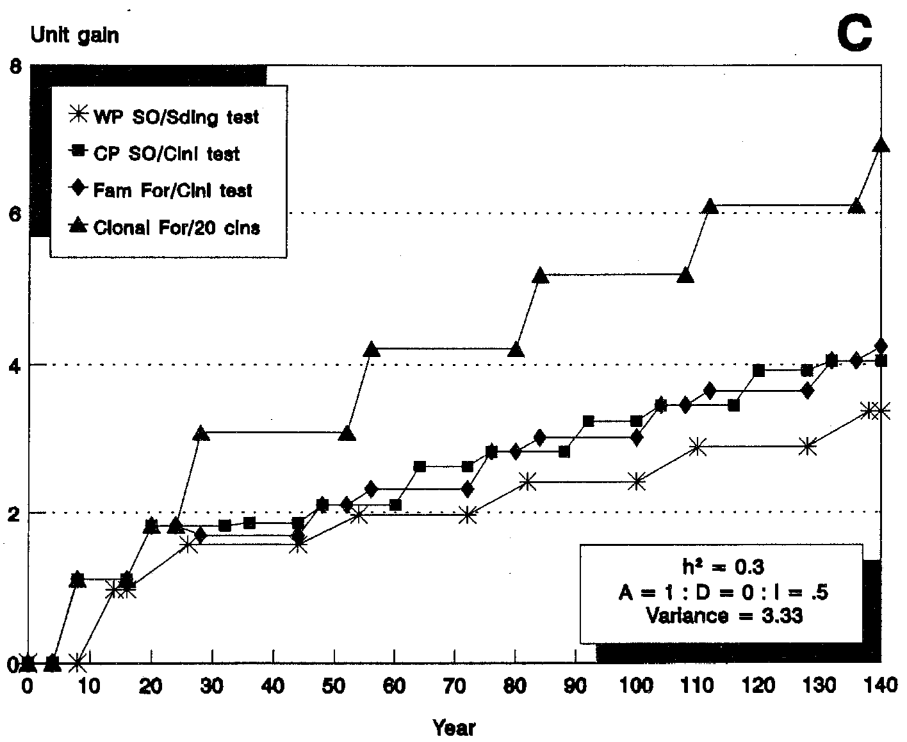


FIGURE 2. Comparison of genetic gain achieved over 140 years by various improvement strategies when initial h^2 is 0.3 and genetic variance structure is composed entirely of additive variance (**A**), and with additional nonadditive variance derived equally from epistasis and dominance (**B**) or exclusively from epistasis (**C**) or dominance (**D**).



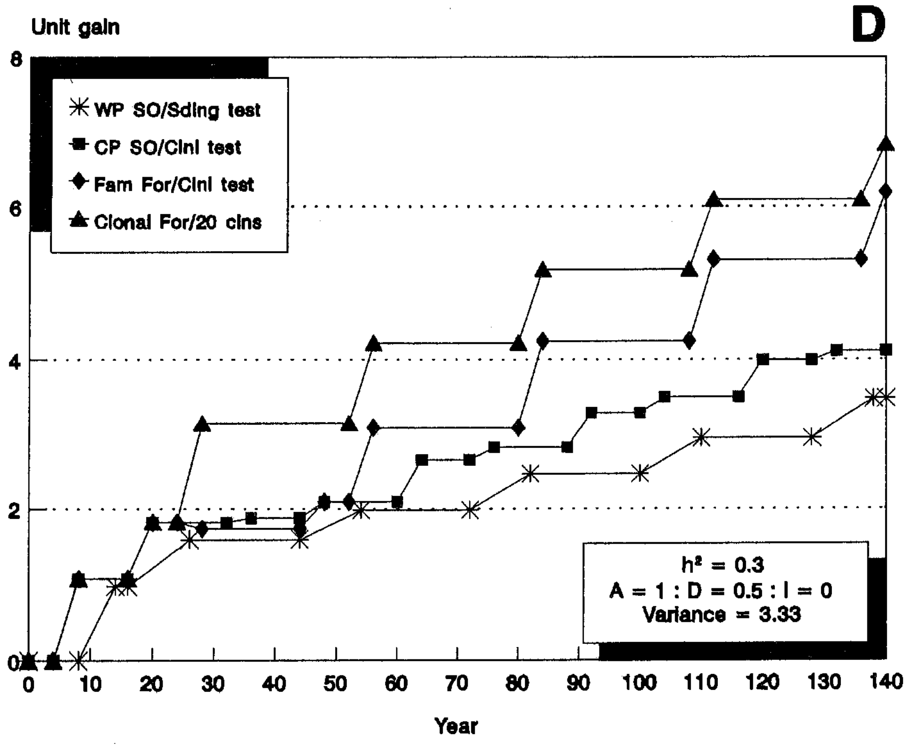


FIGURE 2. *continued*

resulted in less improvement over the gain possible through seedling-based tests. Generally, the use of clonal replicates did not result in any additional gain at heritabilities greater than 0.2, and actually produced less gain when a portion or all of the nonadditive variance was due to epistasis.

As predicted, both the family forestry and clonal forestry strategies were able to capitalize on available nonadditive variance to achieve additional gain. The greatest gains from family forestry were obtained when all of the nonadditive variance was due to dominance. When all of the nonadditive variance was due to epistasis, gains from family forestry with seedling tests were about the same as those achieved under the all-genetic-variance-is-additive case. Although nonadditive variance only made up one third of the total genetic variance, the genetic gains from the clonal forestry strategy when limited to 20 clones was virtually double that possible in the control-pollinated orchard, slightly less at heritabilities less than 0.3, and slightly more at heritabilities greater than 0.3.

In all of the genetic variance scenarios, increasing the number of clones to 40 only resulted in a 5-8% reduction in the genetic gain compared to using 20 clones. This small reduction was observed despite the restriction on relatedness which required that clones be selected from different full-sib families.

Assessment of gains from alternative strategies

The simulation results suggest some important implications for the use of clones in breeding and reforestation programs:

1. The use of a control-pollinated orchard to produce polycross families can achieve average genetic gains in the order of 15 to 30% higher than those estimated for a wind-pollinated seed orchard under ideal conditions, with the greatest difference occurring at higher heritabilities. In practice, the difference between the strategies could be much greater as it will be very difficult to achieve ideal management of the pollen pool in the wind-pollinated orchard. These gains can be realized without the use of clonal techniques, provided that sufficient quantities of control-pollinated seed can be produced. Here, the feasibility and cost of producing large quantities of control-pollinated seed must be balanced against the feasibility and cost of multiplying genotypes by cloning. The technology for each of these approaches is under rapid development and the ideal balance may shift dramatically as innovations become operational and cost reductions are realized.

2. The potential for clonal replicates to increase test efficiency is influenced by the heritability for the trait and particularly by the proportion of genetic variance that is nonadditive. When all of the genetic variance is additive, using clonal replicates in test plantations will increase the average genetic gain, and will be especially effective at lower heritabilities. However, the benefits of clonal replication will be eroded by the proportion of genetic variance that is nonadditive. This erosion will be particularly severe when much of the nonadditive variance is due to epistasis.

3. Where deployment of tested clones is feasible, clonal selection can be integrated with advancement of additive effects in the breeding population to produce higher average genetic gains, particularly when nonadditive variance is substantial. Clonal selection is an option whenever clonal replicates are used in selection plantations, provided that juvenile donor material is adequately stored so that selected clones can be propagated successfully. As indicated earlier, clonal replicates are less effective and sometimes inferior to seedling tests when substantial nonadditive variance is present. However, it is under these same variance conditions that clonal selection is most effective and the net result is a substantial increase in average genetic gain.

Unfortunately, we have little information for any of our important species regarding the level of nonadditive genetic variance for important traits, and even less information concerning the breakdown of dominance and epistatic components. Yet, as demonstrated by the simulation results, this information is critical for decisions regarding the integration of clonal techniques in breeding programs.

Conifers commonly used in large reforestation programs tend to be early successional, pioneering species. It has been suggested in the literature that additive variance would be far more important than dominance variance for growth traits in such species (Rehfeldt and Lester 1969). However, there are indications that dominance variance, which is often minimal for growth traits in young plantations, may increase as trees become larger and inter-tree competition increases (Boyle 1987a, 1987b). Most estimates of genetic variances in forest trees have assumed epistasis to be absent, although its presence could introduce serious bias to estimates of additive and dominance variance (Mullin and Park 1992). Very few direct estimates of epistasis have been made for traits in forest trees, although a clonal study in Nova Scotia reported that up to 35% of the genetic variance for 5-year height growth in black spruce may be due to epistasis (Mullin *et al.* 1992). In another young clonal test in radiata pine, the standard additive-dominance genetic model failed to account for the observed clonal variance for height growth, which was three times larger than expected; one of the explanations proposed was that epistatic variances had caused the clonal variance estimates to be much higher than expected (King and Johnson 1991).

The gains from tree improvement are normally described in terms of genetic gain, although geneticists are frequently cautious and conservative when making predictions of expected gain. The ultimate objective of any tree breeding strategy is the improvement of yield and quality of planted stands; yet breeders are rarely able to evaluate their selections at harvest age. Many estimates of gain are based on assessment of improvement in early height growth. Fortunately, later evaluations often indicate that improvement in volume growth and overall stand value is, in fact, much higher.

Genetic gain is a function of variance structure and selection intensity. These parameters were incorporated in the simulation exercise reported earlier, and alternative strategies compared in terms of relative improvement in a given population. The simulation technique does not account for differences in genetic correlation between assessment traits at young age and mature traits of real commercial importance, and different patterns may well emerge for seedling and clonal test materials. There are also some indications that clonal planting stock may even produce additional non-genetic gain resulting from physiological differences between seedling and cloned planting stock (Arnold and Gleed 1985; Gemmel *et al.* 1991; Menzies *et al.* 1991).

If gains from tree breeding strategies which use seedlings are imprecise, then those for clonal strategies are that much more uncertain. Those strategies which use cloning to amplify seed from controlled crosses strive to capture gains from increased genetic efficiency over wind-pollinated orchards, and hope that additional effects due to cloning are minimal, or perhaps positive. Clonal selection strategies hope to capture nonadditive variances which have been estimated for only a couple of our species: tamarack (Park and Fowler 1987) and black spruce (Mullin *et al.* 1992).

Although absolute gain figures are simply not available, it seems likely that, under realistic variance scenarios, controlled pollination combined with cloning could result in gains which are *double* those obtainable from inefficient wind-pollinated orchards, and clonal selection could result in additional gain. Until more specific data are available, it might be reasonable, at least for purposes of economic comparisons, to assume that conventional seed-orchard approaches will yield a conservative 10% volume gain in the second generation, and that control-pollinated orchards and clonal selection strategies might achieve at least 15% and 20% volume gains, respectively.

Evaluating costs of alternative strategies

One would expect that, because tree improvement costs are incurred earlier in the harvest cycle, uncertainty of cost would be less than for estimates of future benefits (Thomson 1989). Unfortunately, costs associated with many of the strategies considered in this report are likely to change as a result of rapid, ongoing changes in technology. Even rooting of juvenile cuttings, the most well developed cloning method for spruce, has produced cost estimates which vary widely, although there seems to be a tendency for costs to fall as experience is gained and operations are expanded to a larger scale. However, even for rooted cuttings, which are highly labour intensive, costs are not available for operations larger than a few million, and the techniques have not become operational for many conifer species such as jack pine.

This study considered four areas where alternative seedling and clonal strategies might differ in cost: *(i)* breeding and testing; *(ii)* production of improved genetic material; *(iii)* nursery propagation of planting stock; and *(iv)* plantation establishment and management. Cost estimates for each of these components are discussed and form the basic input to the financial analysis procedure developed during the study.

Breeding and testing

The pursuit of genetic gain through recurrent selection in advanced generations is common to all breeding strategies. This will normally involve polycross testing of selected parents to verify genetic quality, followed by controlled crossing among selected parents to produce progeny for establishment in selection plantations. The method of deployment of planting stock has no bearing on the cost of these operations.

If clonal selection is to be used to pursue additional nonadditive gains within a breeding cycle, an additional screening operation is required. Capturing these additional effects contributes nothing to the advancement of gain in the next cycle, and this leads to problems when integrating clonal forestry with management of breeding populations (Burdon 1986, 1989, 1991). It is clear that screening of clonal material will either raise the total cost of testing, or will come at the expense of efficient advancement of the breeding population. Since resources available to breeding operations will normally be constrained, one would expect that clonal testing will likely compete for the same resources used for advancing the breeding population. Obviously, the additional returns from clonal selection must not only compensate for higher costs of deployment, but must also compensate for lost efficiency in testing for advancement of the breeding population.

In the simulations reported earlier, the total breeding effort was held constant, while clonal testing was integrated with the selection plantation phase. Clone-site interactions were regarded as unimportant, and the level of clonal replication was sufficient to achieve gains from clonal selection and often contributed to greater efficiency in advancing the breeding population. In practice, we might expect that additional replication may be required to resolve interaction variances, or perhaps as a legislated requirement designed to ensure biological safety. Such requirements could raise the cost of testing for clonal forestry by a substantial, but as yet undetermined, amount.

When spread over the operational production of planting stock, the contribution of breeding to the cost of reforestation is generally considered to be small. In this report, breeding activities are assumed to be relatively intensive and contribute $5 per thousand to the cost of planting stock.

Production of improved genetic material

The most significant differences in costs among the strategies considered in this study are related to management of the production population and nursery propagation of the planting stock. Current orchard production costs experienced by NBTIC cooperators are, for the most part, confidential, although reasonable estimates are available from several published sources. On the other hand, production costs for alternative control-pollinated orchards and clonal strategies are very difficult to estimate with any degree of accuracy due to lack of experience and the early stage of development of some of the technologies. In the following sections, the current status of cost estimates is reviewed and, where possible, related to the cost of conventional seed-orchard and nursery operations.

Seed orchards - conventional

Costs of production in wind-pollinated seed orchards can, of course, vary widely depending on the species and the productivity of the orchard. Considered separately from the costs of breeding and seed collection, seed-orchard management entails a wide range of operational costs, including land acquisition, site preparation, irrigation, fencing, propagation and establishment of orchard stock, protection, soil amendments, and crop monitoring. While these costs are spread over the average production of the orchard throughout its lifespan, the contribution of these costs to plantation establishment is also strongly influenced by the efficiency of seed usage by the production nursery (South 1986, 1987).

Calculation methods vary, but estimates in the literature evaluate the contribution of seed orchard costs to planting stock production to be in the neighbourhood of $8-15 per thousand (Arnold 1990; McKenney *et al.* 1988; Talbert *et al.* 1985). Allowing for conservative evaluation of additional costs which may be experienced in Maritime orchards, a working cost estimate in the range of $10-20 might be appropriate. The calculations in this report assume that seed-orchard costs contribute $15 per thousand to the cost of planting stock.

Seed orchards - alternative designs

In recent years, several modifications to the classical Syrach Larsen orchard have been proposed and prototypes established. All are characterized by an attempt to achieve higher seed yields with more favourable pollination conditions. The first proposal by Sweet and Krugman (1977) described separate male and female orchards with controlled pollination. The concept of "meadow" orchards, with trees established at ever-increasing densities, was further developed in New Zealand where the first commercial-scale installation was established in 1987 (Arnold 1990). Most recently, the New Zealanders have developed aqueous pollination systems which achieve parental control without the use of isolation bags (Sweet *et al.* 1990) and further breakthrough refinements are now in press (G. Sweet, pers. comm.).

Given the changing state of control-pollinated orchard technology, cost comparisons quickly become outdated and must be viewed with caution. In New Zealand, control-pollinated seed was commercially available in 1989 for about 10x the cost of conventional wind-pollinated orchard seed (Arnold 1990). However, costs are expected to drop substantially, with controlled-pollinated seed from older-style orchards and "meadow" orchards stabilizing at about 5.2x and 3.6x the cost of conventional orchard seed, respectively. When controlled pollination is carried out without isolation, the price is expected to drop to about double the cost of conventional orchard seed, or about $20-40 per thousand plantable trees.

Proponents of indoor, containerized seed orchards feel that similar costs can be achieved by producing seed on intensively managed ramets growing under controlled conditions, and that production levels can be increased rapidly to meet the entire reforestation requirement at reasonable cost (Ross *et al.* 1986; S. Ross, pers. comm.). Certainly, a controlled environment has a clear advantage when it comes to using treatments such as heat, moisture stress, and photoperiod control as a means of stimulating seed production, and would probably enhance the efficiency of gibberellin treatments and aqueous pollen application.

One way or another, it appears that improved orchard technology will make it possible to produce seed of known parentage, for about double the cost of managing conventional wind-pollinated orchards. The main areas of uncertainty appear to be the scaling-up problems and the time required to reach full production.

Management of clonal donor material

The strategies addressed in this study which rely on clonal deployment of planting stock, do not require the management of a large seed-orchard production population. Even if seeds from controlled crosses are used as the starting material, multiplication rates of 50-100x can be achieved by the most crude cloning system, requiring a very small initial amount of seed material. There is however, a requirement for continuing management of clonal donor material. In the case of rooted cuttings, this would be a stool bed where hedged plants are managed as a source of cuttings. For micropropagation and embryogenic systems, tissue must be maintained under suitable culture conditions, or placed in cryo-storage.

Many authors consider these costs to be insignificant, or include them as part of the cost of producing clonal planting stock. McKenney *et al.* (1988) recognized that repeat crossing and maintenance of donor material could be relatively expensive for a small program; up to $10 per thousand plantable trees. However, for planting programs larger than 500 ha per year, these costs should remain constant at about $5 per thousand.

Nursery propagation of planting stock

Most of the planting stock produced in New Brunswick is grown as containerized seedlings; very little is produced as bareroot stock, due to higher production and planting costs. Procedures vary among nurseries and species, but most container-grown trees are started from seed in heated greenhouses and spend at least the first portion of their nursery life in a controlled environment. Accounting procedures vary among nurseries, particularly in terms of how capital costs are assigned to stock output, but general production costs are reported in the range of $135 to $170 per thousand, with $150 as a median figure.

If production costs for seedling stock are poorly documented, then costs for clonally produced planting stock are almost nonexistent and tremendously varied, as illustrated in Table 3. Relatively few estimates are based on actual operational production experience. Black spruce steckling programs in Quebec and Ontario have indicated that their clonal stock produced from juvenile rooted cuttings costs in the range of 3.5 to 4.3x the cost of normal seedling stock. However, both of these programs are limited to about 1 million stecklings per year (Rogers 1990; M. Campagna, pers. comm.) and are using expensive facilities which presumably have a higher capacity.

TABLE 3. Comparison of vegetative propagation costs

Species	Location	Cost per 1000 plants Stecklings	Cost per 1000 plants Micropropagation	Source
Populus tremuloides	USA	US$320-390	US$780-880	Hall *et al.* 1990
Eucalyptus spp.	France		3, 000F (2x cost of seedlings)	Franclet and Boulay 1983
	USA		US$140	Mascarenhas *et al.* 1988
Pinus radiata	New Zealand	NZ$223 (5.6x price of seedlings)		Arnold and Gleed 1985
			7 to 10x cost of seedlings	Smith 1986
			projected NZ$250-300	Aitken-Christie and Jones 1987
		NZ$87 (1.7x cost of seedlings)	NZ$450	Menzies 1985
Picea abies	Russia	25% less than bareroot transplants		Rutkovskii and Kharina 1987
	Germany	1.2 to 1.5x cost of transplants		Kleinschmit and Schmidt 1977
	Sweden	2x cost of seedlings		Bentzer 1986
		1.6 to 1.7x cost of seedlings		B. Bentzer, pers. comm. 1991
Picea sitchensis	U.K.	UK£13-50 (1.8 to 3.6x cost of seedlings)		Gill 1983
Various conifers	U.K.	UK£57-120	UK£80-300	Dixon 1987
Juniperus spp.	USA	US$260		Badenhop 1984
		US$131		Bluhm and Burt 1983
Picea mariana	Ontario	$600+ contract price $325-350 OMNR $203 Orono est. (seedlings = $170)		McKenney *et al.* 1988
	Quebec	$650 (4.3x cost of seedlings)		M. Campagna, pers. comm. 1991
	Nova Scotia	1.5 to 3x cost of seedlings		B. White, pers. comm. 1989

There is a trend towards lower costs associated with programs which have gained practical experience and produce larger quantities of steckling stock. In Nova Scotia, juvenile cuttings were used in the mid-1980s to amplify limited quantities of black spruce seed for planting on the highlands of Cape Breton. Annual production of black spruce stecklings reached 2.3 million at an estimated cost of 1.5 to 3x the cost of container seedlings with costs continuing to decrease as the program was phased out (B. White and K. Thomas, pers. comm.). In Sweden, Hilleshög has considerable experience in the production of steckling stock for Norway spruce (*Picea abies* [L.] Karst.) on a commercial scale. In the mid-1980s, Hilleshög reported that steckling costs were about double those of comparable seedling stock (Bentzer 1986). Since then, annual production has increased to about 3 million and prices for stecklings now run 60 to 70% higher than seedling stock (B. Bentzer, pers. comm.). Other nurseries in Germany and Ontario with considerable experience in steckling production have even reported cost estimates for rooted cuttings as low as 20% higher than regular seedlings (Kleinschmit and Schmidt 1977; McKenney *et al.* 1988).

Production systems are constantly changing and operational programs are actively investigating ways to reduce costs. On the other hand, steckling stock is highly labour intensive and production in the tens of millions could very well introduce new problems as programs attempt to scale up. Nevertheless, it seems that an operational program of sufficient size with experienced management could probably achieve production costs for stecklings which are 1.5x the cost of container-grown seedlings, or roughly $225 per thousand.

Costs for production of micropropagation and embryogenic systems are even less certain. Proponents of these emerging technologies predict great reductions in cost which will make these techniques increasingly attractive, but there are no hard data to support this speculation. Estimates in the literature for micropropagation costs run the range from double to 10x the cost of seedling stock (Table 3). Despite these uncertain costs, some forest companies have made a significant commitment to micropropagation on an operational scale; e.g., Tasman Forestry Ltd in New Zealand opened a tissue culture laboratory in 1988 to produce 2.5 million plantlets per year (Gleed 1991).

Cost estimates for embryogenic systems in conifers are virtually nonexistent, as protocol development for somatic embryogenesis is still at an early stage. Certainly, mechanization is seen as having major potential to reduce the high cost of labour currently associated with tissue culture and embryogenic techniques (Aitken-Christie 1991; Aitken-Christie and Jones 1987; Harrell and Simonton 1986). Liquid culture systems hold the greatest promise for automated handling of somatic embryos (Levin *et al.* 1988), although our important conifers have not responded well to culture in liquid media (J. Bonga, pers. comm.).

It is early yet to speculate the real potential for cost reductions resulting from tissue and embryogenic culture systems. The progress made in the past few years with respect to protocol development has been nothing short of phenomenal, and there seems little doubt that, even if never used for the production of operational planting stock, these techniques will prove invaluable for the long-term maintenance of clones and insertion of new genes, and may assist in the achievement of real rejuvenation of mature material. If used for operational deployment of clonal stock, these new systems will compete on a cost basis with rooted cuttings, and must yet demonstrate favourable, true-to-type performance in the field.

Plantation establishment and management

One might ignore the possibility of cost differences between seedling and clones after the planting stock have left the nursery. To do so would require the assumption that management requirements for clonal plantations will be similar to those established with seedlings; an assumption which has yet to be well tested in our important species. However, at the very least, we might expect that faster growth rates will lead to differences in management costs during the life of the plantation, perhaps reducing the need for competition control and pest protection.

Experience with radiata pine in New Zealand has indicated that other differences may also have an important effect on the cost of plantation management (Arnold and Gleed 1985). It has been determined in this case that initial planting density may be reduced from 1200-1500 stems per ha, to 750, since the cuttings do not require early competition to achieve acceptable form, and this reduces the loss of trees during precommercial thinning operations. Pruning costs were also reduced. Thus, even including the cost of steckling stock, the overall cost of management was reduced and a case could be made supporting clonal deployment, without any expectation of genetic improvement for growth rate.

There are no data available to indicate what differences, if any, may exist in the costs of plantation management between clones and seedlings, for important New Brunswick species. Although the safest assumption at this point would probably be that clonal plantations will be equally expensive to manage, there remains the possibility that important benefits will become apparent once sufficient experience has been gained with clonal stock in the field.

Net cost differences between seedling and clonal strategies

In the financial analysis carried out in this study, the emphasis was on evaluating the present value of benefits, primarily higher per hectare stand value. Since many of the strategy costs contribute directly to higher cost of planting stock, the benefits are also expressed per 1000 planted trees. For purposes of comparing alternative reforestation strategies, only the *differences* in benefits and cost are really important. This simplifies the task somewhat and focuses the decision on identifying a justifiable threshold price for improvement of nursery stock.

In a management environment where costs are changing continually, the decision-maker must constantly re-evaluate the impact of cost on forest management investments. Point estimates of cost components of nursery stock production, used for illustration in this report, are summarized in Table 4. In this summary, the difference between the cost of improved seedlings resulting from a conventional wind-pollinated orchard strategy and unimproved stock is estimated to be $20 per thousand, whereas clonal stock produced from control-pollinated seed will cost $82 more per thousand than unimproved stock. The decision-maker will compare these extra costs against the present value of benefits expected to accrue from the use of improved stock.

TABLE 4. Point estimates of cost components ($ per thousand) for production of unimproved and improved seedlings, and improved clonal planting stock

	Stock type		
Cost component	Unimproved seedling stock	Improved seedling stock	Improved clonal stock
Breeding population	-	$5	$5
Production population			
Seed orchard operations	-	15	-
Donor material management	-	-	2
Nursery propagation			
Seedlings	$150	150	-
Stecklings	-	-	225
	=========	========	========
Total cost per '000	$150	$170	$232
Cost differences	<---- $20 ---->		<---- $62 ---->
	<----------- $82 ----------->		

Other economic factors

The decision to accept or reject clonal techniques as part of a breeding and reforestation strategy depends to a great extent on the manager's objectives and criteria used for evaluation. Conventional investment analysis to determine rates of return on investment in stand establishment may not be appropriate when the primary objective is to manage harvest flows and other benefits from the *whole* forest (Reed and Baskerville 1991). Here the forest manager is most concerned with identifying a regime of silvicultural investment that optimizes the flow of benefits. Having made the decision to plant, the decision-maker can legitimately ask if there are economically attractive ways to enhance the value of planted forests and diversify his silvicultural investment portfolio through tree improvement. The economic value of a given tree improvement strategy can be calculated as the difference between the expected costs and expected benefits. Since these costs and benefits accrue at different points in time, it is normal practice to discount these amounts to their present value (PV).

Although genetic gain and differential costs are important, financial comparisons of alternative improvement strategies requires consideration of several other market and non-market factors, including: *(i)* rate of discount; *(ii)* scheduling of harvest and regeneration activities; *(iii)* stumpage value; *(iv)* expectation of yield from plantations; and *(v)* the size of the planting program (Thomson 1989).

Discount rate

When financial analyses are used in decision making, no factor is more controversial than the choice of discount rate to apply to future costs and benefits. The whole concept that the future ability of the forest to provide benefits is somehow less valuable than present consumption is abhorrent to many and has been attacked by reputable forest management experts, e.g. Baskerville (1991). It could even be argued that discounting of forest management benefits is inconsistent with the philosophy of sustainable development, and therefore inappropriate for modern decision-making in forest management, particularly for publicly owned forests. Nevertheless, analytical practices used for the bulk of decision-making which drives our economy accept the principle of discounting.

Many economists have discussed the selection of an appropriate rate of discount for analysis of forestry investments. Most agree that a "real" rate of interest should be used, i.e., without inflation. It is not the objective of this study, nor is this author competent, to defend an appropriate rate of discounting for forest management investments. It will suffice to state that the real discount rate is affected by many market factors and the social objectives which influence management activity in the forest (see Fraser 1985; Harou 1983). A low "social" rate of discount may be applicable to silvicultural investments, especially when they occur on publicly owned land (Harou 1985). Very low rates may not be acceptable in the real world of corporate business, while high rates will be a strong disincentive against any investment which occurs over a time period as long as a forest rotation. Rates in the range of 3 to 5% have been suggested (see Ondro and Constantino 1990a, 1990b for a discussion of Canadian and US rates.)

A recent report by Deloitte & Touche Management Consultants (1991) used a real interest rate of 4% to discount economic benefits of budworm control in eastern Canada. This same report stated that timber values may appreciate at a higher rate than other goods and services, resulting in an estimated 1% appreciation in stumpage value. In an economic analysis of a tree improvement program for western larch (*Larix occidentalis* Nutt.), Fins *et al.* (1984) used real discount rates of 4 and 6%, and assumed that stumpage rates would appreciate at the rate of 2%.

The effect of stumpage appreciation can be included by adjusting the real interest rate. This effective discount rate does not equal the real interest rate minus the rate of stumpage appreciation; rather, the correct adjustment, as given by Binkley (1980), is

$$i' = \frac{(1+i)}{(1+h)} - 1$$

where

i' is the discount rate adjusted for stumpage appreciation;
i is the real rate of interest; and
h is the stumpage appreciation rate.

Calculations presented in this report were made for real interest rates of 4 and 6%, with and without a 1 or 2% appreciation in stumpage. This resulted in a series of effective discount rates in the range of 1.96 to 6.00%, as shown in Table 5.

TABLE 5. Effective interest rate (%) as a function of real interest rates adjusted by the rate of stumpage appreciation

	Real interest rate	
Stumpage appreciation	4%	6%
0%	4.00	6.00
1%	2.97	4.95
2%	1.96	3.92

Scheduling of forest harvest and regeneration

Tree improvement activities are generally designed to meet the requirements of a given regeneration program. However, the dimensions of a regeneration program can be affected by both market and nonmarket factors (Thomson 1989). Changes in management objectives, market conditions and constraints to forest management will affect the timing of harvest and, thus, the timing of regeneration. Changes in the reforestation program may also come about as a result of losses to fire, disease or insects.

The conventional wind-pollinated orchard is designed from the outset to meet a given seed demand. Its value would be maximized if reforestation requirements were to coincide with the development of orchard productivity. More likely is that orchard output at any point in time will be somewhat below or exceed the actual requirements for stock production, and this will decrease the present value of the investment in orchard establishment. Compared to the conventional seed orchard, clonal production populations, and even other alternative orchard systems, are somewhat more flexible and can more readily accommodate changes in regeneration requirements.

Harvest scheduling also has an impact on the ability to realize early benefits from an improvement program. Planting improved material will result in an increase in the overall productivity of the forest estate, which, in turn, will raise the allowable cut, the so-called Allowable-cut effect (ACE). Provided there is sufficient standing timber to provide an even flow of material throughout the life of the plantation, the ACE will result in an increased allowable harvest equivalent to the increase in growth rate due to the investment. The ability of the forest to provide the required harvest flow throughout the investment period has a major impact on the ACE (Binkley 1980, 1984; Schweitzer *et al.* 1972). Unfavourable age-class distribution in New Brunswick's forest will lead to a wood supply gap in the foreseeable future (V. Zelazny, pers. comm.). This will have an impact on the ability of the forest to maintain the even flow of increased harvest volumes which would be necessary to realize the maximum benefit from the ACE. The present value of any stand establishment treatment, such as tree improvement, will be greatly affected by harvest scheduling and silvicultural investments in *existing* forest stands which will permit the ACE to be realized.

Stumpage value

It is obvious that the future value of stumpage will have a major effect on the benefits realized from investment in tree improvement. Market forces could cause stumpage to appreciate at a faster or slower rate than other goods and services. More surprising is the difficulty that the decision-maker will experience when attempting to make a true determination on current stumpage. The value of stumpage to a woodlot owner selling to a harvesting contractor may be much lower than that determined by a government land-owner who places considerable value on the impact that forest production has on employment and other economic activity. A higher "shadow" price for stumpage may be appropriate when the investor values the investment as being socially attractive (Harou 1984).

In their recent report on the economic benefits of budworm control, Deloitte & Touche (1991) used a residual timber value approach to determine the current value of stumpage on the Restigouche-Tobique license. Starting with the Madawaska Marketing Board mill-delivered prices for pulpwood and sawlogs, deductions were made for harvesting, transportation, additional costs of management on Crown land, and an allowance for profit and risk. The residual value of the average pulpwood-sawlog mix was determined to be \$15.52/m^3. Although considerably higher than stumpage fees paid to the Crown or to private forest owners, this stumpage value is thought to better reflect the *true* value of the material. Even so, stumpage value of wood from genetically improved stands may actually be higher yet, due to value gains from factors such as increased piece size, lower harvesting costs, higher lumber recovery rate, shorter average hauling distance, release of forest land for other purposes, and reduction of risk (Reed and Baskerville 1991). The analysis presented in this report used a stumpage value estimate of \$15.50/m^3, and provided for increases in value resulting from genetic improvement.

Expectation of yield from plantations

Gains from tree improvement, or other plantation management treatments, must be related to the yield from unimproved plantations. Unfortunately, information about the site quality of future planting sites and their expected yields is very poor, although research is under way to rectify this problem. Returns from tree improvement will be maximized if selected stock is established only on the best planting sites. The challenge is to describe growth and yield from the mean site quality expected to receive improved stock.

In an earlier study of black spruce tree improvement in New Brunswick, Cornelius and Morgenstern (1986) considered an "intermediate" site which they described as reaching peak mean annual increment (MAI) at 46 years, with 296 m^3/ha and a mean height of 18.1 m. The New Brunswick plantation growth and yield model has been revised considerably since the Cornelius-Morgenstern study was published (V. Zelazny, pers. comm.), and now describes an "average" spruce site (SI_{50} = 15.2 m) as achieving maximum MAI at 60 years with a merchantable volume of 276 m^3/ha and mean height of 17.5 m. Even an "above average" site (SI_{50} = 17.2 m) does not achieve peak MAI until 51 years, with a merchantable volume of 278 m^3/ha and height of 17.4 m. These yields are much lower than those estimated for sites in Nova Scotia with similar SI_{50} (Anonymous 1988), and one might expect revisions based on ongoing research.

For the purposes of financial analyses in this study, the current New Brunswick model is used, but the assumption is made that improved stock will be directed at "above average" sites (SI_{50} = 17.2 m). Several approaches can be used to determine "optimal" rotation ages (see Newman 1988), but in the present study, only two rotation ages are considered: *(i)* minimum operable age, considered by the NB Department of Natural Resources and Energy to be reached when average tree size exceeds 0.12 m^3; and *(ii)* the age when MAI is maximized. Wood-supply pressures may require that fibre from plantations enter the harvest stream as soon as the stands are operable. According to the NBDNRE model, minimum operable age on "above average" sites is 40 years, yielding a merchantable harvest volume of 211 m^3/ha and MAI of 5.28 m^3/ha. If wood-supply planning will permit, the volume production of the forest will be maximized if harvest is delayed until MAI reaches its peak of 5.45 m^3/ha at 51 years and merchantable volume will be 278 m^3/ha.

Size of the planting program

Gains from improvement efforts do not accrue until improved trees are planted. Obviously, a large reduction in the size of the planting program would have a negative impact on the returns from investment in any tree improvement strategy. This factor is not considered in the financial analyses reported in this study; comparisons are made among strategies which fully utilize the material available from the production population. However, it should be recognized that strategies which require a large capital investment in seed-orchard development or construction of expensive breeding-hall facilities will be particularly vulnerable to changes in planting requirements. Changes in output can be achieved more efficiently when cloning is used to amplify control-pollinated seed or deploy tested clones. Although this flexibility may be a major advantage of clonal strategies, the requirement, and therefore the value, of flexibility may be difficult to assess.

Calculating the present value of improved planting stock

The project developed a financial analysis procedure which extends standard present value techniques to incorporate allowable-cut effects and changes in stumpage value resulting from genetic improvement. The calculations are performed within a spreadsheet which reports present value of improved seedlings growing on a specific site, for a given present stumpage value, with and without allowable-cut effects, over a range of effective discount rates incorporating the effects of stumpage appreciation with the real rate of interest. Realistic ranges of genetic and economic variables were tested to demonstrate the utility of these support tools to decision-making.

Regardless of the vegetative propagation method, stecklings and emblings will likely remain more expensive than planting stock propagated from seed. Assuming that the productivity and quality of this stock is higher, managers should be willing to pay a premium price for such stock. Calculations were made to determine the maximum justifiable increase in the cost of improved planting stock, depending on the expected gain in value at time of harvest. The gain in value is considered to have two components: *(i)* gain from extra volume increment, and *(ii)* gain in stumpage value due to genetic improvement, as discussed earlier.

The present value of these gains may be calculated as the sum of the two components, using standard discount techniques:

$$V_0 = \left[\frac{n \cdot I \cdot G_I \cdot S}{(1+i')^n}\right] + \left[\frac{n \cdot I \cdot (1+G_I) \cdot G_S \cdot S}{(1+i')^n}\right]$$

where:

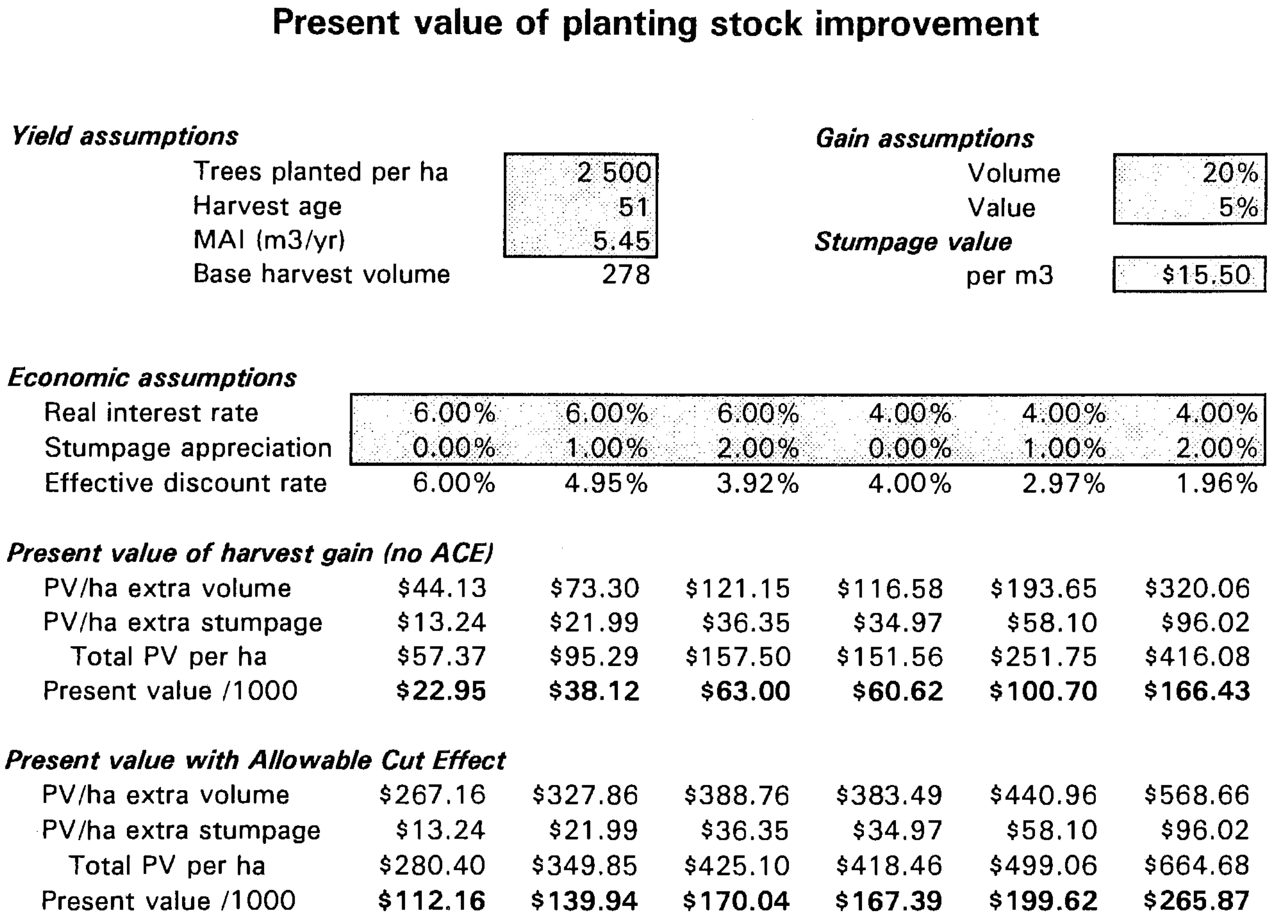
n	is the rotation age;
I	is the mean annual increment at age n;
G_I	is the gain in volume increment, as a proportion;
G_S	is the gain in stumpage value of the stand (as a proportion);
S	is the stumpage value; and
i'	is the discount rate.

In this equation, the first term describes the present value of gains in volume production, while the second term accounts for the increase in stumpage value due to improvement. The assumption is made that no benefit will accrue from the investment until the stand is harvested at year n. However, as discussed earlier, the increase in plantation yield may have an impact on the allowable cut for the entire forest, throughout the rotation of planted trees. Provided that an even flow of increased harvest material can be maintained throughout the rotation, this allowable-cut effect will accrue as an annuity. While the ACE will have an impact on the volume increase component of the present value equation, the stumpage value component remains unchanged:

$$V_0 = \left[I \cdot G_I \cdot S \frac{(1+i')^n - 1}{i'(1+i')^n}\right] + \left[\frac{n \cdot I \cdot (1+G_I) \cdot G_S \cdot S}{(1+i')^n}\right]$$

where the terms are as defined previously.

As part of this project, a spreadsheet template was prepared using Microsoft Excel to calculate the present value of gains from alternative tree improvement strategies. Site quality data and expected gains are accepted as input and the spreadsheet calculates the present value of the gains in terms of \$ per hectare and \$ per thousand trees, for a range of discount rate scenarios. The spreadsheet aids the decision-maker by simplifying the financial analysis of any scenario of site quality, gain, or economic parameters. A sample analysis is presented in Figure 3, where variables which may be modified by the user are indicated by shaded background. In this example, the user has requested an analysis of an "above-average" site where 80% of the original 2,500 planted trees survive to harvest at age 51, the age of peak MAI. Genetic improvement is assumed to result in a 20% increase in volume, and a 5% increase in stumpage value, which is currently set at \$15.50. Calculations are presented for a range of interest rate



Present value of planting stock improvement

Yield assumptions		*Gain assumptions*	
Trees planted per ha	2 500	Volume	20%
Harvest age	51	Value	5%
MAI (m3/yr)	5.45	*Stumpage value*	
Base harvest volume	278	per m3	$15.50

Economic assumptions						
Real interest rate	6.00%	6.00%	6.00%	4.00%	4.00%	4.00%
Stumpage appreciation	0.00%	1.00%	2.00%	0.00%	1.00%	2.00%
Effective discount rate	6.00%	4.95%	3.92%	4.00%	2.97%	1.96%
Present value of harvest gain (no ACE)						
PV/ha extra volume	$44.13	$73.30	$121.15	$116.58	$193.65	$320.06
PV/ha extra stumpage	$13.24	$21.99	$36.35	$34.97	$58.10	$96.02
Total PV per ha	$57.37	$95.29	$157.50	$151.56	$251.75	$416.08
Present value /1000	**$22.95**	**$38.12**	**$63.00**	**$60.62**	**$100.70**	**$166.43**
Present value with Allowable Cut Effect						
PV/ha extra volume	$267.16	$327.86	$388.76	$383.49	$440.96	$568.66
PV/ha extra stumpage	$13.24	$21.99	$36.35	$34.97	$58.10	$96.02
Total PV per ha	$280.40	$349.85	$425.10	$418.46	$499.06	$664.68
Present value /1000	**$112.16**	**$139.94**	**$170.04**	**$167.39**	**$199.62**	**$265.87**

FIGURE 3. Sample calculation of present value of gains from planting stock improvement using a spreadsheet template. The user is permitted to change the values of all variables shown in shaded boxes, and the calculations are updated automatically.

scenarios, both with and without allowable-cut effects.

Results of present value analyses

The spreadsheet was used to explore the effect of various factors on the present value of planted stands under various management and economic scenarios. Figure 4 shows the outcome of present value analysis for unimproved plantations on "above-average" spruce sites. The calculations were made, both with and without allowable-cut effects at the minimum age of operability, 40 years, and at age 51 when MAI reaches its peak. The value of the allowable-cut effect is immediately apparent, as is the dramatic impact of effective interest rate. Without the allowable-cut effect, the value is generally higher if the stand is harvested at the minimum

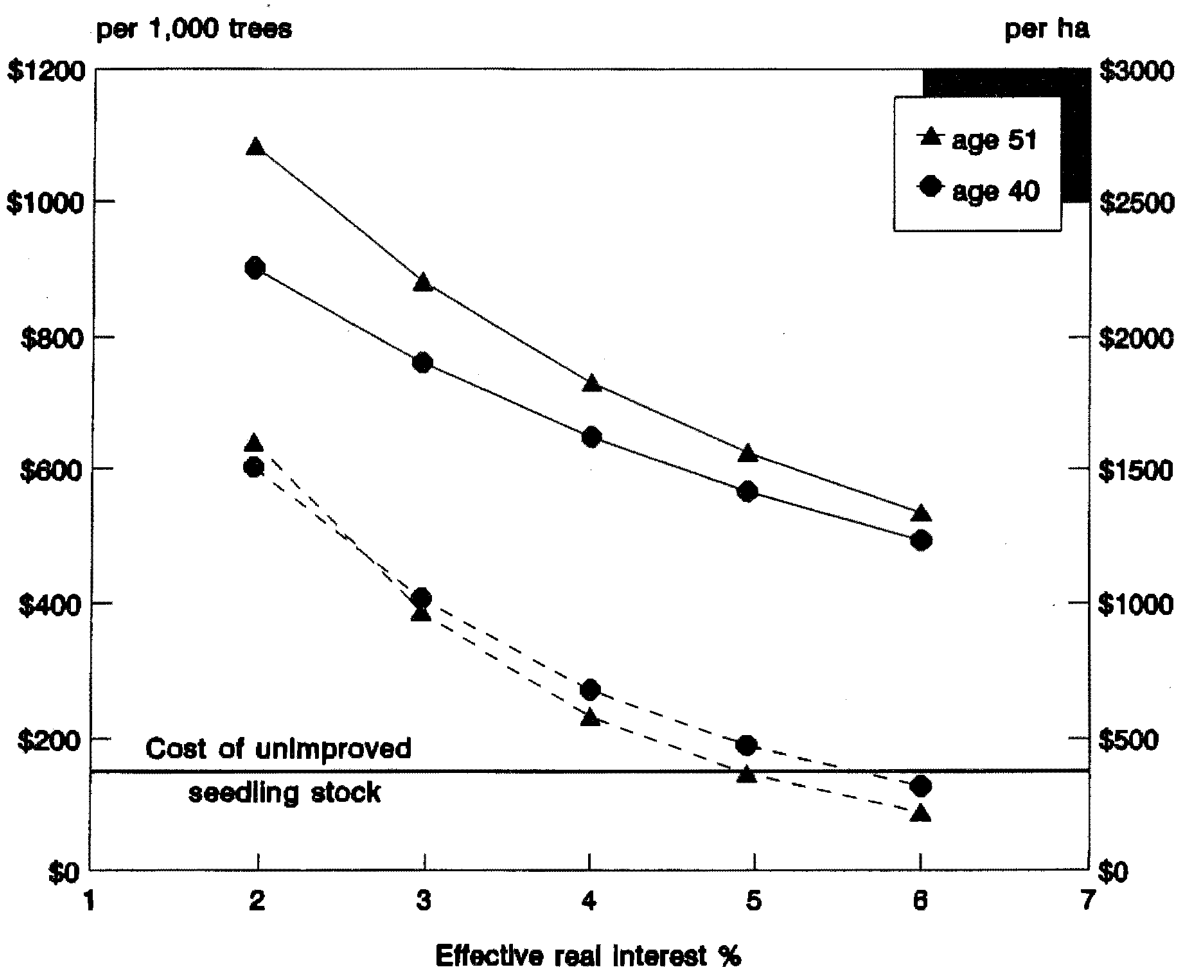


FIGURE 4. Present value of a spruce plantation established with unimproved seedlings on an "above-average" site, harvested at age 40 or age 51, relative to the cost of planting stock production. Calculations assumed stumpage at $15.50 per m^3. Solid and broken lines refer to present values calculated with and without allowable cut effects, respectively.

operable age. However, when the allowable-cut effect is considered, present value continues to increase for harvest ages beyond that of peak MAI. The figure also relates the cost of unimproved seedling stock ($150 per thousand) to the present value of the plantation, and demonstrates that, without the allowable-cut effect, the value of the plantation is not sufficient to cover even the cost of planting stock, let alone other costs of establishment and management, at interest rates higher than 5%. Obviously, present value analysis without allowable-cut effects does not give strong support for investment in plantation forestry under this scenario. The fact that planting programs exist at today's moderately high level is an indication that decision-makers value impact of silvicultural investment on harvest flows from the whole forest, and/or accept a low social discount rate and high shadow price for stumpage. These same values should also be applied to investments which increase the return from plantations.

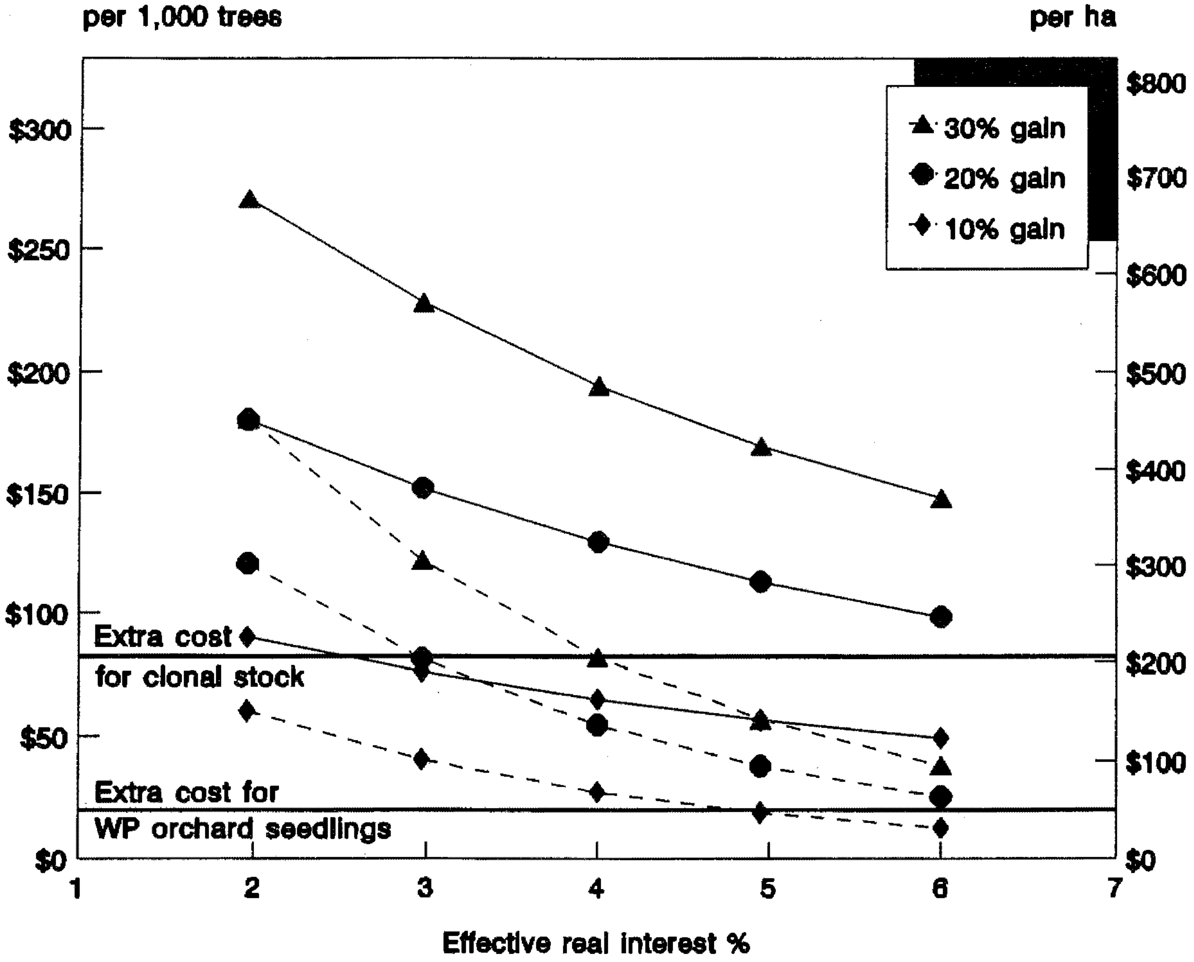


FIGURE 5. Present value of volume gains on an "above-average" spruce site, harvested at age 40 (minimum operable age), relative to the extra cost of producing improved seedling and clonal planting stock. Calculations assumed stumpage at $15.50 per m^3, with no increase in value due to genetic improvement. Solid and broken lines refer to present values calculated with and without allowable cut effects, respectively.

In Figures 5 and 6, the present value of volume gains from different levels of genetic improvement are shown at harvest age 40 and 51, respectively. The figures demonstrate that the assumption of rotation age does not have a critical effect on the economic viability of investment in genetic improvement. This observation supports a similar finding by McKenney *et al.* (1988) who determined that optimal rotation age is *not* significantly affected by tree improvement. The analysis also confirms that returns from wind-pollinated seed orchards can easily justify the extra cost to produce improved stock from wind-pollinated seed orchards. Even without the allowable-cut effect, the conventional seed-orchard program is justified at low levels of genetic gain; 5% gain when an effective interest rate of 3% is used, and about 10% gain when effective interest rate is 5%. If the allowable cut is considered, then conventional orchards are viable at conservatively high interest rates, even if genetic gain is less than 5%.

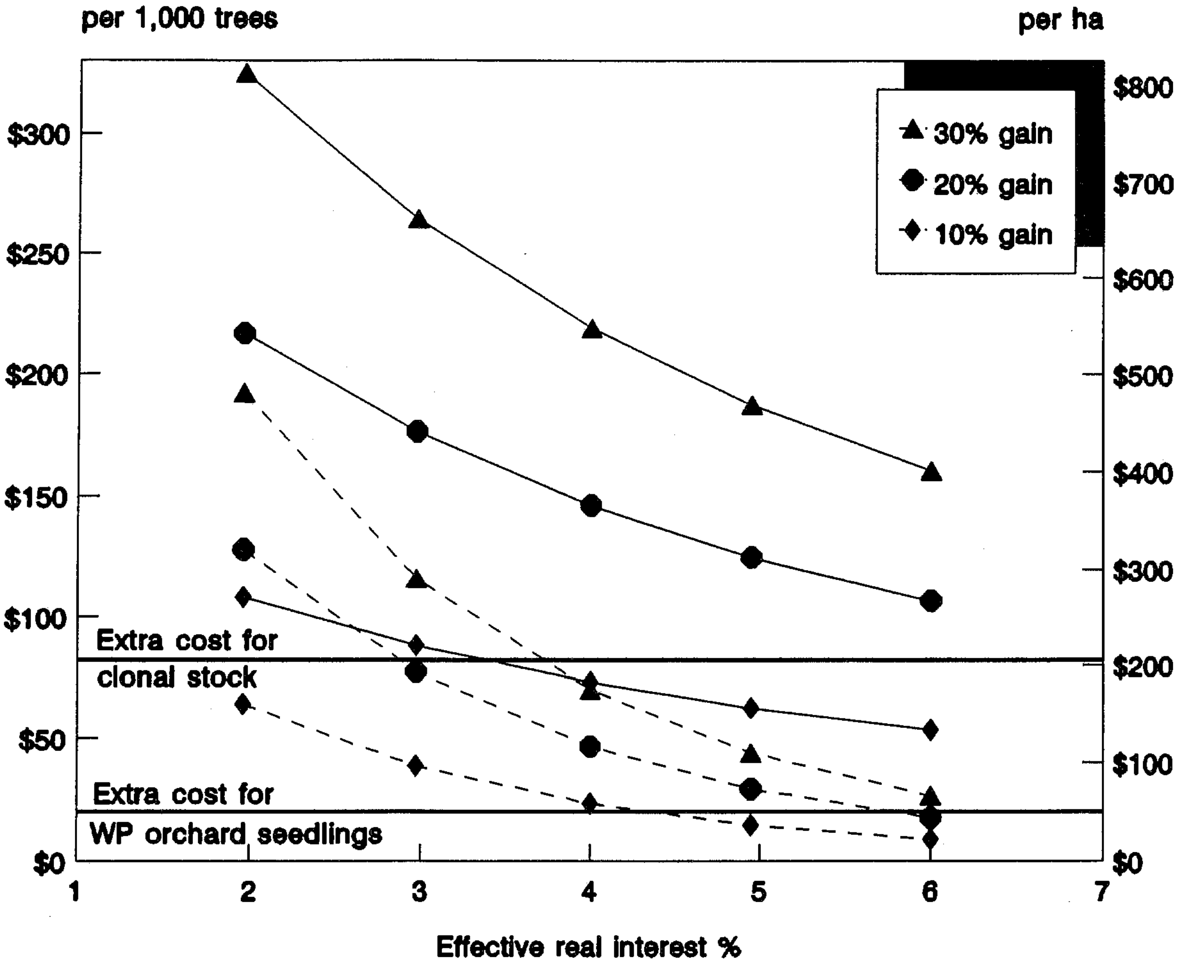


FIGURE 6. Present value of volume gains on an "above-average" spruce site, harvested at age 51 (age of peak MAI), relative to the extra cost of producing improved seedling and clonal planting stock. Calculations assumed stumpage at $15.50 per m^3, with no increase in value due to genetic improvement. Solid and broken lines refer to present values calculated with and without allowable cut effects, respectively.

To be profitable, clonal deployment of improved stock requires much higher levels of genetic gain to be achieved, particularly when the allowable-cut effect is not available. However, if harvest levels can be increased during the rotation, clonal deployment is viable with genetic gains of less than 10% when the effective real interest rate is less than 3.5%, and at 15% genetic gain when the interest rate is 6%. Figure 6 also illustrates the sensitivity of the net present value of investment in clonal deployment to the level of genetic gain achieved and the actual cost of the propagation. If clonal stock production costs are 50% higher than estimated in this study, genetic gain must be 7 to 8 percentage points higher to achieve the same cost-benefit ratio, even if allowable-cut effects can be realized.

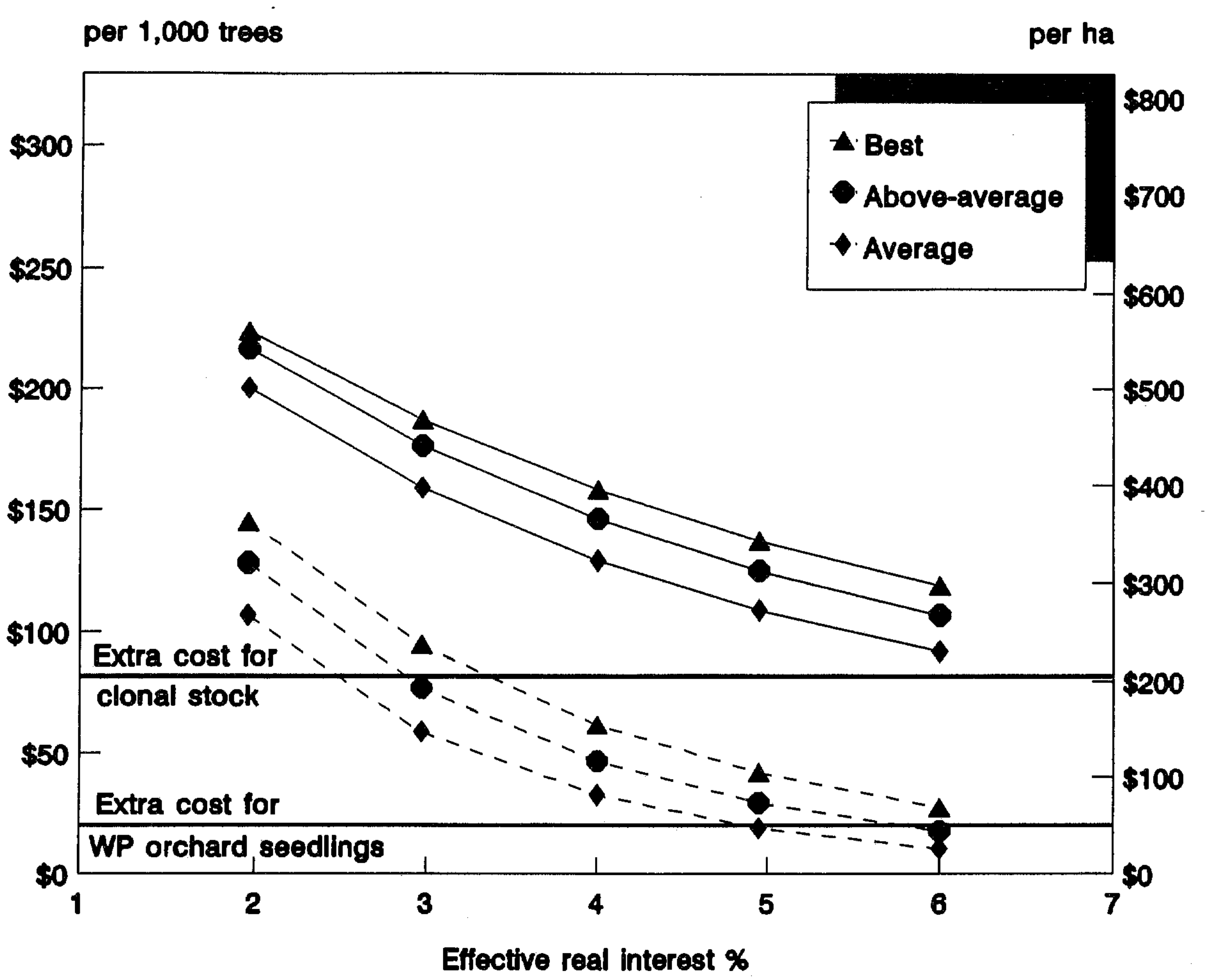


FIGURE 7. Present value of a 20% genetic gain in volume on "average", "above-average", and "best" spruce sites, when harvested at age of peak MAI. Calculations assumed stumpage at $15.50 per m^3, with no increase in value due to genetic improvement. Solid and broken lines refer to present values calculated with and without allowable cut effects, respectively.

One might hope to maximize returns from genetic improvement by concentrating the investment on the best sites. Figure 7 illustrates the range of returns that would be expected on spruce sites ranging from "average" to "best" quality. Upgrading the planting site by one class, equivalent to a change in SI_{50} of 2 metres, would increase the present value of the plantation by roughly $35 per hectare, or $14 per thousand planted trees. This will not only justify a higher cost for nursery propagation, but will also produce additional fibre which may be badly needed to fill a hole in the wood supply.

In additional to the extra volume that genetic improvement would hope to achieve, several factors could also contribute to a higher stumpage value for wood from improved plantations. The concentration of fibre closer to the mill, lower harvesting costs and increased piece size will certainly add to value of harvested material. Depending on the mill process and

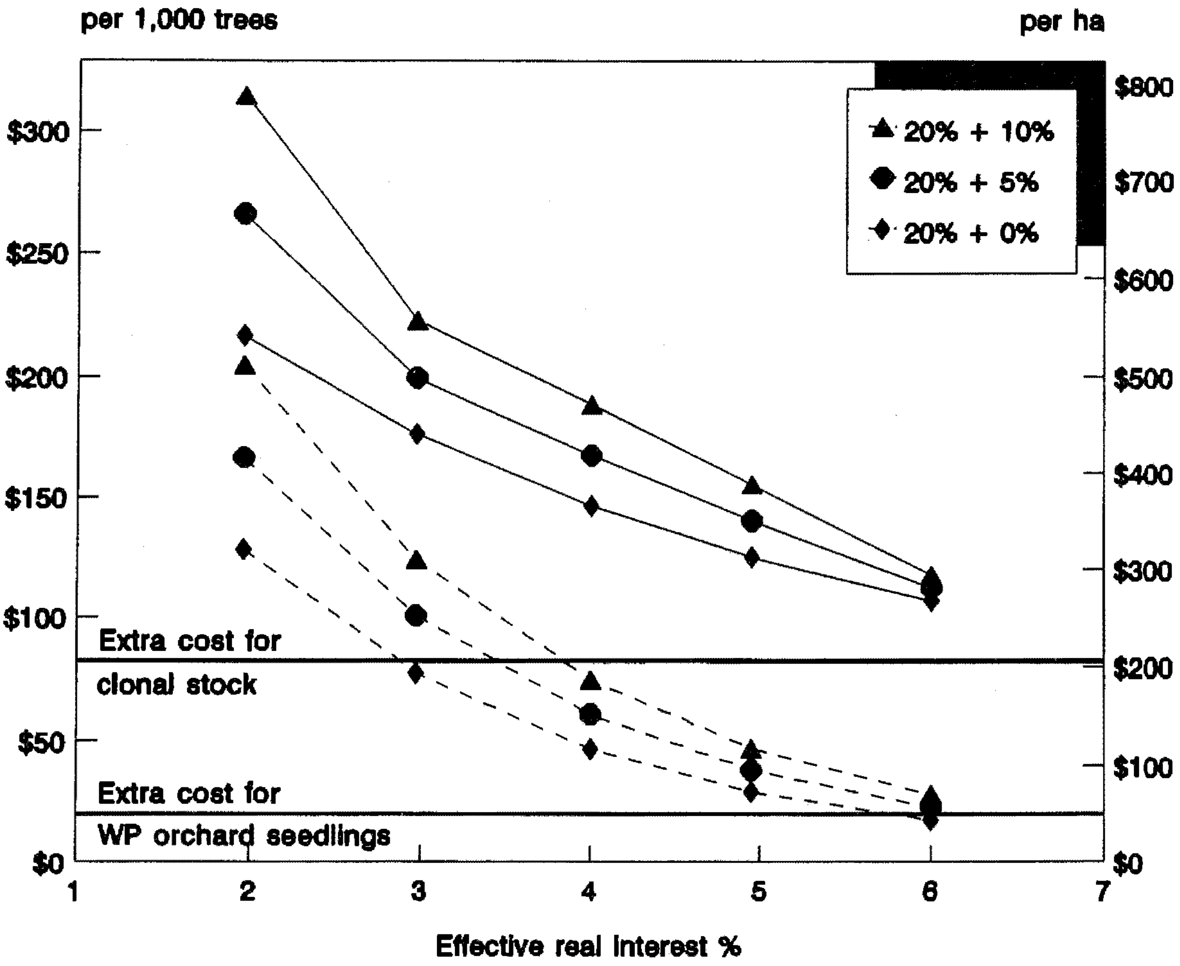


FIGURE 8. Present value of gains on an "above-average" spruce site at age 51, when a 20% gain in volume is combined with 0%, 5% and 10% increases in fibre value due to genetic improvement. Calculations assumed stumpage of unimproved fibre at $15.50 per m^3. Solid and broken lines refer to present values calculated with and without allowable cut effects, respectively.

market, value may also increase due to improvement of fibre quality. Figure 8 illustrates the effect of varying degrees of quality improvement on the present value of investment which results in a 20% gain in volume. In this example, a 10% gain in stumpage value is approximately equal to a 1% reduction in the effective rate. If the effective interest rate were considered to be 4%, this same gain in stumpage value would increase the value of planting stock by $42 or $28 per thousand, with and without the ACE, respectively.

In Figure 9, a sample comparison is given for present value of gains from wind-pollinated orchards, control-pollinated orchards and clonal forestry. If these gain assumptions are considered reasonable, the analysis demonstrates that all of the strategies are economically viable if allowable-cut effects are available. Even when no allowable-cut effect is available, the clonal forestry option is viable at effective rates of real interest below 3.8%. If we assume that,

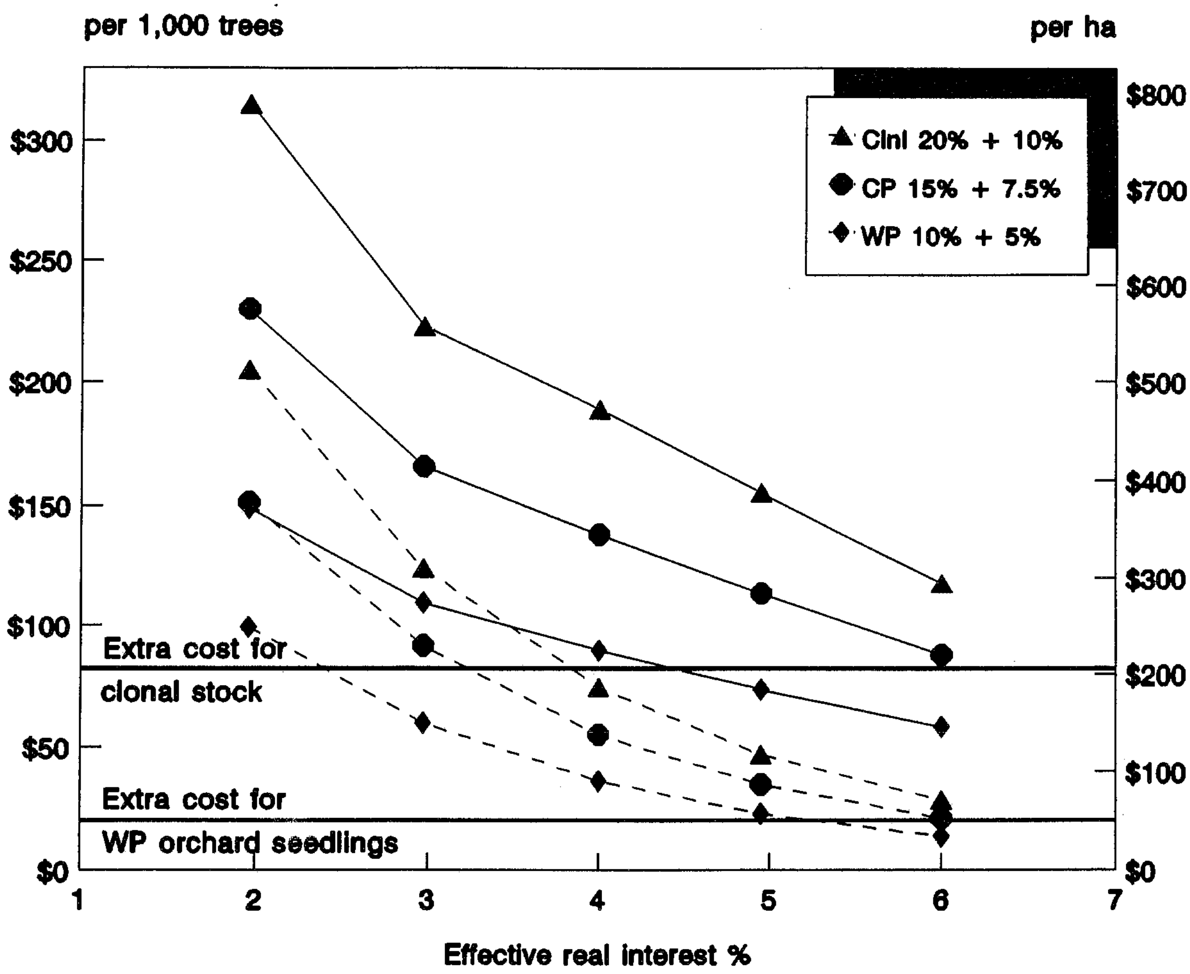


FIGURE 9. Present value of gains on an "above-average" spruce site at age 51, for different breeding strategies where wind-pollinated orchards are assumed to produce a 10% gain in volume, combined with a 5% gain in stumpage value; control-pollinated orchards and clonal forestry are assumed to produce gains equivalent to 1.5 and 2x those achieved by the wind-pollinated orchards. Calculations assumed stumpage of unimproved fibre at $15.50 per m^3. Solid and broken lines refer to present values calculated with and without allowable cut effects, respectively.

compared to wind-pollinated orchards, control-pollinated orchard seed will increase the cost of improved stock by $15 per thousand, this option is viable without allowable-cut effects at interest rates below about 4.75%. The impact of the extra cost of producing clonal planting stock is readily apparent in this figure. Although the 50% premium used here to estimate the cost of clonal stock is probably reasonable for moderate quantities of steckling material, it may not be possible to produce sufficient quantities to supply the majority of reforestation stock as clones, unless automated micropropagation techniques are employed, for which the cost premium is much less certain. If actual clonal propagation costs are double those used in this analysis, viability of clonal forestry would likely require allowable-cut effects to be available, and assurance that gains can actually be achieved would become even more critical.

General conclusions

> *"The conventional seed orchard is finished"* -- Henri Chaperon, AFOCEL, France, speaking at the FRI/NZFP Forests Ltd Clonal Forestry Workshop, 1-2 May 1989, Rotorua, NZ (Sweet 1991)

In making this assertion, M. Chaperon was not claiming that seed orchards should be replaced by clonal forestry. Rather, his point was to recognize the serious inefficiencies of wind-pollinated orchards and to encourage tree breeders to seek other means by which the recombination of genes in production populations can be regulated. Control over pollination should be regarded as a desirable element of any future breeding strategy, regardless of whether or not cloning is used as a deployment method. In many ways, a decision between conventional seed orchards and clonal forestry is fundamentally flawed since it attempts to compare technology which is not quite obsolete, with technology which is not quite operational. A definitive analysis in this kind of situation is simply not possible.

At the beginning of this report, the original question was stated "Does clonal propagation offer potential gains and management benefits which might justify the higher cost anticipated for planting stock production." This project has produced some useful support tools which can help decision-makers evaluate the relative impact of genetic structure and economic factors on the viability of alternative breeding strategies, including those which utilize clones. The techniques employed by these tools go beyond standard gain equations and discount economics, to incorporate the added complexities of long-term breeding plans, and the value generated by the whole forest as a result of investment in tree improvement.

Major findings

In reviewing the major findings of this study, it makes sense to focus on each of the three major applications of clonal propagation in breeding and reforestation, identified earlier: *(i)* clonal replication of test material, *(ii)* vegetative multiplication, and *(iii)* clonal selection.

Clonal Replication

When used to replicate genotypes in genetic tests, clonal propagation can have a major impact on the efficiency of breeding programs, even when clones are not used for deployment of operational planting stock. The simulations carried out in this study indicate that clonal replication will increase test efficiency over a range of genetic variance scenarios, but is particularly effective when most of the genetic variance is additive and/or when heritability is moderately low, ≤ 0.3. In these situations, the extra gain resulting over time from the use of clonal replicates should be 7 to 11% higher than that achieved when tests are established as seedlings. There may, however, be no benefit at higher heritabilities if there is a substantial portion of nonadditive genetic variance, although such heritabilities are not expected for growth traits such as height or volume growth.

For this application, the form and development of clonal test material need not resemble that of seedlings, provided that genotypic rankings are similar. In fact, our experience with spruce stecklings from juvenile donor plants, albeit limited, indicates that they grow very much like "normal" trees and are indistinguishable from seedlings soon after establishment in the field. However, the assumption that genotypic rankings are similar is only just now being tested in a series of experiments established by Dr. Yill Sung Park, Forestry Canada.

The other weak area of knowledge relevant to the use of clonal replicates in testing is the added cost of test establishment and assessment. Although the propagation of steckling test material is not expected to add significantly to the cost of testing, the addition of another level of genetic grouping will add complexity to the field design of experiments and will place higher demand on field staff to properly identify the larger number of unique test units. Whereas current test protocols require plot sizes of 4 to 5 trees, clonal replication would likely require field crews to handle single-tree plot designs. Only field experience with clonal test material will confirm how significant is the cost of this additional complexity.

Vegetative multiplication

Deployment of control-pollinated material is hampered by difficulties in producing the required number of seeds to supply the reforestation requirement. Vegetative multiplication has been used successfully to overcome this problem, but there are other approaches to be considered. Nursery managers can have a major impact on seed requirements simply by increasing their efficiency of seed use. Control-pollinated orchards can be managed more intensively, employing hormonal cone induction and other treatments to increase seed output. Methodology for isolating receptive flowers, improved pollen handling, and better techniques for applying selected pollens can increase the ability of orchard managers to supply demand with control-pollinated genotypes. Technology is advancing rapidly on all of these fronts, and vegetative multiplication may or may not be the method of choice as improvements are made in control-pollinated orchard management.

Regardless of how planting stock is deployed to the field, the use of controlled pollination will produce large increases in genetic gain compared to wind-pollinated seed orchards. Even compared to gains from an "ideal" wind-pollinated orchard, production of polycross seed in control-pollinated orchards should produce genetic gains which are 20 to 30% higher. In fact, pollination conditions in wind-pollinated orchards are such that realized gains and effective population size will be somewhat less than what would be predicted under "ideal" assumptions. Therefore, it would not be unreasonable to expect control-pollinated orchards to achieve gains which are at least 50% higher, perhaps even *double* those of conventional wind-pollinated orchards. If dominance variance contributes a substantial portion to the total genetic variance, the simulations conducted by this study demonstrate that realized gains could be increased even further by deployment of tested full-sib families.

When used as a deployment method, managers will require assurance that vegetative propagules will grow and respond like "normal" trees. The evidence available from our limited experience suggests that this is true for spruce stecklings from juvenile donor plants, but additional field test data are required to confirm this observation. The growth of vegetative propagules will almost certainly differ, at least in subtle ways, from that of seedlings. Identification of the factors responsible for these differences will provide the understanding necessary to lower risk, and may even provide opportunities to achieve additional silvicultural benefits from the use of clones.

Although vegetative mulitplication will have to compete with other orchard technologies as they develop, the economic analysis presented in this report demonstrates that clonal propagation is an economically viable method to pursue the extra gains from controlled pollination when allowable-cut effects are available, even at high rates of real interest. Even without allowable-cut effects, vegetative multiplication will be worthwhile at low to moderate effective interest rates (real interest adjusted for stumpage appreciation), provided that stated assumptions regarding propagation cost, genetic gain, and stumpage value are considered reasonable. The uncertainty about these assumptions is perhaps the greatest deterrent to selecting vegetative multiplication as a deployment option. However, since vegetative multiplication is merely being used as a "packaging" method for deployment of control-pollinated genotypes, there is considerable flexibility to employ new cloning technology, or to reverse the commitment to vegetative multiplication entirely in favour of other improvements in control-pollinated orchard seed production, as they develop. One way or another, the objective of breeding programs should be to ensure that recombination of genes in production populations is genetically efficient and that effective population size is controlled so as to guarantee a target level of diversity.

Clonal selection

The simulations described in this report demonstrate that true *clonal forestry* will only be attractive when there is a substantial component of nonadditive genetic variance. Clonal selection will be equally effective at any given level of nonadditive variance, regardless of the relative contributions of dominance and epistatic components. When all of the nonadditive variance is derived from dominance, clonal selection will still be superior to selection of full-sib families, since gain is achieved from the entire dominance variance component, whereas selection among families will capture gain from only one quarter of this component. If all or most of the genetic variance is additive and without an increased effort devoted to additional field testing, clonal selection strategies will not achieve higher gains than control-pollinated orchards, except at the expense of genetic diversity.

Data from young genetic tests in spruce and jack pine suggest that most of the genetic variance is additive. However, the limited data available from older tests grown from seed and the few clonal tests reported in the literature suggest that the nonadditive component may account for as much as one third of the total genetic variance; somewhat more than was thought even a few years ago. If these extra gains are to be captured by means of clonal selection, there is no operational alternative to clonal deployment.

At present, operational cloning of planting stock is limited to production of stecklings from rooted cuttings, and is further limited to spruces and larch; no operational cloning technology currently exists for jack pine. However, developing technology in the areas of tissue culture and somatic embryogenesis show promise to offer alternatives which may expand the feasibility of clonal propagation to other species, and may lead to reductions in production costs. In all cases, assumptions regarding relative performance of clonal propagules compared with seedlings must be tested more thoroughly before decision-makers are likely to make a significant commitment to clonal forestry.

Assuming that a substantial portion of the genetic variance is, in fact, nonadditive and that additional wood fibre or quality is required to meet forest management objectives, the economic analysis presented in this report suggests that clonal forestry will be worthwhile pursuing if allowable-cut effects are available. Even in the absence of allowable-cut effects, there is a reasonable expectation that clonal forestry would be viable at low to moderate effective rates of real interest. Nevertheless, the high degree of uncertainty with respect to actual genetic gains and costs of propagation makes it unlikely that clonal forestry will be attractive to forest managers until further information is gathered to confirm assumptions made in this analysis.

Major difficulties for decision-makers

Although this study has identified many *potential* gains and benefits, there clearly are not sufficient data available to provide anything but fuzzy answers. The most significant extra genetic gains which will be achieved by cloning will be derived from nonadditive effects, but we know very little about the nonadditive genetic structure of *any* of our species. The simulation exercise demonstrated that the relative magnitude of additive and nonadditive components of genetic variance will have a tremendous impact on the gains which are achievable from different breeding strategies.

Colouring all decisions regarding the deployment of clones is the question of what differences in performance will result from the use of clonal propagules as compared with seedlings. Here again, there are some positive indications that performance of clones from juvenile ortets will be similar to seedlings, and that differences which do exist may even be favourable. As limited as it is, all of this evidence has been derived from steckling material; no data exist for plants propagated from tissue culture or somatic embryos.

Although useful for comparing genetic approaches for enhancing plantation performance, the discounted investment analysis fails to identify the optimal place of genetic improvement in a strategic silvicultural plan that seeks to achieve a stated objective for the sustainable flow of benefits from the whole forest. In developing a strategic silviculture plan, one would first identify lowest cost, short-term treatments that have a high probability of contributing to the overall harvest requirement, while satisfying constraints imposed by non-fibre objectives. If the wood supply objective has not been met once all available areas have been identified for treatment, additional higher-cost, longer-term and higher-risk treatments must be added to the silviculture strategy until the objective is satisfied. The cost of individual treatments added to the mix may be very high, but what is really important is the overall cost of the silvicultural strategy designed to meet the objectives of the whole forest. This is the real cost of doing business in forestry. Once the optimal mix of treatments has been identified, additional investment opportunities can then be assessed in terms of their potential to provide attractive returns and opportunity for additional economic activity. Although qualitative statements can be made regarding benefits such as risk reduction, release of forest land for other uses, and maintenance of biodiversity, quantitative techniques which bring these factors into decision-making are not well developed.

Recommendations for further work

Develop practical experience with clonal material

> *"... sexual reproduction has been the way to do things for a long time, and most of us are pretty comfortable doing things that way. But even with good information, we don't always get it right the first time, and theory is a poor substitute for hands-on experience."* (Libby 1991)

The practice of reforestation with nursery-grown seedlings developed slowly in New Brunswick, as it did elsewhere. Foresters had to develop a "feel" for the technology and required time to convince themselves that the impact of plantation silviculture on the flow of benefits from the whole forest was indeed positive. As Libby states above, no amount of theory can replace the value of experience. This study has described scenarios where the use of clones in tree breeding and reforestation programs would be highly attractive. Unfortunately, our practical experience with this technology is very limited. As important as the contribution that additional theoretical research may lend to decision-making for clonal strategies, is the familiarity and practical understanding that will develop as foresters work with clones in the field. Then, as our genetic gain data become more reliable and propagation technology further developed, forest managers will be in a position to identify the optimal place for clonal techniques in the silvicultural investment portfolio.

Incorporate clonal replication in genetic testing

A logical place to develop experience with clonal deployment is with field testing in breeding programs. This study indicated that clonal replicates can greatly increase testing efficiency under many, although not all, genetic variance scenarios. As propagation technology continues to evolve, every opportunity should be taken to establish clonal replicates of genetic test materials alongside seedling stock. These combined seedling/clonal tests will be particularly valuable when a family structure has been provided which allows the resolution of additive and nonadditive components of genetic variance. Incorporating vegetative propagules as an adjunct to progeny tests with seedlings will help to resolve the nonadditive genetic variance structure in the breeding population and will confirm the suitability of clonal materials for selection of breeding materials.

Test critical assumptions regarding clonal performance

It has been commonly observed that clonal variances are larger than might be expected from our experience with seedling-based tests. Our analysis procedures are invariably qualified by assumptions regarding the impact of C-effects, maturation, and the growth behaviour of clonal material compared to seedlings. These assumptions must be formally tested, and these tests should be replicated with various types of clonal material as propagation technology develops. Comparative field experiments can be established now with seedlings and stecklings produced from spruce and larch, and emblings should be incorporated as soon as they are available. Investigation of C-effects will require powerful experiments to distinguish among true maternal effects, environmental covariances and variation in condition of plants from different propagation cycles.

Storage protocols for clonal material

Clonal propagation presents many challenges which must be addressed before clonal forestry can become a reality for important New Brunswick species. Field testing of clonal material takes time, during which the clone must be maintained in a constant physiological state to guarantee the ability to produce vigorous planting material once the best clones have been identified. Techniques such as hedging and serial propagation have only been partly successful in accomplishing this objective, as maturation of clonal material is not arrested, but merely retarded. Long test periods will require better storage techniques. This are will probably be the first major application of somatic embryogenesis technology, combined with cryopreservation. Perfection of cryostorage protocols will be useful, even if current embryogenic techniques are expensive and characterized by low recovery rates, as valuable genotypes could be stored in a truly juvenile state while clones undergo field testing and operational propagation techniques are developed further.

Expand application of simulation technique

The population simulation technique developed for this project is tremendously flexible and has promise for application to other theoretical problems in breeding. Although several strategy options are currently available in the simulator, changes will no doubt be desired by some users to accommodate other selection schemes, such as combined-index selection, and other mating designs such as incomplete diallels or factorials. A useful addition for multiple-generation simulations would be index selection which incorporates ancestral performance in earlier breeding cycles. The simulation approach could also be used to test strategies for the management of inbreeding or the maintenance of genetic diversity in breeding and production populations, and may be useful for evaluating the optimal allocation of testing effort in breeding programs. The approach could also be developed further to incorporate the effects of genetic correlation between traits evaluated at early ages and those at maturity.

Optimization tools for strategic planning of silviculture

The financial analysis spreadsheet developed by the project goes beyond the standard discounted cost-benefit techniques commonly applied at the stand level and incorporates the impact of increased fibre value and the allowable-cut effect derived from the investment in genetic improvement. This modification of the traditional approach to economic analysis may be quite appropriate for some landowners, but those with large capital investment in processing facilities and managers of publicly owned forests must also consider objectives to maintain harvest flows to sustain economic activity. For these decision-makers, a strategic planning approach to silviculture is most appropriate; one that seeks to minimize the cost of achieving a sustainable harvest objective, rather than simply analysing investment opportunities. Unfortunately, few tools exist to optimize a strategic plan for silviculture over the whole forest. Quantitative tools which analyze the distribution of inventory and treatment opportunities are required to determine the least-cost mix of silviculture expenditures to satisfy objectives for the sustained flow of benefits from the whole forest, while remaining faithful to other constraints imposed by social values. Such a technique would help to identify where high-cost, long-term treatments such as clonal forestry are warranted to deal with shortfalls in harvest objectives which cannot be overcome by low-cost treatments alone.

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Rutkovskii, I.V., and Kharina, L.V. 1987. Growing plants from rooted cuttings of commercially valuable forms of Picea abies without lining out in the transplant section of the nursery. Lesnoe Khozyaistvo 10: 27-29.

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Schooley, H.O., and Mullin, T.J. 1988. Seed production strategies: current vs. future. Proc. Can. Tree Improve. Assoc., Part 2, 21: 155-169.

Schweitzer, D.L., Sassaman, R.W., and Schallau, C.H. 1972. Allowable cut effect: some physical and economic implications. J. For. 70: 4.

Shaw, D.V., and Hood, J.V. 1985. Maximizing gain per effort by using clonal replicates in genetic tests. Theor. Appl. Genet. 71: 392-399.

Smith, D.R. 1986. Radiata pine (*Pinus radiata* D. Don.). *In* Biotechnology in agriculture and forestry. Vol. 1. Trees I. *Edited by* Y.P.S. Bajaj. Springer-Verlag, Berlin. pp. 274-291.

Smith, D.R. 1991. Economic benefits of vegetative propagation. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. *Edited by* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 158-160.

South, D.B. 1986. Economics of seed efficiency. J. For. 84: 33-34.

South, D.B. 1987. Economic aspects of nursery seed efficiency. South. J. Appl. For. 11: 106-109.

Sweet, G.B. 1991. Summing up. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, New Zealand. *Edited by* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 164-168.

Sweet, G.B., and Krugman, S.L. 1977. Flowering and seed production problems - and a new concept of seed orchards. *In* Proceedings of the Third World Consultation on Forest Tree Breeding, Canberra, Australia, 21-26 March 1977. FAO/IUFRO. pp. 749-759.

Sweet, G.B., Bolton, P., and Litchwark, H. 1990. A meadow orchard in radiata pine - research and reality. *In* Proceedings reproductive processes working group S.2.01-5, XIX IUFRO world congress, Montreal, Canada, 7-11 August 1990. .

Szmidt, A.E. 1987. Genetic composition of seed orchard crops. For. Ecol. Manage. 19: 227-232.

Talbert, J.T., Weir, R.J., and Arnold, R.D. 1985. Costs and benefits of a mature first-generation loblolly pine tree improvement program. J. For. 83: 162-166.

Thomson, T.A. 1989. Evaluating some financial uncertainties of tree improvement using the capital asset pricing model and dominance analysis. Can. J. For. Res. 19: 1380-1388.

Thorpe, T.A., Harry, I.S., and Kumar, P.P. 1991. Application of micropropagation to forestry. *In* Micropropagation: technology and application. *Edited by* P.C. Debergh and R.H. Zimmerman. Kluwer Academic Publishers, The Netherlands. pp. 311-336.

Timmis, R. 1985. Factors influencing the use of clonal material in commercial forestry. *In* Crop physiology of forest trees. Proceedings of an international conference on managing forest trees as cultivated plants, held in Finland, 23-28 July 1984. *Edited by* P.M.A. Tigerstedt, P. Puttonen and V. Koski. Department of Plant Breeding, University of Helsinki., Helsinki, Finland. pp. 259-272.

Tremblay, F.M. 1990. Somatic embryogenesis and plantlet regeneration from embryos isolated from stored seeds of *Picea glauca*. Can. J. Bot. 68: 236-242.

von Arnold, S. 1987. Improved efficiency of somatic embryogenesis in mature embryos of *Picea abies* (L.) Karst. J. Plant Physiol. 128: 233-244.

Webster, F.B., Roberts, D.R., McInnis, S.M., and Sutton, B.C.S. 1990. Propagation of interior spruce by somatic embryogenesis. Can. J. For. Res. 20: 1759-1765.

Wilhelmsson, L. 1991. Propagation of bred material - costs and benefits. *In* Pollen contamination in seed orchards: proceedings of the meeting of the Nordic Group for Tree Breeding in Sweden, August 1991. *Edited by* D. Lindgren. Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology, Uppsala, Sweden. pp. 100-119.

Appendix I

Annotated bibliography

Ahuja, M. 1986. What can biotechnology offer for forest tree breeding? [Was kann die Biotechnologie der Forstpflanzenzüchtung bieten?]. Allg. Forstzeit. 41(51/52): 1307-1309.

Language(s): German (English summary)

Abstract: In addition to large-scale propagation of a number of tree species (including protoplast culture), in vitro techniques which show promise include: production of haploids, conservation of germplasm, early testing for resistance, virus-free propagation, fusion of protoplasts for production of somatic hybrids, utilization of somaclonal variation, and gene transfers by recombinant DNA technology.

Aitken-Christie, J. 1991. Automation. *In* Micropropagation: technology and application. *Edited by:* P.C. Debergh, and R.H. Zimmerman. Kluwer Academic Publishers, The Netherlands. pp. 363-388.

Abstract: Automation in tissue culture covering automation in laboratory and greenhouse management, automated assessment of tissue cultures, automation in vitro and ex vitro, and robotisation was reviewed. Problems and prospects for the future are discussed.

Aitken-Christie, J., and Gleed, J.A. 1984. Uses for micropropagation of juvenile radiata pine in New Zealand. *In* International symposium of recent advances in forest biotechnology: June 10-13, 1984, Grand Traverse Resort Village, Traverse City, Michigan. Michigan Biotechnology Institute, East Lansing, MI. pp. 47-57.

Abstract: This paper presents a summary of the uses and potential future for micropropagation of juvenile Pinus radiata D.Don (radiata pine) in New Zealand. It covers such topics as the cold storage of shoots in culture micropropagation research, research plantations, introduction of new material, in vitro selection, and the commercial development of micropropagation. The financial benefits of micropropagation have been seen to be sufficient to justify commercialisation by two New Zealand companies. Micropropagation as a valid research tool and a doorway to clonal forestry has an exciting potential in New Zealand forestry.

Comments: Proposes using cold-storage of shoots in vitro (4 degrees C) as alternative to maintenance of clones for 6-8 years during field testing. Calculations of break-even price per 1000 micropropagated seedlings.

Aitken-Christie, J., and Jones, C. 1987. Towards automation: radiata pine shoot hedges in vitro. Plant Cell Tissue Org. Cult. 8(3): 185-196.

Comments: Describes procedures for maintaining clonal "hedges" in a culture vessel. Mini-hedges can be maintained for 18 months providing a continuous supply of new shoots for rooting. This would lend itself to automation of micropropagation as an alternative to somatic embryogenesis.

"While no costings from commercial embryogenesis operations are available to substantiate claims of cost reduction, some researchers still consider this to be the only approach. However, we have clearly demonstrated that reductions in cost may be possible through improvement of organogenic methods."

Standard shoot production using "normal" transfer method is 90 shoots/h. Hedges in vessels could increase this rate to 672 shoots/h - a seven-fold increase. If system automated, the main labour cost would be for shoot harvesting/transfer. Projected cost for micropropagated stock with shoot hedges would be NZ$250-300/1000.

Aitken-Christie, J., Singh, A.P., and Davies, H. 1988. Multiplication of meristematic tissue: a new tissue culture system for radiata pine. *In* Genetic manipulation of woody plants. *Edited by:* J.W. Hanover, and D.E. Keathley. Plenum Publ. Corp. pp. 413-432.

Comments: A subculturable meristematic tissue system capable of plantlet regeneration for Pinus radiata.

Also discuss genetic stability and automation as prerequisites for commercial use -- neither of which are yet demonstrated.

Anonymous. 1987. Tree improvement master plan for Ontario. Ontario Ministry Natural Resources, Queen's Printer for Ontario. 81 pages.
Comments: Outlines tree improvement plan under the headings:
- Principles and practices
- Species priorities
- Goals
- Strategies
- Standards
- Economics
- Supportive research

Note in particular the economic analysis methods used to calculate cost benefit ratios for "area" and "rotation age" models.

Arnold, R.J. 1990. Control pollinated radiata pine seed - a comparison of seedling and cutting options for large scale deployment. N.Z. Forestry 35(3): 12-17.
Abstract: Controlled pollination, CP, of radiata pine seed orchard clones is required to realise their full potential genetic gain. Vegetative multiplication of CP seedlots has been the usual practice till the present. However, this was found only to be economic for seed costs exceeding NZ$1,800 per kg, or where seed quantities are limited. Recent developments in radiata pine seed orchard management will enable large-scale production of such seed at costs projected to be as low as NZ$900 per kg. Isolated siting of future orchards could enable CP seed to be produced without a requirement for bag isolation of individual female cone whorls, decreasing costs even further. Given such costs, CP seed utilisation for seedling production can have significant advantages over its vegetative multiplication by cuttings from nursery seedling stools.

Arnold, R.J., and Gleed, J.A. 1985. Raising and managing radiata pine cuttings for production forests. Aust. For. 48(3): 199-206.
Abstract: Methods of producing rooted radiata pine cuttings are described. Nursery production of these cuttings in New Zealand was shown to be 5 times more expensive than that of one-year-old seedlings. However, comparison of costs of plantations established with cuttings or seedlings showed that at age 7 yr discounted costs per hectare were $200 in favour of cuttings. At age 12 yr, wood density of cuttings was 7% lower than for comparable seedlings, and heartwood content was 4% lower. Stem form of cuttings was significantly better than that of seedlings, especially for branch index and butt sweep.
Comments: Quotes total cost of seedling and steckling stock of NZ$40 and 223 respectively. However, initial planting density can be decreased from 1,200/ha with seedlings, to only 750/ha with cuttings. This greatly reduces cost of plantation establishment and early silvicultural costs.

Askew, G.R. 1988. Estimation of gamete pool compositions in clonal seed orchards. Silvae Genet. 37(5-6): 227-232.
Abstract: Nineteen loblolly clones monitored for flowering activity during three successive years, and data used to develop model to predict the genetic composition of the resulting seed crops. Variation in pollen production, female cone production, contamination by foreign pollen and numbers of clones found to impact on final gamete distribution.

Badenhop, M.B. 1984. How much does it cost to produce a rooted cutting? Amer. Nurseryman 160(8): 104-111.
Abstract: Studies were made of the costs of raising rooted cuttings of Juniperus horizontalis cv. Plumosa Compacta Youngstown, Ilex crenata cv. Hetzii and Euonymus alatus cv. Compactus using (1) 4 X 50-foot outdoor propagation beds, (2) 12 X 98-foot plastic-covered hoop houses each containing two 5 X 96-foot propagation beds or (3) a combination of 12 X 98-foot hoop houses each containing two 4 X 96-foot propagation beds, and 4 X 48-foot outdoor propagation beds. In all systems the cuttings were misted until rooted. Systems 2 and 3 had the highest survival rates (80-90%), compared with 60-70% in system 1.

The production cycle lengths were 18 months for J. horizontalis and I. crenata in all systems, but 9 months for E. alatus in systems 1 and 2 and 24 months in system 3. The average costs of raising each of the 3 species were 26, 31 and 23 cents, respectively. Labour costs amounted to about 30-50% of the total and overhead costs to about 25%. The various costs are itemized in detail.

Baskerville, G.L. 1991. Concluding comments: Proceedings of the Technical Session of the Forest Economics and Policy Working Group, CIF Annual General Meeting, Fredericton, New Brunswick, August 1990. For. Chron. 67(2): 117-118.

Comments: "... the idea of sustainable development is in conflict with fundamental economic principles and beliefs. The Brundtland definition of sustainable development says it is not reasonable to discount the values available from a resource in the future. Much of the problems our profession has had in introducing timber management have stemmed from the prevalence of the economic doctrine that the future is not as valuable as the present, and therefore timber management is not a reasonable thing to undertake."

Bentzer, B. 1986. Operational cutting production of Norway spruce *Picea abies* (L.) Karst. Mitt. der Bundesforschungsanst. Forst- Holzwirtsch. 152: 134-141.

Comments: The average height superiority of (Norway spruce) clones compared to standard seedlings is c. 20%.

"The development of a rational technique for production of cuttings still has a long way to go before it is perfected. Methods of mechanizing the harvest of cuttings and their insertion into the rooting media have to be developed. These procedures today constitute expensive bottlenecks in the production chain. The market price for a container cutting is thus now roughly double that of a container seedling of comparable size."

[NOTE: Five years later in 1991, Bentzer (pers. comm.) reports that "stecklings are sold at a price of between 60 to 70% over and above the price of comparable seedlings. Production volume is c. 3 million in 1991/92 - all Norway spruce. Capacity for production is c. 10 million, but the market is simply not ready yet."]

Binkley, C.S. 1980. Economic analysis of the allowable cut effect. For. Sci. 26(4): 633-642.

Comments: "Demonstrates the mechanics of the allowable cut effect and analyzes alternative criteria for evaluating investments in timber production."

" if maximizing present net worth is the objective of investments in timber production ... then their net benefits should be computed with the ACE."

Public policy may impose restrictions on timber flow." Public investment will most likely attempt to maximize timber production subject to a budget constraint. "... the fact that the shadow price of timber might not equal its market price should not cause economists alarm."

Also demonstrates the calculation of an effective discount rate by adjusting the real discount rate for appreciation of stumpage prices.

Binkley, C.S. 1984. Allowable cut effects without even flow constraints. Can. J. For. Res. 14(3): 317-320.

Abstract: "Allowable cut effects are a general pert of the harvest scheduling problem. Valid economic analysis of forest management programs requires the inclusion of the positive or negative incomes associated with them."

Bluhm, W.L., and Burt, J. 1983. Cutting propagation costs for Fraser photinia and Tam juniper. Combined Proceedings International Plant Propagators' Society 33: 83-87.

Abstract: Data from a group of Oregon nurserymen showed that propagation costs for Photinia X fraseri and Juniperus sabina var. tamariscifolia (2 widely grown subjects) were 20.5 and 13.1 cents per salable rooted cutting, respectively. Sticking, rooting and growing cuttings amounted to 71.2 and 73.3% of the total cost. Labour was the principal cost factor (> 50% of total).

Boyle, T.J.B. 1987. A diallel cross in black spruce. Genome, 29: 180-186.

Abstract: A complete 7 x 7 diallel of black spruce, without selfs, planted at three locations, was measured for height growth at several ages. Analysis using Griffing's method 3, model II, demonstrated that general combining ability (GCA) was the dominant genetic component of variation, although specific combining ability (SCA) appeared to be proportionately increasing in importance with age. When data from all locations were combined, the GCA x environment interaction proved to be highly significant. If the trend of increasing proportional importance of SCA continues, existing improvement strategies exploiting only GCA may need to be radically altered. Greater genetic gain would result from crosses among a few clones of high specific combining ability. Whatever approach is used, it appears likely that genotypes will have to be carefully matched to sites. Imbalance in the data appeared to invalidate F-tests. As a result of heterozygosity in the parents and the likely presence of epistasis and linkage disequilibrium, the interpretation of GCA and SCA variance components in terms of additive and dominance genetic variance cannot be made.

Comments: By age 14, 30% of the total genetic variance for height growth was due to dominance variance.

Burdon, R.D. 1982. The roles and optimal place of vegetative propagation in tree breeding strategies. *In* Proceedings of the IUFRO Joint Meeting of Working Parties on Genetics about Breeding Strategies including Multiclonal Varieties, Sensenstein, September 6-10, 1982. Lwr. Saxony For. Res. Inst., West Germany. pp. 66-83.

Abstract: Vegetative propagation can play various roles in tree improvement, and even several within one program. The possible roles are: holding of genotypes in archives; providing clonal seed orchards; mass propagation either of selected clones for crop uniformity and full utilizations of nonadditive gene effects, or of scarce or expensive seedling stock; provision of genetic information, by testing candidate genotypes for mass clonal propagation, or screening seed parents for breeding value, or estimating genetic parameters; providing material for research into physiology and pathology; potentially, novel applications such as genetic engineering.

The appropriate role or combination of roles in an improvement program must depend on the particular set of circumstances, which include: the biological constraints for the species on the different modes of propagation, the nature of the selection criteria and the genetic parameters for those criteria, and various silvicultural factors beyond the outright constraints. In a breeding program, different roles can be complementary or alternatives to each other or to seed propagation.

Burdon, R.D. 1986. Clonal forestry and breeding strategies - a perspective. *In* Conference Proceedings IUFRO Joint Meeting of Working Parties on Breeding Theory, Progeny Testing and Seed Orchards. Oct. 13-17, 1986, Williamsburg, VA. pp. 645-659.

Abstract: Clonal forestry entails large-scale planting of selected clones. Such clones should be sought within control-crosses between intensively select parents. Without going as far as clonal forestry, control-crosses can be mass-produced direct, or else vegetatively multiplied. The potential impacts of these developments on breeding strategies are examined after a review of the nature and historical evolution of breeding strategy. The shift from open pollination (as in conventional seed orchards) to controlled crossing may influence breeding strategies far more than the extension to clonal forestry. Neither development, however, would overturn certain basic requirements of a strategy, which include: pursuit of cumulative additive genetic gains by recurrent selection, and management of genetic material to assure the continued gains and to cover a wide range of contingencies.

Comments: Tree breeding - clonal

Burdon, R.D. 1989. When is cloning on an operational scale appropriate? *In* Breeding tropical trees: population structure and genetic improvement strategies in clonal and seedling forestry: Proceedings of a conference held in Pattaya, Thailand 28 November - 3 December 1988, by IUFRO Working Parties S2.02-08 Tropical species provenances and breeding, and S2.02-09 Eucalypt provenances and breeding. *Edited by:* G.L. Gibson, A.R. Griffin, and A.C. Matheson. Oxford Forestry Institute, Oxford, UK and Winrock International, Arlington, VA. pp. 9-27.

Abstract: Large scale use of a finite number of selected clones is the essence of clonal forestry (CF), which must be clearly distinguished from vegetative multiplication (VM) of unidentified genotypes starting with limited amounts of seed. To be worthwhile, CF must be biologically safe, technically feasible and economically advantageous.

Biological safety depends heavily on using enough clones to give a satisfactory spread of risks. In the longer term, both safety and future genetic gains depend on CF being founded upon an adequate genetic base, in the form of managed breeding populations and even gene resources.
Technical feasibility depends on achieving extremely high multiplication of individual clones and repropagating them over an extended period. This may be no problem with species where vegetative propagation is more convenient than using seed. Otherwise, one must overcome or circumvent problems posed by inherent difficulties of vegetative propagation, by maturation, or other forms of cultivar decline. Apart from purely biological problems, major logistical problems may have to be solved, so that feasibility depends on extensive development work. Even when problems are solved, clonal forestry is likely to carry additional costs that need to be outweighed by enhanced returns.
The prospective economic advantages of clonal forestry relating to genetic gain can involve: non-additive gene effects for some traits giving greater directional gains, advantages relating to genetic uniformity of stands, and other advantages of being able to exploit non-linear economic worth functions. The advantages of exploiting non-additive gene effects depend greatly on the importance of such effects relative to additive gene effects, while the other advantages will depend strongly on minimising non-genetic variation in the field. Further potential advantages include being able to capture desirable but low frequency segregants soon after F1 hybrid generations, and use of experience with particular clones both to extend the selection criteria beyond those for which conventional screening measures work and to generate favourable interactions between clones and management systems. The advantages, however, need searching analysis to ensure that efforts towards clonal forestry are profitably directed, and they must be shown to accrue in practice and not just theory. The advantages must be considered relative to those alternatives which include not only use of seedlings but also VM.

Burdon, R.D. 1990. Implications of non-linear economic weights for breeding. Theor. Appl. Genet. 79(1): 65-71.

Abstract: Applicable to both plant and animal breeding, relationships were studied theoretically between phenotypic values of selection candidates ('parents') and economic worth of the 'offspring' that would belong to production populations. The candidates could include individuals, crosses or clones, and the offspring could be produced either sexually or vegetatively. Cases considered included 3 systems for generating production populations (clonal propagation, pair (full-sib) crosses and half-sib crosses), 3 economic-worth (profit) functions for individual offspring (linear, intermediate optimum, acceptable vs. cull) and independently varying heritabilities for both parents and offspring. The heritabilities were varied in the model against a background of fixed genetic variance. Parental values were considered in terms of phenotypic standard deviations from the population mean, assuming normality. Lower heritabilities and, to a lesser extent, genetic segregation severely damped down the non-linearities of economic worth in relation to measured parental values, such that the linear weightings for traits in a selection index should usually be a good approximation, provided the profit function for individual offspring is monotonic. The economic advantages of corrective mating within a select population may be minimal if both heritabilities are low and the profit functions apply to the individual offspring. The economic advantages accruing from genetic uniformity of clones (or crosses between inbreds) in conjunction with non-linear profit functions are strongly dependent on achieving high broad-sense heritabilities, particularly in the offspring (production population).

Burdon, R.D. 1991. Expected impact of varying rates of propagation failure on genetic gain. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 104-105.

Abstract: Genetic gains from clonal selection are liable to severe erosion by significant losses of clones through propagation failures, unless the number of candidates per final selection is very large.

Burdon, R.D. 1991. Genetic parameters in seedlings and juvenile clones of *Pinus radiata*: some preliminary estimates. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 95-97.

Abstract: Estimates of variances and heritabilities were compared between juvenile clones (cuttings from

3-year-old ortets hedged to 55 cm) and seedlings in four natural and two cultivated populations. Discrepancies occurred but could be explained by the mating patterns in different populations combined with some nonadditive gene effects. Good comparisons need powerful experiments.

Burdon, R.D. 1991. Position statement -- clonal forestry with *Pinus radiata*. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, New Zealand. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 187-198.

Abstract: Clonal forestry (CF) has the crucial feature or requiring very high multiplication of single clones over an extended period. For it to be worthwhile it must produce extra benefits that outweigh any extra costs and complications.

In Pinus radiata, maturation creates major problems for developing CF. These involve, in varying degrees, logistical feasibility, developing valid predictions of genetic gains, screening of clones, and, ultimately, integrating the clonal system with breeding population management.

While certain of the commonly cited theoretical advantages of CF remain in question, there are potentially special advantages for P. radiata in fine-tuning branching patterns, effective screening for traits like resistance to wind damage, and, eventually, utilizing desirable alien genes incorporated by introgressive crossing with other species or by genetic transformation.

The various issues involved in developing a successful CF system for P. radiata are set out, and total coverage of those issues by the various agencies is reviewed as an aid to planning further work. Ulterior issues are: use of clonal material for probing genotype-site interaction, use of same as an aid to ideotype definition, and the prospect of Plant Variety Rights being granted to clonal material. Implications of existing institutional structures for the development of CF are also considered.

The range of issues, and the complexity of certain of the issues, argue strongly for a closely coordinated approach among all the interested parties, with a pooling of both the technology and the resultant clonal selections. Development work for CF and routine testing of clones must be done on top of breeding-population and gene-resource management, and not instead of it.

Comments: Contains summary of conditions which must be satisfied for CF, compared with vegetative multiplication, to be worthwhile, and a concise discussion of the problems of integrating CF with breeding population management.

Biological safety precepts: "not to concentrate on too narrow a base of clones, to retain the back-up of a large breeding population and gene resources, and to be in no immediate hurry to mass-propagate and genetic transformants that may come available."

Burdon, R.D. 1991. Some common assumptions in genetic gain expectations. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 44-45.

Abstract: It is commonly claimed that clonal forestry offers greater genetic gains than other breeding options. This is on the basis of expectations according to the customary quantitative genetic model. It is appropriate to examine the model and the expectations, and to consider certain underlying assumptions that relate to the potential advantages of clonal forestry. For clonal forestry options, particular concern must exist over the assumption that variances and genotypic rankings are the same in seedling and clonal material.

Comments: In the discussion that followed at the workshop, Burdon made observations about the equivalence of variances and rankings between clones and seedlings. The environmental variances do not appear to be comparable in many cases, although rankings are. Anecdotal reports however from Brazil suggest poor correlation between seedling and clone performance in eucalypts.

Burdon, R.D., and Namkoong, G. 1983. Multiple populations and sublines. Silvae Genet. 32(5-6): 221-222.

Abstract: Multiple populations and sublines are two concepts that have developed in recent years for tree breeding. They relate to subdividing breeding populations, and are defined as follows:

"multiple populations" represent different selection criteria, to ensure that at least one such population will correspond roughly to any future selection goal;

"sublines" represent replicate breeding populations that can be intercrossed to ensure completely outbred offspring at any time in the future.

Carlisle, A., and Teich, A.H. 1978. Analysing benefits and costs of tree-breeding programmes. Unasylva, 30(1): 34-37.

Comments: "Using a mathematical model, it has been shown that, allowing for interest and inflation, accumulated establishment costs far exceed management cost in a plantation operation at time of harvest". "In the literature the evidence that these benefits (from tree improvement) considerably exceed the costs in cash terms is overwhelming".

Carson, M.J. 1986. Advantages of clonal forestry for *Pinus radiata* - real or imagined? N.Z. J. For. Sci. 16(3): 403-415.

Abstract: The advantages of using tested clones in P. radiata stands were compared with current open-pollinated and control-pollinated seed orchard strategies in New Zealand. Clonal forestry shares with control-pollinated orchard strategies the advantages of shorter plant production times, control of pedigree, flexibility of deployment, multiplication of valuable crosses, and efficient capture of additive genetic gains. It may have additional advantages in increasing uniformity, allowing clone/site matching, controlling growth habit, and capturing non-additive genetic gains. However, a control-pollinated orchard strategy coupled with vegetative multiplication is currently proving to be more cost-efficient in establishing managed stands. Use of a clonal strategy requires evidence for greater economic gains.

Carson, M.J. 1986. Control-pollinated seed orchards of best general combiners - a new strategy for radiata pine improvement. Chap. 26. *In* Plant breeding symposium DSIR 1986. (Special Publ. No. 5) *Edited by:* T.A. Williams, and G.S. Wratt. N.Z. Agronomy Society. pp. 144-149.

Abstract: Results from a diallel test of improved Pinus radiata planted on two Central North Island (New Zealand) sites indicate that general combining (GCA) effects are more important than specific combining ability effects (SCA) for tree growth rate, stem form, and resistance to Dothistromia pini. These results support current use of well-isolated open-pollinated clonal seed orchards of the best general combiners for the production of improved radiata pine seed. Mass controlled pollination and vegetative multiplication will soon allow large-scale production of crosses. Given the moderate levels of SCA and the finite number of crosses that can be tested, maximum gains seem attainable for parental GCA. Parental GCA estimates have previously been obtained from trials of open-pollinated progenies. In future, control-pollinated polycross progenies will be used for GCA ranking of parents. Greater gains should result from large-scale production of the best general combiners, rather than selection and multiplication of best full-sib families.

Comments: Shows comparison of gain from different testing and selection strategies with equal amounts of effort. Good approach to comparison of methods on based on equal, finite resources.

Carson, M.J. 1987. Improving log and wood quality: the role of the radiata pine improvement programme. N.Z. Forestry 31(4): 26-30.

Abstract: The radiata pine improvement programme in New Zealand was begun in the 1950s with plus-tree selection to establish clonal seed orchards. The main emphasis in tree improvement has been on growth rate, stem form, disease resistance, branching habit and log and wood quality. Increased growth rate and better stem form will significantly increase profitability through reductions in growing costs and increases in piece size, but in timber coming on the market in the 1990s there will be an increase in knotty grades at the expense of a reduction in clearcuttings grades. Despite the possibility of producing special-purpose breeds, the main emphasis of the tree improvement programme in future will continue to be a general-purpose radiata breed with wide site tolerance, superior vigour and stem form, and moderate resistance to Dothistroma [Scirrhia] pini and Cyclaneusma minus. Greater flexibility is possible by concentrating on developing the techniques of controlled pollination and subsequent vegetative multiplication.

Carson, M.J. 1991. From improved breeds to clonal ideotypes. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 47-50.

Abstract: *Pinus radiata* ideotypes (trees with a specific combination of attributes) developed as improved breeds should also prove suitable for use in clonal forestry. Selection will be for relatively few ideotypes, since each distinct ideotype will be subject to the acid test of economic justification. Greater gains and cost efficiencies will result from integrating clonal development with breeding operations.

Carson, M.J., and Burdon, R.D. 1991. Relative advantages of clonal forestry and vegetative multiplication. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 41-43.

Abstract: Clonal forestry shares with control-pollinated orchard systems advantages of shorter plant production times, control of pedigree, flexibility of deployment, multiplication of valuable crosses, and efficient capture of additive genetic gains. It may have additional advantages of greater crop uniformity, better exploitation of genotype-environment interaction, controlling resource allocations, working with known clones, meeting non-traditional breeding goals, and capturing nonadditive genetic gains. However, a control-pollinated orchard system coupled with vegetative multiplication is currently more cost-effective. Adoption of a clonal system should await the development of cheaper delivery systems, and greater evidence for economic gains.

Carson, M.J., Burdon, R.D., Carson, S.D., Firth, A., Shelbourne, C.J.A., and Vincent, T.G. 1990. Realising genetic gains in production forests. *In* Joint meeting of Western Forest Genetics Association and IUFRO working parties S2.02-05, 06, 12 and 14, Douglas-fir, contorta pine, Sitka spruce and Abies breeding and genetic resources, Olympia, WA, August 20-24, 1990. (Paper presented during "Genetic gains in production forests", but not included in proceedings)

Comments: Describes reasons for failure of conventional OP clonal orchards to deliver gains:

- pollen contamination from outside orchard
- unequal pollen contribution from orchard parents
- late initial seed production (poor siting)
- attrition of clones due to graft incompatibility
- failed attempts to establish orchards with cuttings rather than grafts
- large number of clones considered necessary to ensure out-crossing

Also discusses use of control-pollinated and meadow orchards.
Selection of families at age 5 was too early for optimal gains.
Assortative mating and "nucleus" breeding options.
Mixed results from early selection attempts.
Accelerated realisation of gain from vegetative multiplication.

Carson, S.D., and Carson, M.J. 1991. Clonal forestry and durability of disease resistance. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 134-138.

Abstract: Clonal forestry would probably reduce genetic variability and increase the risk of disasters. Few, if any, tools exist for assessing the risks of genetic uniformity. Risks will depend on many characteristics of the reproductive biology of the host and pathogen species, and on the genetic structures of both the host and pathogen populations. Since resistance is overcome because pathogen populations evolve in response to changes in the host population, the mechanisms involved work at the level of populations rather than at the level of genes or genotypes. A theoretical population model that incorporates some or all of the above parameters could assist in risk assessment.

Comments: "No forest can ever be completely "safe". Disasters have occurred in highly diverse forests, as when chestnut blight was introduced to the American chestnut. But risk clearly increases if large stands are planted with single clones."

Chaperon, H. 1991. Open-pollinated seed orchards: tested families or tested clones for tomorrow's forests? *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 15-24.

Abstract: Interest in vegetative propagation of forest trees has been revitalised recently because of the success achieved with some tropical eucalypts. The application of these techniques to pines (particularly Pinus pinaster - Maritime pine in France) is more difficult because of:

- a different silviculture: longer rotations, with thinning for controlling stocking of stands;
- maturation, which still impedes the multiplication and growth rate of clones selected when mature;
- inheritance of selection criteria, mainly additive.

The multiplication of selected families from controlled crosses is the best method at present for achieving genetic gains in pines.

Controlled crosses should be carried out on a large scale in seed orchards specially designed for this purpose; the seed can be multiplied by vegetative propagation (somatic embryogenesis, micropropagation, or rooted cuttings) for as long as required while seed production from the seed orchards remains insufficient.

The cloning of pines may probably develop in the future because of renewed interest in inter-specific and inter-provenance hybrids and because additional selection criteria are likely to be adopted.

Chee, R. 1984. Micropropagation: can nurserymen afford to ignore it? Am. Nurseryman. 159(8).

Comments: Up to 90% of the micropropagation cost due to labour.

Cheliak, W.M., and Klimaszewska, K. 1991. Genetic variation in somatic embryogenic response in open-pollinated families of black spruce. Theor. Appl. Genet. 82: 185-190.

Abstract: Zygotic embryos from open pollinated seeds of 20 black spruce families were used to investigate the proportion of genotypes that would give rise to embryogenic tissue (ET) and mature somatic embryos. Eighty-five percent of the maternal genotypes gave rise to embryogenic tissue. Within-family rates of ET induction ranged from 0 to 17%, with an average of 8%. The largest proportion of variation was among families, indicating the additive nature of the genetic variation. On a medium of 6% sucrose and 3.7μM ABA, 90% of the embryogenic lines gave rise to abundant (> 100/100mg of ET), well-formed, mature somatic embryos. These were grown in the greenhouse and have now been established in field trials.

Cheliak, W.M., and Rogers, D.L. 1990. Integrating biotechnology into tree improvement programs. Can. J. For. Res. 20(4): 452-463.

Abstract: Time is a major constraint in the progress of tree improvement programs. Four ways in which time influences the tree improvement process are (i) evolutionary time, (ii) time to harvest, (iii) time to achieve phenotypic stability, and (iv) time to reach reproductive maturity. The ways in which each of these affects the three phases of a tree improvement program (conservation, selection and breeding, and propagation) are identified and discussed. How biotechnological techniques, as well as other enabling technologies, address the time constraint problem is also discussed. The biotechnological approaches include tissue culture, molecular genetics, and genetic engineering; the enabling technologies include early testing and flower induction. Through tissue culture it is possible to increase genetic gain per unit time and increase total genetic gain by using more of the total genetic variation. Development of high-resolution linkage maps, through application of molecular genetics technology, will provide new approaches to early screening, testing, and selection. Additionally, molecular probes will be useful in improving methods that genetically fingerprint germplasm. Genetic engineering has considerable potential to reduce time constraints. However,because of the diverse breeding and production populations typically employed, much basic work needs to be done to integrate genetically engineered materials into tree improvement programs. Early selection and flower induction address the time constraints imposed by age-stable performance and reproductive maturity. When used in combination with the previously described biotechnologies, a powerful system is created that can dramatically reduce the time required to integrate genetically improved material into forest regeneration programs. An example of integrating tree improvement, clonal forestry and biotechnology is described for an existing black spruce regeneration program.

Comments: "Through tissue culture it is possible to increase genetic gain per unit time and increase total genetic gain by using more of the total genetic variation."

"Only limited data are available, but in some estimates 30-50% of the total genetic variation is in the form of nonadditive effects (Boyle 1987; Cotterill et al. 1987; Timmis et al. 1987)"

"... some of the genetic gain can be incorporated in as little as 20% of the time that it would take from conventional seed orchards (Hasnain and Cheliak 1986)"

Chu, I.Y.E., and Kurtz, S.L. 1990. Commercialization of plant micropropagation. Chap. 6. *In* Handbook of plant cell culture. Volume 5. Ornamental species. *Edited by:* P.V. Ammirato, D.A. Evans, W.R. Sharp, and Y.P.S. Bajaj. McGraw-Hill, Inc., New York. pp. 126-164.

Abstract: The subject is reviewed. The commercial advantages of micropropagation are seen in terms of product development (allowing rapid multiplication, product uniformity and high volume production, but also propagation of heterozygous, genetically engineered or germplasm materials), product enhancement (improving the phenotype and producing disease-free plants), and marketability of the product (making available to growers a range of products from microcuttings to established plants, ease of product movement and non-seasonal production). The limits to and cost of micropropagation are set out as are the available production systems (axillary shoot multiplication, adventitious shoots and somatic embryogenesis), the production stages and the necessary production facilities. The economics of micropropagation systems are examined in terms of reducing production costs and current world activity and markets.

Constantine, D.R. 1986. Micropropagation in the commercial environment. Chap. 17. *In* Plant tissue culture and its agricultural applications. *Edited by:* L.A. Withers, and P.G. Alderson. Butterworths, London. pp. 175-186.

Comments: Logistical impact of scaling-up production often escapes attention by academic workers. Comments on problems and opportunities from variation in micropropagated plants.

Copes, D.L., and Sniezko, R.A. 1991. The influence of floral bud phenology on the potential mating system pf a wind-pollinated Douglas-fir orchard. Can. J. For. Res. 21(6): 813-820.

Abstract: Reproductive bud phenology from 1983 through 1989 limited potential outcross efficiency to a maximum of 58 to 87%, in a Douglas-fir clonal orchard near Monmouth, Oregon. Potential outcross efficiency was calculated for 20 clones from dates of male and female bud opening and pollination mechanism information. Cool weather before bud opening of the earliest clones delayed and compressed the breeding period and resulted in a greater percentage of trees having synchronous periods of pollen release and receptive seed strobili. Outcrossing was greatest in clones with intermediate phenology and least in the earliest clones. The breeding system appears to be an almost continuous series of overlapping breeding subpopulations. Each year's breeding subpopulations were different from those of other years because of large shifts in rank order of bud opening by 10 to 20% of the clones and because of great differences in the length of breeding season. Seed crops produced in years with compressed breeding seasons have potential of being more diverse than crops produced during years with extended breeding seasons.

Cornelius, J.P., and Morgenstern, E.K. 1986. An economic analysis of black spruce breeding in New Brunswick. Can. J. For. Res. 16(3): 476-483.

Abstract: A representative black spruce breeding program was formulated using information collected from New Brunswick Tree Improvement Council cooperators. This "base program" was subjected to program profitability and program efficiency analyses. Costs and revenues were computed for a range of real discount rates. The results showed that variation in discount rates did not greatly influence the break-even level of gross discounted revenue, which was fairly stable at around $100 000 for the base orchard of 5.2 ha. Projected gross discounted revenue ranged from about $100 000 at 4.5% discount rate to $36 at 16%. With the internal rate of return at 4.4%, it was concluded that black spruce breeding is probably and economic means of securing extra wood supplies. The program efficiency component concentrated on resource allocation between plus-tree and family selection. The results suggested that current strategies are close to optimum; for a wide range of numbers of families selected within a constant budget, gross returns remained within about 10% of the maximum possible for each assumption set. It was concluded that current breeding programs should be continued, with present recommended strategies retained.

Comments: Growth and yield information used in this report has since been adjusted downwards. States that an "intermediate" black spruce site will reach peak MAI at 46 years, with 296.4 m3/ha and mean height of 18.1 m. Current model results for "above average" site indicates that peak MAI is reached at 51 years with TV of 304.7 and MV of 278 m3/ha and mean height of 17.4 m. An "average" site reaches peak MAI at 60 years with TV of 302.8 and MV of 276 m3/ha.

Cotterill, P.P. 1984. A plan for breeding radiata pine. Silvae Genet. 33(2-3): 84-90.
Abstract: A plan for improving radiata pine in SE South Australia is proposed, which would remove the conflict between achieving rapid gains in genetic quality of seed from orchards while attempting to maintain genetic diversity. One large breeding population should be gradually improved over the generations, while a more highly selected seed orchard population of superior individuals is developed from this population. Features of the plan which may be new are: low-cost gene conservation areas which contain the pooled progeny of all parents in the first-generation breeding population; a two-stage selection scheme, where 4 individuals are selected from each family in the breeding population, and then from progeny tested using open-pollinated seed, before finally deciding which two individuals from each family are best for future breeding; an index using estimates of general combining abilities to pair potential parents, so that more superior families may be generated from single-pair matings.

Cotterill, P.P. 1986. Genetic gains expected from alternative breeding strategies including simple cost options. Silvae Genet. 35(5-6): 212-223.
Abstract: Gain equations are developed and used to calculate genetic gains expected in the breeding population each generation and each decade from 10 breeding strategies. Half-diallel mating with combined index selection can maximize expected genetic gain per generation. However, the simpler and less expensive strategy of single-pair mating with combined index selection has a shorter generation interval and produces substantially greater gains per decade. Polycross mating with combined index selection also produces good expected gains per decade. Strategies which rely solely on within-family selection produce poor gains per generation and per decade.

Cotterill, P.P., and Jackson, N. 1989. Gains expected from clonal orchards under alternative breeding strategies. For. Sci. 35(1): 183-196.
Abstract: Gain equations were developed under the assumption of an additive genetic model and were used to calculate responses from clonal seed orchards under six strategies for breeding trees. The six strategies involve combinations of phenotypic or combined index selection to establish orchards, and polycross, single-pair, or half-diallel mating for progeny testing to cull orchards and for regenerating the breeding population. Open-pollinated mating was considered for progeny testing only. Combined index selection with half-diallel mating produced the greatest gains from orchards. Single-pair mating used in conjunction with open-pollinated progeny testing proved to be the next best option under the range of heritabilities studied (heritabilities from 0.05 to 0.06). However, combined index selection with single-pair mating (and no open-pollinated testing) was also very efficient. Combined index selection with polycross mating produced substantial gains from culled orchards but was less appealing for unculled orchards.

Cunningham, M.W. 1986. Evaluation of the potential of clonal forestry for a population of American sycamore. Ph.D. Dissertation, North Carolina State University, Raleigh, NC. 89 p.
Abstract: A population of American sycamore (Platanus occidentalis) comprising 13-yr-old progenies from 30 open-pollinated families was evaluated to determine the potential of using rooted cuttings as planting stock. Rooting ability of cuttings from 1-yr-old coppice was 6.5-99.2%, with a population mean of 56.3%. Family effects were not significant for any of the rooting traits evaluated, but clone-family effects were significant for all traits. Rooting traits and ortet growth traits were not correlated. Results implied that genetic variation in rooting ability was predominantly nonadditive and that recurrent selection would cause little change in these traits. Selection at 5 or 9 yr to improve volume at 13 yr resulted in greater expected gains on a per year basis than selection for any trait at age 13. Economic analysis indicated that a ratio of nonadditive to additive variance of 0.4-1.2 was needed for the use of rooted cuttings to be more profitable than the use of seed orchard seedlings. The profitability of the clonal system was highly dependent on the number of individuals selected from progeny tests for evaluation in clonal tests.

Danbury, D.J. 1972. Economic implications of selection for seed production in radiata pine seed orchards. Aust. For. Res. 5(4): 37-44.

Comments: Suggests that selecting best seed producing clones in orchard will increase seed production and thus lower seed costs. If seed production is negatively correlated with volume prod'n, the selection would still be worthwhile provided that volume loss did not exceed 0.5%.

Davis, L.S. 1969. Economic models for program evaluation. *In* Proceedings 2nd World Consultation on Forest Tree Breeding, Washington, 7-16 August 1969. FAO/IUFRO. pp. 1524-1543.

Comments: Presents basic models for analysis of quantitative and qualitative improvement of pulp fibre. Shows that a small increase (5%) in wood quality from tree selection would raise mill profits by 15 to 41% by increasing yield per unit of wood processed and reducing mill processing time.

de Fossard, R.A., and Bourne, R.A. 1977. Reducing tissue culture costs for commercial propagation. Acta Hortic. 78: 37-44.

Comments: Tissue culture uses considerably less space at all stages, than rooted cuttings, but is associated with expensive equipment and costly labour. Costs may be reduced by using alternative equipment, supplies and methods, and lower cost-labour.

Dekker-Robertson, D.L., and Kleinschmit, J. 1991. Serial propagation in Norway spruce (*Picea abies* (L.) Karst.): results from later propagation cycles. Silvae Genet. 40(5/6): 202-214.

Abstract: Maturation state can adversely affect the success of vegetative propagation, insofar as more mature material is difficult to root and tends to grow plagiotropically. One method used to retard maturation of trees in clonal tree improvement programs is serial vegetative propagation, which has the advantage of being practical for large-scale operations. Norway spruce ramets first rooted in 1968 have been re-rooted seven times, while new clones have been added regularly. Growth traits such as height, root-collar diameter and fresh and dry weight, as well as form traits such as habit, tropism, root development and number of branches are compared on four trees of each three-year-old clone to evaluate the success of serial propagation in retarding maturation. There are distinct differences in the performance of seedlings and cuttings. Cuttings are generally superior in total dry matter production, even in higher propagation phases (cycles) where a decrease in height can be observed. While clones that have been rooted from one to four times show fast growth and good form, some clones within later propagation phases show decreases in both traits, indicating a higher maturation state. It may be possible to select against fast-maturing clones, thus prolonging the possible period for vegetative propagation, but a restriction of repropagation to seven or eight phases seems to be necessary.

Deloitte & Touche. 1991. Economic benefit assessment of spruce budworm control in eastern Canada. Deloitte & Touche Management Consultants, Guelph, Ontario. 101 pages. (Draft final report, prepared for the Forest Pest Management Caucus)

Comments: Page 78-80: Describes calculation of residual timber value for the Restigouche-Tobique license, resulting in a weighted value of $15.52/m3. Also, "that real timber values have tended to increase by 1 percent per year, while real costs (i.e. harvesting and transportation) have remained relatively constant." Therefore, conducted analysis under two situations: no increase in real timber value, and with 1 percent/year increase.

Used a 4 percent discount rate.

Di-Giovanni, F., and Kevan, P.G. 1991. Factors affecting pollen dynamics and its importance to pollen contamination: a review. Can. J. For. Res. 21(8): 1155-1170.

Abstract: Pollen contamination causes major losses to genetic improvement from selection and breeding of "plus" trees in conifer seed orchards. Genetic losses arise by the influx of "wild" conspecific pollen into seed orchards and its deleterious fertilization of superior genetic lines. This review firstly addresses the basis of the problem: pollen, conifer reproduction, and the concept of seed orchard management, especially in regard to reduction of contamination. Secondly, the physical processes of pollen liberation, dispersal, and deposition are described, and examples of previous studies illuminating these phenomena given. Thirdly, past research on measuring pollen dispersal in natural stands and seed orchards is discussed in the light of modelling techniques used to predict these types of dispersal pattern. Work on the other facets of contamination measurement, gene-flow studies, are listed. It is concluded that a detailed study that combines both the physical and gene-flow aspects of pollen dispersal should be initiated to compare and contrast the two methods, and that attempts to model pollen contamination should be sought.

Dixon, G.R. 1987. The practicalities and economics of micropropagation for the amenity plant trade. *In* Micropropagation in horticulture: practice and commercial problems. Proceedings of the Institute of Horticulture Symposium, University of Nottingham School of Agriculture, 24-26 March 1986. *Edited by:* P.G. Alderson, and W.M. Dullforce. Institute of Horticulture, London, UK. pp. 183-196.

Abstract: The amenity plant industry in the UK is discussed in relation to its development, products and markets. Results are reported from a small survey of nurseries to determine the range of costs of rooted cuttings and the economic suitability of micropropagated plants (including trees and shrubs) for the amenity sector is considered.

Comments: Selling prices of amenity plant material in 1986 (£UK):

Trees - conifer 2+0	.03-.04
Trees - conifer 2+2	.07-.09
Trees & shrubs - microprop.	.20-.70

Production costs in 1986:

Rooted cuttings	.057-.120
Micropropagation	.08-.30 (avg. .12)

Donnan, A., Jr. 1986. Determining and minimizing production costs. *In* Tissue culture as a plant production system for horticultural crops. *Edited by:* F.A. Bliss. (Current Plant Science and Biotechnology in Agriculture.) Martinus Nijhoff, Dordrecht. pp. 167-173.

Comments: "Labor is by far the largest cost involved in producing tissue culture plants at the present time, accounting for 60% up to 85% in extreme cases."

El-Kassaby, Y.A., and Askew, G.R. 1991. The relation between reproductive phenology and reproductive output in determining the gamete pool profile in a Douglas-fir seed orchard. For. Sci. 37(3): 827-835.

Abstract: A 15-year-old, Douglas-fir, full-sib seed orchard with 97 families was studied to establish the relation between reproductive phenology and reproductive output. Both male and female strobili development was monitored throughout the flowering season, and seed-cone counts and male strobili productions were determined. The overall potential gametic contributions of each family were estimated in terms of proportional contributions to the seed crop and parental balance.

Families varied greatly in both seed-cone and pollen contributions. The top 5 contributors of cones were different from the top 5 pollen contributors. Assessing seed-cone and pollen contributions prior to cone induction or supplemental mass pollination will be valuable for increasing the genetic value of orchard seed. Estimates of the genetic value of the orchard crop should be calculated after completion of a parental balance study focused on both seed and pollen contributions and their reproductive phenology timing.

El-Kassaby, Y.A., Rudin, D., and Yazdani, R. 1989. Levels of outcrossing and contamination in two Pinus sylvestris L. seed orchards in northern Sweden. Scand. J. For. Res. 4(1): 41-49.

Abstract: The joint levels of outcrossing and contamination two young northern Swedish Scots pine (Pinus sylvestris L.) seed orchards were studied with the aid of allozyme markers. High levels of contamination (21-36 %) were estimated and were attributed to the observed low within orchard pollen production. Outcrossing rate estimates were high (0.957-0.961), though they departed significantly from complete outcrossing (t = 1.0) in spite of the observed high contamination levels. These results confirmed reported relationships between outcrossing and contamination levels in open-pollinated seed orchards. It was concluded that a crop management option relying on supplemental mass-pollination would be effective in reducing both contamination and inbreeding levels.

Eule, H.W. 1984. Plant propagation in a forest district-owned nursery - example of the Delliehausen nursery in the Uslar Forest District [Pflanzenanzucht im forsteigenen Kamp dargestellt am Beispiel des Kampes Delliehausen im Staatl. Forstamt Uslar]. Forst und Holz 39(12): 310-312.

Abstract: A report on centralized nursery facilities initiated at this site in Lower Saxony in 1967. In 1980, some 266 000 rooted cuttings (of several species) were produced, at an av. total cost of DM99.27 per thousand cuttings.

Farthing, J.G. 1988. Propagation techniques for Ficus robusta. Acta Hortic. 226: 489-498.

Abstract: Four methods of propagation (air layers, unrooted top cuttings, leaf cuttings and micropropagation) for this pot plant species were examined over a 24-month period. The economics of the production techniques were evaluated, taking into account energy requirements, space, uniformity of crop, and losses. The micropropagated material was clearly the most economic option.

Comments: The micropropagated material was more economic than other forms of vegetative propagation, but no data are presented on seedling production costs.

Fins, L., Moore, J.A., Medema, E.L., and Hatch, C.R. 1984. Economic analysis of a tree improvement program for western larch. J. For. 82(11): 675-679.

Abstract: Data collected from genetically improved stands of Larix occidentalis (produced by a tree improvement programme in N. Idaho) and from unimproved stands were analyzed using an individual tree simulation model (Prognosis) [see FA 45, 5788] and the economic subroutine CHEAPO [Medema, E.L.; Hatch, C.R. (1979) Computerized help for the economic analysis of prognosis-model outputs (CHEAPO). Research report prepared for Intermountain Forest & Range Experiment Station, Ogden, UT. Prepared by the College of Forestry, Wildlife & Range Sciences, Univ. Idaho, Moscow. 71 pp.] to determine volume and values of timber at the age of financial rotation (when net present value is maximized). Three hypothetical functions were tested on 2 site classes. Sensitivity analyses showed that the investment in tree improvement was likely to be profitable at 4 and 5% discount rates on excellent sites and at 4% on good sites. The analysis was most sensitive to changes in discount rate, site quality and cone production rate; and moderately sensitive to variation in time to seed production, number of productive orchard years, and differences among the assumed biological functions.

Comments: Assumed a 2% stumpage price appreciation, and real discount rates of 4 to 6%.

See formulae used for present value of a series of payments. (Use to calculate the $value of the allowable-cut-effect from planting higher quality stock??)

Florkowski, W.J., Lindstrom, O.M., Robacker, C.D., and Simonton, H.R. 1990. Analysis of pricing plants grown in tissue culture. Hortscience, 25(10): 1306.

Comments: Reports wholesale selling price of $0.47 of Stage IV plantlets of Ficus Benjamina (avg. 6 producers)

Florkowski, W.J., Lindstrom, O., Robacker, C., and Simonton, W. 1988. Biological, technical, and economic aspects of commercial micropropagation. Georgia Agricultural Experiment Station, Griffin, GA. 17 pages. (Res. Rep. No. 556)

Abstract: Information is surveyed under the following headings: (1) history of micropropagation, (2) micropropagation of plants (including stages of micropropagation, advantages and disadvantages, and opportunities for commercialization), (3) location of tissue culture operations, (4) establishment of a commercial tissue culture operation (including details of facilities, equipment, supplies, personnel, operating expenses and required laboratory capabilities), (5) marketing of tissue-culture grown plants, (6) pricing of tissue culture plants, (7) export of tissue culture products, and (8) patents for tissue culture laboratories. The text is illustrated with examples of mostly horticultural plants and tropical fruits. A glossary of technical terms is included. Although intended for use in Georgia, USA, the publication is of general interest to workers involved with tissue culture and micropropagation.

Comments: Quotes selling prices (including profit) or US$0.40-0.68 per established plantlet from tissue culture (1988).

Foster, G.S., Campbell, R.K., and Adams, W.T. 1985. Network analysis of research and development for evaluating a clonal reforestation programme. Chap. 23. *In* Crop physiology of forest trees. Proceedings of an international conference on managing forest trees as cultivated plants, held in Finland, 23-28 July 1984. *Edited by:* P.M.A. Tigerstedt, P. Puttonen, and V. Koski. Dept. Plant Breeding, Univ. Helsinki, Helsinki, Finland. pp. 273-283.

Abstract: Network analysis holds promise for coordinating the large number of research and development activities required to carry through a clonal reforestation program. The activities are subdivided into four increasingly complex sections separated by decision points. In this way, research costs are kept down until there are sufficient indications of eventual success. The research and development program described in this analysis can provide a reforestation manager with information on the basis of which he can decide whether and when to start clonal reforestation with a selected species.

Comments: Part of Sam Foster's PhD thesis, Oregon State Univ.

Discusses the use of Network Analysis to guide the sequence of research activities (critical path) leading to decisions regarding the use of clonal forestry for a given species.

Fowler, D.P. 1986. Strategies for the genetic improvement of important tree species in the Maritimes. Can. For. Serv. - Maritimes, Inf. Rep. M-X-156. 30 pages.

Abstract: Multigeneration breeding strategies for the genetic improvement of tree species that are important for reforestation in the Maritimes Region of Canada are presented. The species include black spruce, white spruce, red spruce, Norway spruce, jack pine, and tamarack. The strategies presented here are based on available biological and genetic information and can be modified or changed as more information or improved techniques become available.

Frampton, L.J., Jr., and Hodges, J.F. 1989. Nursery rooting of cuttings from seedlings of slash and loblolly pine. South. J. Appl. For. 13(3): 127-132.

Comments: Describes techniques for rooting of slash and loblolly pines from 1-0 seedlings. About 52% of the cuttings produced plantable trees (these species are known to be very difficult to propagate vegetatively).

Franclet, A., and Boulay, M. 1983. Micropropagation of frost resistant Eucalypt clones. Aust. For. Res. 13(1): 83-89.

Abstract: A method is described for the production of approx. 20 000 plants per month from clones selected for frost resistance. Only clones of Eucalyptus gunnii, E. dalrympleana and their hybrids are involved at present, though clones of E. pauciflora and E. delegatensis are to be tested. Multiplication of axillary buds in culture is by a method similar to that of de Fossard [see FA 41, 7133] with activated charcoal added to the second medium to promote elongation. Rooting is achieved by 7 days in the dark at lower temp. (20°C) followed by a few days in the light at 25°C. A special container is described for acclimatizing plantlets to growth under greenhouse conditions. Plants raised in this way cost approx. twice that of conventionally raised material.

Comments: Note reference to cost of in vitro plantlet production (3 F per) is about 2x that of seedlings.

Fraser, G.A. 1985. Benefit-cost analysis of forestry investment. Can. For. Serv., Pacific Forestry Centre. 20 pages. (Inf. Rep. BC-X-275)

Abstract: Reviews development and application of benefit-cost analysis to forestry investments. Leads reader through measurement of costs and benefits, discounting, and the sensitivity of the method to changes in the underlying assumptions, and clearly states the limitations of benefit-cost analysis.

Friedman, S.T., and Adams, W.T. 1985. Levels of outcrossing in two loblolly pine seed orchards. Silvae Genet. 34(4-5): 157-162.

Comments: Found that outcrossing (orchards had 23-27 clones) was very close to 1; higher than found in surrounding natural stands. Possible factors: number of clones, density, design, species, contribution by outside pollen.

Gemmel, P., Örlander, G., and Högberg, K.A. 1991. Norway spruce cuttings perform better than seedlings of the same genetic origin. Silvae Genet. 40(5/6): 198-202.

Abstract: Growth and survival for seedlings and cuttings of Norway spruce were compared. The two different plant lots originated from the same seed source, and the selection of plants for cutting propagation gave a negligible reduction of genetic variation. Eight years after planting, both survival and height were superior for cuttings for cuttings compared to seedlings. The differences in performance for the two plant materials can be explained by differences in morphology and physiology. The results indicate that genetic selection for growth, based on clonal tests, can be improved by using growth in a later stage than from the first eight years when comparing different clones.

Comments: Height growth was 10-20% higher for cuttings over seedlings, although size at time of planting was roughly the same.

"... referring to present rules in Sweden, the acceptance of cutting propagated clones for commercial use is determined by the total gain compared to recommended seedling material without separating the genetic gain from other components. This means that the total gain when using mixtures of accepted clones includes effects of cutting propagation method as well as genetic selection effects. There is reason to believe that the propagation effect is variable, which makes it difficult to generalize single quantifications of this effect."

Gill, J.G.S. 1983. Comparisons of production costs and genetic benefits of transplants and rooted cuttings of *Picea sitchensis*. Forestry, 56(1): 61-73.

Abstract: A system has been developed by the British Forestry Commission for bulking-up plant numbers from scarse seedlots by rooted cuttings. Commercial-scale trials of the system are now under way. This paper describes a comparison of costs of producing planting stock by two methods; traditional nursery rearing of transplants (1+1) and vegetative propagation of stock material to produce cuttings (C1+1). Genetic gains are predicted and compared for both systems, predictions being based on quantitative estimates of genetic variables from progeny tests and on the current progress of the breeding programme. The implications of the economic comparison for the future breeding programme of Sitka spruce are discussed.

Comments: Bulking-up - "while the genetic quality of the material is identical (assuming panmictic pollination, etc.) to that which could be produced by orchards composed of compatible clones, it is available in a much shorter time - thus enhancing the all important concept of genetic gain per unit-of-time in economic terms."

"Plants raised from cuttings are 1.8 to 3.6 times more expensive than conventional transplants. This compares with a differential of 1.2 to 1.5 reported by Kleinschmit and Schmidt (1977) for Norway spruce."

Gleed, J.A. 1991. Toward clonal afforestation. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. p. 61.

Abstract: Tasman Forestry Limited commenced operations in 1962 and now manages 150 000 ha of radiata pine plantations. Progress towards clonal forest management is being achieved by means of a programme of commercial exploitation of the genetic resources. A chronological summary of this programme is provided.

Comments: New tissue culture lab facility was commissioned in 1988 to produce 2.5 million plants per year (50 000 per week). By 1993, expect to plant 5 000 ha per year with tissue-cultured clonal material (at 500 per ha).

Hall, R.B., Colletti, J.P., Schultz, R.C., Faltonson, R.R., Kolison, S.H., Jr., Hanna, R.D., Hillson, T.D., and Morrison, J.W. 1990. Commercial-scale vegetative propagation of aspens. *In* Proceedings of aspen symposium, Duluth, MN, July 25-27, 1989. (Gen. Tech. Rep. NC-140) *Edited by:* R.D. Adams. USDA For. Serv., North Central For. Exp. Sta. pp. 211-219.

Comments: Includes some production costs relevant to tissue culture, rooted cuttings, and root segments for clonal propagation of hybrid poplars. Root sprouts forming from root segments are known as "rootlings".

Harju, A., and Outi, M. 1989. Background pollination in Pinus sylvestris seed orchards. Scand. J. For. Res. 4(4): 513-519.

Abstract: The proportion of background pollen grains in the seed crops of two Pinus sylvestris seed orchards in Central Finland was estimated with the aid of multilocus allozyme markers. The orchards studied were more than 30 years old and in full pollen production. For the bulked seed crops of the seed orchard with southern clones the estimated average of background pollination over four years was 26%. There were statistically significant differences between years. No significant heterogeneity in the degree of background pollination between clones was found. Among single ramets there was significant heterogeneity in the estimated contamination rates, but the variation was not related to position in the orchard. For the seed orchard with northern clones the bulked seed crop was studied only for one year and the level of background pollination was found to be 33%. These estimates are fairly high, but lower than for many other orchards. Background pollination at this level will cause losses in expected genetic gains. Part of the seeds from northern orchards will not be adapted to the intended area of use.

Harou, P.A. 1983. A note on the real rate of discount. For. Sci. 29(2): 249-252.

Abstract: One of the main factors affecting the profitability of investment in forestry is certainly the rate of discount. Because of the long time span of forestry projects, a small variation in this rate can affect substantially their benefits and costs. As inflation is difficult to foresee, it is preferable to use real values in projecting the cash flows of a forestry investment. In this case, a real rate of discount has to be used. If a correct multiplicative, not additive, relation is used between the real and nominal rates of discount, inflation can be appropriately disregarded. If the inflated cash flows were used this same multiplicative relationship would make the analyses done in real or nominal terms equivalent.

Harou, P.A. 1984. Possibilities for shadow pricing forestry investments. For. Ecol. Manage. 8: 59-73.

Comments: Discusses concept of "shadow pricing" which is applicable to long-term forestry projects which may socially attractive, even if they are not financially profitable.

Harou, P.A. 1985. On a social discount rate for forestry. Can. J. For. Res. 15(5): 927-934.

Abstract: After a review of the literature on the discount rate in economics and forestry, a methodology is proposed to arrive at an appropriate social discount rate to appraise public forestry investments. In the proposed approach, the opportunity cost of capital is considered in the establishment of a shadow price of investment. The social discount rate, which should weight the project net social benefits through time, is an unknown of the net present worth equation set to zero.

Harou, P.A. 1987. Quantification of the uncertainty and risk of forestry projects. *In* Essays in forestry economics: appraisal and evaluation of forestry investment, programs and policies. *Edited by:* P.A. Harou. Wissenschaftsverlag Vauk Kiel, Kiel, Germany. pp. 54-59.

Abstract: The duration of forestry investments has impact not only on the discounting of their benefits and costs, but also on the certainty surrounding their estimates. What will a tree plantation or a natural regeneration yield over time and what will be the value of these yields? Deterministic sensitivity analysis of Net Present Worth or other criteria of a forestry investment will give a good basis for assessing the uncertainty surrounding that project profitability. An expected Net Present Worth obtained through simulation is an appropriate criterion for choosing among risky forestry projects, whereas the adjusted discount rate should be avoided.

Harrell, R., and Simonton, W. 1986. Automation opportunities in plant tissue culture operations. Amer. Soc. Agric. Engineers, St. Joseph, MI. 12 pages. (Paper No. 86-1596)

Abstract: Opportunities for automation in commercial and experimental plant tissue culture techniques were examined. It was concluded that, excluding the plantlet excision task, commercial micropropagation unit operations can be automated with existing technology, but automation alone cannot lower commercial micropropagation production costs to a point that it can be economically applied to most agricultural and forestry crops.

Hartney, V.J., and Kabay, E.D. 1984. From tissue culture to forest trees. Combined Proceedings International Plant Propagators' Society 34: 93-99.

Abstract: The feasibility of commercial micropropagation of eucalypts and other forest trees is discussed. Salinity in crop production is a world-wide problem and a table is given listing salt-tolerant clones of Eucalyptus camaldulensis (34), E. macarandra (1), E. spathulata (1) and E. wandoo (10). All clones tolerated a NaCl concentration above 640 mmol/litre under laboratory conditions. Means of reducing the costs of tissue culture by rationalization and mechanization are suggested.

Comments: Several suggested aspects of the culture process are targets for cost reduction: (1) Labour (75% of total cost of production); (2) Media (preference for liquid-based media); (3) Space; (4) Container maintenance and labelling; (5) Contamination; (6) Record-keeping.

Hasnain, S., and Cheliak, W. 1986. Tissue culture in forestry: economic and genetic potential. For. Chron. 62(4): 219-225.

Abstract: It is argued that vegetative propagation of Canadian conifers by tissue culture methods will allow rapid commercial exploitation of the genetic gain achieved in breeding programmes. It is shown that micropropagation should be economically feasible in Canada.

Hasnain, S., Pigeon, R., and Overend, R.P. 1986. Economic analysis of the use of tissue culture for rapid forest improvement. For. Chron. 62(4): 240-245.

Abstract: Results of the analysis (with reference to Canadian conifers) show that the cost of tissue culture plantlets will be relatively high, but that this cost will be more than compensated for by savings realized by reduced rotation age.

Herrick, O.W. 1981. Economics of pitch x loblolly pine hybrids. Silvae Genet. 30(1): 1-7.

Abstract: Promising results from developmental testing of pitch x loblolly pine hybrids prompted an evaluation of the economic potential for investment in hybrid seed production. A least-total-cost model was derived to provide guides for cost effective investment in seed orchard and planting phases of hybrid production. The incremental analysis, based on least-cost-plus-loss economic theory, indicates that pitch x loblolly hybrid seed production would yield net gains at interest rates up to 9 percent. The model can be used to find the combination of annual planting area, seed orchard capacity, and expenditure that increased forest yields would justify at different interest rates.

Comments: Requires careful reading, particularly portions on decision-making models.

Hollowell, R.R., and Porterfield, R.L. 1986. Is tree improvement a good investment? J. For. 84(2): 46-48.

Comments: "Typical costs for tree improvement are $4-$6/acre regenerated."

Horgan, G.P. 1991. Risk analysis for forestry. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 155-157.

Abstract: Techniques for managing pure risk seek either to remove it through increased knowledge, or to adapt to it by minimising its potential adverse impacts. No technique, however, can absolve the investor from the necessity of analysis. Analysis will often reveal that it is uncertainty, not risk, that is being faced. It is not a good idea to leave analysis of risk solely to "experts". Many disciplines can make worthwhile contributions and experts often tend to understate the risks associated with their own subject area.

Comments: Definitions "risk" and "uncertainty":

"A risky situation is one where the set of possible outcomes is well known, and where a probability distribution for this set of outcomes is agreed."

"An uncertain situation is one where either the set of outcomes is unknown or where agreement as to an appropriate probability for these outcomes cannot be reached."

Three strategies to manage risk:
(1) reduce risk by increasing knowledge;
(2) minimize risk by varying the length of exposure to it; or
(3) reduce its impact by diversification of investment.

Jiang, I.B.-J. 1987. Early testing in forest tree breeding: A review. For. Tree Improv. 20: 45-78.

Abstract: The methods that give genetic evaluation of selected genotypes are reviewed. The theoretical background of early testing is examined. The importance of early testing the forest tree breeding activities is analyzed in connection with a synthetic tree breeding model. A comparative review is made between various early-testing studies. It is contended that the choice of both characters and testing environments is crucial to an early testing study. The (in)stability of juvenile-mature correlations under multi-generation selections is questioned.

Johnsen, O. 1985. Successive bulk propagation of juvenile plants from full-sib families of Norway spruce. For. Ecol. Manage. 11(4): 271-282.

Abstract: The results of bulk propagation of Norway spruce for one year are presented. The number of cuttings produced per seedling ranged from 21 to 38 (avg. 30) between different families, with large within-family variation. No clear relationship between family field performance and production of cuttings. Established cuttings produced more propagules per plant than seedlings in the first propagation. Misting gave about 92% rooting, with no significant differences between rooting media used. A bulk propagation program is proposed with a potential of about 1000-1500 plants per germinated seed within 3-years from sowing.

Johnson, G.R. 1988. A look to the future: clonal forestry. *In* Workshop on growing radiata pine from cuttings. (FRI Bulletin No. 135) *Edited by:* M.I. Menzies, J.P. Aimers, and L.J. Whitehouse. Forest Research Institute, Rotorua, NZ. pp. 79-84.

Abstract: Clonal forestry offers the possibility of greater genetic gains in traits of economic importance because genotypes, actual gene combinations, can be selected, and not lost through gene recombination. But clones from high-performing families require an additional testing phase, so potential gain must be weighed against the additional testing costs.

Because clonal forestry utilises only a limited number of clones, stand uniformity may increase. This reduction in genetic variation does have risks associated with pests adapting to particular clones.

Before clonal forestry can become a reality with radiata pine, methods of storage to maintain juvenility or rejuvenation of older material, and methods to economically multiply clones in great numbers, must be further developed and tested.

Johnson, G.R. 1988. Marginal costs and benefits of using cuttings to amplify improved seed. *In* Workshop on growing radiata pine from cuttings. (FRI Bulletin No. 135) *Edited by:* M.I. Menzies, J.P. Aimers, and L.J. Whitehouse. Forest Research Institute, Rotorua, NZ. pp. 173-178.

Abstract: Switching from a system raising 1-year-old seedlings from open-pollinated orchard seed to a system which produces cuttings from genetically superior control-pollinated seed will increase the cost of planting stock but should result in increased revenues at harvest. The decision to plant cuttings must be determined on a site by site basis. The maximum benefit gained from planting cuttings of superior genetic quality will be seen in stands which have been planted on the best sites, and are being managed for high value products.

Comments: Increases in value of cutting plantations was a combination of 10% increase in volume increment and lower planting density.

Jones, J.B. 1990. Economic considerations in tissue culture propagation of ornamentals. Chap. 7. *In* Handbook of plant cell culture. Volume 5. Ornamental species. *Edited by:* P.V. Ammirato, D.A. Evans, W.R. Sharp, and Y.P.S. Bajaj. McGraw-Hill, Inc., New York. pp. 165-178.

Abstract: The chapter focuses on the economics of producing ornamental plants using tissue culture, why they are bought, and the margins between the laboratory propagator-grower-shipper of linings and the wholesale nursery and the retailer. Two products are examined in detail: Nandina domestica, a landscape nursery shrub, and Syngonium podophyllum, White Butterfly, an indoor green foliage potted plant. It is found that, until somatic embryogenesis or other cost-reducing systems for producing these plants become technically or economically feasible, management skill will be the major factor in laboratory performance.

Kang, H. 1989. Inbreeding effective population size under some artificial selection schemes. II. Normal distribution of breeding values. For. Sci. 35(2): 303-318.

Abstract: Two selection systems, truncation selection followed by a balanced mating (truncation selection) and a selection scheme that assigns mating frequencies to individuals according to their breeding values (weighting system), were compared with respect to inbreeding effective population size. This comparison was made with the condition that both selection schemes give the same expected performance of selected individuals (selection differential). Breeding values of selected individuals were assumed to be normally distributed on a performance scale. Two functions, linear and Beta, were used to represent weighting systems. The results showed that (1) depending on the distribution of breeding values, inbreeding effective population number of some weighting systems can be greater than that of a truncation selection that generates the same selection differential, and (2) because the difference in inbreeding effective population size using different systems can be substantial, it is worth examining for the presence of desirable weighting systems in practical tree breeding situations.

King, J.N., and Johnson, G.R. 1991. Computer simulation of clonal selection gains. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 51-52.

Abstract: Gains from conventional seed orchards versus clonal selection gains were compared using computer simulation. The simulation followed features and selection intensities represented in the New Zealand radiata pine breeding programme. Assuming known levels of nonadditive genetic variance in radiata pine ($<25\%$ of additive variance), it was calculated that substantially greater gains over seed orchard options can be delivered only with intensive clonal selection ($<5\%$).

Comments: Notes that estimates of nonadditive genetic variance appear to be high and poorly estimated from assessments of progeny trials younger than age 12.

King, J.N., and Johnson, G.R. 1991. Genetic parameter estimates from a young clonal test. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 98-100.

Abstract: Early results (including height up to age 3) are reported from the first of the new series of clonal tests using juvenile ortet material. The trial involved 10 clones in each of 19 full-sib families, and was replicated on two pumice-land sites. Variance components for heights up to 3 years were estimated, including additive and nonadditive genetic variances. Clonal variance estimates were up to three times larger, relative to family variance estimates, than what would be expected from standard genetic models. Differential clonal responses to the vegetative propagation process (C effects?) may have inflated clonal variances, although prior selection could have severely truncated variance between families.

Comments: The full-sib families used in this experiment were unrelated. Gives three possible reasons for the failure of the genetic model: (i) epistatic variance was ignored, (ii) parents were not a random sample, hence effect of truncation of variance by selection, and (iii) C effects were ignored.

"It could be that early genetic parameter estimates in clonal tests are inflated by genotype x mode-of-propagation interaction, just as early seedling parameters can be inflated by maternal effects.", i.e. they are inflated by C effects.

Klomp, B.K. 1988. Some silvicultural aspects of cuttings. *In* Workshop on growing radiata pine from cuttings. (FRI Bulletin No. 135) *Edited by:* M.I. Menzies, J.P. Aimers, and L.J. Whitehouse. Forest Research Institute, Rotorua, NZ. pp. 152-161.

Abstract: Deals with pruning and thinning practices for cuttings and seedlings of radiata pine. Cuttings from younger stool beds produce stecklings which perform more like seedlings than cuttings from older (>4 years old) beds.

Koski, V. 1987. Long geographic transfers, a possible way of eliminating pollen contamination in advanced-generation seed orchards of *Pinus sylvestris*. For. Ecol. Manage. 19(1): 267-271.

Comments: "Since new (next generation) seed orchards will be more genetically differentiated than the old ones, the effect of pollen contamination will be more harmful; therefore serious efforts should be made to eliminate undesirable pollen contamination." Suggests relocating orchards south to areas where different surrounding species and flowering times will guard against contamination. "Only feasible way of avoiding pollen contamination."

Krogstrup, P. 1989. Micropropagation of juvenile Norway spruce. For. Tree Improv. 22: 1-10.
Abstract: Cotyledons taken from 7-day-old NS to form adventitous buds in culture. Plantlets were successfully established in soil. Liquid medium would allow for automation to change medium without disturbance to explants.

Krugman, S.I. 1988. Guidelines for research and development in biotechnology. *In* Somatic cell genetics of woody plants. Proc. IUFRO Working Party S2.04-07, held in Grosshansdorf, Fed. Rep. Germany, 10-13 Aug. 1987. *Edited by:* M.R. Ahuja. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 221-225.
Abstract: Describes preparation of US guidelines to regulate laboratory research, containment and field testing of genetically engineered products.

Levin, R., Gaba, V., Tal, B., Hirsch, S., De-Nola, D., and Vasil, I.K. 1988. Automated plant tissue culture for mass propagation. Bio/Technology 6(9): 1035-1040.
Abstract: The economics of mass propagation are discussed, and the advantages of growing plants in liquid medium (easily monitored and uniform growth conditions, minimization of contamination, easier automation and greater efficiency) are stressed. The integration of a liquid medium bioreactor with a bioprocessor which segregates, sizes and dispenses propagules (100 000 in 8 h) and an automated transplanting machine is described.
Comments: Automated transplanting machine transfers about 8,000 plantlets per hour
Plantlets produced by "conventional" in vitro methods must sell for $0.25+. 40-60% of the cost is for labour. Automation cut production costs in order of 60%

Libby, W.J. 1988. Testing and deployment of brave new plantings. *In* Somatic cell genetics of woody plants. Proc. IUFRO Working Party S2.04-07, held in Grosshansdorf, Fed. Rep. Germany, 10-13 Aug. 1987. *Edited by:* M.R. Ahuja. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 201-209.
Abstract: Responsible field testing (of trees resulting from genetic manipulation or somatic cells) requires long periods of time, and it evaluates the total performance of the tree or clone. Widespread deployment can responsibly commence only following successful field testing/ Field testing will be more efficient and deployment can commence sooner if the genetically engineered clones come from well-known clones, or from well-known families, or from well-tested families, or at least from trees of well-known provenance.
Comments: Three guidelines:
(a) Mixtures of large numbers of clones are about as safe as similar mixtures of genetically diverse seedlings;
(b) mixtures or regional deployment of very small numbers of clones are not safe, and commitment to 2-4 clones is often worse than monoclonal deployment;
(c) regional deployment of modest numbers (in range of 7 to 99 clones) is about as safe as deployment of larger numbers of clones and offers substantial additional advantages as well.

Libby, W.J. 1991. Opening comments. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 11-12.
Comments: "Clonal forestry and breeding are not incompatible. An appropriate breeding programme should be maintained in support of a clonal forestry programme, with outstanding candidates from each generation tested against the current "first team".
"... there is an interesting contest of strategies between the practice of clonal forestry and continued breeding. If very aggressive breeding, using early testing and rapid generation turnover, proves so successful that it routinely produces average offspring better than the best clones of a few generations back, these new breeds, or the better clones among them, will replace the older clones before test information and management experience accumulate sufficiently to justify full clonal forestry. Thus,

whether the full benefits of clonal forestry are likely to be attained or not will depend on how good the aggressive breeders are."
"We are comfortable with our sexually produced seedlings, and we think that we know how to do good forestry with them."
"... sexual reproduction has been the way to do things for a long time, and most of us are pretty comfortable doing things that way. But even with good information, we don't always get it right the first time, and theory is a poor substitute for hands on experience."

Lindgren, D. 1977. Possible advantages and risks connected with vegetative propagation for reforestation. *In* Vegetative propagation of forest trees -- physiology and practice. *Edited by:* L. Eliasson. Institute of Forest Improvement and Department of Forest Genetics, Swedish University of Agricultural Sciences, Stockholm. pp. 9-16.

Abstract: With vegetative propagation a superior genetic gain may be obtained and quickly utilized in practical forestry. It is a flexible way of breeding. There are risks connected with this method, due to the possibility that a vegetatively propagated material could differ from that which is sexually propagated as follows:

- seedlings and cuttings of the same genotype may behave differently
- the extreme selection possible may have undesirable side effects
- the genetic structure may be quite different; the most extreme form is cultures from a single clone
- the characteristics making the clone suitable for vegetative propagation may make it less productive
- the clones may change their characteristics during testing and propagation

Lindgren, D. (Editor). 1991. Pollen contamination in seed orchards: proceedings of the meeting of the Nordic Group for Tree Breeding 1991. Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology, Uppsala, Sweden. (Report 10)

Löfgren, K.-G. 1988. On the economic value of genetic progress in forestry. For. Sci. 34(3): 708-723.

Abstract: Previous analyses of the economics of tree improvement are extended by introducing a number of general theorems on the properties of the present value function as a function of biotechnological parameters. More specifically, it is shown how the economic gains from the improvement can be given upper and lower bounds, which, to a certain extent, are expressible in entities known from current management practices. The general theorems are derived from a model of a present value maximizing forestry firm with an initial endowment consisting of trees in different age classes, which is facing a competitive environment. A special section is devoted to the economics of genetic progress at the stand level, since certain types of improvements are handled more easily at that level. The core results show that straightforward calculation methods often have theoretical support. An empirical application shows that the theory has practical implications.

Comments: Very difficult to follow -- requires firm understanding of calculus and matrix algebra

Loo-Dinkins, J.A. Undated. Minimum number of parents required for British Columbia seed orchards. 22 pages. (Unpublished file report for the B.C. Ministry of Forests)

Comments: Calculates the minimum "effective" number of parents required in a clonal seed orchard to be in range of 24-29.

Assuming that only 30% of the parents produce 80% of the seed, and that proportions of cones and pollen are correlated (r=.60), it is safe to assume that no more than 70% of the parents will be contributing gametes. If all of these produced equally, the actual number of clones to achieve an effective number of 24-29 would be 34-41.

Due to selfing (10%) and unequal distribution of gametes, actual numbers required are more likely in the range of 60-70.

Loo-Dinkins, J.A. Undated. Simulated advanced generation breeding populations: options for coastal Douglas-fir. Quantgen Forest Consulting, Vancouver. 45 pages. (Unpublished file report for B.C. Ministry of Forests)

Comments: Simulation model constructed to compare gain and rate of inbreeding for a number of options.

Lowe, W.J., and van Buijtenen, J.P. 1989. The incorporation of early testing procedures into an operational tree improvement program. Silvae Genet. 38(5-6): 243-250.

Abstract: Seedlots that have both good germination and a small shoot dry weight in greenhouse tests tend to have average or below average volume growth in field tests. This relationship allows the use of shoot dry weight in the greenhouse to be used as a trait for culling some progenies prior to field testing in a tree improvement programme. Two-step testing procedures combine independent culling at the end of the first test (greenhouse) with assortative mating for the second test (field) to both reduce progeny testing costs and increase genetic gain. These procedures increase the efficiency of an operational tree improvement programme by reducing the funding required for field testing to obtain the same or slightly greater genetic gain. The implementation of shoot dry weight as an early testing trait in the first and second generation loblolly pine (Pinus taeda) breeding programme for the Western Gulf Forest Tree Improvement Program is discussed. In the first generation, a 17% cost reduction was obtained by removing crosses containing the parent with the smallest shoot dry weight in each partial diallel prior to field testing. In the second generation, selections with the smallest shoot dry weight based on polymix crosses were deleted, resulting in a 24% reduction in established costs of the polymix progeny test. Further savings would be gained from a reduction in the partial diallel breeding and testing activities for the third generation selection population.

Lundkvist, K., and Gullberg, U. 1981. Initiated genetic research on clonal forestry in Norway spruce. *In* Symposium on clonal forestry: Uppsala, Sweden, April 8-9, 1981. *Edited by:* G. Eriksson, and K. Lundkvist. Swed. Univ. Agric. Sci., Dept. For. Gen., Res. Note 32. pp. 85-100.

Comments: At cost levels necessary for bulk propagation, there is no clear indication that cuttings are, in the long-run, any better than the seed orchard alternative.

Maethe, H. 1989. In vitro culture : solving one problem creates another [In vitro-Kultur: gelöste Probleme gebaren neue]. Deutsche Baumschule 41(8): 384-385.

Language(s): German

Abstract: Problems associated with in vitro propagation of woody plants are outlined, with particular reference to competition from conventional multiplication methods using cuttings. They are related to higher cost, and genetic modifications which often arise in callus cultures. Commercially viable examples of in vitro propagation are listed, such as peach rootstocks in Italy, virus-free raspberries, and Vaccinium in the USA and Canada. Rhododendron is cited as producing very variable results in vitro. The future of in vitro propagation will depend on the speed and cost of regeneration methods, and the relative merits of automating the procedure, and on meristem culture or cloned seed grown in a bioreactor. The latter produces spherical cell agglomerations which will ultimately be enclosed in a capsule containing a fungicide or insecticide. It was noted that automation of the in vitro process could lead to automation of the conventional multiplication techniques and thereby to intensified competition.

Mahalovich, M.F. 1990. Modelling positive assortative mating and elite populations in recurrent selection programs for general combining ability. Ph.D. Dissertation, NC State Univ. 129 p.

Comments: Used FORTRAN model to additive and partial dominance effects at 50 loci controlling a quantitative trait. Used to simulate PAM under alternative breeding strategies.

Martin, B. 1985. Human impacts on forests: ecology or economics? [Impact de l'homme sur la foret. Ecologie ou economie?]. Revue Forestiere Francaise 37(1): 5-16.

Language(s): French

Abstract: The conflict between extensive forestry and intensive plantation forestry is discussed. It is becoming increasingly difficult to get investment in extensive forestry. However, an extensive system protects genetic resources and ecological systems. Intensive forestry is more productive and therefore more profitable, and is more attractive to investors. Nevertheless, financial decisions are closely related to the state of the forest capital, which means that large well-managed forests will probably survive. The success of clonal forestry, a highly economic type of management, could help to stabilize forestry, by freeing most forests from excessive economic pressure and thus making it possible to strengthen their biological value through the establishment of genetic and ecological protection areas.

Mascarenhas, A.F., Khuspe, S.S., Nadgauda, R.S., Gupta, P.K., and Khan, B.M. 1988. Potential of cell culture in plantation forestry programs. *In* Genetic manipulation of wood plants. Vol. 44. *Edited by:* J.W. Hanover, and D.E. Keathley. Plenum Press, New York. pp. 391-412.

Abstract: Results are summarized of field evaluations in India of plantlets produced by tissue culture of material from mature trees of Eucalyptus tereticornis, E. torelliana, E. citriodora, Tectona grandis and Salvadora persica. Economic and other benefits of these procedures are discussed.

Comments: Running costs for tissue culture plantlets (Eucalyptus) were US$70 per 1000, compared to US$30 for seedlings. If capital costs are also considered, the price per 1000 rises to US$140. Cost:benefit ratio was favourable due to increased yield, despite higher nursery stock and planting costs.

Matheson, A.C., and Brown, A.G. (Editors). 1983. Radiata pine breeding manual. Division of Forest Research, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia. 128 pages.

Abstract: A manual produced for use in Australia by 6 members of the CSIRO Division of Forest Research (the editors, with Eldridge, K.G.; Hand, F.C.; Griffin, A.R. and Wright, P.J.) There are 11 chapters: Executive statement; Introduction; Genetic resources available; Strategy and tactics; Selection; Vegetative propagation and breeding arboreta; Controlled pollination; Progeny testing; Seed orchards; Assessing gain; and Economic analysis. There are 4 appendices: Computing facilities and programs [describing CSIRONET and including a brochure]; Notes for searchers; Plus tree register [stored on a computer by CSIRO Division of Forest Research on behalf of Research Working Group No. 1 - a sample printout and record forms are provided]; and Progeny test register [maintained as part of the plus tree register, a sample record form is provided].

Comments: Unable to obtain copy of this document.

Matyas, C., and Rauter, R.M. 1987. Feasibility of seed orchard establishment, rogueing and lifespan. For. Ecol. Manage. 19(1-4): 247-256.

Abstract: Apart from genetic gains, the feasibility of seed orchards is influenced by cost factors, management decisions and rates of propagation. The authors investigate the establishment, rogueing and lifespan of seed orchards, with emphasis on investment and operating costs, optimal assessment age and expected seed yields. Expenditures for establishment of seed orchards are compared to present values of savings on reduced regeneration areas, due to gains from improved stock. Lambeth's selection efficiency and age correlation formulae are used for optimizing the timing of rogueing. For the decision as to the economic lifespan of the seed orchards, the costs of investment and operation were distributed over the cone yield produced. The case studies presented refer to operational conditions in Canada and Europe.

Comments: Presents actual costs (1983 $s) of establishment and maintenance of both clonal and seedling seed orchards, based on 8 ha orchard size. (see also Tree improvement master plan for Ontario (Anon. 1987)). Uses Lambeth's formulae (Lambeth 1980: For. Sci. 26:571-580) for calculating optimum age for roguing based on maximizing selection efficiency as a function of age correlation and selection cycle.

McCown, D.D. 1986. Plug systems for micropropagules. *In* Tissue culture as a plant production system for horticultural crops. *Edited by:* R.H. Zimmerman, R.J. Griesbach, F.A. Hammerschlag, and R.H. Lawson. Martinus Nijhoff, Dordrecht. pp. 53-60.

Comments: Discusses requirements of plug systems compatible with establishment of microcuttings. Indicates two commercial plug systems available for microcuttings: Techniculture plugs (Castle & Cooke, Techniculture Inc., Salinas, CA) and Oasis Horticubes (Smithers-Oasis, Kent, OH).

McKenney, D., van Vuuren, W., and Fox, G. 1988. The economics of tree improvement: a comparison of clonal forestry and seed orchards for black spruce in Ontario. Dep. Agric. Econ. and Bus., Univ. Guelph. 61 pages.

Abstract: The seed orchard and the clonal forestry/rooted cuttings approaches to black spruce tree improvement were compared using cost/benefit analysis. The approach developed in this study separates research and development activities that identify superior trees to be included in the breeding program from operational tree improvement activities. Operational tree improvement is the means of mass producing genetically improved planting stock for plantations. Optimal economic rotation ages were calculated for unimproved and improved plantations. Operational tree improvement costs were included with the other plantation establishment and management costs. The difference in the net present value of unimproved and improved plantations is compared with the research cost to determine the total net worth of tree improvement. The most important economic factor determining the net worth of tree improvement is stumpage value, but other important factors include magnitude of the genetic gain, size of the improved planting program, quality of the land base, and the discount rate. Over 500 scenarios were considered using sensitivity analysis.

Neither the seed orchard approach nor the rooted cuttings approach are economically worthwhile at current stumpage prices in Ontario, but it is unlikely that current stumpage prices are an accurate reflection of the future worth of standing timber. The seed orchard approach can be profitable at much lower stumpage values than the rooted cuttings approach and is therefore the recommended method of black spruce tree management. Even though rooted cuttings have the potential of capturing more genetic gain, the high cost of cutting production relative to seedling production makes the clonal forestry approach economically unattractive at this time.

Comments: At 4% discount rate, seed orchard operational costs are $16.78 per hectare of plantation (when 2 000 ha per year planted) -- this assumes only 0.5 million plantable trees per year per ha of seed orchard. Managing the donor material for a clonal program costs $4.00 per hectare planted.

"Tree improvement should not be viewed as having a major impact on optimal rotation age. Optimal economic rotation ages for improved and unimproved plantations do not differ significantly. Lower rotation ages in improved plantations is often cited as a benefit of tree improvement. Given current knowledge of growth rates in plantations, lowering rotation ages versus those of unimproved plantations may not be economically warranted."

Menzies, M.I. 1985. Vegetative propagation of radiata pine. Proc. Inter. Plant Prop. Soc. 35: 383-389.

Comments: Systems used in NZ are described.

Quotes cost of stock in NZ$/000:

seedlings	NZ$50
juvenile cuttings	87
micropropagation	450

Menzies, M.I., and Klomp, B.K. 1988. Effects of parent age on growth and form of cuttings, and comparison with seedlings. *In* Workshop on growing radiata pine from cuttings. (FRI Bulletin No. 135) *Edited by:* M.I. Menzies, J.P. Aimers, and L.J. Whitehouse. Forest Research Institute, Rotorua, NZ. pp. 18-40.

Abstract: Early field trials with cuttings to evaluate clonal forestry options showed that cuttings from parent trees of various ages could be an attractive option because of their uniformity of growth, stem straightness, and freedom from malformation. However, further trials also showed that cuttings from older trees (5 years or older) had slower early diameter growth, and a consequent loss of volume which could be undesirable. Further field trials have been established on a range of sites to compare the growth and from of seedlings with cuttings from parent trees aged up to 5 years (from seed).

Results from trials planted in 1983 show that cuttings from 1-year-old seedlings are similar to seedlings in growth rate and form. Cuttings from 3-year-old trees (without sealed buds when collected) have similar growth rates to seedlings, but have improved form. Cuttings from 4- and 5-year-old trees are showing slower early growth rates, particularly diameter growth, but excellent tree form compared with seedlings of the same genetic stock.

Menzies, M.I., Klomp, B.K., and Holden, D.G. 1991. Optimal physiological age of propagules for use in clonal forestry. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 142-145.

Abstract: Some form of vegetative propagation will be necessary to propagate tested clones for clonal forestry. Field trials have shown that cuttings from young parents (1- to 3-years old) can perform as well as or better than seedlings on both farm and forestry sites. Although there is some loss of early diameter growth with cuttings from older parents (4- to 5-years old), there are indications that these cuttings have better form, with less malformation, especially on fertile farm sites.

Comments: Ideal physiological age is considered to be 3.

Morgenstern, E.K., and Park, Y.S. 1991. Breeding of *Picea mariana* (Mill.) B.S.P.: seed orchard and clonal approaches. *In* Proceedings of the IUFRO meeting in Helsinki, Finland, August 1991. (Pre-publication manuscript)

Abstract: Advanced generation breeding of black spruce will make greater use of alternative clonal strategies in lieu of conventional seed orchard procedures. The second generation selections will be made in the previous family tests. The best parents are crossed in breeding halls, and subsequently the best progenies are vegetatively multiplied. To increase the efficiency of genetic parameter estimation, clonal replicates will be used in the genetic testing. Although clonal propagation is expensive, the extra cost is partially offset by eliminating inefficiencies of conventional seed orchards, as well as additional genetic gains.

Muhs, H.J. 1988. Rules governing the release of forest reproductive material derived from in vitro culture. *In* Somatic cell genetics of woody plants. Proc. IUFRO Working Party S2.04-07, held in Grosshansdorf, Fed. Rep. Germany, 10-13 Aug. 1987. *Edited by:* M.R. Ahuja. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 211-219.

Abstract: A discussion of rules currently in force in Sweden and W. Germany and the proposal to amend the rules of the OECD (Organization for Economic Cooperation and Development) Scheme and EEC Directives.

Comments: Institute of Forest Genetics and Forest Tree Breeding, 2070 Grosshansdorf 2, German Federal Republic.

Describes the minimum numbers of clones required in Sweden and Germany, depending on species, testing procedures used, etc. Clone testing in both countries is on single-clone basis, but deployment is only permitted as mixture. Note that "bulk propagation" of seeds is not permitted in Germany and is limited to 100 ramets per genotype in Sweden.

Number of genotypes required for clone mixtures in Sweden:
level 1 (tested 2 sites, 6 years) = 120 clones (up to 250,000/clone)
level 2 (tested 4 sites, 9 years) = 60 clones (up to 750,000/clone)
level 3 (tested 6 sites, 6+12 years,
- replicated in time at level 1) = 30 clones (up to 1,500,000 per)

Germany generally requires mixtures of 500 tested clones for large-area reforestation projects; may be reduced to 100 on special sites. Individual clones are approved for use for 10 years, with possible extension for additional 10 years.

Mullin, T.J., Morgenstern, E.K., Park, Y.S., and Fowler, D.P. 1992. Genetic parameters from a clonally replicated test of black spruce (*Picea mariana*). Can. J. For. Res. 22(1). (In press)

Abstract: A clonally replicated field test of full-sib black spruce progeny was established at four locations in Nova Scotia. Estimated variance components for five-year height growth and survival were interpreted according to am additive-dominance-epistasis genetic model, and used to derive estimates of gain from various selection and deployment strategies. Five years after striking, 64% of the total genetic variance for height growth was due to additive variance. Virtually all of the remaining non-additive variance was composed of epistatic variances; dominance variance was negligible. Narrow-sense heritability for five-year height growth was low at 0.059. Substantial non-additive variance contributed to a somewhat higher estimate of broad-sense heritability at 0.093. Family-mean heritabilities were much higher: 0.823 and 0.697 for half-sib and full-sib family means, respectively. Comparable heritabilities for survival were estimated with high standard errors and were considered unreliable. Results from this study indicate that clonal selection may provide large increases in genetic gain by capturing genetic variance due to epistasis, as well as a greater portion of the additive variance. Genetic gains for five-year height growth in the order of 22.6% might be achieved, using the best 1% of tested clones for operational planting. Clonal propagation may also be a preferred method to capture substantial genetic gain (about 11%) from selection at the family level, resulting in simplified management of breeding populations while reducing costs associated with conventional soil-based orchards.

Mullin, T.J., and Park, Y.S. 1992. Estimating genetic gains from alternative breeding strategies for clonal forestry. Can. J. For. Res. 22(1). (In press)

Abstract: Concepts and procedures are presented for the analysis of progeny trials that incorporate clonal replication as a means to resolve variance arising from non-additive gene effects. Components of variance from the linear model may be expressed in terms of expected covariances among relatives, and these, in turn, may be used to derive approximations of additive, dominance and epistatic components of genetic variance. In addition to the usual assumptions applied to conventional progeny trials, the use of this expanded genetic model in the analysis of tests with clonal replicates assumes that the greatest portion of the total epistasis is due to interactions involving groups of more than two or three loci. If this assumption is not satisfied, estimates of additive and dominance variance, including those from trials without clonal replicates, will be contaminated by a large fraction of epistasis, and total epistasis will be underestimated by a corresponding amount. Heritability and gain formulae for alternative selection and deployment schemes are developed and illustrate the use of genetic parameters in the comparison of seedling and clonal reforestation strategies.

Newman, D.H. 1988. The optimal forest rotation: a discussion and annotated bibliography. USDA For. Serv., Gen. Tech. Rep. SE-48. 47 pages.

Abstract: The literature contains six different criteria of the optimal forest rotation: (1) maximization of single-rotation gross yield, (2) maximization of single-rotation annual yield, (3) maximization of single-rotation discounted net revenues, (4) maximization of discounted net revenues from an infinite series of rotations, (5) maximization of annual net revenues, and (6) maximization of the rate of growth of capital (internal rate of return). First-order conditions for maximization show the rotation effects of the criteria. Various authors have extended basic models and discussed effects of externalities, imperfect markets, changing parameters, and taxes.

Newman, D.H., and Williams, C.G. 1991. The incorporation of risk in optimal selection age determination. For. Sci. 37(5): 1350-1364.

Abstract: This paper explores the effect of decision-making criteria on optimal selection age determination in a loblolly pine tree breeding program. Three different selection ages, 2, 4, and 6 years, are compared using biological, economic, and risk-adjusted simulation methods. The 4-year selection option is found to be superior to the other options by virtually all criteria used in this analysis. This choice of 4 years is also quite robust regarding the assumptions used in the analysis such as prices, costs, gain estimates, and breeding strategy.

Nielsen, C. 1988. An economic analysis of tree improvement strategies for Norway spruce. On Line (Ont. Min. Nat. Res.) 5(1): 1-2.

Comments: Used economic analysis approach developed for the OMNR Master TI Plan (Anon. 1987). Serial propagation is superior at 5.5% real interest if gain is at least 2%; at 7% interest with 4% gain, and at 8% interest with 6% extra gain. Details on economic analysis were to be published in a separate report which has not yet been released.

Ondro, W.J., and Constantino, L.F. 1990. Benefits, costs, and profitability of precommercial thinning of three lodgepole pine stands in Alberta. For. Can., Northern For. Cen., Inform. Rep. NOR-X-. 49 pages. (MS in press)

Comments: Benefits evaluated included:

(1) Market value of increased yield;
(2) Premiums for larger log size;
(3) Logging cost reductions;
(4) Rotation age reduction.

Ondro, W.J., and Constantino, L.F. 1990. Financial returns from fertilizing 70-year-old lodgepole pine near Hinton, Alberta. For. Chron. 66(3): 287-292.

Comments: Demonstrates use of internal rate of return (IRR), present net worth (PNW) and profitability index criteria to identify and rank profitable treatments. (Note in particular page 289-290; also rational for selecting discount rates).

O'Regan, M., and Sar, L. 1989. The vegetative propagation of radiata pine: economic gains and policy implications.; Discussion Paper - Australian Bureau of Agricultural and Resource Economics (1989) (No. 89.2) v + 24 pp. 28 ref.

Abstract: A case study is presented based on data from a field trial in the Australian Capital Territory which enabled 40-year-old radiata pine (Pinus radiata) trees from cuttings and seedlings to be compared in terms of log yields and final products. For those factors quantifiable from the trial, growing radiata pine from cuttings was a more profitable investment than the seedlings alternative, in terms of both net present value and internal rate of return. Although establishment costs were higher for cuttings, they generated more net revenue than seedlings, due mainly to a higher proportion of the logs being allocated to higher valued uses, as a result of straighter stems, smaller branches and less stem taper. The relative profitability of cuttings as compared with seedlings could be increased by greater genetic selection and improved methods of obtaining and treating cuttings. There would be substantial economies in processing logs from cuttings as compared with seedlings, because of improved recovery rates and higher quality of output. This implies that logs from cuttings are of higher value than equal sized logs from seedlings, and should therefore command a royalty premium. However, in the core analysis the prices for logs from cuttings were assumed to be the same as for those from seedlings. If royalty systems were sufficiently market-oriented, and provided price premiums for superior logs, then again the profitability of cuttings would be considerably higher than estimated in the core analysis. A sensitivity analysis of the profitability of growing cuttings with respect to these two factors confirmed that modest increases in yield relative to that observed in the trial, and the addition of a royalty premium for log quality, would make investment in growing cuttings considerably more profitable relative to seedlings than the basic analysis indicated. To the extent that growth of cuttings is more rapid than that of seedlings, the optimum rotation period may be shortened. From a sensitivity analysis of the effects of rotation length on profitability this appears to be the case, with consequent further gains in net revenue per hectare.

Comments: Australian Bureau of Agricultural and Resource Economics, Canberra, ACT 2601, Australia. Out-of-print and not available in any library in North American or UK.

Ottens, J., and Carlisle, A. 1976. Tree improvement does pay--but more economic analyses and application programs are needed to ensure this. Pulp. and. Pap. Can. 77(8): 60-64.

Comments: Need for economic analyses to optimize strategies (as opposed to program justification?).
(1) cost per acre is low, (2) cost occur only once in rotation, (3) carries over to next generation

Paques, L.E. 1989. Tree improvement strategies: modelling and optimization: the model. Silvae Genet. 38(3-4): 101-107.

Abstract: A model of a complete cycle of tree improvement is proposed, combining in the equivalent annual rent (EAR) genetic and economic factors affecting tree improvement strategies. The model is used to study the effect of the mutual interactions of various technical and management alternatives on the economic response for any pattern of genetic variability. The EAR is used to determine the efficiency of tree improvement strategies and as a measure for optimization. Examined are the effects on selection alternatives of annual seed yield in the seed orchard (40-80 lb/acre), size of the land base (300 000-1 200 000 acres), length of the rotation of forest plantations (25 and 30 years) and techniques of breeding, consisting of the accelerated method (treatments combining physical stresses and growth substances applied to seedlings in the greenhouse) or traditional methods in an orchard.

Park, Y.S., and Bonga, J.M. 1990. Conifer micropropagation: its function in tree improvement programs. *In* Micropropagation of woody plants. *Edited by:* M.R. Ahuja. Kluwer Academic Publishers. (In press)

Comments: "More efficient micropropagation systems will have to be developed before micropropagation of conifers will become a viable technique in tree improvement and reforestation operations ... prospects that this will be achieved have improved considerably over the last few years."
Discuss strategies that employ cloning, either for clonal selection, or for amplification of limited numbers of seeds.

Pfeifer, A.R. 1988. Clonal forestry - a review to the future. Irish For. 45(2): 101-111.

Abstract: A brief review under the headings: the potential uses of clones in forestry, techniques of propagation, the development of clonal varieties, juvenility, bulking up, deployment of clones, and cost of production.

Pierik, R.L.M. 1988. Handicaps for the large scale commercial application of micropropagation. Acta Hortic. 230: 63-71.

Abstract: It is suggested that widespread use of micropropagation is handicapped by the following factors:

(1) frequent mutations occur, particularly when using the adventitious bud technique and callus systems;

(2) basic knowledge concerning factors affecting organ and somatic embryo formation in various types of cultures is often lacking;

(3) woody species (shrubs and trees) are extremely difficult to clone in vitro because rejuvenation can often not be induced; rooting of adult shoots is rarely possible;

(4) internal infections are still a serious handicap;

(5) problems such as vitrification and exudation of toxic compounds in the medium may occur;

(6) in vitro ethylene and CO2 levels may increase to an unacceptable level, often resulting in poor quality plants;

(7) the role of physical factors (light, temperature, humidity, the gas phase) is often neglected;

(8) during transfer from the test tube or container to soil a high percentage of plants may be lost, because the micropropagated plants are not well adapted to the in vivo climate;

(9) mass propagation in vitro is very labour intensive, resulting in high costs (70% of cost);

(10) the techniques developed are not always economically viable; and

(11) during large-sale micropropagation timing of production is often poorly controlled.

Pierik, R.L.M. 1988. In vitro culture of higher plants as a tool in the propagation of horticultural crops. Acta Hortic. 1(226): 25-40.

Abstract: A brief review and discussion under the following headings: in vitro cloning in the Netherlands; analysis of micropropagation; requirements of vegetative propagation in vitro; advantages of cloning in vitro; cloning systems in vitro; basic problems when propagating plants in vitro; handicaps for the commercial application of in vitro cloning; and factors affecting the cost price of in vitro produced plants.

Comments: Differences between herbaceous and wood plants.

Development restricted to single genotype may not be appropriate to mixture.

Labour intensive: 70% of production cost is for labour.

Pirrie, A., and Gordon, A.M. 1987. Tree biotechnology and the future potential applications of clonal forestry. OFI Occasional Papers, Oxford Forestry Institute, University of Oxford (34): 5-10.

Abstract: A discussion of micropropagation (initiation, multiplication and establishment) as a method of vegetative propagation, including economic and technical aspects of genetically manipulating forest tree species (somaclonal variation, somatic hybridization, transformation).

Porterfield, R.L., and Ledig, F.T. 1977. The economics of tree improvement programs in the Northeast. Proc. Northeast. For. Tree Improve. Conf. 25: 35-47.

Abstract: A simple break-even, benefit-cost analysis is presented which will provide an initial evaluation of profitability associated with tree improvement programs. White spruce and black spruce are used as case studies. Several ideas for increasing the profitability of tree improvement work are discussed in relation to sensitivity analysis of initial assumptions.

Redenbaugh, K. 1990. Application of artificial seed to tropical crops. Hortscience, 25(3): 251-255.

Abstract: Current progress in research concerning artificial seeds (somatic embryos enclosed in a protective coating) is discussed with particular reference to the status of somatic embryogenesis techniques in tropical crops, notably coffee. Vegetative propagation can only be used to produce a small number of coffee plants as orthotropic shoots must be used. Development of artificial seeds will markedly reduce the cost per propagule in comparison to traditional vegetative methods. A list of tropical crops in which somatic embryogenesis has been achieved is included.

Redenbaugh, K., Fujii, J.A., and Slade, D. 1988. Encapsulated plant embryos. *In* Biotechnology in agriculture. *Edited by:* A. Mizrahi. Alan R. Liss, Inc., New York. pp. 225-248.

Abstract: The development of 'artificial seeds' is reviewed, beginning with a consideration of their potential. It is argued that low costs and high genetic uniformity, even with unstable genotypes or where seed fertility is low, will make artificial seed production a viable proposition. Horticultural, field and forestry crops which are particularly suited because a good somatic embryogeny system is available or because of the value of vegetative propagation are listed. Fluid drilling, desiccated coatings, hydrogels and other techniques are considered and methods for hydrogel encapsulation of plant embryos surveyed. Production of lucerne somatic embryos is described. Requirements for commercialization of artificial seed production are outlined.

Reed, F.L.C. 1989. The potential economic impact of biotechnology and related research on the forest sector. For. Chron. 65(3): 185-189.

Abstract: The Canadian forest sector is at a critical juncture in maintaining its competitive position internationally. One reason is the difficulty that we are experiencing in holding the line on the costs of timber and its processing. The expenditure on silviculture alone is often in the range of 10-20% of the cost of delivering roundwood to manufacturing plants. The entire forest community is counting on forestry science, and especially biotechnology, to enhance industry viability and provide solutions to problems with environmental quality. However, the funding of forestry R&D has always been handicapped by our inability to argue persuasively for science budgets. The central theme of this paper is that the application of biotechnology and other science to forestry certainly does pay. A synthesis of traditional and newer approaches to benefit-cost analysis is recommended to assist science managers making their case for financial support.

Reed, F.L.C., and Baskerville, G.L. 1991. A contemporary perspective on silvicultural investments. J. Bus. Admin. 19(1-2): 161-185.

Comments: "One of the principal reasons for the ineffectiveness of forest management in dealing with this supply problem has been the persistent use of stand silviculture investment criteria which are both narrow in scope and flawed in their application. That is, *forest* management design has been overridden by *stand* silviculture economics."

"... when you have a large forest already in place, the correct question is not 'Shall we invest in a new stand on a clearcut?' Instead, we should be asking, 'Are we going to liquidate an entire forest as a valuable capital asset, or live off the annual increment of the forest?' If the answer is to live off the increment, then the appropriate analysis is to discover the silviculture regime that optimizes the sustainable flow from the whole forest. In projecting the outlook for coming decades, we must also ask, 'Are there economically attractive opportunities to enhance the value of the forest which is already in place?' The analysis can also be framed in this way, 'Which silvicultural regime will result in the largest set of benefits for a given budget?'"

Rensema, T.R., and Carter, K.K. 1984. Economic analysis of three regeneration alternatives in Maine's spruce-fir forest. Proc. Northeast. For. Tree Improve. Conf. 29: 168-176.

Abstract: This study investigates three regeneration regimes using the present net worth criterion and mill-delivered cost per cord. These three systems are: (1) tree-improvement programs for Japanese larch (Larix leptolepis (Sieb. and Zucc.) Gord.); (2) natural spruce-fir precommercially thinned at ten years; and (3) a natural spruce-fir stand unmanaged. Real discount rates, percent gain in volume because of the program used, and real increases in the value of the pulpwood (mill-delivered price) were varied for sensitivity analysis. The net present value criterion indicated at what year the stands should economically be harvested. Results indicated that as discount rates increased, economic rotation length decreased. Percent volume gain had little effect on the rotation length. Real increase in mill-delivered prices however, did affect rotation length.

Risbrudt, C.D., and McDonald, S.E. 1986. How effective are tree improvement programs in the 50 States? USDA For. Serv., NC For. Exper. Sta., Res. Pap. No. NC-276. 6 pages.

Abstract: Data were collected from all 50 State Foresters on the extent and cost of activities in producing genetically improved trees for timber production, the use of State and Private Forestry funds for such activities and the species being improved. Future timber volume attributable to genetic improvement and benefit/cost ratios were estimated. Only the benefits of planting on nonindustrial private forest lands are considered. Loblolly pine improvement accounted for 40% of the total annual expenditure of $4 million. Improvement of loblolly pine, Douglas fir, slash pine and ponderosa pine represented 80% of all expenditure. Analysis showed the high sensitivity of the benefit/cost ratios to the discount rate because of the long time before tree improvement benefits are realized. It is concluded, however, that the tree improvement programme is a logical public effort because of the significant long-term benefits of increased timber harvests.

Roberds, J.H., Friedman, S.T., and El-Kassaby, Y.A. 1991. Effective number of pollen parents in clonal seed orchards. Theor. Appl. Genet. 82: 313-320.

Abstract: A method for quantifying mating behaviour in clonal seed orchards of forest trees is presented. It involves the estimation of effective numbers of pollen parents from seed samples collected from individual ramets in such orchards. These effective numbers are variance effective numbers for populations of male gametes that are successful in uniting with ovules to produce viable seed. Three such effective numbers are defined for clonal seed orchards: (a) for male gamete populations for ramets within clones, (b) for male gamete populations for clones, and (c) for male gamete populations for entire orchards. Estimators for these effective numbers and for standardized variances of allele frequencies in the male gametic populations are presented. Expressions are also given for confidence intervals for each of the three effective numbers. Estimates of these parameters and the corresponding confidence intervals for two seed orchards are presented and interpreted.

Roberds, J.H., Namkoong, G., and Skrøppa, T. 1990. Genetic analysis of risk in clonal populations of forest trees. Theor. Appl. Genet. 79: 841-848.

Abstract: A major concern arising from the culture of clonally propagated crops of forest trees is risk of catastrophic loss due to an agent or event not anticipated at the time of population establishment. Since danger of such a catastrophe depends to some degree on the genetic variability within clonal mixtures, attention has been focused on the number of clones needed to keep the risk of catastrophic loss below specified levels. In this paper, we describe a genetical analysis of susceptibility to a destructive agent and the effect that frequency of genes for susceptibility have on the number of clones needed to effectively manage this risk. As a part of the analysis, parameters representing the minimum acceptable mortality rates in plantations (β) and acceptable levels of risk (α) are defined, and their effects on the number of single-pair matings needed for the production of clonal stock are evaluated. Dominance and recessive gene action models for a single two-allele genetic locus are investigated. Probabilities for plantation failure are functions of the gene frequency for the allele conferring susceptibility. These functions converge to zero for allele frequencies less than β but to one for frequencies greater than or equal to β. This convergence is periodic rather than monotonic, since probabilities for plantation failure increase rather than decrease over restricted ranges of increasing numbers of clones. Recessive and dominance gene actions are found to have different effects on the minimum number of clones needed to attain acceptable risk levels. For conditions in which substantial numbers of clones are required, selecting multiple clones per mating is an effective method for reducing the number of matings necessary to achieve acceptable risks.

Rogers, D.L. 1990. The black spruce clonal program: recent developments and future direction. *In* Proceedings from the annual meeting of the black spruce clonal forestry program, February, 1990. *Edited by:* D.L. Rogers. OMNR North. For. Develop. Grp., Timmins, Ont. pp. 1-6.

Comments: Northern Clonal Forestry Centre (Moonbeam, Ontario) opened in 1984, and now produces about 1 million black spruce stecklings per year for Northern Ontario.

Ross, S.D., Eastham, A.M., and Bower, R.C. 1986. Potential for container seed orchards. *In* Proceedings -- Conifer tree seed in the Inland Mountain West symposium, Missoula, Montana, August 5-6, 1985. (Gen. Tech. Rep. INT-203) *Edited by:* R.C. Shearer. USDA For. Serv., Intermountain Research Station, Ogeden, UT. pp. 180-186.

Abstract: Results are presented for Englemann spruce and western hemlock which demonstrate the practical advantages of producing genetically improved seeds on small potted trees within a plastic-covered house. Relative to conventional soil-based orchards, these advantages include: earlier and more consistently abundant flowering; improved protection of cones and seed; and strict control of pollen parentage, together with flexibility of clonal composition for maximum genetic gains. Because of more efficient space utilization and the greater ease and flexibility of management, production costs also promise to be lower.

Russell, J.H., and Libby, W.J. 1986. Clonal testing efficiency: the trade-offs between clones tested and ramets per clone. Can. J. For. Res. 16: 925-930.

Abstract: Three contrasting simulation models were developed to investigate testing efficiencies in a clonal selection program. The variables investigated were total number of plants tested, number of candidate clones tested, number of ramets per clone, number of clones selected, selection intensity, and broad-sense heritability. The model deemed appropriate to most clonal forestry situations selected a fixed number of clones in an experiment with the total number of plants in the test held constant. In this model, as the number of ramets per clone was varied, the number of candidate clones tested and selection intensity necessarily also varied. This model indicates that cloning individuals for testing is useful when selection is based on a characteristic or index with broad-sense heritability less than about 0.6. At the lower heritabilities, two to six ramets per clone per site usually produces the optimum level of cloning, the exact number depending on the selection intensity and heritability. Predictions generated by this fixed number of selected clones model were compared with average phenotypic values of selections using different subsamples of data for 8-year height and for 8-year diameter in a radiata pine clonal experiment. Agreement between predictions and average phenotypic values in both these two comparisons was close.

Russell, J.H., and Loo-Dinkins, J.A. 1991. Distribution of testing effort among computer simulated clonal populations. . (Manuscript under review)

Comments: "... a tree improvement strategy which involves clonal testing as a separate, add-on component of the mainline recurrent selection program may not be feasible, especially if generation turnover is relatively rapid."

Rutkovskii, I.V., and Kharina, L.V. 1987. Growing plants from rooted cuttings of commercially valuable forms of Picea abies without lining out in the transplant section of the nursery. Lesnoe Khozyaistvo 10: 27-29.

Language(s): Russian

Abstract: In trials in the USSR to produce planting stock from cuttings within 3 years, cuttings were taken from plants, 4-7 yr old, of valuable forms of spruce selected for rapid growth and a second (summer) increment, and also from the best 9-yr-old seedling progeny of plus trees. Rooting was not improved by the use of growth regulators (IBA and IAA, with or without vitamin C). On the basis of these trials and data in the literature, the following procedure is recommended for the production of planting stock from rooted cuttings: seeds of plus-trees are sown under plastic (frame or greenhouse); seedlings are transplanted after 2 yr and in the spring of their fifth growing season individuals are selected for rapid growth and a second increment; in the spring of the 5th-8th growing season (i.e. at biological age 4-7 yr) cuttings are taken from selected plants and rooted in frames; after 3 years growth the rooted cuttings are suitable for planting out. These rooted cuttings are 25% cheaper than normal planting stock which has been lined out in transplant beds.

Comments: Only reference in the literature reporting lower propagation costs for stecklings than for "normal planting stock". Comparison is between large, 3-year-old steckling stock and bareroot transplant stock.

Schachler, G., and Matschke, J. 1984. Status and prospects of the vegetative propagation of Norway spruce [Stand und Perspektiven zur autovegetativen Vermehrung von Fichte]. Beitrage fur die Forstwirtschaft 18(1): 19-24.

Language(s): German

Abstract: A discussion of methods used in E. Germany for the propagation of selected clones in plastic greenhouses. Effects of age of stock on rooting of cuttings, and economic efficiency of the operation, are reported. Experience is reported in the use of growth hormones to promote rooting, shoot production etc.

Schweitzer, D.L., Sassaman, R.W., and Schallau, C.H. 1972. Allowable cut effect: some physical and economic implications. J. For. 70(7): 4.

Comments: Allowable cut effect is defined and illustrated.

Shelbourne, C.J.A. 1988. The role of cuttings in the genetic improvement of forest trees. *In* Workshop on growing radiata pine from cuttings. (FRI Bulletin No. 135) *Edited by:* M.I. Menzies, J.P. Aimers, and L.J. Whitehouse. Forest Research Institute, Rotorua, NZ. pp. 7-14.

Abstract: The control-pollinated (CP) orchard, in which crosses are made artificially between a few of the best, progeny-tested parents, is the key source of seedlings for multiplication by rooted cuttings. These orchards yield higher gains than open-pollinated (OP) orchards because the latter are affected by pollen contamination from unimproved trees outside the orchard. CP orchards also have other advantages in allowing the production of a variety of different breeds of radiata pine for different end-uses, with reduced lead-times, all from the same area of orchard.

The extra costs of producing 1-year-old cuttings from CP and VM, compared with using OP orchard seed, lie mainly in the cost of raising cuttings, provided numerous cuttings (10 or more) result from each CP seed. The cost of such cuttings should be between 50 to 100% greater than the cost of 1-year-old seedlings.

Shelbourne, C.J.A. 1990. Incorporating clonal forestry in the breeding strategy. Draft paper (not for publication) presented at: Proc. Joint Meeting of Western For. Genet. Assoc. and IUFRO Working Parties S2.02-05,06,12 and 14, August 20-24, 1990, Olympia, WA.

Comments: Discusses alternative ways to incorporate clonal forestry in the breeding strategy, particularly when propagation must be made from "juvenile" trees

Shelbourne, C.J.A. 1991. Clonal testing *Pinus radiata* in New Zealand. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 25-40.

Abstract: Extensive clonal tests of radiata pine have been planted in New Zealand since 1968. Up until 1986, physiological ages of clones planted in tests were always greater than 5 years, with concomitant reduction in diameter growth and alteration of other traits relative to seedling performance. This paper reviews and summarises the oldest assessment data from all trials and tabulates heritability of clone means and expected and realised gains from a selection of the best 10% of the clones in each test.

There is good agreement between predicted and realised gains in each trial, and these were high for all traits except malformation. There is some suspicion that clones-in-families variance has been inflated relative to that expected from the genetic model and this may have been caused by C effect variance, a non-genetic clonal variance imposed by such factors as ageing and propagation method.

Comments: The assumption that epistasis is absent results in Shelbourne's warning that C effects may be both common and relatively large. The additional variance in clones-within-families may be explained by epistatic variance if an expanded genetic model were used. How can one tell the difference?

Shelbourne, C.J.A. 1991. Genetic gains from different kinds of breeding population and seed or plant production population. Paper to be presented at the IUFRO meeting on Management and Improvement of Eucalypts, Durban, South Africa in September 1991. (Unpublished draft manuscript)

Comments: Discussion of gain calculations and evaluation of five breeding-population options and 12 plant-production populations options. Unfortunately, the author only considers additive variance, assuming dominance and epistasis to be absent, and only considers gain achieved in one cycle of breeding. Although gain per dollar is calculated, the derivation of costs is not given. Detailed the comparisons are not made among strategies with equivalent expenditure of effort, e.g., low cost alternatives often gave greater gain per dollar, but the total gain achieved per unit time was much less. Even with these flaws, the paper is an excellent illustration of how markedly different breeding and production population strategies may be compared.

Shelbourne, C.J.A., Carson, M.J., and Wilcox, M.D. 1989. New techniques in the genetic improvement of radiata pine. Commonw. For. Rev. 68(3): 191-201.

Abstract: This paper examines recent developments in breeding, particularly breeding strategy, reviews new techniques in vegetative propagation, seed production and clonal forestry, and assesses genetic gains as a preliminary to discussing costs and benefits of tree improvement. Examples are drawn from experience with radiata pine (Pinus radiata) in New Zealand.

Comments: Describes the implementation of "family forestry" by means of control-pollinated orchards (500/ha) and "Meadow orchards" (5,000-10,000/ha). Pollination is by hand in both cases. In meadow orchards, females are not isolated and pollen is applied by hand to clonal blocks. Males are not produced in large numbers on young grafts. Meadow orchard results in less control over contamination and parentage (therefore, loss of gain) but the cost of seed production is much lower than with control-pollinated orchards ($400-600 compared with $2,500 per kg - 1989 NZ$)

Sluis, C.J., and Walker, K.A. 1985. Commercialization of plant tissue culture propagation. Newsletter, International Association for Plant Tissue Culture (47): 2-12.

Abstract: The structure of the existing micropropagation industry is assessed from the standpoints of biology, technology, economics and marketing. It is concluded that major technological advances in micropropagation processes and reduction of production costs are essential before plants of economic crops derived from tissue cultures become widely available to growers. The best prospects for automation are thought to be offered by somatic embryogenesis systems, where embryo encapsulation could result in the mass availability of somatic seeds at significantly low costs.

Smith, D.R. 1986. Forest and nut trees. 1. Radiata pine (*Pinus radiata* D. Don.). *In* Biotechnology in agriculture and forestry. Vol. 1. Trees I. *Edited by:* Y.P.S. Bajaj. Springer-Verlag, Berlin. pp. 274-291. (515 pp.)

Comments: Estimates that micropropagated radiata pine stock would be 7-10x as expensive as normal seedling stock. Even at this high price, the extra genetic gain (estimated at 20%) and the lower initial planting density would make this a cost effective means of growing extra wood.

Smith, D.R. 1991. Economic benefits of vegetative propagation. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 158-160.

Abstract: Several vegetative propagation systems are now available for vegetative amplification of superior seedlots. All of these are potentially capable of supplying New Zealand's requirement of *Pinus radiata* planting stock, even if as few as twenty clones were used.

South, D.B. 1986. Economics of seed efficiency. J. For. 84(3): 33-34.

Comments: The best genetic orchard stock is of little value until planting stock is produced. The present value of increasing seed efficiency (# seeds/plantable tree) is substantial, and will be even greater when output of higher quality genetic stock is enhanced.

South, D.B. 1987. Economic aspects of nursery seed efficiency. South. J. Appl. For. 11(2): 106-109.

Abstract: Costs and value of improved seeds are discussed in relation to some economic benefits that could be gained by increasing the number of plantable seeds for a given number of pure live seeds sown.

Comments: Demonstrates calculation of present value of gain in volume by genetic improvement as a function of interest rate, stumpage value, rotation age and site quality.

Stomp, A.M. 1988. Sex, designer genes, and tree improvement. TAPPI, 71(7): 115-120.

Comments: Describes the futuristic techniques that will be made available to the tree breeder, such as: recombinant DNA genetic engineering, RFLPs, somaclonal variation, somatic cell fusion, gene transfer, biochemical assays, and in vitro screening.

Sweet, G.B. 1991. Summing up. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, New Zealand. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 164-168.

Comments: "... the prospect in the 1950s and 1960s was in many ways simpler than it is today: then it was simply a matter of whether we were going to have clonal forests or seedling forests. We were still at a stage of conventional Syrach Larsen-type seed orchards, and ..." vegetative amplification of control crossed material "... really was not available. It was not until the mid to late 1970s that we developed the concept of the control-pollinated seed orchard which, with the high expense of seed production, led us to thoughts of vegetative amplification of what we expected to be scarce seed."

"... I suspect that very few of the participants at this meeting, and maybe none of you, see large-scale clonal forestry as being just around the corner in terms of time."

"... maturation effects clearly represent a significant constraint ... complete rejuvenation is possible. It is in fact extremely easy; plants do it without our help every time they undertake meiosis."

Henri Chaperon: "The conventional seed orchard is finished".

Sweet, G.B., Bolton, P., and Litchwark, H. 1990. A meadow orchard in radiata pine - research and reality. *In* Proceedings reproductive processes working group S.2.01-5, XIX IUFRO world congress, Montreal, Canada, 7-11 August 1990.

Abstract: NZ is currently establishing a commercial meadow orchard of radiata pine on a very productive site in the South Island. Based on research results presented, it is expected that strobili (enhanced by gibberellin treatment) will be controlled pollinated, without isolation, using an aqueous pollen solution. Projections have been made for the production of 50kg of seed per hectare per annum from age 3, at a direct cost of $500 per kg. Genetic quality should be comparable with that from present bagged controlled pollinated orchards.

Sweet, G.B., and Krugman, S.L. 1977. Flowering and seed production problems - and a new concept of seed orchards. *In* Proceedings of the Third World Consultation on Forest Tree Breeding, Canberra, Australia, 21-26 March 1977. FAO/IUFRO. pp. 749-759.

Abstract: This paper reviews the problems of present day seed orchards and suggests that a number of them can be overcome with existing technology. To accomplish this, it proposes a new form of seed orchard, designed for more intensive management. The system visualizes separate male and female orchards, with the use of artificial pollination. The female orchards consist of clonal hedges maintained at a height which is low enough for management operations to be carried out easily and cheaply. The male orchards contain a limited number of clones, selected either for a high general combining ability or specific combining ability.

Comments: This is the classic paper which introduced the concept of control-pollinated orchards, later developed by Sweet and others to the present-day meadow orchard with pollination by means of an aqueous pollen suspension.

Szmidt, A.E. 1987. Genetic composition of seed orchard crops. For. Ecol. Manage. 19(1): 227-232.

Comments: This paper documents the loss of parental variation in seed from three Scots pine orchards due to non-panmictic mating and outside contamination. Also document the effect of seed grading which they found might be used to remove excessive homozygosity from the crop by culling lighter seeds.

Talbert, J.T., Weir, R.J., and Arnold, R.D. 1985. Costs and benefits of a mature first-generation loblolly pine tree improvement program. J. For. 83(3): 162-166.

Abstract: A discussion of a series of trials (NC State University-Industry Cooperative Tree Improvement Program) in which the final first-generation progeny tests were established in 1983. Gains from tree improvement in growth rate and quality traits such as wood density, resistance to fusiform rust [Cronartium fusiforme] and stem straightness are briefly reviewed. Gain estimates for height were 3-4%, increasing to about 7% in an orchard subjected to intensive roguing based on test information, in which improvement in volume and harvest value were estimated as 12 and 32% respectively. Rates of return on investment after tax depended on seed orchard yields: estimates ranged from 14.3% at a seed yield of 10 lb/acre to 18.7% at 150 lb/acre.

Comments: Tree improvement (seed orchard) costs per acre of plantation are in range of $5-8/acre. These are in line with those quoted by Gleed (1982). Extra cost highly dependent on seed crops. In general, anything that will hasten deployment of improved seed will be profitable.

Thomson, T.A. 1989. Evaluating some financial uncertainties of tree improvement using the capital asset pricing model and dominance analysis. Can. J. For. Res. 19(11): 1380-1388.

Abstract: Although uncertainty considerations are of prime importance in capital budgeting, forestry investments are often evaluated without comparing their uncertainty level with their rates of return. This paper examines some financial uncertainties of a west coast Douglas-fir tree improvement program. Biophysical uncertainties such as amount of genetic gain or uncertainty of site quality are determined by *a priori* assumption to be nonmarket; thus, use of expected value adjusts for these risks. The market uncertainties of tree improvement are found to be reasonable, vis-à-vis other investments as sensitivity analysis shows that the financial risks were small, or the measured β was low. This paper concludes that the tree improvement investment is worthwhile, considering its risk as well as return.

Comments: NON-MARKET UNCERTAINTIES:

(1) Genetic gain: "Because genetic gain is dependent on selection intensity and heritability, its risk is not market related and this sensitivity suggests the point estimate of NPV is a valid estimate of its expected NPV."

(2) Site quality: "... the mean site index yields a correct calculation of expected NPV."

(3) Number of hectares to be regenerated: "... regenerating fewer hectares has a greater impact (negative) on NPV than regenerating more hectares (positive impact)."

MARKET-RELATED UNCERTAINTIES:

(1) Cost: "... the spread of IRR is less than 1% for a cost increase of 50% or a decrease of 25%."

(2) Regeneration timing: affects planning of program output; "... uncertainty about harvest pattern (and hence regeneration requirements) ... does not appear to seriously affect the evaluation of the tree improvement investment."

(3) Appropriate discount rate: unclear, anyone's guess

(4) Future stumpage value: "Although future stumpage price is unknown, it will be the same for both tree improvement and forest management investments. ... in the case of uncertain prices, tree improvement will almost certainly dominate forest management. ...Tree improvement is a better investment in terms of downside risk (low future price), so a risk-averse investor will prefer tree improvement to forest management on additional hectares. ... because the market has accepted forest management, it should accept the addition of tree improvement to the forest management portfolio, for tree improvement as a marginal investment compares favourably with investment in forest management without tree improvement."

Thomson, T.A., Lester, D.T., and Martin, J.A. 1987. Marginal analysis and cost effectiveness in seed orchard management. Can. J. For. Res. 17(6): 510-515.

Abstract: Marginal analysis was used for 3 management decisions. Examples were developed from data from a Douglas fir tree improvement programme. In a seed orchard established with many untested trees, analysis indicated that inferior parents should be rogued to the point where the number of orchard trees times the av. expected vol. gain of trees produced by that orchard is maximized. The method was also useful in choosing the number of trees to establish in an orchard planted after progeny tests have identified superior parents. The cost of establishing many ramets to meet early seed production goals was balanced with the projected value of the seed. In the example given, an additional orchard tree was cost effective if its seed was needed at an orchard age of 12-15 yr. Finally, marginal analysis was used to determine whether to induce a seed orchard to increase its seed production when there is an excess demand for seed. This decision was guided by balancing the cost of the induction treatment with the combined effect of expected increase in seed harvest, the genetic gain and the discount rate. A 4-quadrant decision diagram is presented for estimating this balance.

Thomson, T.A., Lester, D.T., Martin, J.A., and Foster, G.S. 1989. Using economic and decision making concepts to evaluate and design a corporate tree improvement program. Silvae Genet. 38(1): 21-28.

Abstract: Economic and decision making techniques were used to evaluate an existing Pseudotsuga menziesii improvement programme and to plan its future direction. Tree improvement alternatives to meet the projected seed requirements over time were designed. The alternatives differed in the amount of gain they will provide and in their cost. The collection of cones from designated parents in wild stands is considered, as are first-generation seed orchards of 2 types, second-generation seed orchards of 2 types, and combinations of first and second generation orchards. After ensuring that each alternative is cost-effective, its net present value is calculated to determine the economically desirable alternative. For the specific case examined it was recommended that interim seed collection be made from designated parents in wild stands, the existing first generation seed orchard be retained and work towards a second generation orchard continued.

Thorpe, T.A., Harry, I.S., and Kumar, P.P. 1991. Application of micropropagation to forestry. *In* Micropropagation: technology and application. *Edited by:* P.C. Debergh, and R.H. Zimmerman. Kluwer Academic Publishers, The Netherlands. pp. 311-336.

Abstract: Reviews micropropagation methods in approximate order of chronological development, including: organogenesis (axillary budbreaking, adventitious budding, development and multiplication of buds, rooting and hardening of plantlets), asexual embryogenesis. Also discusses the major problems associated with micropropagation technology: juvenility-maturation problems, culture problems, field performance, and cost of plantlet production.

Thorpe, T.A., and Hasnain, S. 1988. Micropropagation of conifers: methods, opportunities and costs. Proc. Can. Tree Improve. Assoc., Part 2, 21: 68-84.

Abstract: Clonal propagation is an integral part of any tree improvement programme. During the last 10 years lab-scale protocols have been developed for the micropropagation of nearly 25 conifers via the multi-staged organogenic route; and in the last two years, somatic embryogenesis has also been achieved in six species. Success has mainly been with embryogenic and juvenile tissues, but progress is being made with tissues from mature trees. Several opportunities exist for the application of presently available micropropagation technology to specific forestry problems, but some limitations exist. Based on certain assumptions, it appears that micropropagation is economically feasible in Canada, and can play a role in producing the superior planting stock required for reforestation. However, the technologies and the infrastructure for delivery needs to be developed.

Timmis, R. 1985. Factors influencing the use of clonal material in commercial forestry. *In* Crop physiology of forest trees. Proceedings of an international conference on managing forest trees as cultivated plants, held in Finland, 23-28 July 1984. *Edited by:* P.M.A. Tigerstedt, P. Puttonen, and V. Koski. Department of Plant Breeding, University of Helsinki., Helsinki, Finland. pp. 259-272.

Abstract: A discussion of the technology available for vegetative propagation of commercially important conifers, schemes for using it, genetic gain, costs and long-term business aspects. Net present value of the investment involved is most sensitive to assumptions about genetic gain.

Timmis, R., Abo El-Nil, M.M., and Stonecypher, R.W. 1987. Potential genetic gain through tissue culture. *In* Cell and tissue culture in forestry. Vol. 1. General principles and biotechnology. *Edited by:* J.M. Bonga, and D.J. Durzan. Martinus Nijhoff, Dordrecht, The Netherlands. pp. 198-215.

Comments: "Each term in the genetic gain equation for forest improvement can be changed in a favourable way through current or projected tissue culture technology. Gain can be increased with current technology by (1) addition of dominance and epistatic components of genetic variance through the cloning of elite individuals, and (2) reduction of the effect of environmental variance components through clonal testing."

Tisserat, B., and Vandercook, C.E. 1985. Development of an automated plant culture system. Plant Cell Tissue Org. Cult. 5: 107-117.

Abstract: An apparatus was constructed that could be used to automate the growing of plant tissues, organs, and whole plantlets under sterile conditions. Control of the automated plant culture system is through interfacing with a microcomputer.

Tombleson, J.D., and Carson, M.J. 1991. Family forestry vs clonal forestry -- a case study. *In* Proceedings: FRI/NZFP Forests Ltd clonal forestry workshop, 1-2 May 1989, Rotorua, NZ. (FRI Bulletin No. 160) *Edited by:* J.T. Miller. Forest Research Institute and NZFP Forests Ltd., Rotorua, NZ. pp. 150-153.

Abstract: A case study comparing current radiata pine vegetative multiplication strategies (family forestry) with clonal forestry is described. The primary constraint to clonal forestry is considered to be a delay of at least 10 years before the best clones can be tested, identified, and vegetatively multiplied to supply planting programme requirements. By this time, a further generation of breeding and selection may have taken place in the breeding population, yielding similar or greater genetic gains. On this basis, family forestry using nursery stool-bed propagation techniques appears to be a superior alternative to clonal forestry.

Vanderschaeghe, A.M., and Debergh, P.C. 1988. Automation of tissue culture manipulations in the final stages. Acta Hortic. 227: 399-401.

Abstract: As the major cost in plant propagation by tissue culture is the manual labour, especially in later stages when individual shoots are handled, a production scheme is outlined and data on trials with Prunus avium are presented.

Automation of addition of liquid medium directly to container.

von Wuehlisch, G., Muhs, H.-J., and Geburek, T. 1990. Competitive behaviour of clones of *Picea abies* in monoclonal mosaics vs. intimate clonal mixtures: a pilot study. Scand. J. For. Res. 5: 397-401.

Abstract: The effect of competition on five Norway spruce clones of different provenances growing monoclonally (intragenotypic competition) and in intimate mixtures (intergenotypic competition) at close spacing were studied until the age of five years. In height, root collar diameter, dry weight, and mortality rate, clones reacted differently to the treatments, showing significant inherent competitive differences. A positive competitive reaction between certain clones can raise total increment by overcompensation and can reduce risks by maintaining genetic diversity until harvest.

Webber, J.E. 1987. Increasing seed yield and genetic efficiency in Douglas-fir seed orchards through pollen management. For. Ecol. Manage. 19(1): 209-218.

Comments: Supplemental mass pollination (SMP) can be used to increase both the yield and genetic quality of Douglas-fir orchard seed. Factors: density of competing pollen clouds (ineffective under high pollen-cloud density, SMP should be reserved for treating early- and possibly late-flowering individuals) and timing of application (early - "first on, first in").

Wilhelmsson, L. 1991. Propagation of bred material - costs and benefits. *In* Pollen contamination in seed orchards: proceedings of the meeting of the Nordic Group for Tree Breeding in Sweden, August 1991. (Report 10) *Edited by:* D. Lindgren. Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology, Uppsala, Sweden. pp. 100-119.

Abstract: Investments in bred material may be judged by strategic analysis. Long-term business economic analyses may give good support for this if reasonable real interest rates (1-4%) are used. Costs per cubic metre of stem wood produced will, in most cases, decrease if bred materials are used instead of unbred stand materials. Investments in propagation methods that really utilize the genetic gain in bred materials often seem more profitable than forest plantations in general. At today's breeding level, this seems to be true up to a propagation cost of 0.5 - 1 SEK (US$0.08 - 0.16). Survival calculations may be regarded as short-term investments if the decision to reforest has been made. In this situation, the establishment costs per surviving tree may be directly compared. As forest tree breeding continues, materials with increased breeding values will become available, and investments in improved propagation methods will be even more profitable.

Zimmerman, R.H. 1985. Application of tissue culture propagation to woody plants. *In* Proceedings of the third Tennessee symposium on plant cell and tissue culture held Sept. 9-13, 1984 at the University of Tennessee, Knoxville. *Edited by:* R.R. Henke, K.W. Hughes, M.J. Constantin, and A. Hollaender. Plenum Press, New York. pp. 165-177.

Abstract: A discussion covering the historical development, the economic and technical problems and future prospects of the commercial propagation of fruit trees, ornamental plants, forest trees and plantation crops.

Comments: Economic problems: (1) labour costs -- requires simplification and automation; (2) Scaling-up.

Technical problems: (1) Cultural establishment (primarily maturation state); (2) culture contamination; (3) Field performance and phenotypic stability.

Somatic embryogenesis is a promising technique, however, "the requirement for clonal fidelity means many years of field testing will be required once methods are developed."

Appendix II

FORTRAN program listing for POPSIM -- Forest Tree Breeding Population Simulator

```
c       PPPPPPP     OOOOOO    PPPPPPP     SSSSSS   III   MM     MM
c       P      P   O      O   P      P   S          I    M M   M M
c       P      P   O      O   P      P   S          I    M  M M  M
c       PPPPPPP    O      O   PPPPPPP     SSSSS     I    M   M   M
c       P          O      O   P                S    I    M       M
c       P          O      O   P                S    I    M       M
c       P           OOOOOO    P          SSSSSS    III   M       M


c                                    by

c                              Dr T.J. Mullin

c                             under contract to
c                   Forestry Canada - Maritimes Region
c                                   1991


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c    consequential, indirect or similar damages resulting for the use of this
c    program.  The person using the program bears all the risk as to the
c    quality and performance of the software.


c * Declaration Statements:

      INTEGER*1 KFLAG(450),KCFLAG(450,200)
      INTEGER*2 IHR,IMIN,ISEC,I100TH,IYR,IMON,IDAY
      INTEGER IDEN(450),DAM,SIRE,MALE(450),FEMALE(450),FTMP
      REAL IBAR,IVAR,VAL(5,450),FAMMEAN(450),CLNMEAN(450,200),IPROG,
     +EFFBAR(4),EFFVAR(4),PBAR(5),PVAR(5),TVAL(5),X(5)
      REAL*8 XT,XSUM(45,4),XSUM2(45,4)
      CHARACTER*11 EFFECT(5)/'Additive','Dominance','Epistasis',
     +'Environment','Phenotype'/

c * FORMAT Statements:

901   FORMAT(//,22x,'FOREST TREE BREEDING POPULATION SIMULATOR',
     +/, 22X,     '               Version 1.0α3'
     +//,    22x,'           (c) T.J. Mullin, 1991',//
     +'  PLEASE NOTE:'/
     +'    The distribution of this program is intended for scientific p
     +urposes only.'/
     +'    Dr T.J. Mullin and Forestry Canada - Maritimes Region hereby
     +disclaim'/
     +'    all warranties relating to this software, whether express or
     +implied,'/
     +'    including without limitation any implied warranties of mercha
     +ntability or'/
     +'    fitness for a particular purpose.  Neither will Dr T.J. Mulli
     +n or Forestry'/
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     +'    Canada - Maritimes Region be liable for any special, incident
     +al,'/
     +'    consequential, indirect or similar damages resulting for the
     +use of this'/
     +'    program.  The person using the program bears all the risk as
     +to the'/
     +'    quality and performance of the software.'/)
 902  FORMAT(1H0, 'Select hardcopy output option ->',/
     +'                1 - summary only, 2 - full: ',\)
 903  FORMAT(1H0,'Enter a seed number for random number generator: ',\)
 904  FORMAT('0INITIALIZATION ->'//,4X'Random seed number used for this
     +run : ',I7)
 905  FORMAT(1H0,'Enter mean and variance of additive effects: ',\)
 906  FORMAT(1H0,'Enter mean and variance of dominance effects: ',\)
 907  FORMAT(1H0,'Enter mean and variance of epistatic effects: ',\)
 908  FORMAT(1H0,'Enter mean and variance of environmental effects: ',\)
 909  FORMAT('0POPULATION PARAMETERS ->',//,7X
     +'Effect                Mean              Variance',5(/4X,A11,2F18.3))
 910  FORMAT(1H0,'   Narrow-sense heritability (h2) =',F5.2,/
     +1H ,      '    Broad-sense heritability (H2) =',F5.2,/)
 911  FORMAT('0Enter number of trees in breeding population: ',\)
 912  FORMAT(/,' Generating genotypic and environmental values for',/,
     +1H ,I4,' trees in breeding population')
 920  FORMAT(/' TIMING ->',/'    First iteration started:  ',I4,'.',
     +I2.2,'.',I2.2,' at ',I2.2,I2.2,' hours.')
 921  FORMAT(/' GENERATION #',I1,//,
     +'     Breeding population of',I5' trees:',//,
     +'      Effect              Mean          Variance        Maximum
     +   Minimum')
 922  FORMAT('0Enter number of iterations to be completed: '\)
 923  FORMAT(//'0UNTESTED Production Population ->')
 925  FORMAT(4X,A11,4F15.3)
 926  FORMAT ('0Enter trees/sub-line and number of sublines to'/
     +'  be maintained in the breeding population: ',\)
 927  FORMAT(1H1,///' ITERATION #', I2)
 928  FORMAT(1H1,///' AVERAGE SIMULATION RESULT (with 1 SD in parenthese
     +s) FOR',I3,' ITERATIONS')
 930  FORMAT(1H0,'Enter minimum number of selections required for orchar
     +d: ',\)
 933  FORMAT(//'0POLYCROSS-TESTED Production Population ->')
 935  FORMAT(4X'Breeding population structure:'/5X,I3,
     +' sublines, each with',I4,' trees, for total of'I4' trees.')
 936  FORMAT(3I7,6F10.5)
 937  FORMAT(/,4X'Seed orchard or clone mixture composed of',
     +I5,' best untested phenotypes:',//,
     +'      Effect              Mean          Variance        Maximum
     +   Minimum')
 938  FORMAT('0Enter number of males represented in polymix: '\)
 939  FORMAT(/,' POLYCROSS TESTING ->',/,4X'Pollen mix for polycross tes
     +ting represents',I4,' random individuals.')
 941  FORMAT(1H0,'Enter number of polycross progeny per tree: ',\)
 943  FORMAT(/,4X,'Polycross test of breeding population with 'I3,
     +'-tree polymix',/,
     +I8,' test trees per parent, for total of',I7,' test progeny.')
 948  FORMAT(1H0,'Generating',I4,' progeny for each of',I5' parents,'
     +/'    for a total of',I6,' test progeny',/
     +'0  This will take awhile ... please be patient!',/)
 949  FORMAT('0Enter your preferred sorting method for pair matings',/
     + '    Random = 0, EQUAL Positive = 1, UNEQUAL Positive = 2 : ',\)
 950  FORMAT(/4X'Seed orchard or clone mixture composed of',
     +I5,' best polycross-tested trees:'//,
     +'      Effect              Mean          Variance        Maximum
     +   Minimum')
 951  FORMAT('0Enter number of genotypes tested per cross: '\)
 952  FORMAT('0Enter number of ramets per genotype: '\)
 953  FORMAT('     RANDOM pair-mating to produce')
 954  FORMAT('     EQUAL POSITIVE-ASSORTATIVE pair-mating to produce')
 955  FORMAT('     UNEQUAL POSITIVE-ASSORTATIVE pair-mating to produce')
 956  FORMAT(I8,' full-sib families with',I5' genotypes per family, and'
     +/,     I8,' ramets per genotype, for total of',I7' test progeny.')
 957  FORMAT('0',40X,'... please be patient!')
 958  FORMAT(///,1H1,//'0Deployment of TESTED FAMILIES ->')
```

```
 959  FORMAT(/4X'Full-sib family mixture composed of',I5,
     +' best families:'//
     +'       Effect             Mean          Variance        Maximum
     +   Minimum')
 960  FORMAT(/////,' Try another subline or testing scenario = 1, else 0
     +: ',\)
 961  FORMAT(//'0Deployment of TESTED CLONES ->')
 962  FORMAT(/4X'Clone mixture composed of best clone from each of',I5,
     +' best families:'//
     +'       Effect             Mean          Variance        Maximum
     +   Minimum')
 964  FORMAT(/'0Please specify variance structure of original breeding p
     +opulation ...')
 965  FORMAT('0Enter number of generations for simulation: ',\)
 966  FORMAT(/4X,'The simulation will be repeated'I3' times,'/,
     +'          and will cycle through',I3,' generations.')
 967  FORMAT(//' Please specify structure for breeding and production po
     +pulations ...')
 970  FORMAT(///,' Simulate a new population = 1, else 0: ',\)
 973  FORMAT(//,' Please specify make-up of pollen mix used for polycros
     +s testing ...')
 974  FORMAT(//,' Please specify test design for selection plantations .
     +..')
 978  FORMAT('0Enter number of selections per full-sib family: ',\)
 979  FORMAT(' Sorry ... must divide evenly into ',I3)
 980  FORMAT('0Include half-sib relatives? = 1, else = 0 : ',\)
 981  FORMAT(// ' Progeny and summary data will be written to disk files
     + as they are generated.'/'  Storage requirements are 30K per 1,000
     + trees in selection plantations per'/'  generation, plus 5.3K for
     +each generation simulated.  The simulation will be'/'  faster if a
     + RAM Disk (drive F:) is available with sufficient space.'/
     +'    Select location for these files ->'/
     +'      0 - default drive, 1 - drive F: ',\)
 983  FORMAT(/,' ADVANCED-SELECTION PHASE ->',/,
     +4X,'Selection plantations established using')
 984  FORMAT(/////,/////,/////)
 985  FORMAT(/4X'Selection of next breeding population composed of best'
     +,/,I9,' trees from each of best'I3' FS families/subline;')
 986  FORMAT('    Last iteration completed: ',I4,'.',I2.2,'.',I2.2,
     +' at ',I2.2,I2.2,' hours.')
 988  FORMAT('0SIMULATOR PROGRESS ->')
 989  FORMAT('0    Iteration #'I3)
 990  FORMAT('           Generation'I3)
 995  FORMAT(4X,A11,2X,4(2X,F6.3,'(',F5.3')'))

c  Locations of files used by simulator:

      WRITE(*,984)
      WRITE(*,901)
      WRITE(*,981)
      READ(*,*)I
      IF(I.EQ.1)OPEN(3,FILE='F:\PROGENY',FORM='UNFORMATTED')
      IF(I.EQ.1)OPEN(4,FILE='F:\SUMMARY',FORM='UNFORMATTED')
      IF(I.NE.1)OPEN(3,FORM='UNFORMATTED')
      IF(I.NE.1)OPEN(4,FORM='UNFORMATTED')
      WRITE(*,902)
      READ(*,*) IPRN
      IF(IPRN.EQ.2)OPEN(6,FILE='outfile')
      IT=0
    1 REWIND 3
      REWIND 4

c  Initialize random number generator

      IF(IPRN.EQ.2)WRITE(6,901)
      WRITE(*,903)
      READ(*,*) IISEED
      IF(IPRN.EQ.2)WRITE(6,904) IISEED
      ISEED=IISEED
      SEED = RANDOM(ISEED)
      WRITE(*,965)
      READ(*,*)NCYCLE
```

```
      WRITE(*,922)
      READ(*,*)ITERS
      IF(IPRN.EQ.2)WRITE(6,966)ITERS,NCYCLE

c  Specify initial effects and variances for breeding population

      WRITE(*,964)
      WRITE(*,905)
      READ(*,*) EFFBAR(1), EFFVAR(1)
      WRITE(*,906)
      READ(*,*) EFFBAR(2), EFFVAR(2)
      WRITE(*,907)
      READ(*,*) EFFBAR(3), EFFVAR(3)
      WRITE(*,908)
      READ(*,*) EFFBAR(4), EFFVAR(4)
      SEFFBAR=EFFBAR(1)+EFFBAR(2)+EFFBAR(3)+EFFBAR(4)
      SEFFVAR=EFFVAR(1)+EFFVAR(2)+EFFVAR(3)+EFFVAR(4)
      IF(IPRN.NE.2)GO TO 2
      WRITE(6,909) (EFFECT(I),EFFBAR(I),EFFVAR(I),I=1,4),
     +EFFECT(5),SEFFBAR,SEFFVAR
      WRITE(6,910)EFFVAR(1)/SEFFVAR, (SEFFVAR-EFFVAR(4))/SEFFVAR


c * Generate initial genetic and environmental effects

    2 WRITE(*,967)
      WRITE(*,911)
      READ(*,*)NT
      IF(NT.LE.400)GO TO 200
      WRITE(*,*)'Sorry ... maximum number of trees is 400.'
      GO TO 2
  200 IF(NT.EQ.INT(NT/4)*4)GO TO 199
      WRITE(*,*)'Sorry ... number of trees must be a multiple of 4'
      GO TO 2
  199 WRITE(*,912) NT
  401 IT=IT+1
      IGEN=0
      DO 3 J=1,NT
        VAL(5,J)=0.
        FEMALE(J)=-9
        MALE(J)=-9
      DO 3 I=1,4
        VAL(I,J) = EFFBAR(I)+SQRT(EFFVAR(I))*RANNOR(ISEED)
    3   VAL(5,J) = VAL(5,J) + VAL(I,J)
      IF(IT.GT.1)GO TO 402

c * Specify subline structure for breeding population

   15 WRITE(*,926)
      READ(*,*) NTS, NS
      IF(NTS.EQ.INT(NTS/4)*4)GO TO 16
      WRITE(*,*) 'Sorry ... trees/subline must be a multiple of 4'
      GO TO 15
   16 IF(NTS*NS.EQ.NT)GO TO 17
      WRITE(*,*) 'Sorry ... total number of trees must equal:',NT
      GO TO 15

   17 CONTINUE
      WRITE(*,930)
      READ(*,*) NSEL
      IF(NSEL.EQ.NSEL/NS*NS)GO TO 18
      WRITE(*,*) 'Number of selections must be multiple of',NS
      GO TO 17
  18  CONTINUE
      NSEL=NSEL/NS

c  Print out subline structure

      IF(IPRN.EQ.2)WRITE(6,935)NS,NTS,NT

c  Generate genetic and environmental values for trees in polymix
```

```
      WRITE(*,973)
 201  WRITE(*,938)
      READ(*,*) NP
      IF(NP.LE.100)GO TO 202
      WRITE(*,*)'Sorry ... maximum number of males in polymix is 50.'
      GO TO 201

c  Generate additive effect for each male in polymix

 202  WRITE(*,941)
      READ(*,*) NX

 402  SUMX=0.
      SUMX2=0.
      PMAX=-9.00*10.**10.
      PMIN=+9.00*10.**10.
      DO 46 J=NT+1,NT+NP
        VAL(1,J) = EFFBAR(1)+SQRT(EFFVAR(1))*RANNOR(ISEED)
        SUMX=SUMX+VAL(1,J)
        SUMX2=SUMX2+VAL(1,J)*VAL(1,J)
        IF(VAL(1,J).GT.PMAX)PMAX=VAL(1,J)
  46    IF(VAL(1,J).LT.PMIN)PMIN=VAL(1,J)
      RN=NP
      SS=SUMX2-(SUMX*SUMX/RN)
      PBAR(1)=SUMX/RN
      PVAR(1)=SS/(RN-1)
      IF(IT.GT.1)GO TO 403
      IF(IPRN.EQ.2)WRITE(6,939)NP
      IF(IPRN.EQ.2)WRITE(6,943)NP,NX,NX*NT

c * Is assortative mating to be used for selection plantations?

      WRITE(*,974)
  56  WRITE(*,949)
      READ(*,*)ISORT
      IF(ISORT.GE.0.AND.ISORT.LE.2)GO TO 57
      WRITE(*,*)'Illegal entry ... try again.'
      GO TO 56
  57  IF(ISORT.LT.2.OR.NTS.GE.12)GO TO 205
      WRITE(*,*) 'Unequal positive assortative mating not available for
     +sublines of less than 12 trees.'
      GO TO 56

c * Specify numbers of test progeny and ramets per clone

 205  WRITE(*,951)
      READ(*,*) NC
      IF(NC.LE.200)GO TO 206
      WRITE(*,*)'Sorry ... no more than 200 genotypes per family'
 206  WRITE(*,952)
      READ(*,*) NR
      IF(IPRN.NE.2)GO TO 95
      WRITE(6,983)
      IF(ISORT.EQ.0)WRITE(6,953)
      IF(ISORT.EQ.1)WRITE(6,954)
      IF(ISORT.EQ.2)WRITE(6,955)
      WRITE(6,956)NT, NC, NR,NT*NC*NR

c  *  How many selections per family (must divide evenly into NTS)

  95  WRITE(*,978)
      READ(*,*)NSF
      IF(NTS/NSF*NSF.EQ.NTS)GO TO 96
      WRITE(*,979)NTS
      GO TO 95
  96  NF=NTS/NSF
      WRITE(*,980)
      READ(*,*)IH

c Date and time started:

      CALL GETDAT(IYR,IMON,IDAY)
```

```
      CALL GETTIM(IHR,IMIN,ISEC,I100TH)

      IF(IPRN.NE.2)GO TO 404
      WRITE(6,985)NSF,NF
      IF(IH.EQ.0)WRITE(6,*)'       selected families MAY NOT have common
     + parent.'
      IF(IH.EQ.1)WRITE(6,*)'       selected families MAY have common par
     +ent.'
      WRITE(6,920)IYR,IMON,IDAY,IHR,IMIN
 404  WRITE(*,920)IYR,IMON,IDAY,IHR,IMIN
      WRITE(*,988)
 403  CONTINUE
      WRITE(*,989) IT

c  Generate population statistics

 300  IGEN=IGEN+1
      WRITE(*,990) IGEN
      IF(IPRN.EQ.1.AND.ITERS.GT.1)GO TO 350
      WRITE(6,927)IT
      WRITE(6,921)IGEN,NT
 350  DO 12 I=1,5
        SUMX=0.
        SUMX2=0.
        PMAX=-9.00*10.**10.
        PMIN=+9.00*10.**10.
        DO 11 J=1,NT
          SUMX=SUMX+VAL(I,J)
          SUMX2=SUMX2+VAL(I,J)*VAL(I,J)
          IF(VAL(I,J).GT.PMAX)PMAX=VAL(I,J)
  11      IF(VAL(I,J).LT.PMIN)PMIN=VAL(I,J)
        RN=NT
        SS=SUMX2-(SUMX*SUMX/RN)
        PBAR(I)=SUMX/RN
        PVAR(I)=SS/(RN-1)
        IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))
     +  WRITE(6,925)EFFECT(I),PBAR(I),PVAR(I),PMAX,PMIN
  12    WRITE(4)PBAR(I),PVAR(I),PMAX,PMIN

c  Select NSEL top-ranking untested phenotypes

      IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))WRITE(6,923)
      NSX=NSEL

c  Re-set selection flags to zero

      DO 20 I=1,NT
  20    KFLAG(I)=0

c  Check if this is the first generation

  28  IF(IGEN.GT.1)GO TO 24
      DO 23 J=1,NSEL*NS
        PMAX=-9.00*10.**10.
        DO 22 K=1,NT
          IF (VAL(5,K).GT.PMAX.AND.KFLAG(K).LT.1)GOTO 21
          GOTO 22
   21     PMAX=VAL(5,K)
          KMAX=K
   22     CONTINUE
   23   KFLAG(KMAX)=1
      GO TO 29

c  Select unrelated trees within sublines for second and subsequent generations

  24  DO 27 I=1,NS
        KX = I*NTS-NTS+1
       DO 27 J=1,NSEL
        PMAX=-9.00*10.**10.
        DO 26 K=KX,KX+NTS-1
          IF (VAL(5,K).GT.PMAX.AND.KFLAG(K).LT.1)GOTO 25
          GOTO 26
```

```
c * Tree related to a previous selection in this subline?
   25      IF(J.EQ.1)GO TO 427
           IR=0
           DO 426 KK=KX,KX+NTS-1
             IF(K.EQ.KK.OR.KFLAG(KK).NE.1)GO TO 426
             IF(FEMALE(K).EQ.FEMALE(KK).OR.FEMALE(K).EQ.MALE(KK))IR=1
             IF(MALE(K).EQ.FEMALE(KK).OR.MALE(K).EQ.MALE(KK))IR=1
  426        CONTINUE
           IF(IR.EQ.1)GO TO 26
  427      PMAX=VAL(5,K)
           KMAX=K
   26      CONTINUE
   27    KFLAG(KMAX)=1
   29   CONTINUE

c Generate population statistics for selected trees

      IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))WRITE(6,937)NSX*NS
      DO 42 I=1,5
        N=0
        SUMX =0.
        SUMX2=0.
        PMAX =-9.00*10.**10.
        PMIN =+9.00*10.**10.
        DO 41 J=1,NT
          IF(KFLAG(J).LT.1)GO TO 41
          N = N+1
          SUMX =SUMX+VAL(I,J)
          SUMX2=SUMX2+VAL(I,J)*VAL(I,J)
          IF(VAL(I,J).GT.PMAX)PMAX=VAL(I,J)
          IF(VAL(I,J).LT.PMIN)PMIN=VAL(I,J)
  41      CONTINUE
        RN=N
        SS=SUMX2-(SUMX*SUMX/RN)
        PBAR(I)=SUMX/RN
        PVAR(I)=SS/(RN-1)
        IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))
     +  WRITE(6,925)EFFECT(I),PBAR(I),PVAR(I),PMAX,PMIN
  42    WRITE(4)PBAR(I),PVAR(I),PMAX,PMIN

      NSX=NSX+NSX
      IF(NSX.LE.2*NSEL)GO TO 28

c  Derive family dominance effect for each possible cross

      DO 52 K=NT+1,NT+NP
  52    VAL(2,K) = EFFBAR(2)+SQRT(0.25*EFFVAR(2))*RANNOR(ISEED)

c  Generate NX progeny from polycross

      DO 55 I=1,NT
        FAMMEAN(I)=0.
        DAM=FEMALE(I)

c    Generate the genetic and environmental effects for each
c       individual in polycross family

        DO 50 J=1,NX

c    First, choose a male parent at random:

          SIRE = IRANDOM(NT+1,NT+NP,ISEED)

c    Then, generate the individual's values:

      APROG=(VAL(1,I)+VAL(1,SIRE))/2.+SQRT(0.5*EFFVAR(1))*RANNOR(ISEED)
          DPROG=VAL(2,SIRE)+SQRT(0.75*EFFVAR(2))*RANNOR(ISEED)
          IPROG=EFFBAR(3)+SQRT(EFFVAR(3))*RANNOR(ISEED)
          EPROG=EFFBAR(4)+SQRT(EFFVAR(4))*RANNOR(ISEED)
          PPROG=APROG+DPROG+IPROG+EPROG
  50      FAMMEAN(I) = FAMMEAN(I)+PPROG
        ZX=NX
```

```
         FAMMEAN(I) = FAMMEAN(I)/ZX
   55   CONTINUE
        REWIND 3

c * If assortative mating is to be used, sort the trees by FAMMEANs

        IF(ISORT.EQ.0)GO TO 65

c * If this is the first generation, sort all trees:

        IF(IGEN.GT.1)GO TO 659
        LATEST=NT
   60   LAST=LATEST
        DO 62 J=2,LAST
          IF(FAMMEAN(J-1).GE.FAMMEAN(J)) GO TO 62
          LATEST = J-1
          FTMP=FEMALE(J-1)
          FEMALE(J-1)=FEMALE(J)
          FEMALE(J)=FTMP
          MTMP=MALE(J-1)
          MALE(J-1)=MALE(J)
          MALE(J)=MTMP
          FMTMP=FAMMEAN(J-1)
          FAMMEAN(J-1)=FAMMEAN(J)
          FAMMEAN(J)=FMTMP
            DO 61 I=1,5
            TVAL(I)=VAL(I,J-1)
            VAL(I,J-1)=VAL(I,J)
   61       VAL(I,J)=TVAL(I)
   62     CONTINUE
        IF(LATEST.LT.LAST.AND.LATEST.GT.1)GO TO 60
        GO TO 65

c * Otherwise, sort trees within sublines

  659   DO 863 K=1,NS
        LATEST=K*NTS
  860   LAST=LATEST
        DO 862 J=K*NTS-NTS+2,LAST
          IF(FAMMEAN(J-1).GE.FAMMEAN(J)) GO TO 862
          LATEST = J-1
          FTMP=FEMALE(J-1)
          FEMALE(J-1)=FEMALE(J)
          FEMALE(J)=FTMP
          MTMP=MALE(J-1)
          MALE(J-1)=MALE(J)
          MALE(J)=MTMP
          FMTMP=FAMMEAN(J-1)
          FAMMEAN(J-1)=FAMMEAN(J)
          FAMMEAN(J)=FMTMP
            DO 861 I=1,5
            TVAL(I)=VAL(I,J-1)
            VAL(I,J-1)=VAL(I,J)
  861       VAL(I,J)=TVAL(I)
  862     CONTINUE
        IF(LATEST.LT.LAST.AND.LATEST.GT.1)GO TO 860
  863   CONTINUE

c * If this is the first generation of PAM

   65   IF(IGEN.GT.1.OR.ISORT.EQ.0)GO TO 770

c * Generate tree identifiers for first generation PAM, so that
c       trees are sorted and assigned uniformly to sublines

        DO 68 J=1,NTS
        DO 68 I=1,NS
          K = J*NS-NS + I
   68     IDEN(K) = IGEN*100000+I*1000 + J
        LATEST=NT
   70   LAST=LATEST
        DO 72 J=2,LAST
```

```
        IF(IDEN(J-1).LE.IDEN(J)) GO TO 72
        LATEST = J-1
        FTMP=FEMALE(J-1)
        FEMALE(J-1)=FEMALE(J)
        FEMALE(J)=FTMP
        MTMP=MALE(J-1)
        MALE(J-1)=MALE(J)
        MALE(J)=MTMP
        FMTMP=FAMMEAN(J-1)
        FAMMEAN(J-1)=FAMMEAN(J)
        FAMMEAN(J)=FMTMP
        IDTMP=IDEN(J-1)
        IDEN(J-1)=IDEN(J)
        IDEN(J)=IDTMP
        DO 71 I=1,5
          TVAL(I)=VAL(I,J-1)
          VAL(I,J-1)=VAL(I,J)
  71      VAL(I,J)=TVAL(I)
  72    CONTINUE
      IF(LATEST.LT.LAST.AND.LATEST.GT.1)GO TO 70
      GO TO 772

c Otherwise, assign IDs in order, by subline

 770  DO 771 I=1,NS
      DO 771 J=1,NTS
        K=I*NTS-NTS+J
 771    IDEN(K)=IGEN*100000+I*1000+J

c  Select NSEL top-ranking GCA parents from each subline

 772  IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))WRITE(6,933)

      NSX=NSEL

c  Re-set selection flags to zero

      DO 74 I=1,NT
  74    KFLAG(I)=0

c  Check if this is the first generation

 728  IF(IGEN.GT.1)GO TO 724
      DO 723 J=1,NSEL*NS
        PMAX=-9.00*10.**10.
        DO 722 K=1,NT
          IF (FAMMEAN(K).GT.PMAX.AND.KFLAG(K).LT.1)GOTO 721
          GOTO 722
  721     PMAX=FAMMEAN(K)
          KMAX=K
  722     CONTINUE
  723   KFLAG(KMAX)=1
      GO TO 729

c  Select unrelated trees within sublines for second and subsequent generations

 724  DO 78 I=1,NS
        KX = I*NTS-NTS+1
       DO 78 J=1,NSEL
        PMAX=-9.00*10.**10.
        DO 77 K=KX,KX+NTS-1
          IF (FAMMEAN(K).GT.PMAX.AND.KFLAG(K).LT.1)GOTO 76
          GOTO 77
c * Tree related to a previous selection in this subline?
   76     IF(J.EQ.1)GO TO 727
          IR=0
          DO 726 KK=KX,KX+NTS-1
            IF(K.EQ.KK.OR.KFLAG(KK).NE.1)GO TO 726
            IF(FEMALE(K).EQ.FEMALE(KK).OR.FEMALE(K).EQ.MALE(KK))IR=1
            IF(MALE(K).EQ.FEMALE(KK).OR.MALE(K).EQ.MALE(KK))IR=1
  726       CONTINUE
          IF(IR.EQ.1)GO TO 77
```

```
  727     PMAX=FAMMEAN(K)
          KMAX=K
   77     CONTINUE
   78   KFLAG(KMAX)=1
 729  CONTINUE

c Generate population statistics for selected trees

      IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))WRITE(6,950)NSX*NS

       DO 82 I=1,5
        N=0
        SUMX =0.
        SUMX2=0.
        PMAX =-9.00*10.**10.
        PMIN =+9.00*10.**10.
        DO 81 J=1,NT
          IF(KFLAG(J).LT.1)GO TO 81
          N = N+1
          SUMX =SUMX+VAL(I,J)
          SUMX2=SUMX2+VAL(I,J)*VAL(I,J)
          IF(VAL(I,J).GT.PMAX)PMAX=VAL(I,J)
          IF(VAL(I,J).LT.PMIN)PMIN=VAL(I,J)
  81      CONTINUE
        RN=N
        SS=SUMX2-(SUMX*SUMX/RN)
        PBAR(I)=SUMX/RN
        PVAR(I)=SS/(RN-1)
        IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))
     +  WRITE(6,925)EFFECT(I),PBAR(I),PVAR(I),PMAX,PMIN
  82    WRITE(4)PBAR(I),PVAR(I),PMAX,PMIN

      NSX=NSX+NSX
      IF(NSX.LE.2*NSEL)GO TO 728

c * Pair mating procedure:

      REWIND 3
      IX=0
      KT=(NTS/5)*2
      KL=NTS-(NTS/5)
      DO 97 I=1,NS
      DO 97 J=1,NTS,4
      KX=I*NTS-NTS+J
      KK=4
      IF(ISORT.NE.2)GO TO 90
      IF(J.GE.KL)GO TO 97
      IF(J.LE.KT)KK=6
  90  DO 94 K=1,KK
      IX=IX+1
      DAM=4
      SIRE=1
      IF(K.EQ.1)DAM=2
      IF(K.EQ.3)DAM=3
      IF(K.EQ.3)SIRE=2
      IF(K.EQ.4)SIRE=3
      IF(K.EQ.5)DAM=3
      IF(K.EQ.6)SIRE=2
      LF=KX+DAM-1
      LM=KX+SIRE-1

c *  Produce NC genotypes


      FSUMX=0
      ZR=NR
      ZC=NC
      DO 93 L=1,NC

c *  Generate random mean family dominance effect with variance = 1/4 population D

       DFAM = PBAR(2)+SQRT(0.25*PVAR(2))*RANNOR(ISEED)
```

```
c * Now generate the individual genotype values:

        APROG=(VAL(1,LF)+VAL(1,LM))/2.+SQRT(0.5*PVAR(1))*RANNOR(ISEED)
        DPROG=DFAM+SQRT(0.75*PVAR(2))*RANNOR(ISEED)
        IPROG=PBAR(3)+SQRT(PVAR(3))*RANNOR(ISEED)

c *  Produce NR ramets of this genotype

        CSUMX=0
        DO 92 LL=1,NR
          EPROG=EFFBAR(4)+SQRT(EFFVAR(4))*RANNOR(ISEED)
          PPROG=APROG+DPROG+IPROG+EPROG
          WRITE(3)IDEN(LF),IDEN(LM),APROG,DPROG,IPROG,EPROG,PPROG
  92      CSUMX=CSUMX+PPROG
          CLNMEAN(IX,L)=CSUMX/ZR
  93    FSUMX=FSUMX+CLNMEAN(IX,L)
        FEMALE(IX)=IDEN(LF)
        MALE(IX)=IDEN(LM)
  94    FAMMEAN(IX)=FSUMX/ZC
  97  CONTINUE

c  *  Reset the selection flags to 0

      DO 101 I=1,NT
      KFLAG(I)=0
      DO 101 J=1,NC
 101  KCFLAG(I,J)=0
      IFL=0
      IML=0

c  *  Select the NF best families

      DO 121 I=1,NS
        KX = I*NTS-NTS+1
        DO 121 J=1,NF
          PMAX=-9.00*10.**10.
          DO 108 K=KX,KX+NTS-1
            IF (FAMMEAN(K).GT.PMAX.AND.KFLAG(K).LT.1)GO TO 106
            GO TO 108

c     Check if this is a half-sib relative of previously selected family

 106        IF(IH.EQ.1.OR.K.EQ.1)GO TO 107
            IREL=0
            IIF=FEMALE(K)
            IIM=MALE(K)
            DO 110 KI=1,NT
            IF(KFLAG(KI).EQ.0)GO TO 110
            IF(FEMALE(KI).EQ.IIF.OR.MALE(KI).EQ.IIF)IREL=1
            IF(FEMALE(KI).EQ.IIM.OR.MALE(KI).EQ.IIM)IREL=1
 110        CONTINUE
            IF(IREL.EQ.1)GO TO 108
 107        PMAX=FAMMEAN(K)
            KMAX=K
 108        CONTINUE
        IFL=FEMALE(KMAX)
        IML=MALE(KMAX)
        KFLAG(KMAX)=J

c  *  Now select the NSF best trees (clones) in each selected family

        DO 120 L=1,NSF
         PMAX=-9.00*10.**10.
         DO 118 LL=1,NC
          IF(CLNMEAN(KMAX,LL).GT.PMAX.AND.KCFLAG(KMAX,LL).LT.1)GO TO 116
          GO TO 118
 116      PMAX=CLNMEAN(KMAX,LL)
          LMAX=LL
 118      CONTINUE
 120    KCFLAG(KMAX,LMAX)=L
 121  CONTINUE
```

```
c *  Initialize array to accumulate best family/clone stats

      DO 1010 J=1,16,4
      DO 1010 I=1,5
        VAL(I,J)  =0.
        VAL(I,J+1)=0.
        VAL(I,J+2)=-9.*10.**10.
 1010   VAL(I,J+3)= 9.*10.**10.

c * Go to progeny file and retrieve info for best families and clones

      REWIND 3

      DO 1130 K=1,NT
      DO 1130 J=1,NC
      DO 1130 I=1,NR
        READ(3)IFL,IML,(X(L),L=1,5)
        IF(I.NE.NR)GO TO 1130

c * Is the tree from one of the best families?

        IF(KFLAG(K).EQ.0.OR.KFLAG(K).GT.NSEL*2) GO TO 1130
        JJ=5
 1119   DO 1120 II=1,3
          VAL(II,JJ)  = VAL(II,JJ)+X(II)
          VAL(II,JJ+1)= VAL(II,JJ+1)+X(II)*X(II)
          IF(X(II).GT.VAL(II,JJ+2))VAL(II,JJ+2)=X(II)
 1120     IF(X(II).LT.VAL(II,JJ+3))VAL(II,JJ+3)=X(II)
        VAL(5,JJ) = VAL(5,JJ)+CLNMEAN(K,J)
        VAL(5,JJ+1)=VAL(5,JJ+1)+CLNMEAN(K,J)*CLNMEAN(K,J)
        IF(CLNMEAN(K,J).GT.VAL(5,JJ+2))VAL(5,JJ+2)=CLNMEAN(K,J)
        IF(CLNMEAN(K,J).LT.VAL(5,JJ+3))VAL(5,JJ+3)=CLNMEAN(K,J)
        V4 = CLNMEAN(K,J)-(X(1)+X(2)+X(3))
        VAL(4,JJ) = VAL(4,JJ)+V4
        VAL(4,JJ+1)=VAL(4,JJ+1)+V4*V4
        IF(V4.GT.VAL(4,JJ+2))VAL(4,JJ+2)=V4
        IF(V4.LT.VAL(4,JJ+3))VAL(4,JJ+3)=V4

c * Is this the best clone in the family?

        IF(KCFLAG(K,J).NE.1) GO TO 1125
        KK=JJ+8
        DO 1122 II=1,3
          VAL(II,KK)  = VAL(II,KK)+X(II)
          VAL(II,KK+1)= VAL(II,KK+1)+X(II)*X(II)
          IF(X(II).GT.VAL(II,KK+2))VAL(II,KK+2)=X(II)
 1122     IF(X(II).LT.VAL(II,KK+3))VAL(II,KK+3)=X(II)
        VAL(5,KK) = VAL(5,KK)+CLNMEAN(K,J)
        VAL(5,KK+1)=VAL(5,KK+1)+CLNMEAN(K,J)*CLNMEAN(K,J)
        IF(CLNMEAN(K,J).GT.VAL(5,KK+2))VAL(5,KK+2)=CLNMEAN(K,J)
        IF(CLNMEAN(K,J).LT.VAL(5,KK+3))VAL(5,KK+3)=CLNMEAN(K,J)
        V4 = CLNMEAN(K,J)-(X(1)+X(2)+X(3))
        VAL(4,KK) = VAL(4,KK)+V4
        VAL(4,KK+1)=VAL(4,KK+1)+V4*V4
        IF(V4.GT.VAL(4,KK+2))VAL(4,KK+2)=V4
        IF(V4.LT.VAL(4,KK+3))VAL(4,KK+3)=V4

 1125   JJ=JJ-4
        IF(JJ.EQ.1.AND.KFLAG(K).LE.NSEL)GO TO 1119
 1130 CONTINUE

c Generate statistics for selected families:

      IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))WRITE(6,958)

      JJ=1
      NSX=NSEL
 1149 IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))WRITE(6,959)NSX*NS
      RN=NSX*NS*NC
      DO 1150 I=1,5
      SS=VAL(I,JJ+1)-(VAL(I,JJ)*VAL(I,JJ)/RN)
      PBAR(I)=VAL(I,JJ)/RN
```

```
      PVAR(I)=SS/(RN-1)
      IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))
     +WRITE(6,925)EFFECT(I),PBAR(I),PVAR(I),VAL(I,JJ+2),VAL(I,JJ+3)
 1150 WRITE(4)PBAR(I),PVAR(I),VAL(I,JJ+2),VAL(I,JJ+3)

      NSX=NSX+NSX
      JJ=JJ+4
      IF(NSX.LE.2*NSEL)GO TO 1149

c Generate statistics for selected clones:

      IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))WRITE(6,961)

      JJ=9
      NSX=NSEL
 1159 IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))WRITE(6,962)NSX*NS
      RN=NSX*NS
      DO 1160 I=1,5
      SS=VAL(I,JJ+1)-(VAL(I,JJ)*VAL(I,JJ)/RN)
      PBAR(I)=VAL(I,JJ)/RN
      PVAR(I)=SS/(RN-1)
      IF(IPRN.EQ.2.OR.(IPRN.EQ.1.AND.ITERS.EQ.1))
     +WRITE(6,925)EFFECT(I),PBAR(I),PVAR(I),VAL(I,JJ+2),VAL(I,JJ+3)
 1160 WRITE(4)PBAR(I),PVAR(I),VAL(I,JJ+2),VAL(I,JJ+3)

      NSX=NSX+NSX
      JJ=JJ+4
      IF(NSX.LE.2*NSEL)GO TO 1159

c  *  Go to the progeny file and retrieve information for selected trees (clones)
c      for next generation's breeding population.

      IF(IGEN.EQ.NCYCLE)GO TO 301
      REWIND 3
      KX=0
      DO 130 K=1,NT
      DO 130 J=1,NC
       DO 130 I=1,NR
        READ(3)IFL,IML,APROG,DPROG,IPROG,EPROG,PPROG

c  * If this is a selected tree, transfer info, otherwise skip to next record

        IF(KCFLAG(K,J).EQ.0)GO TO 130


c  * If this is last record for this genotype, transfer to array

        IF(I.NE.NR)GO TO 130
        KX=KX+1
        VAL(1,KX) = APROG
        VAL(2,KX) = DPROG
        VAL(3,KX) = IPROG
        VAL(5,KX) = CLNMEAN(K,J)
        VAL(4,KX) = VAL(5,KX)-(APROG+DPROG+IPROG)
        FEMALE(KX)= IFL
        MALE(KX) = IML
 130  CONTINUE

c * Finished NCYCLE generation

      GO TO 300
 301  IF(IT.LT.ITERS)GO TO 401

c  * Produce summary of all interations

 600  CONTINUE

      IF(IPRN.NE.1)GO TO 1599
      OPEN(6,FILE='PRN')
      WRITE(6,901)
      WRITE(6,904) IISEED
      WRITE(6,966)ITERS,NCYCLE
```

```
      WRITE(6,909) (EFFECT(I),EFFBAR(I),EFFVAR(I),I=1,4),
     +EFFECT(5),SEFFBAR,SEFFVAR
      WRITE(6,910)EFFVAR(1)/SEFFVAR, (SEFFVAR-EFFVAR(4))/SEFFVAR
      WRITE(6,935)NS,NTS,NT
      WRITE(6,939)NP
      WRITE(6,943)NP,NX,NX*NT
      WRITE(6,983)
      IF(ISORT.EQ.0)WRITE(6,953)
      IF(ISORT.EQ.1)WRITE(6,954)
      IF(ISORT.EQ.2)WRITE(6,955)
      WRITE(6,956)NT, NC, NR,NT*NC*NR
      WRITE(6,985)NSF,NF
      IF(IH.EQ.0)WRITE(6,*)'       selected families MAY NOT have common
     + parent.'
      IF(IH.EQ.1)WRITE(6,*)'       selected families MAY have common par
     +ent.'
      WRITE(6,920)IYR,IMON,IDAY,IHR,IMIN

 1599 CALL GETDAT(IYR,IMON,IDAY)
      CALL GETTIM(IHR,IMIN,ISEC,I100TH)
      WRITE(*,986)IYR,IMON,IDAY,IHR,IMIN
      WRITE(6,986)IYR,IMON,IDAY,IHR,IMIN
      IF(ITERS.LE.1)GO TO 671
      RN=ITERS
      DO 670 I=1,NCYCLE
      REWIND 4
      WRITE(6,928) ITERS
      WRITE(6,921)I,NT
      DO 602 J=1,45
      DO 602 K=1,4
        XSUM(J,K)=0.
 602    XSUM2(J,K)=0.
      DO 641 II=1,ITERS
      DO 641 IK=1,NCYCLE
      DO 641 J=1,45
        READ(4)(X(KK),KK=1,4)
        IF(IK.NE.I)GO TO 641
        DO 640 KK=1,4
         XSUM(J,KK)= XSUM(J,KK)+X(KK)
 640     XSUM2(J,KK)=XSUM2(J,KK)+X(KK)*X(KK)
 641  CONTINUE

      DO 650 J=1,45
      DO 650 K=1,4
        XT=(XSUM2(J,K)-(XSUM(J,K)*XSUM(J,K)/RN))/(RN-1)
        XSUM2(J,K) = SQRT(XT)
 650    XSUM(J,K)  = XSUM(J,K)/RN

      DO 660 J=1,5
 660  WRITE(6,995) EFFECT(J),(XSUM(J,K),XSUM2(J,K),K=1,4)

      WRITE(6,923)
      NSX=NSEL
      JO=0
 661  WRITE(6,937) NSX*NS
      DO 662 J=1,5
      JJ=J+5+JO
 662  WRITE(6,995) EFFECT(J),(XSUM(JJ,K),XSUM2(JJ,K),K=1,4)
      NSX=NSX+NSX
      JO=JO+5
      IF(NSX.LE.2*NSEL)GO TO 661

      WRITE(6,933)
      NSX=NSEL
      JO=10
 665  WRITE(6,950)NSX*NS
      DO 666 J=1,5
      JJ=J+5+JO
 666  WRITE(6,995) EFFECT(J),(XSUM(JJ,K),XSUM2(JJ,K),K=1,4)
      NSX=NSX+NSX
      JO=JO+5
      IF(NSX.LE.2*NSEL)GO TO 665
```

```
      WRITE(6,958)
      NSX=NSEL
      JO=20
  668 WRITE(6,959)NSX*NS
      DO 669 J=1,5
      JJ=J+5+JO
  669 WRITE(6,995) EFFECT(J),(XSUM(JJ,K),XSUM2(JJ,K),K=1,4)
      NSX=NSX+NSX
      JO=JO+5
      IF(NSX.LE.2*NSEL)GO TO 668

      WRITE(6,961)
      NSX=NSEL
      JO=30
 1668 WRITE(6,962)NSX*NS
      DO 1669 J=1,5
      JJ=J+5+JO
 1669 WRITE(6,995) EFFECT(J),(XSUM(JJ,K),XSUM2(JJ,K),K=1,4)
      NSX=NSX+NSX
      JO=JO+5
      IF(NSX.LE.2*NSEL)GO TO 1668

 670  CONTINUE

c  * Terminate program

 671  WRITE(6,9002)
 9002 FORMAT(1H1)

      STOP
      END

      FUNCTION IRANDOM(ILO,IHI,ISEED)
c       Returns a random integer between ILO and IHI.
c       Based on the algorithm provided with MS-FORTRAN 4.3
        IRANDOM=ILO+(IHI-ILO+1)*RANDOM(ISEED)
        RETURN
        END

      FUNCTION RANNOR(ISEED)
c       Returns a normally distributed deviate with zero mean and unit variance,
c       using RANDOM(ISEED) as the source of uniform deviates.
c       Based on the GASDEV algorithm given by:  Press,W.H., Flannery,B.P.,
c       Teukolsky,S.A., and Vetterling,W.T.  1986.  Numerical recipes: the art
c       of computer programming.  Cambridge Univ. Press, Cambridge, UK.
      DATA ISET/0/
      IF (ISET.EQ.0) THEN
    1    V1=2.*RANDOM(ISEED)-1.
         V2=2.*RANDOM(ISEED)-1.
         R=V1**2+V2**2
         IF(R.GE.1.)GO TO 1
         FAC=SQRT(-2.*LOG(R)/R)
         GSET=V1*FAC
         RANNOR=V2*FAC
         ISET=1
      ELSE
         RANNOR=GSET
         ISET=0
      ENDIF
      RETURN
      END

       FUNCTION RANDOM(ISEED)
c       Returns a uniform random deviate between 0.0 and 1.0.  Set ISEED to
c       any negative value to initialize or reinitialize the sequence.
c       Based on the RAN2 algorithm given by:  Press,W.H., Flannery,B.P.,
c       Teukolsky,S.A., and Vetterling,W.T.  1986.  Numerical recipes: the art
c       of computer programming.  Cambridge Univ. Press, Cambridge, UK.
      PARAMETER (M=714025,IA=1366,IC=150889,RM=1./M)
      DIMENSION IR(97)
c Initialize on first call even if ISEED is not negative.
      DATA IFF /0/
```

```
      IF (ISEED.LT.0.OR.IFF.EQ.0)THEN
         IFF=1
         ISEED=MOD(IC-ISEED,M)
c  Initialize the shuffle table.
         DO 11 J=1,97
            ISEED=MOD(IA*ISEED+IC,M)
            IR(J)=ISEED
  11        CONTINUE
         ISEED=MOD(IA*ISEED+IC,M)
         IY=ISEED
      ENDIF
c  Here is where we start except on initialization
      J=1+(97*IY)/M
      IF(J.GT.97.OR.J.LT.1)PAUSE 'Random number generator not functionin
     +g correctly.  Press <ENTER>'
      IY=IR(J)
      RANDOM=IY*RM
      ISEED=MOD(IA*ISEED+IC,M)
      IR(J)=ISEED
      RETURN
      END
```