



June 19th, 1998

TO WHOM IT MAY CONCERN:

Re: Independent Evaluation of Somatic Embryogenesis for the Propagation of B.C. Conifers

The Forest Genetics Council of British Columbia (formerly the Tree Improvement Council of B.C.) has commissioned an independent evaluation (review) of the process of somatic embryogenesis for the propagation of genetically improved coniferous genotypes in British Columbia.

This is to introduce Dr. Don Lester and Dr. Bill Libby who will work as a team to accomplish the evaluation task under contract to the Forest Genetics Council. Part of their work will involve interviewing a cross section of persons in industry and government who work directly or indirectly in various aspects of reforestation and management of crown forest lands. Please give these gentlemen your cooperation so that they might proceed with the task at hand. If you have any questions, concerns or comments, please call me at (250) 260-4767 or Fax (250) 542-2230.

Sincerely,

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**External Evaluation of Somatic Embryogenesis
for Enhancing Genetic Gains from
British Columbia's Tree Breeding Programs**

A Report to the Forest Genetics Council of BC
by
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EXECUTIVE SUMMARY

Commercially valuable genetic variation has been identified in several forest tree species of British Columbia. To date, the “packaging” of that variation for delivery to forest plantations has been through wind-pollinated orchard seed or, in a few cases, rooted cuttings. A variety of additional methods exist and differ in expected genetic gain, feasibility of implementation, cost effectiveness, time to implementation, and required additional research and development to achieve a level of large-scale production.

Somatic embryogenesis (SE) is one of the alternative methods for delivery of genetic gain. It is an emerging technology that offers, potentially, large advantages in genetic gain, rapid access to superior gene combinations, long-term storage of specific genotypes, a higher degree of control of genetic diversity, and possibly lower cost of planting stock. We have considered the potential of SE for multiplication of seed that is difficult to produce in large quantities, for providing and preserving an array of clones for clonal forestry, and for providing a method for large-scale production of genotypes altered by transgenic manipulation. Much of our detailed discussion is focussed on clonal forestry. We suggest that the level of comprehension required for successful implementation of clonal forestry requires a long and serious commitment and is not work for amateurs.

In Section 1, we point out that the theoretical advantages of SE need to be considered in the context of BC forestry. Section 2 notes BC is in a very favorable position from a genetic perspective in that many genetically superior individuals are available for each of several commercial conifers.

Section 3 discusses why SE is attractive in theory and what are the elements of an operational system of embling production and deployment.

Section 4 offers our views on the current status of SE in British Columbia. We were impressed with the progress being made in producing large numbers of emblings. While noting some of the problems yet to be solved, we are optimistic that SE has the potential to produce planting stock in large quantities and to provide the basis for clonal forestry. Development of SE is most advanced for interior spruce. The main issues with interior spruce seem to be embling price and the frequency of recalcitrant genotypes. Development of SE for Sitka spruce is likewise well advanced. Progress with Douglas-fir has been less and with western white pine, much less.

Section 5 addresses the issue of cost effectiveness using a form of benefit/cost analysis. Benefits are discussed in terms of both direct and indirect effects, although the analytical model uses only volume at harvest added by tree improvement as the measure of benefit. Costs are additional costs added to the price of unimproved nursery seedlings as a consequence of costs required to achieve the expected genetic gain through SE. We accept the possibility that SE will eventually produce planting stock for which no added cost is required. At that point, cost effectiveness as analysed here would be moot.

Five cases are presented: interior spruce, Sitka spruce, coastal and interior western white pine and coastal Douglas-fir. Graphs illustrate major differences among species, largely due to different growth rates and rotation ages. In some cases, substantial increases in cost of planting stock are offset by achievable genetic gains. In other cases, only small increases in the cost of planting stock would allow a financially attractive outcome.

Section 6 identifies various issues that we encountered. These include aspects of administration, finance, perceptions of the general public and of forestry professionals, and biology.

Fourteen recommendations are given, with comments, in Section 7. Two recommendations relate to delivery of genetic gain in general, five are focused on SE, and seven concern clonal forestry. Recommended actions include additional analytical work, Council facilitation of the development of an operational SE system(s) and development of activities to educate the forestry community and public about clonal forestry.

PREFACE

Fifteen years ago, somatic embryogenesis appeared on the horizon as a promising technology that might become available sometime in the next millenium (Libby 1985). Today, it has progressed very far through research and development, and seems almost here as a delivery system for genetically improved trees in operational forestry. Much of this progress has been made in British Columbia, with two BC firms occupying the cutting edge. As this new technology began to surface, there was some concern that programs were racing ahead without sufficient planning and review. We therefore were asked to provide such a review.

To evaluate the potential of somatic embryogenesis (SE) as a way to deliver genetic gains in BC forest trees requires more than a consideration of the present and likely future success of SE as a propagation method. Assuming that there will be additional costs, at least for several years, one must ask whether the BC forest economy can extract sufficient benefits to make the method financially attractive. For each of these topics, we must proceed with a mixture of fact, experience, and opinion (and probable bias).

It should be noted that some claims about the current status of the SE process and about future prospects were not possible for us to validate. The recent history of SE in BC has been marred by overzealous claims and poor quality control, not unusual in the more competitive fields of biotechnology. Some of the problems thus created seem to have been solved and the market, combined with regulation of reforestation on public lands, probably will force the solution of other current problems if the method is to become commercially viable here. Likewise, market response to the potential for improvement in a wide range of traits will determine whether cost or genetic value is the primary market force.

To achieve our evaluation, we have interviewed, together or singly, about two dozen people. Included were producers developing and using SE for planting stock production, planners who approve the choice of planting stock, scientists directly or indirectly involved with SE, and local foresters who have chosen to plant trees produced from SE. We have had too little opportunity to talk with potentially interested parties outside of those most involved with SE, i.e. the general public and the environmental community.

You will find in reading our report that we have not answered all the questions posed, and perhaps have raised some new ones deserving further attention. Nevertheless, we were pleasantly surprised and even excited by how far somatic embryogenesis has come, and think that there may be some valuable uses awaiting it in BC.

ACKNOWLEDGEMENTS

Participants in various aspects of this evaluation are listed below. We appreciate the contributions of each one. Particular thanks go to Chris Hawkins who provided a very useful weekend day of test site visits. Jordan Tanz, Executive Director, Forest Genetics Council, provided substantial assistance in mailing letters of introduction and in supplying addresses of potential contacts.

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1 INTRODUCTION

For centuries cloning, as a way to quickly access and maintain desirable combinations of genes, has been a standard practice in horticulture and for a few forest tree species. Features of biology (maturation) and of cost have limited the usefulness of cloning for most forest trees. Somatic embryogenesis (SE) has the potential to overcome biological limitations by approximating the developmental pathway of zygotic embryos, and by providing embryonic tissue that can be stored for long periods and then recovered in an embryonic and embryogenic state. In addition, regeneration of large numbers of plants from stored cultures may result in lower costs for planting stock.

Somatic embryogenesis, for forest trees, is an emerging technology. For several species, SE has moved from the biological phase of "Can it be done?" to the phase of refinement for trial on an operational scale. The time needed to achieve an operational scale will vary with the species and with whether SE is used only to multiply random embryos from families of established genetic performance, or to multiply clones for clonal forestry.

Several large issues cloud the theoretical appeal of SE for delivering genetic improvement in BC. Most often cited is cost effectiveness. The present cost of planting stock from SE (emblings) is a major concern, although we expect that costs soon could be markedly reduced. Users generally agree that they would use emblings if emblings were available at a cost-effective price. "Cost-effective price" includes not only the price of planting stock, but also possible near-term reductions in silviculture costs, and increases in the harvest value of wood produced by that stock. The issues of future cost reductions and various mid-term and long-term increases in values, however, are major uncertainties. Forests of BC, relative to regions currently practicing highly intensive forestry, have moderate growth rates at best and are managed at a relatively low intensity for products that are currently relatively low in value. The ability to reliably reproduce specific combinations of many traits will be attractive only if the value of those traits is likely to be recognized by distant-future markets. Because of the current low intensities of management of many British Columbia forests, there is not much room to reduce silviculture costs (although increases in such costs might be avoided by using better planting stock).

A related question is the form in which wood will be used in the foreseeable future. Some foresters interviewed noted that the trend in many wood products is toward manufactured wood. Traditionally, wood technologists have devised ways to utilize available wood resources no matter how malformed or how poor its technical qualities. Whether this is preferable to selecting and deploying families or clones with better stem-form and wood properties, thus modifying the raw material resource, is beyond our analysis but not irrelevant to the question of cost effectiveness of SE for British Columbia.

In this report, we will present some theory and rationales for using vegetative propagation, and some of the particular advantages and concerns that somatic embryogenic techniques bring to this option. Not surprisingly, it appears that: (a) deployment of emblings will soon be warranted with some species in some BC situations; (b) use of SE is unlikely to soon (or ever) be justified in other BC situations; and (c) for a large number of BC situations, the decision to proceed with SE will not depend so much on biological and financial analyses as on the forest policies then in place, and perhaps on some long-term economic decisions responding to a greater range of values than those of producing more or less wood at some time in the distant future.

2 CURRENT STATUS OF TREE IMPROVEMENT IN BRITISH COLUMBIA

2.1 Identification of genetic value

Over the last forty years, tree improvement has progressed from the demonstration of genetic differences among clones and the phenotypic selection of parents in wild stands to estimation of genetic value from formal progeny testing and the incorporation of multi-trait selection methods. For each of eight coniferous species, there are from hundreds to thousands of selected parents under test. Some test plantations exceed 20 years in age.

Progeny tests have shown abundant genetic variation in a variety of traits for all eight species. This variation has prompted the application of various methods for “packaging” genetic improvement to be delivered in forest plantations. Most commonly, seed produced in wind-pollinated orchards has been the method chosen for packaging. For a few species, rooted cuttings are preferred.

2.2 Delivery of genetic gain

Currently, there is in place the ability to produce improved planting stock to meet about 38% of projected needs. This stock will have an estimated potential genetic gain in volume averaging 8% (Lester 1998). With implementation of plans for the next decade, production is estimated to rise to 55% of needs with an average gain of 13%. The stated goals of the Forest Genetics Council are improved planting stock for 75% of needs with an average genetic gain of 12% in volume (Tree Improvement Council 1998). Nearly all of this improved planting stock is to be delivered in the form of seedlings.

Within the last decade, several developments have prompted interest in other methods for delivery of genetic gain. These developments include the recognition of immediate harvest incentives for use of improved planting stock in forest management planning, recognition of genetic variation in tolerance to major pests, and advances in methods for vegetative propagation. In addition, increased genetic gain and reduced time to deliver genetically improved planting stock are attractive features of vegetative propagation.

3 DELIVERY OF GENETIC GAINS THROUGH SOMATIC EMBRYOGENESIS

3.1 Theory

Somatic embryogenesis (SE) is an advanced technique first reported in mid-century with carrots, and recently greatly advanced using a broader range of economically important and model species. Its importance is not so much in creating useful genetic variation as in enabling such variation to be found, or incorporated, or kept, or rapidly and massively duplicated.

Zygotic embryos are created when, surrounded by the organism’s nutritive tissue, an egg nucleus unites with a sperm or pollen nucleus. The egg and pollen nuclei have undergone meiosis, each thereby sampling half the genes of the female and male. Zygotic embryos thus combine different gene samples of the parents and, typically, no two are alike. The rest of the organism’s cells, called somatic cells, do not undergo meiosis. Their divisions are mitotic, which

simply duplicate the genetic material of the cell. Except for occasional mutations, the somatic cells in an organism all carry the same genetic information.

The techniques of successful SE deflect somatic cells from their normal path of development. Instead of becoming some part of the original developing plant (or, in the case of suspensor cells, being left behind entirely), they can be made to develop into new embryos and ultimately into entire new plants. Such embryogenic cells or tissues can be stored for uncertain but probably very long periods of time. Or, such embryogenic cells can be made to repeatedly grow and divide, producing tens, hundreds, thousands or millions of essentially identical embryogenic clumps of tissue. Or, such embryogenic cells can be the recipients of specific genes from other organisms through the techniques of genetic engineering. Or, given certain cues under the control of the biotechnologist, the development of pulsed clumps of embryogenic tissue can be channeled to produce embryos.

SE enables useful genetic variation to be found by providing relatively small numbers of essentially identical genotypes for selection experiments (see testing, 3.2.3b, below).

Cryogenic storage of some of the embryogenic tissue of each clone under test allows these genotypes to be kept, hopefully in a fully-juvenile embryonic maturation state, until they can be confidently used. For proven clones in large-scale production, such storage also allows the line to be renewed periodically, and provides a reserve for recovering the line in the case of a production disaster (such as occurred at the Te Teko tissue-culture lab (New Zealand) in the Edgecumbe earthquake).

Once good clones are identified, they can then be recovered from cryostorage and propagated. Whether this will be done using SE to produce millions of embling copies per clone, or whether the route will be from cryostorage of selected clones through modest numbers of somatic embryos to modest numbers of hedged emblings to massive numbers of cuttings to deployment as stecklings, will depend on the relative cost-effectiveness of these two routes (see 6.2 below).

Our present state of knowledge indicates that embryogenic tissue is a uniquely attractive option for inserting a few chosen genes into a recipient clone or species. Once incorporated, a miniclone line will have been created that differs from the original macroclone with respect to only a very few genes and those specific traits they influence. The successful recipient cells can be triggered to produce embryos and then trees, where the performance of the transgenic miniclone can be evaluated. If favorable, the miniclone can be massively propagated using SE or other clonal techniques, or some of these trees can be used as parents to transmit the new genetic variation by sexual means. In these options, useful new genetic variation can be created, and SE will contribute to such events.

Mutational genetic variation will occur in culture in some or all of the clones being propagated by SE. Mutation is normal in any sexual or clonal line, and most mutations are deleterious. Occasionally favorable mutations occur and are discovered, another way of adding useful genetic variation. It is possible, even likely, that mutational variation will occur at unusually high rates during multiplication of the embryogenic tissue in culture. If so, SE lines will need to be “cleaned up” even more often than clonal lines or full-sib families produced by cuttings or seed; of course, more favorable mutations may show up in embling lines as well.

It is possible, even likely, that the embling propagule-type will be “different” from the seedling, steckling or plantling propagule-types. Such differences may be due to maturation state, or simply because emblings have taken a different developmental pathway than have seedlings, stecklings and plantlings. Such differences are not necessarily bad, but they need to be understood before the embling propagule-type can be used with confidence (see 3.2.3 and 4.5, below).

Finally, we were informed that only about 25% of the interior spruce embryos entered

into SE protocols produce embryogenic tissue. This low success percentage may have genetic implications and it clearly has financial implications. Costs per embryogenic line would clearly be less if (say) 75% of the attempts were successful. The genetic implications are less clear. If successful embryogenesis is unrelated to other genetic attributes (i.e., random), then there are no genetic consequences of a low success rate. It simply takes more work and costs more to get the same quality of genetic material with 25% SE success compared to if 100% of viable embryos successfully produced embryogenic tissue. We know of no theoretical reasons to expect that embryogenic success will prove to be related to other elements of performance within the population being propagated or, if so, whether the better-performing or poorer-performing members of that population would be selected in the SE process. Data on this point will be hard to get, as the genotypes that die during the SE attempt can't then be grown and compared to those that successfully produce emblings. If the embling propagule-type is intrinsically (i.e. developmentally) identical to the seedling propagule-type in field performance (see 3.2.3a below), then seedling and embling samples from sets of the same full-sib families could be compared. However, at present, it seems likely that such comparisons will be confounded with intrinsic propagule-type differences. (Note also that, if there is genetic selection for subsequent field performance in the SE process, this will confound the propagule-type tests described in 3.2.3a.) To begin to resolve this question, it will be necessary to await the propagule-type test results. If the embling and seedlings field performances are similar, genetic selection and intrinsic developmental differences may be canceling each other, but the practical conclusion will be to accept emblings as similar to seedlings. If emblings differ substantially from seedlings, then the better of the two will be preferred, and it will be up to scientists to try to sort out the causes of the differences.

3.2. Elements of an Operational System

In order to bring a new technology into production, one needs not only knowledge about the new technology, but the situation and timing need to be right for it to fit into ongoing operations. Many of these elements need to occur in sequence, and some can not begin until others have been essentially completed. The following sections explore five of a longer list of such elements.

3.2.1. *Basic research through R&D.*

The basic research that leads to technological breakthrough is often curiosity-driven rather than problem-driven. As such, it often occurs in universities or government labs, and the knowledge produced has typically been in the public domain. As people begin to think about how to use such new curiosity-driven findings, the research and development (R&D) leading to useful applications often moves to the private sector, and the findings may be closely-held secrets or intellectual property that is sold or licensed rather than freely made available. The development of SE technology and of genetically improved tree material both follow this general trajectory (see 6.1, below)

3.2.2. *Client Infrastructure.*

Before either tree-improvement or clonal forestry can hope to succeed, potential users of these technologies have to either have, or have access to, operational knowledge and procedures that underpin their application. For the species of interest, provenance testing must be sufficiently advanced so that groups of families or clones are not deployed to inappropriate sites.

The transportation network must be sufficient, and sufficiently maintained, so that an appropriate network of tests can be installed and repeatedly monitored. Sites must be evaluated and mapped, so that appropriate species or species mixes are deployed to them. Plantation technology (site preparation and aftercare) must be sufficiently advanced so that tests are successfully established and provide meaningful results. Nursery practice for the propagule-type being considered must have completed sufficient R&D so that the planting stock survives and grows well. Finally, the professionals responsible for evaluating and implementing the use of improved sexual or clonal planting stock must be well enough informed to do so effectively.

3.2.3. *Testing*

With respect to the deployment of emblings in production forests, (a) one kind of testing is essential, and (b) the second is needed if full clonal forestry is contemplated.

3.2.3a. *Testing the Embling Propagule-type.*

Using clones in production forestry has long been an attractive idea (Larsen 1956; Ahuja & Libby 1993a, b). The early enthusiasts for each kind of clonal propagule generally focused on the advantages offered, only to be thwarted by unanticipated problems. Advocates of grafting were soon discouraged by the problem of stock-scion incompatibilities. Rooting enthusiasts soon encountered the problems of early plagiotropic growth of stecklings and maturation of the clones. Tissue-culture enthusiasts soon found that tissue origin and culture conditions greatly affected the quality of plantlings. And now emblings are becoming available.

Recognizing that differences among propagule-types can be expected to be both favorable and unfavorable, we suggest that the differences might be characterized and evaluated as follows:

- (i) The differences are such as to disqualify the embling propagule-type under test (advances in SE protocols improving embling quality would require a new set of tests).
- (ii) The differences are such as to make the embling propagule-type acceptable but less desirable than the seedling and/or steckling propagule-type.
- (iii) The differences are either small or balanced, such as to clearly favor neither the emblings, nor the better of the steckling and seedling propagule-types.
- (iv) The differences on balance moderately favor the embling propagule-type among similar genotypes (i.e., within full-sib families).
- (v) The differences strongly favor the embling propagule-type among similar genotypes (i.e., within full-sib families).

It seems reasonable for the near future that, for deployment approval to be given, the embling propagule-type should first have been evaluated for at least 5 years in the field, and for longer if the results are inconclusive after 5 years.

With outcomes (iii, iv or v), approval for full deployment could then be given, with the caveat that significant changes in embling production protocol will require additional testing of emblings produced under the changed protocol. As additional species become available as emblings, if the outcomes of such tests with similar species have consistently been (iii, iv or v), testing requirements for the embling propagule-type could be relaxed or even waived.

One may wonder how outcomes (iv or v) might occur. The sort of favorable differences that might lead to (iv or v) evaluations are well illustrated by the steckling propagule-type in radiata pine. When stecklings at maturation state about 4-to-6 years are deployed, their bole form is better, their branches are smaller, and they are less likely to topple, compared to seedlings from the same families. This allows fewer to be planted per hectare, and saves on planting, thinning and pruning costs (Gleed 1993). The Te Teko clonal forestry operation was

justified to management by showing that these combined savings reduced costs of silviculture for the company about NZ\$4,000,000 per year in the first 8 years after planting. Such early-adolescent stecklings cost more to produce than do more-juvenile stecklings. At least some clients are willing to pay such producers as the FRI nursery in Rotorua a substantial premium for the early-adolescent stecklings.

If the propagule-test outcome is (ii), a client wishing to deploy the embling propagule type in normal production plantations would be required to apply for conditional registration for use of that embling propagule-type, the application stating and accepting the relative advantages and disadvantages as evaluated in the test(s).

If the propagule-test outcome is (i), registration of the embling propagule-type in the test would be denied.

We advise that propagule-type testing not be officially initiated until the quality of the emblings for that species is sufficient to not require aborting the test. We so advise in order to avoid major commitments to premature testing, but support small unofficial trials while the producers are developing embling quality.

Where SE is used for vegetative multiplication of known good families, the price (cost) of plantable emblings will probably need to be substantially less than the price (cost) of seedlings of those same good families for (ii) to be attractive; slightly less than for seedlings to justify emblings if (iii); but could be a little to a lot more for (iv) and (v), respectively.

3.2.3b. Testing for genetic value

For vegetative multiplication of known good families, no further genetic testing is required.

By “full clonal forestry” is meant the deployment of well-tested well-understood clones. Testing of these clones has two purposes: identifying outstanding clones; and characterizing them so that they can be effectively deployed, managed and utilized. A thoughtful and extensive analysis of clonal forestry and vegetatively-multiplied family forestry for British Columbia was recently completed (Dobbs 1997).

Recent and current tree-breeding generally focuses on a relatively few traits, such as height growth, stem form and sometimes resistance to a specific pest (Lester 1993). “Gains” are recorded as changes for the better in these traits, and usually their impact on volume per tree or (more problematic) volume per hectare (Libby 1987b) is estimated. Progeny tests provide the basis for family selection (backward) and within-family selection (forward) to fine-tune the selection of future parents for seed orchards and for breeding, often by weighting values for the selected traits in some sort of index. They also allow the characterization of families thus produced.

Clonal testing and selection are quite different from the testing and selection commonly done during tree breeding. For example, in the testing, selection and clonal characterization program at Te Teko, we recently identified and characterized (among others) two very promising clones. Somewhat to our surprise, they are full-sibs. They belong to a family known (by the Radiata Pine Breeding Coop) to have outstanding individual-tree growth, good bole-form, and generally above-average wood quality. Because of sexual recombination, in theory about half of the additive genetic variation in the selected traits and almost all of the non-additive genetic variation in those traits should be varying among sibs within such full-sib families. These two sibs are both well above their family averages in both early growth and bole form, and thus additional gains in these index traits were indeed captured by their clonal testing and selection (evaluation of their wood-quality traits will occur soon, when they are somewhat older). One has a classic “growth and form” ideotype, with evenly-spaced moderate-angled branch whorls and a ruler-straight bole. The other gives promise of having that rare and valued long-internode

binodal ideotype, with an almost-straight bole. This binodal trait was not part of the breeding cooperative's selection index, nor were other observations on these clones' propagabilities, frequencies of forks and ramicorn branches, a list of disease, insect, and environmental-damage susceptibilities, and other traits that were observed and considered by the foresters who first identified and then evaluated and characterized these two outstanding clones. It is likely these cloned sibs will serve very different market niches, and they will probably be deployed to rather different sets of plantation sites. They are unlikely, except in further tests and demonstrations, to ever be grown together. Had vegetative multiplication of this excellent family been used instead of full clonal forestry, these two clones would have just been a bit of noise adding to the within-family genetic variability, and it is unlikely they could have been effectively managed to take advantage of their exceptional specific qualities. It is very difficult to predict the financial benefits of opportunistically captured traits that are not part of the breed index (Dobbs 1997), but in many cases they are substantial.

Clonal testing strategies were extensively discussed and generally agreed-upon in a 1986 IUFRO workshop (Libby 1987a), and the hierarchical scheme developed seems valid today for use in a steady-state mature clonal program. This is essentially a numbers game. To find spectacularly outstanding clones, the first step in testing a new pulse of candidate families would screen very large numbers of clones, and would include only a very few ramets of each (Russell & Libby 1986). In the first round of selection, the "best few" clones would be neither confidently selected nor characterized. But one could be reasonably assured that some spectacular clones would be forwarded to the next step of the testing hierarchy, where such confident selection and characterization would occur.

However, British Columbia is in the very early stages of considering and perhaps adopting full clonal forestry for species until now either sexually propagated, or that have at most had good families "bulked up" using vegetative multiplication. We suggest a different early goal and thus modification of the IUFRO testing strategy early in each species' program.

When one is assembling the first set of clones to be deployed in full clonal forestry, the goal of NOT massively deploying an embarrassing below-average clone probably outweighs the goal of deploying spectacularly outstanding clones. The first pulse of clonal tests for interior spruce includes only 1400 clones (called "lines", a term that unfortunately can be confused with sexually-propagated inbred lines). These were initially selected from promising available families based on successful SE propagability. Each clone has been deployed as 12-to-24 ramets, distributed on 2 or 3 sites for second-round testing. That is too many ramets for efficient second-round field-testing in the IUFRO scheme. But it is pretty good for selection and characterization of a set of 50 or so clones that are all likely to be reasonably above average in single-tree height growth, with a high degree of various kinds of weevil resistance. Furthermore, and perhaps more important, these clones can be well characterized as to other attributes of their ideotypes as these become apparent.

Then, in a few years, if clients find full clonal forestry attractive, additional pulses of candidate families can be clonally tested in accordance with the IUFRO scheme. The original 50 or so clones can be slowly replaced with new clones. This will occur as those new clones are confidently found to be sufficiently superior to the poorer-performing clones in the then-current deployment set. If the promise of SE with respect to cryogenic storage holds up, the best few of that "first 50" may be continued in production deployment as increasingly well-known clones for centuries or even millennia.

3.2.4. Development of Deployment Sets

A sports analogy is perhaps useful in discussing the development and continuation of the

deployment set in clonal forestry. Usually, when a new sport is invented, the first people who play it seriously aren't very good by later standards of performance. But they are the best then available. As younger players with better training and longer experience come up, the original "first team" is soon largely replaced by them. Later, as the sport becomes well established, there is still a turnover in the first team. This is partly because the players age, a problem we hope SE will solve for trees by keeping excellent clones in a juvenile maturation state through cryostorage. It is also because the opposition learns the weaknesses of the veteran players (analogous to insects or diseases adapting to a previously resistant clone). But even so, most sports managers will play a veteran whose skills are known and reliable, rather than a potentially better but not fully understood rookie. This means a new clone must be substantially better than the clone it replaces, because of the value well-known clones will have to management.

Important questions to be addressed when developing the set of clones to be deployed are: How many clones per "region"? How many kinds of clones? To which sites should each clone be deployed?

3.2.4a. How Many Clones Per Region?

Economies of scale during production, the genetic gains achieved by using only the very best clones, and management comprehension of the attributes of each clone, all argue for small numbers. Although diversity considerations would seem to argue for large numbers, a consistent and convincing case can be made that diversity concerns are well served by "effective numbers" in the 7-to-20 range (Libby 1982, 1991, 1998 and references therein). If vegetative multiplication is used, the diversity calculations must be done on the number of the families; the kinds of families, i.e., selfed, full-sib, half-sib or open-pollinated; the relatedness of the families to each other; and the approximate clonal composition of the deployed set from each family. Although as few as 7 unrelated clones can be justified in a region, many professionals are settling for "first team" numbers nearer to 50, with perhaps 10-to-20 of them being deployed in any given year. These numbers correspond well with guidelines already developed for BC (Anon. 1997).

3.2.4b. How Many Kinds of Clones?

Managers will probably want a variety of clones of any given species. Some clones may be able to better handle specific kinds of sites within the region (frost pockets, high weevil-risk areas, particular soils). Others may be chosen because they exhibit different solutions to the same problem (for example, different mechanisms of weevil resistance). Others may serve different markets, or be deployed to guard against the risk of market changes (perhaps some with high-density wood and others with low-density wood). As the number of kinds of clones one desires in a region's deployment set goes up, so does the number one maintains on the region's "first team".

3.2.4c. To Which Sites Should Each Clone Be Deployed?

In many cases, the answer to this question is pretty obvious. For example, one of a region's first-team clones may only have marginally above-average growth and form, but it exhibits excellent weevil resistance. That clone should only be deployed to sites in its region with high weevil-risk.

Seed-transfer rules provide first-approximation guidelines for how far from its origin a clone can be deployed. But testing and experience will soon show that some clones can be deployed over a much wider range of sites, while others are much more restricted. This comes under the general topic of genotype-by-environment interaction (GxE). Abundant experience shows that, while research often reports a GxE value for a species or population, specific

interactions vary enormously among families and among clones within families.

It is sometimes thought that clones are highly interactive but seedlings are not. This seems to be nonsense. Clones can be shown to be highly interactive (or not), while seedlings can be planted and grown in only one place (where some seedlings with strong GxE by chance end in places where they are highly adapted, and others by chance end in places where they are poorly adapted). Bruce Zobel maintains that about half the second-generation gain in the Aracruz eucalypt clonal program was obtained by identifying and eliminating the clones that exhibited strong GxE interactions, while sexual propagation of course continues to segregate interactive seedlings, and those planted by chance on their downside-interactive sites hold down overall seedling performance.

Two decades ago, a common strategy was to attempt to know enough about highly-interactive “prima donna” clones to deploy them to the sites where their performance was excellent, and keep them off sites where their performance collapsed. However, as concerns about climate change gained credence, it became plausible that environments would change enough within the rotation period of a plantation to make planting climate-sensitive interactive clones a poor option.

The characterization of a clone’s GxE sensitivity is generally done at the third (productivity testing) level of the IUFRO testing scheme. However, see 3.2.5 below.

3.2.5. *Management Feedback.*

It is crucial that client management be involved in the testing and subsequent deployment of clones. The majority of this, once the first-team clones have been chosen, will probably be informal, given that a MOMS (Mosaics Of Monoclonal Stands) rather than a WIMPs (Widespread Intimately Mixed Plantations) deployment is used. Regional technical and professional staff will quickly become familiar with the performances of the deployed clones in the MOMS configuration. If a WIMPs configuration is used, then some areas will have to be designated as test areas, with many ramets of each of the clones individually labeled and monitored within the mixtures. In either case, management personnel will soon have a basis both for ordering clones and for deploying those clones that are working well for them. Their feedback to the producers, which might take the form of meetings or questionnaires but is effectively done through the reorder (or not) process, will guide the producers in fine-tuning their offered “first team” for each region.

(Please note that mixed-species plantations, often desired or mandated in British Columbia, might use only one clone for one or more of the species in the mixture in a particular plantation compartment. This not only can match compatible clones of the different species, but it retains many of the MOMS advantages within each of the species present as only one clone per compartment.)

3.3 *Experience Elsewhere*

Some fruit tree species have been clonally propagated for well over a millennium. A forest conifer, Chinese fir, has been clonally propagated for over 800 years in Hubei and nearby provinces of China. Full clonal forestry seems to have begun in Japan with *Cryptomeria* about 5 centuries ago (Ohba 1993). In the past three centuries, many species of both forest and urban trees have been clonally propagated as either the exclusive or an important means of their reproduction and deployment (Ahuja and Libby 1993b). We thus have abundant examples to draw upon and learn from.

Our experience with SE is a much different story. Although the technique is about 50

years old, and much effort has gone into its development in the past 25 years, thus far no species is extensively propagated by means of somatic embryos (Grossnickle, Cyr & Polonenko 1996). It appears that interior spruce, in British Columbia, may be the most advanced species on Earth in this regard. Thus, many people will learn from this British Columbia program, but it has little experience elsewhere to draw on. For this reason, the first steps in certifying the embling propagule-type for widespread deployment should be both cautious and careful.

4 CURRENT STATUS OF SOMATIC EMBRYOGENESIS IN BC

4.1 Access to Improved Families and Specific Genotypes

The individual plants chosen for clonal propagation can vary across a wide range of genetic knowledge and value, from completely random within the species, through random plants of known and appropriate provenance, through random members of open-pollinated families available from the wild or in seed-orchards, through random members of families produced as prescribed crosses of progeny-tested parents with desired combinations of breeding values, through early-tested promising clones drawn from any of the preceding sources, to thoroughly-tested well-characterized clones that are among the very best then known and available (see 3.2.3b and 3.2.4, above, this report). The further one proceeds through these options, the longer it takes, the more it costs, and the higher the values captured by cloning.

Compared to many other regions and programs, British Columbia is in a favorable position with respect to the R&D already accomplished in developing genetic knowledge about many forest-tree species of interest. For some species, this process is well advanced, for others less so (see Lester 1993 and section 5.3 in this report). As in many other parts of Earth, the history of organizing and funding this R&D in British Columbia was driven by resource stewardship and long-term economics, with a goal of increasing the health and value of future British Columbia forests. The funding predominantly has been public.

As elsewhere, the British Columbia fiscal environment has been changing to one of shorter-term accountability. Some of the issues raised by this and other policy changes will be addressed briefly in this section and the following 4.2 section, and more broadly in sections 5 and 6. While we were not commissioned to comment on forest policy in British Columbia, we can't escape some of its important implications.

Among of the most important and troubling of the issues we encountered are *access* to currently available improved families and genotypes, and the *continued production and deployment* of new and better families and genotypes.

Since the mid-1950s, the Research Branch of the BC Ministry of Forestry has been the major player in developing both technical knowledge and genetically improved biological material, with substantial contributions from Forestry Canada, universities and several private companies, functioning independently and/or cooperatively. It is our opinion that leadership by the MOF and cooperation with and among other organizations is the appropriate way to achieve continued identification of better families and genotypes. Those families and genotypes are the future of British Columbia's planted forests (particularly those on better sites) that are to be managed for timber as well as for other values.

To be clear, we think it neither necessary nor wise for organizations providing delivery mechanisms, such as SE, to be required to take primary responsibility for developing and later fine-tuning the genetic material to be delivered. While public organizations are less stable and

less committed than they once were, instability in BC industry has been in evidence for at least the last 15 years and does not seem to be decreasing. Despite criticism (some justified) of the MOF program, MOF should be encouraged to maintain its role in breeding, selection, and testing.

Surely when the forest-genetic experiments, seed orchards, progeny tests and trials, and analyses of data therefrom were established and executed during the 1950s-1980s, the intent was to broadly benefit the forests and the long-term economy of British Columbia. Genetic knowledge and materials thus produced were freely available to whatever organizations could effectively deliver them to the forests. But the concept of intellectual property arrived and was embraced. Under this concept, those who develop knowledge of genotype or technique should be able to financially benefit from it and even control it. The increasingly important concept of fiscal accountability can lead to the requirement that techniques and genotypes developed with public funds should return dollars to the public organization that created them, and they surely should not be freely given away for private profit. As the planting-stock business is privatized, producers or clients could develop proprietary advantages through exclusive access to genetic resources that were identified wholly or in part with public funding. There are other issues of fairness, for example that organizations contributing technical or genotypic value may not be appropriately acknowledged.

These are difficult issues. We have probably not raised all of them, and surely can't presume to resolve them. We do offer some suggestions.

We suggest that the BC genetic-worth rating system continue to be developed. It could be used as a basis for valuing genetic material accessed for testing and deployment, and particularly as a basis for licensing, royalty payments and/or similar methods of sharing returns among those who selected, propagated, tested and characterized valuable families and clones.

We further suggest that various options of partnerships, licensing, royalties and/or contract pay-for-services might be appropriate to facilitate the movement of better trees from research to the forest. In-kind contributions from industry and government forests (i.e., clients) during the later testing and characterization of deployed clones should also be appropriately encouraged and recognized.

4.2. Mass Production of Emblings

The ability to reliably and cost-effectively mass-produce emblings may arrive before either British Columbia regulations or an appropriately cautious approach to their deployment by clients will allow it to be fully implemented. Both of the major SE producers in British Columbia have demonstrated to us some remarkable advances in the mass-production of emblings. There are, however, some components of the process that need further scrutiny before we can unreservedly recommend that embling mass-production proceed.

It is easy to recommend patience, and a phased scaling-up as the technology is fine-tuned and confidence in it is developed. The realities of cash flow suggest that, until commercial levels of emblings can be responsibly deployed, each SE-producing organization needs to secure some sort of bridging funding. This can be accomplished with the organization's internal funds, or perhaps with sponsorship or partnership involving other players. In the foreseeable future, this awkward phase of bridging financing will probably characterize the arrival of SE for each new species or genus, as the 5+ years needed to first develop quality embling planting stock and then to test embling performance is endured. If full clonal forestry is chosen, this financially awkward bridging period will stretch to over 10 years in each region, while candidate clones undergo field testing.

Cost and price are important issues for clients and producers alike. Cost is influenced by

economies of scale, and by propagability of the clones being produced. If all clones have similar propagability, then the numbers of clones to be deployed in each region (set by some combination of regulation and client demand) will influence economies of scale. We were assured that the percentages of ramets in clones successfully propagated by SE that will develop as quality emblings are now similar to percentages of seeds that can be germinated and successfully grown to BC MOF specifications in a nursery as seedlings (over 80% for interior spruce, currently less for other species). However, we do not have a good sense of the relative propagability of clones successful in SE. For example, if it turns out during clonal testing that the best clone in a family propagates only half as well as the third-best (the same effort to produce 1,000,000 emblings of the third-best produces only 500,000 emblings of the best), the consequent relative costs of producing them may decide for the third-best, with some possible gain in genetic quality of the plantations foregone. Experience will give us better data on this latter issue.

4.3. Cryogenic Storage

For full clonal forestry, cryogenic storage is the most important feature that is offered by SE, given that maturation state is maintained during storage and various abnormalities don't develop in high frequencies. Embryogenic tissues of spruce and other conifers have been successfully cryostored since about 1986 (most more recently), then recovered and induced to form normal plants. So far, the signs are good. But 12 years is too short a storage period to be useful for full clonal forestry, and those recovered apparently-normal plants still need to be watched to see if they develop any unpleasant surprises. Thus, we need to wait and hope that the early results hold up. We can think of no shortcuts.

If high-fidelity cryogenic storage of genotypes with maintenance of maturation state proves to be a reality, this could provide a valuable niche for SE even if cost-effective mass-propagation favors stecklings or plantlings over emblings. If that occurs, then the SE-production facilities would become service providers to the segments of their (or other) organizations that mass-produce field-ready plantlings or stecklings. The cryostored embryogenic tissue would be periodically accessed to produce pulses of (presumably) juvenile material that would then be rapidly multiplied by tissue-culture, or that would become serially-propagated or hedged cutting donors.

4.4. Production of Planting Stock

Inadequate planting-stock quality was a problem early in the development of interior spruce emblings, and it will probably be a similar early problem as each species' production by SE is developed. We think the producers are now fully aware of the negative impact of marketing planting-stock of poor quality and will solve quality problems before promoting emblings for operational deployment.

British Columbia's two major producers of emblings are PRT/PBI and BCRI/Silvagen. PBI, by virtue of PRT being a very large producer of tree planting-stock, has quality control of planting-stock exercised by PRT's experienced nursery personnel. BCRI's origins and organization are different. Their group of scientists is learning the lessons of planting-stock quality using laboratory analyses, observations and field trials.

BCRI research on embling physiology is an excellent approach to understanding what makes a high-quality field-ready embling, and to learning how to better mass-produce such emblings. The clonal stock-quality characterizations beginning to be supplied to clients and others by Silvagen is a step in the right direction. These will provide clients with information that can be field-verified during the establishment phase of nursery pulses of each clone.

However, some see these clonal stock-quality profiles more as a marketing tool than as reliable science at the current stage of knowledge acquisition.

We remind all concerned that embling-quality traits, as assessed by nursery personnel and/or by scientists, may not be identical to those of seedlings. Thus, there is a need to rigorously link embling traits to field performance. One possible outcome of this work might be the modification of BC MOF nursery standards for seedlings when applied to emblings. Such modification might allow known clones of a particular propagule-type to be acceptable even though they do not meet all seedling criteria for being field-ready, but are known to perform well when field-planted. Conversely, meeting all seedling criteria may not guarantee acceptable field-ready performance by emblings.

There is still much to learn, and it is too early to give unqualified assurance that embling stock production is fully reliable. The programs addressing this phase of the SE process now seem increasingly well-conceived, and recent trials are apparently being done better than were the first attempts.

4.5. Performance of Emblings

Part of the field performance of emblings depends on their having been given appropriate nursery care (4.4, above).

It also depends on whether details of the developmental pathway of the emblings makes them intrinsically different from other propagule-types (3.2.3a, above). Some of these intrinsic differences between the embling propagule-type and seedlings, stecklings and/or plantlings may be due in spruce or other genera to such things as: (a) the origin tissue and developmental pathway followed; (b) clone-specific propagule-type differences; (c) whether the somatic embryo is encapsulated and, if so, with which nutritive and regulatory chemicals; (d) whether the somatic embryo receives a controlled dehydrated storage period before further growth commences; (e) variables in the media composition as SE production techniques advance; and (f) whether the somatic embryos have a history of being frozen. We are too early in the interior-spruce (or any other) program to do more than identify these as interesting and possibly important questions, noting that early tests now in the ground are just beginning to supply a few of the answers. If the intrinsic propagule-type differences prove to be non-trivial, it will be important to characterize them for emblings in order to minimize the effects of their negative features and to take advantage of their positive features. These investigations probably need to be done only once per species, with the expectation that intrinsic propagule-type differences won't greatly differ among regions. (However, it should be noted that intrinsic properties of the steckling propagule-type do non-trivially differ among provenances of radiata pine.)

Embling performances also will depend in substantial measure on their genotypes. Deciding on the level of genetic improvement to be captured by SE and, in the case of full clonal forestry, finding and characterizing the individual outstanding clones, will be crucial to this aspect of their performance (see 3.2.3b and 3.2.4, above).

Finally, embling performance will be strongly influenced, particularly for full-clonal-forestry, by management comprehension of each deployed clone, and by management's ability to put that comprehension to effective use (see 3.2.5, above).

British Columbia regulations currently require 5 years' testing in field conditions for new propagule-types. Early tests of the embling propagule-type were begun 5 years ago with interior spruce. However, nursery practices necessary to produce quality emblings were not yet worked out, giving a perhaps misleading advantage to the comparison seedlings. In retrospect, those early tests were established prematurely and should be considered preliminary without penalty. More recent tests are better, with good-quality emblings paired with good-quality seedlings of

the same full-sib families, and stecklings are included in some replications. These propagule-type tests are now established successfully on appropriate sites in the Prince George area with emblings of interior spruce. These should be monitored yearly, and a comprehensive propagule-type comparison done after 5 years in the field.

For interior spruce, British Columbia is probably about 3 years from determining how the embling stock-type compares with the seedling stock type, 6 years from initial genetic comparisons of emblings and seedlings from the same full-sib seed, 15 years from initial clonal deployment and 30 years from the management comprehension needed to effectively deploy specific clones. But that probably still leads the world in progress along this trajectory of modern production forestry.

4.6. Performance of Clones

With the exception of some hybrid poplar clones, and some research and demonstrations with yellow-cedar, there is little basis for knowing just how wonderful or how ordinary highly selected clones might be in most of British Columbia's forest species. Some hints may be gathered from looking at clonal seed-orchards, discounting the problems that grafted seed-orchards are generally propagated using mature scions and the grafted clones are not on their own root systems. An example is the identification of genetic variation in response to nutrition in mid-crown yellowing of radiata pine.

If full clonal forestry is chosen as an option, we suggest the following steps. First, scan the available breeding values of tested parents in the region. Second, produce full-sib families giving a set of contrasting desired combinations of values. Third, put appropriate numbers of each family into efficient clonal testing protocols (see 3.2.3b, above). Fourth, once selected and deployed, develop a system of management feedback (see 3.2.5, above) from operational plantations, so that the performance of each deployed clone can be increasingly known and understood.

5 COST EFFECTIVENESS IN DELIVERY OF GENETIC GAINS

5.1 Benefits and Costs

Markets ultimately determine benefits from genetic improvement. Currently, market values are most easily estimated when the improved trait is volume. SE offers the potential for simultaneous improvement in a wide variety of traits but estimation of benefits becomes much more difficult. The effects of increased pest tolerance on volume may be roughly estimated (see below). The value of increased wood density for structural lumber is, however, dependent on market recognition through machine stress rating or other tests, which are not widely used at present. Intuitively, improved straightness is valuable but difficult to value quantitatively.

A second category of benefits is likewise difficult to value. These benefits derive from the impact of tree improvement on forest management. The period of statutory liability for reforestation is reduced when improved trees grow faster. Brushing costs also may be reduced. Faster growth can be beneficial through shortening the time until mature timber adjacent to young plantations can be harvested. Valuing this effect is especially complex because value is dependent on allowable cut and on specific harvest plans for specific forests. We are unaware of any attempt to estimate the value of improved growth on the "adjacency" question although a

general “what if” approach was taken in the Council Business Plan (Tree Improvement Council 1998). There, 8% genetic gain in growth rate was established as a threshold and volume at harvest was increased in the ratio $\% > 8/8$.

For the evaluation here, benefits are expressed as genetic gain in volume incremental to wild-stand seed. Benefits incremental to control-pollinated seed probably would be appreciably lower.

Costs include even more uncertainty. Producers of emblings have assured us that within a few years, production costs of emblings will be similar to those of seedlings from control-pollinated seeds. We cannot verify this but, on the basis of what we have seen, we accept that major reductions in production cost are likely. There is even the possibility that emblings from clones that propagate easily could be produced at lower cost than seedlings from wild seed.

There are several issues interwoven in the production cost of emblings. Reviewing the sequence of activities, as in Section 4 above, helps to highlight them. Development of cultures for cryopreservation involves gaining access to an adequate sample of the population to be reproduced. It should be noted that this process must be repeated each time that new genotypes are introduced, either to improve an existing population, or to develop a population for another “seed” zone. Moving from cryopreservation to reproduction on an operational scale involves economies of scale (suggested to be in the range of a few million emblings in total). Moving from cryopreservation to reproduction on an operational scale for clonal forestry requires field testing of clones (at least for deployment on public land). Therefore there is a significant time lag before cash flow from large-scale embling production can be achieved.

Alternative marketing strategies further complicate the estimation of cost. Reducing production cost to a level where emblings are priced competitively with alternative methods of delivering genetic gain is one approach. A different approach is to attempt to increase the value of emblings by adding improvement in more traits. Interpretation of the benefit-cost graphs which follow would be different for the two approaches.

In constructing benefit-cost graphs, a range of hypothetical values has been chosen to encompass what we expect to be actual values. Where the reader locates a point of maximum likelihood will vary with time, traits chosen, current status of SE for species-zone or trait combinations, and personal beliefs.

5.2 A General Model

The cost of planting is treated by all companies as an operating cost. Tree improvement is treated by some as an operating cost (most conveniently where the cost is included in the price of stock purchased from other organizations). Some companies treat tree improvement as an investment (especially where they have in-house tree improvement programs). Correspondents suggested that where the cost of improved stock is high, there would be more interest in choosing an investment approach. In analysis of cost effectiveness, several approaches have been used, all aimed at an estimated present net value, return on investment, or other measures of the relationship of benefit to cost. Few, if any, analyses have attempted to compare cost effectiveness of a comprehensive array of ways to deliver genetic gain.

We have chosen to treat the question from a generic perspective which estimates only the impact of genetic gain in volume (benefit) and added cost per planted tree (cost). The values chosen for benefits and costs are intended to cover a plausible range so that the limits of likely outcomes are established.

5.2.1 Benefits

The model defines benefits in terms of incremental volume at harvest resulting from genetic gain. Volume is a trait of nearly universal interest and is the most common measure of forest productivity. Other traits of interest, e.g. stem form and pest tolerance, contribute to merchantable volume although traits such as wood density do not. Volume per hectare for unimproved trees is calculated using the standard yield tables for a given species, site index, and rotation age (Mitchell et al 1995). Incremental volume is then estimated as the volume added to a hectare of unimproved trees by genetic improvement. For the following analyses, site index is the value (meters at age 50) that represents the lower boundary of “good” site quality. The assumption here is that planting stock of high genetic quality will be used on “good” and better sites only.

Rotation ages were chosen at 10 years before the decade of maximum mean annual increment. This is intended to approximate an “economic rotation”. The rotation ages used here assume that stock planted in year one carries the expected potential for genetic gain. Where clonal testing would be required, “the present”, for purposes of estimating incremental benefits and costs of genetic gain) may be many years in the future.

Other assumptions influencing calculation of expected yields for unimproved planting stock are:

- planting rate of 1100 trees per hectare
- no regeneration delay
- an operational reduction in yield of 15% to approximate unproductive areas
- a minimum merchantability of 7.5 cm at d.b.h.
- a discount rate of 4%
- eight levels of genetic gain from 20 to 170%

It should be noted that the choice of discount rate has a marked impact on cost effectiveness, higher rates resulting in lower benefits. Four percent is the rate most commonly used in MOF analyses.

5.2.2 Costs

The model assumes that the production cost of emblings will be more expensive than for unimproved seedlings. If that is not the case, cost effectiveness is moot. For analyses presented here, added cost of production is assumed to be in the present. These analyses are intended to include only incremental costs of production. The analytical approach could, however, be modified to include costs of research and development. If research and development costs were to be included, the model would have to be expanded to include discounting of some costs (time to harvest also would be increased). Six levels of incremental cost per planted tree were used with the range from 25% to 375% of seedling cost per unimproved seedling. The range of added cost of production for vegetative propagation is appreciably less than that suggested by Talbert et al. (1993).

5.3 Model Results

5.3.1 Interior spruce – Site index 19.2m, Rotation age 80 years

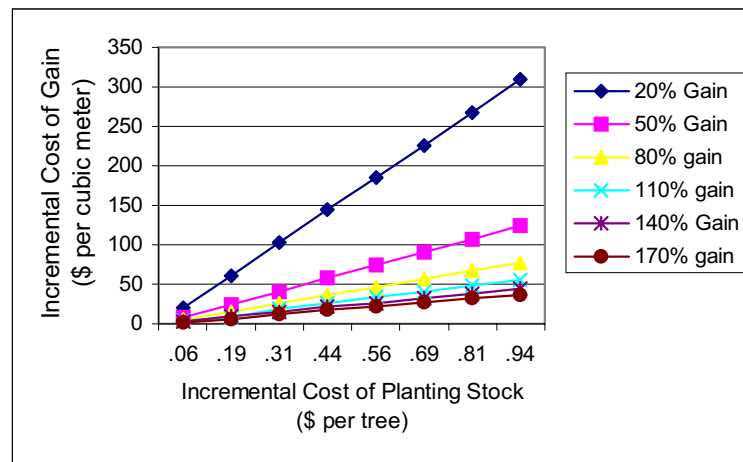


Figure 1. Cost per cubic meter of incremental volume from tree improvement at six levels of genetic gain in volume and eight values of added cost per tree.

Interpretation

Benefits – Current traits of interest are volume growth and weevil resistance. There are wide differences of opinion about how important is weevil resistance and about how widely tolerant planting stock needs to be planted. A positive correlation between growth rate and weevil resistance has been reported (Kiss and Yanchuk 1991) and confirmed in a different genetic test series. Differences in risk of attack are associated with different biogeoclimatic zones (Spittlehouse et al. 1994), and recovery of apparently acceptable stem form after attack has been observed. By contrast, plantations where the majority of trees are multi-stemmed shrubs also are present.

Projected annual demand for planting stock in the Prince George Planning Zone is 34 million (Tree Improvement Council 1998). Assuming that 10% of planting would benefit from weevil tolerance, demand for planting stock would be above levels suggested to us as thresholds for economies of scale.

To provide a first approximation of benefits from planting of weevil resistant trees, it was assumed that for high hazard areas, a maximum annual weevil attack rate of 33% was sustained over 35 years. For the McGregor Model Forest, this rate resulted in a reduction of about 25% in volume over unattacked trees (Taylor et al. 1994). With the positive correlation between height

and weevil tolerance, benefits from combined selection would not be fully additive and a benefit, in volume, of 25 to 35% for vegetative amplification of full-sib families chosen for growth and resistance may be a plausible first approximation.

Costs – A system for SE of interior spruce is more advanced than SE for the three other species in our review. Planting stock quality is now apparently adequate although government approval of embling stock quality will require another 3 to 4 years of testing. Genetic worth for vegetative amplification can be estimated from existing progeny-test data which are in abundant supply for many areas.

The prospects for reforestation with individual clones (clonal forestry) are less immediately encouraging. Although more than 1000 clones are under test, the quality of the earlier tests is compromised by planting stock quality questions and it is not clear how many of these clones are drawn from the best families available in the interior spruce program.

Research and development of SE for vegetative amplification of interior spruce would most likely now focus on increased efficiency in embling recovery, and completion of stock quality testing. If clonal forestry were the goal, a review of the quality of existing test plantations and the genetic quality of clones under test would be required.

With volume gains of 35% from combined selection for growth and weevil tolerance, and an incremental cost per cubic meter at harvest of \$50, a break-even added cost per tree for nursery stock might be about \$0.20.

It should be noted that currently, interior spruce genotypes in culture represent only the Prince George area. For vegetative amplification in other areas using SE, cultures from genotypes appropriate to each area would have to be established. For clonal forestry, clonal testing would have to be initiated.

5.3.2 Sitka spruce – Site index 29.2, Rotation age 70 years

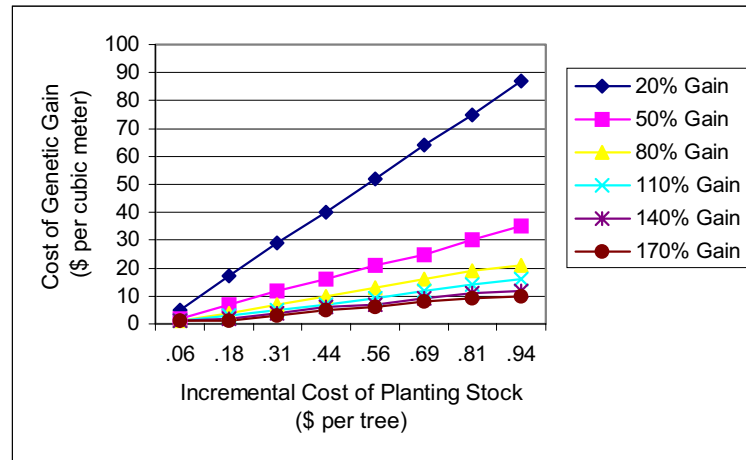


Figure 2. Cost per cubic meter of incremental volume from tree improvement at six levels of genetic gain in volume and eight values of added cost per tree.

Interpretation

Benefits – Provenance and progeny tests of Sitka spruce suggest a very large potential for genetic gain in volume. Weevil damage, however, is so great in some areas that Sitka spruce is not planted. Current plans identify the area of medium weevil hazard as the area for planting of tolerant stock and an estimated planting demand of 3 to 5 million has been suggested (King, pers. comm.). Projected planting demand is at or above the threshold for economies of scale in embling production although strategies of deployment which include susceptible genotypes to stabilize weevil-feeding preferences would influence planting demand.

More information on genetically based tolerance to weevil attack and on expected attack frequency as a function of geographic location is available for Sitka spruce than for interior spruce. Maximum annual attack frequency in the medium hazard zone is expected to be about 50% (Alfaro 1996). Seed from tested provenances has an estimated annual frequency of attack of 25% and tested clones vary to nearly 0% attack. One approach would be to establish an objective of reducing weevil attack in the medium hazard zone to a level similar to average attack frequency of the low hazard zone where genetic improvement in weevil tolerance is considered to be unnecessary (King pers. comm.) For the low hazard zone, attack frequencies are 5 to 10% for plantation ages from 10 to 35 years (Alfaro, 1996). If selection could reduce attack frequencies to 5%, the resulting gain in volume would be 24% above that to be achieved with seed from wild stand seed collections having tested levels of weevil tolerance (Alfaro 1994).

Costs – Emblings of Sitka spruce have been produced in relatively small numbers and will be available for planting on an experimental basis in 1999. Given the success of SE in other spruce species, problems of planting stock quality are not anticipated. Vegetative amplification with stecklings using seed from provenances known to have significant tolerance to weevil attack is

being practiced. Stecklings and seedlings with improved tolerance to weevil attack provide the current cost competition for emblings. When advances in breeding combine weevil tolerance and volume growth, vegetative amplification will have even greater appeal. Clonal forestry, on the other hand, would require a full clonal testing program. From Figure 2, an incremental cost of \$50 per cubic meter for tree improvement would balance an incremental cost of about \$0.60 per tree for planting stock where genetic gains in volume were about 25%

5.3.3 *Western white pine (coastal) – Site index 31.6, Rotation age 60 years*

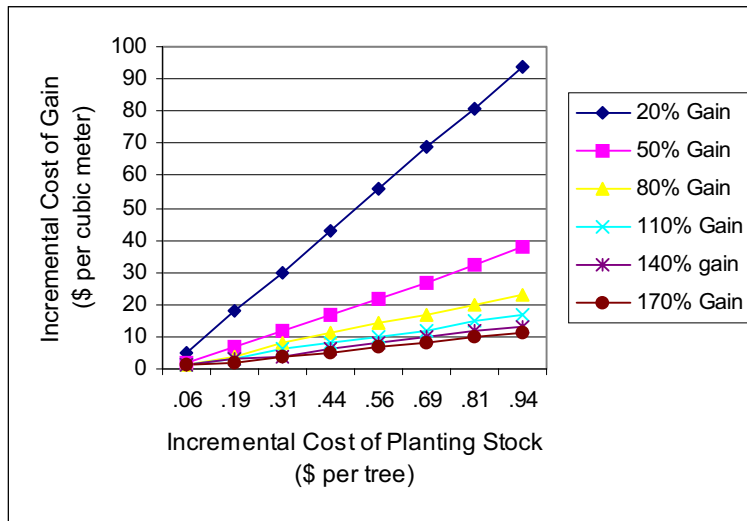


Figure 3. Cost per cubic meter of incremental volume from tree improvement at six levels of genetic gain in volume and eight values of added cost per tree.

5.3.4 *Western white pine (interior) – Site index 20.8, Rotation age 100 years*

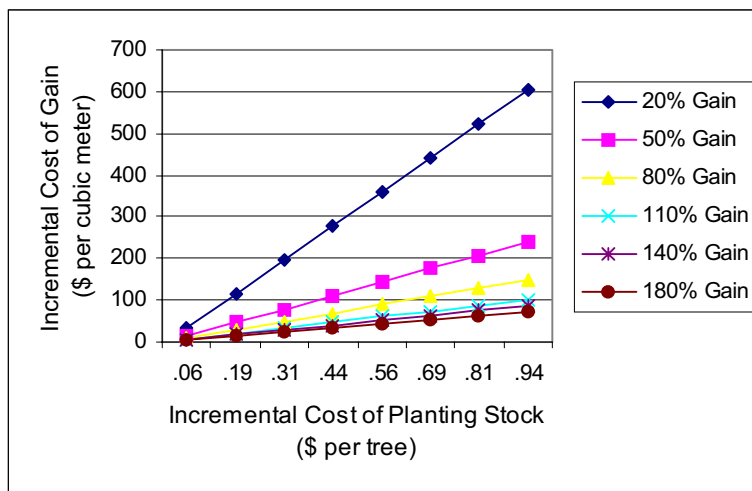


Figure 4. Cost per cubic meter of incremental volume from tree improvement at six levels of genetic gain in volume and eight values of added cost per tree.

Interpretation

Benefits - Three advantages are suggested for developing western white pine with adequate resistance to blister rust – higher product value, resistance to root rots, and increased species diversity. Estimates of potential financial benefits can be viewed in two very different ways. In the first, raising rust resistance from 15% to 65% is a genetic gain of more than 400%. While gains at such levels are outside of the range of values represented in Figures 3 and 4, it would seem that with very high costs of planting stock there could still be a financial benefit.

A very different approach is to use the “best guess” outlined in Table 1. There are no managed stand yield tables for western white pine in BC. Yields, therefore, were assumed to be about the same as the principal intolerant species represented in TIPSY, Douglas-fir (suggested by Mitchell pers. comm.). Combining projected yields and estimated levels of resistance in Table 1 provides an approach to estimating benefits. It is assumed that Douglas-fir is the alternative species for planting on sites, which might be planted with western white pine.

For this analysis, western white pine is awarded a 35% premium in the lumber market (J. Cook, MOF Valuation Branch, pers. comm.). Even with that premium, rust resistance would have to be nearly 10% higher than currently projected to match the expected value of interior Douglas-fir as an alternative in reforestation. Projected levels of genetic gain in volume from current tree improvement in interior Douglas-fir, from 0 to 25% depending on planning zone (TIC, 1998), would add to the favorable position of Douglas-fir, whereas increased root-rot hazard and emphasis on increased species diversity would increase the value of pine. It would seem that either resistance levels must be appreciably higher or reasons for choosing white pine over Douglas-fir must be compelling before significant additional cost for planting stock would be cost effective. This is especially true for the interior.

Costs: The process of embling production would require substantial development. One family has produced many cultures, other families have produced very few. No tests of embling stock quality have been established. The current view of how SE might be applicable requires clonal testing. Therefore, research and development costs will be high and an operational system would not be in place for at least 15 years. Renewed funding would be required to continue research and development.

5.3.4 Douglas-fir (coast) – Site index 31.6, Rotation age 60 years

Graph is identical to Figure 3.

Interpretation

Benefits – Volume growth is of primary interest in Douglas-fir with maintenance of average wood density as a second criterion. The highest breeding value for volume growth of second-generation selections is 26% with a breeding value of –4.7% for wood density (Xie, 1997). The strong negative correlation between volume growth and wood density results in reduced genetic potential for growth due to an improvement objective that requires maintenance of average wood density. Assuming a fully additive model of gene action for both traits, vegetative amplification of full-sib families could result in maintenance of average wood density with gains of about 15% in growth. The degree to which a program of clonal selection for both

Table 1. Estimated benefits from genetic improvement in blister rust resistance of western white pine. A premium of 35% was awarded to pine in recognition of higher wood value.

Species	Amount Planted (%)	Rust Resistance (%)	Amount Harvested (m ³ /ha)	Relative Value (m ³ /ha)	Total Relative Value (m ³ /ha)
<i>Coast</i> - Current practice with unimproved pine					
Douglas-fir	70	100	415	415	
Western white pine	30	15	27	36	
					451
Planting options with materials from Idaho resistance selections					
Douglas-fir	70	100	415	415	
Western white pine	30	65	116	157	
					572
Douglas-fir	100	100	593		
					593
Western white pine	100	65	385		
					385
<i>Interior</i> - Current practice with unimproved pine					
Douglas-fir	70	100	309	309	
Western white pine	30	15	20	27	
					336
- Planting options with materials from Idaho resistance selections					
Douglas-fir	70	100	309	309	
Western white pine	30	65	86	116	
					425
Douglas-fir	100	100	442		
					442
Western white pine	100	65	287		
					287

traits could increase volume growth is unknown. Figure 3 suggests that volume growth benefits would have to be very substantial before the costs of a clonal program would be cost effective.

Costs – To date, cultures of Douglas-fir have been more difficult to establish than cultures of spruces. About 50% of genotypes in culture have produced substantial numbers of emblings. The need to use immature embryos may introduce difficulties of variable maturation state. Stock-type testing would be required for any emblings and clonal testing would be required for a clonal program. High growth rates of coastal Douglas-fir and relatively short rotations, however, suggest that genetic gains could balance a substantial added cost per tree for planting stock.

5.4 Summary

Results from the general model quantify the intuitive expectation of how benefits (genetic gains in volume) balance costs (added cost of genetic gain). Species differences are large, however, as a consequence of differences in growth rates and rotation ages. For Sitka spruce, coastal Douglas-fir and coastal western white pine, substantial incremental costs for genetic improvement of planting stock would be cost effective if the resulting cubic meter of wood was worth at least \$50 at rotation age. For interior spruce and western white pine in interior BC, incremental costs would have to be low, genetic gains very high and/or wood value would have to be very high. It should be noted that these analyses are based only on direct estimates of wood volume. The results do not include benefits from earlier release of harvest constraints on adjacent timber, earlier release of legal obligations for reforestation or reduced costs to achieve “free-to-grow” status. Percentages of “genetic gain in volume” therefore could be higher than those predicted from progeny-test data.

6 FUTURE PROSPECTS FOR SOMATIC EMBRYOGENESIS IN BC

At various points in our review, we have expressed optimism for the potential of SE to enhance BC forests. Development of the process of SE (for spruce and Douglas-fir) is beyond the point of uncertainty as to whether it *can* be done. The ability to produce emblings will not, however, automatically result in operational use of this technology. In the following comments, we summarize several issues that the Forest Genetics Council may want to address in deciding to what level it wishes to encourage development of SE on an operational scale.

6.1 Administrative Issues

The raw material for SE (genotypes and field performance data) is almost exclusively in the public domain and is likely to remain there. Moreover, the regulatory control of deployment of emblings is a provincial responsibility for Crown lands which comprise more than 90% of the forest lands of BC. The technical capability, control of process patents, and marketing of emblings are in the private sector and are likely to remain there. At present, a protocol for transfer of tested genetic material for use in SE is in place but is not universally accepted. This could represent a major block to the use of SE. Here, as elsewhere we note that product objectives of different embling producers influence development of an operational system. Where the producer serves as a contracted manufacturer of emblings, proprietary issues remain

solely with the supplier of embryos. Where the producer seeks to add genetic value to supplied material, ownership is less clear.

6.2 Financial

There are several ways to deliver genetic improvement to forest plantations. Where cost effectiveness is one criterion in the choice of delivery method, we suggest that estimates using best available data should be made to at least identify a plausible range of benefits and costs for different methods. Such analyses could guide both producers and buyers toward financially attractive methods for genetic enhancement of BC forests. Producers would be better informed of price ranges that are likely to be accepted by buyers.

For SE, BC appears to be approaching a gap in funding for research and development that could block further development. Substantial research and development will be required before benefits and cost may approach a financially attractive balance. For interior spruce, refinements to the embling production process, completion of stock quality testing, and continued clonal testing remain. For other species, the list is longer.

We asked potential corporate users of emblings how much they would be willing to spend to advance research and development on SE. The strong and consistent response, with respect to Crown lands, was “Zero!”; “Nothing”; “We’re not willing to accept higher costs of stock or testing.” Government policy, including lack of title to planted trees, is at the heart of these responses. While investment in forest regeneration only to the legal minimum may not be the universal approach of forest industry, there would seem to be little flexibility for substantial direct financial contribution from industry to advancing SE toward an operational scale on public lands. Moreover, in the absence of substantial demonstrated benefits from planting of emblings, resistance to current pricing is wide spread. One noteworthy comment from industry was that outside funding, i.e. from FRBC, should not fully cover current additional purchase costs for emblings. Rather, purchasers should be required to pay some portion of the current additional price to force individual judgements on whether the price is cost effective.

We got a somewhat different answer with respect to private lands. There was some willingness to accept higher costs during R&D in order to help bring the technology along. This seemed to be driven more by the hopes of blockbuster gains through genetic engineering, and the recognition that SE was an important component of that, than the expectation that SE would contribute through the conventional route of delivering improved material from current tree-improvement programs. How an increase in R&D costs would be handled varied substantially among those interviewed, from a reduction in various current silvicultural treatments to a simple add-on from a higher corporate level.

Respondents in our interviews put the percentage of genetics R&D in forestry that is appropriate for pursuing SE in the range 5% to 30% in the near future, until it is clearer whether it will work. A related issue reflects experience that has become common elsewhere, namely that traditional tree-breeding programs have been shortchanged in order to support instead this exciting field of genetic engineering. In addition, the allocation of funds and programs from tree breeding to biotechnology may create another problem. Tree breeders are usually a whole lot better at designing, installing and evaluating field trials than are laboratory-oriented genetic engineers.

From the producers’ point of view, fiscal realities dictate that research and development will be focussed on opportunities that offer the quickest or greatest return on investment. Both producers made it clear that they are working in international markets and that BC is not necessarily essential to their success. Several existing BC projects are scheduled to be dropped in the absence of renewed financial commitments. This perspective (combined with resistance to

investment by potential users of emblings) leads to our view that funding of the current research and development needs, leading to operational production of emblings, is a serious issue.

It may make a difference to some potential users of emblings whether added costs for stock with demonstrated additional genetic improvement can be treated as a cost of logging, or must be treated as a compound-interest investment to be recovered in a future harvest. Whether the purchase of such more-expensive planting stock could be mandated (thus qualifying as a current cost of logging) under the policy of using the “best available at reasonable cost” will probably depend on interpretations of “best available” and of “reasonable cost”.

6.3 Social

We found little opposition to SE on grounds of potential reductions in genetic diversity. We were, however, unable to identify responsible members of the environmental community for interviews. The one specific reference to social concern was mention that the topic of potential reductions in genetic diversity and its possible consequences had been discussed in Land Resource Planning Meetings for the Prince George Region. It should be noted that our correspondent had attended presentations that sought to allay concerns but did not find the mathematical explanations given to be convincing.

We did ask clients, producers, and scientists whether they are concerned about adverse public reaction or harassing lawsuits. Almost without exception, these concerns were rated as minor or absent. Experience in the United States has been very different, with such concerns ranking very high in all three groups on similar topics, and they have all-too-frequently proved to be well founded. We suggest that, if British Columbia decides to move forward with SE technology, there should be substantial attention given to first ascertaining public worries, and then proactively mounting a campaign to inform your diverse publics as to the risks and advantages of using SE technology.

Interestingly, although we attempted to contact a list of foresters who might or should be aware of SE, few replied to our email messages outlining our questions and requesting a suitable time for contact. Whether this indicates that British Columbia foresters are seriously overworked, or whether they are not interested, was not clear. However, one client interview provided the opinion that upper-management is well informed about SE developments, but that field foresters are not only poorly informed but also resistant to this and other new technologies. This was not surprising, since foresters deal with very long time-frames and are therefore rightly conservative about hastily adopting new and untried ways of doing things. It does indicate that, if British Columbia forestry moves ahead with SE, a substantial educational campaign will need to be mounted among established field foresters as well as for the general public.

6.4 Biological

For species other than spruce, issues include recalcitrant genotypes, potential variation from sampling of immature embryos, planting stock quality, and field performance. The spruce model may serve as a guide to solution of these problems but substantial research and development seems to be required before SE for other species is available in BC.

Risks of reduced biodiversity and the related increased risks of catastrophic loss to physical or biotic events were a concern frequently mentioned during our interviews. These issues were addressed for forest plantations in general, and for clonal plantations in particular, in

a 1994 SRIEG meeting (Libby and others 1997, plus following papers *CJFR* 27). While increased genetic control of the tree components of a forest allows management opportunities for serious errors, it does not require management to make such errors. The strong consensus at the 1994 SRIEG meeting, and in other analyses since (Libby 1998), may be paraphrased as follows. *By combining good planning, monitoring and genetic control, clonal plantations will likely be safer than seedling plantations; furthermore, such clonal plantations will likely be safer than most naturally-regenerated forests.* This requires good theory, good data and good execution. This is not work for amateurs. If British Columbia is to make its clonal forests more productive and safer than its natural forests, and be able to convince a likely-to-be-doubting public that it is doing so, the professional effort devoted to this topic cannot be low priority. Thus, it must not be supported only in good times but neglected in hard times. The commitment to clonal forestry must be long-term and serious.

Another biological issue needs to be put in perspective. In some of our interviews we found considerable enthusiasm for SE as a vehicle for genetic engineering. In the long term it may well be, and even in the short term there are a few attractive ideas involving transgenic manipulation. But we think this enthusiasm has its priorities wrong. Compared to most other organisms, most conifer species contain relatively large amounts of genetic variation. We are not very far along in the process of sorting it out. This has two consequences.

First, tree-improvement programs can probably access many-fold greater amounts of useful genetic variation by analyzing, recombining and selecting available *adapted* natural variation, and can do it quicker and cheaper than can genetic engineering bring new variation on line for confident deployment to the forest.

Second, genetic engineering is particularly attractive for tinkering with already-excellent clones that have a few recognized and genetically understood shortcomings. Except perhaps for poplars, British Columbia does not yet have such excellent well-characterized clones as targets for this promising technology, nor is the genetic understanding of many traits of interest yet sufficient.

Finally, please note that SE can serve both traditional tree-breeding and genetic engineering, and its development should be in the context of what these complimentary fields can provide for SE to preserve and deploy.

7. RECOMMENDATIONS

All Methods of Delivery for Genetic Gain

RECOMMENDATION 1. The Forest Genetics Council should initiate a comparison of benefits and costs for alternative methods of delivery of genetic gain.

Comments: a) While the quality of data for this comparison will vary among methods, plausible limits should emerge and can provide guidance on the potential of various methods.

b) This exercise should include design of a model clonal forestry program including clonal testing, number of propagules to be produced, and generation of new genetic variation by crossing, laid out along a timeline in the manner used for seed-orchard planning.

RECOMMENDATION 2. The BC genetic-worth rating system should continue to be

developed (4.1).

Comment: a) Besides serving as a tool for breeders, such a system has heuristic value in encouraging clients to pay for genetic advances, and it may serve as a basis for such things as license fees and royalties (4.1).

Somatic Embryogenesis in General

RECOMMENDATION 3 – The Forest Genetics Council should strongly support continued research and development in SE focused on interior spruce and Sitka spruce (2, 3, 4, 5, 6).

Comments: a) Interior spruce currently has the most advanced SE protocols, and thus will serve as a model species where advances can first be made and mistakes learned from (4, 5.3.1).

b) From the analyses of cost effectiveness, Sitka spruce appears to offer as large an opportunity as any BC species (5.3.2)

c) We currently see the most immediate potential value for SE in vegetative amplification of proven families where control-pollinated seeds are very expensive or in short supply. In addition, development of a financially attractive SE system would enhance the potential for clonal forestry.

d) We favor near-term emphasis on cost reduction in embling production, with the expectation that within two years plausible estimates of market price for spruce emblings will be available (4.2, 5.2.2, 5.3.1).

RECOMMENDATION 4. R&D for SE protocols should proceed at lower priorities with additional species of importance to BC, with appropriate funding and support (6.2).

Comments: a) This should be done for species such as yellow-cedar for its value in cryostoring material that may be propagated as stecklings or plantlings (4.3).

b) It should be done for other species, such as Douglas-fir and western white pine for its possible cost-effective mass-propagation as emblings.

RECOMMENDATION 5. Ways should be found to encourage at least two producers to engage in healthy competition in supplying SE propagules and technology to British Columbia.

Comments a) We recognize the efficiency and pricing values of having competing suppliers of SE technology and production emblings.

b) We would not necessarily limit that support to existing BC organizations engaged in SE.

RECOMMENDATION 6. Clear responsibilities should be developed and assigned for testing propagule-types (3.2.3a).

Comment: a) Although producers' long-term interests are well served by reliable

characterization of embling performance, there may be a short-term conflict of interest (or perhaps distrust of the results by clients) if producers do the testing. At minimum, propagule-type testing of emblings should be supervised and audited by persons or organizations other than the producers.

b) The task might be assigned to some appropriate branch of the MOF, or to some contracted independent certifying organization.

c) Technical standards should be understood by developers of SE technology as well as producers of emblings.

RECOMMENDATION 7. A small working group should be appointed to find creative solutions to fairly and effectively facilitate the use of SE technology at an operational level in BC (4.1, 6.1.1).

Comment: a) Producers, clients, scientists and perhaps others would sit down together to work out their concerns and goals, and then find mutually-agreeable solutions.

b) This group could address related topics, such as genetic engineering.

Clonal forestry

RECOMMENDATION 8. The Forest Genetics Council should determine where the intensity of plantation forest management in BC can accommodate full clonal forestry (3.2.4, 3.2.5, 4.6).

Comment: a) As SE now seems likely to allow long-term storage of clones in an embryonic state (4.3), and their subsequent mass-production (4.2), it is timely that full clonal forestry be considered for appropriate regions of several BC species. Enhanced Forest Management Pilot Projects may offer opportunities for field testing of clonal forestry.

b) In the near future, this can probably only be justified on highly productive sites with relatively short rotations (5).

c) It becomes more likely if massive propagation of relatively few selected clones with good propagability can be achieved (3.2.4a).

RECOMMENDATION 9. The Forest Genetics Council should estimate the degree to which traits in addition to volume growth, wood density, and pest resistance are of major significance in plantation forestry in BC (3.2.3b, 3.2.4, 5.1).

Comment: a) Clonal forestry offers access to an amazing range of trait combinations. Whether this access is important depends on existing problems in plantation forestry and on market recognition in forest products (3.2.3b).

RECOMMENDATION 10. Only high-fidelity full-sib families should be entered into clonal tests if selection for full clonal forestry is a possible option (3.2.3b, 4.6).

Comment: a) Although deployment of vegetatively multiplied open-pollinated or polycross families can seem attractive as an alternative to full-sib families, monitoring of genetic diversity

will be more effective where full pedigree is known (6.2).

b) By “high fidelity” is meant effective crossing protocols that minimize pollen contamination and identify mixups, backed by genetic fingerprinting of candidate families matched for consistency with fingerprinting of selected clones.

RECOMMENDATION 11. For full clonal forestry, if clones are to be marketed to multiple clients, or deployed to Crown lands, the testing and characterization should be audited by either MOF or some independent certifying agency (3.2.3b)

Comment: a) If a clone is to be used exclusively by a single client on private land, the testing and characterization of that clone can be the responsibility of that client.

RECOMMENDATION 12. Clonal testing strategies and guidelines should be developed that are appropriate for early stages of full clonal forestry in British Columbia (3.2.3b, 4.6).

Comment: a) These would then be phased into the IUFRO testing strategies and guidelines as programs mature (3.2.3b, 3.2.4)

b) Some attention may need to be given to ways to encourage management feedback during advanced testing and characterization of the clones (3.2.5).

RECOMMENDATION 13. Convene a workshop or symposium on genetic diversity and ecosystem diversity issues (6.3)

Comment: a) Several respondents interviewed noted that these topics are not well understood in BC

b) It could focus on comparisons of natural regeneration, seedling plantations and various levels of clonal deployment with respect to genetic diversity of the keystone (forest tree) species, diversity in the developed forest ecosystems, and risk avoidance.

c) However, workshops and symposia don’t attract many of those who should be there. The results of such a meeting, therefore, should be designed to complement efforts recommended in Recommendation 14.

RECOMMENDATION 14. A small working group should be appointed to coordinate and implement a proactive education campaign on SE and clonal forestry, to be offered through planned extension activities sponsored by the Forest Genetics Council (6.1.2).

Comments: a) This should be a long-standing group, as these issues will continue to need attention.

b) The efforts should be directed both within the forestry community and to the concerned public.

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