Future Options for the Genetic Improvement of Conifers

Part I: Current and Near-Term Technologies

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Summary

Natural forest ecosystems are less productive than their theoretical net productivity rates. This difference between actual and theoretical productivity can be lessened by silvicultural methods, including genetic improvement. This paper summarises current and near-term (within 5 years) technologies including early selection, flower stimulation, vegetative propagation and crop ideotypes and describes how these are used to reduce the time required to breed and put into use genetically improved material.

Introduction

Compared to the long history of man's use of forests, techniques to breed and select trees with desired growth rates and qualities are comparatively recent developments. Although the basic goals of tree improvement programmes are reasonably clear (increasing yield, production of a high quality product and reduction of production costs) the way to accomplish these objectives is rather unclear (Faulkner, 1987). Most of the current concepts of tree improvement can be traced to work in Scandinavia in the the early 1950's. These methods have served us well for the last 40 years and have resulted in significant gains in the potential productivity of our forests. Unfortunately, due to the long time required to breed and test new genotypes (25 to 35 years in spruce), new methods are needed to reduce the length of time required to improve forest tree species.

The purpose of this paper is to review current methods of tree improvement, and then to examine techniques that will be used in the near future (next 5 years) and suggest how these techniques will affect tree improvement programmes. Part II of this paper will attempt to look further into the future and will discuss technologies that will affect tree breeding in 10 to 20 years and beyond, including molecular biology and genetic engineering.

IRISH FORESTRY, 1992, Vol. 49 (1 & 2): 27-39

Productive Potential of the Forest

Before a discussion of what improvements have been accomplished in breeding forest tree species, it is important to understand the theoretical potential productivity of forests and to determine what levels of improvement might be possible. Such an attempt was made in 1983 by Farnum and co-authors when they calculated the theoretical maximum primary net productivity for two major softwood species in the United States, Douglas-fir (*Pseudotsuga menziesii*) and loblolly pine (*Pinus taeda*).

The theoretical maximum primary net productivity rate is calculated by multiplying the rate of photosynthetic efficiency of a species by the amount of photosynthetic light absorbed by photosynthetic tissue. Then the respiration rate is subtracted, an adjustment is made for temperature and rate of inorganic nutrient uptake and the loss of material due to mortality, shedding and consumption by insects and mammals. This calculation results in a theoretical productivity rate for most land plants of 55 Mg/ha/year (1 Mg= 1 million grams or one metric ton). For temperate conifers this figure is estimated at 45 Mg/ha/year (Farnum *et al.*, 1983).

There is a difference between the mean annual yields (actual observed yields) and the theoretical maximum productivity rate of about 2.5 times. This means that in theory the mean annual yields for temperate conifers should be about 18 Mg/ha/year. In reality natural Douglas-fir and loblolly pine stands produce about 5.7 and 3.6 Mg/ha/year respectively. The difference between the theoretical maximum primary net productivity and the observed mean annual yield is the rate of improvement that should be our target. Farnum and his co-authors have suggested 25 and 30 Mg/ha/year as targets for improvement in Douglas-fir and loblolly pine respectively.

The major way to decrease the gap between these two numbers is by increasing the photosynthetic efficiency of the species which will result in increased growth. The rate of photosynthesis in conifers is about ½ that of most other plant species, possibly because they represent an early form of land plants. Among the ways to improve their efficiency would be by increasing site occupancy, thinning to reduce mortality, improved cultural practices such as fertilisation, avoidance of water stress and by selecting for certain biological processes that can be made more efficient by genetic manipulation. Farnum and his co-authors have presented data to illustrate the mean annual yield of natural stands (base case) for both Douglas-fir and loblolly pine and the effect of silvicultural treatments and genetic improvement on yield (Table 1). Clearly there is a large opportunity to increase the productivity of our forest land through silvicultural treatments and genetic improvement. However, while new silvicultural treatments will undoubtedly improve forest productivity, genetic improvement is a cumulative process whereby a certain increase in the level of improvement results with each new generation.

Table 1: Productivity Increases Attributable to Intensive Management of Douglas-fir and Loblolly pine. From Farnum *et al.*, 1983

Treatment	Douglas-fir Max. Mean Annual Yield (Mg/ha/yr)	Cumulative Increase (percent)
Natural Stand	5.7	–
Silvicultural Treatments		
Plantation Establishment	7.2	30
Nitrogen Fertilizer	8.8	50
1st Generation Genetic Improvement	9.7	70
TARGET	25.0	340

Treatment	Loblolly pine Max. Mean Annual Yield (Mg/ha/yr)	Cumulative Increase (percent)
Natural Stands	3.6	–
Silvicultural Treatments		
Drain and plant	7.0	90
Bedding	8.6	140
Preplant Phosphorous	10.5	190
Nitrogen Fertilizer	11.8	230
1st and 2nd Generation Genetic Improvement	14.3	300
TARGET	30.0	730

Current Tree Improvement Methods

Briefly, these methods depend on the selection of superior individuals from essentially "wild" populations. Natural variations in physiological, morphological and chemical characteristics serve as the source of variation utilized in genetic improvement. The easiest and cheapest improvement method depends on the selection of the proper species (native or exotic) and provenance. Further refinement can take place by selecting trees with superior characteristics ("plus" trees) to become part of a breeding population. Comparative "progeny" tests are established with their offspring on uniform sites in several locations. Seedlings of unselected parents are used as a check or control. Periodically the heights and diameters of the individuals in the progeny tests are measured and compared with the check or control seedlings. After a period of time, which is traditionally ⅓ of the full rotation age of the species (10 to 20 years), the performance of the progeny will reasonably predict the progeny performance at maturity. Trees which consistently perform above the check or control seedlings can be identified. These individuals then become part of the production population. Although height and volume growth are typically the major desired characteristics, other factors include stem form, branching habit, pest resistance and wood properties (Table 2).

Table 2: Douglas-fir traits under genetic control. From Silen, 1978

Strong Genetic Control
Graft incompatibility
Cone Production
Moderate to Strong Genetic control
Stockiness
Terpene Composition
Spiral Grain
Animal Resistance
Survival
Moderate Genetic Control
Stem Diameter
Stem Straightness
Tracheid Length
Percent Summerwood
Frost Resistance
Insect Resistance
Cotyledon Number
Weak to Moderate Genetic control
Total Height
Branching
Weak Genetic Control
Dry Weight
Percent Heartwood
Wood Permeability
Fertiliser Response

Scion material from "plus" trees selected in "wild" populations is grafted onto rootstocks to establish a collection of selected germplasm or a "clone bank". Seedling progeny or grafted scions of plus trees which have demonstrated their superior qualities in progeny tests are used to establish seed production areas or "seed orchards". The natural cross pollination between these individuals within the orchard produces seed with the improved characteristics. Seed orchard site selection is important in order to encourage early flowering and good cone yields. Despite this, many seed orchards (especially seedling seed orchards) are slow to produce practical amounts of seed. Sitka spruce typically requires 15 to 20 years to flower from seed and may need to be 30 to 35 years old before they begin to produce seed in commercial quantities.

Unfortunately, the products of most tree improvement programmes have, as yet, to be put into large-scale use in our production forests. This is because by its very nature the selection, breeding and testing of trees is a long-term activity. In some pioneer species such as pine, which flower early, a breeding cycle may require as little as 7 to 8 years. Subclimax and climax species such as spruce, are among the slowest to reach sexual maturity,typically requiring 15 to 20 years to flower from seed. Combined with a 15 year progeny test period, one breeding cycle in spruce may require 25 to 35 years. Thus TIME is the greatest limiting factor in tree improvement.

Using these methods, varying levels of genetic improvement have been achieved with most major conifers of economic importance in Europe. With increasing costs for both the establishment and continued operation of these long-term tree improvement programmes, geneticists have begun looking at ways to both shorten the breeding cycle and increase the availability of this improved material. This requires the development of a new set of techniques that will allow a reduction in the time required to get improved material into production forestry.

Near-term Technologies

Early Selection

Originally it was believed that about ⅓ of the rotation age (10 to 20 years) was required to be able to identify superior individuals. Studies with Sitka spruce have shown that at least 6 years of field growth (8 years from seed) are required before differences between progeny can be seen (Samuel and Johnstone, 1979; Gill, 1987). Researchers, however, have been attempting to reduce this period still further.

Work by the Forest Commission on Sitka spruce in the early 1970's (Herbert, 1971) attempted to identify superior families early by growing them in a glasshouse. Initially there appeared to be a correlation between height growth in the glasshouse and field growth rate, but these could not be confirmed in larger trials and the method was later abandoned (Samuel and Johnstone, 1979; Faulkner, 1987). It can be argued that the technology has improved so much in the last 20 years that these type of studies with Sitka should be repeated, especially in light of recent results with other species where good correlations have been found (Waxler and van Buijtenen, 1981; Williams *et al.*, 1987; Pharis *et al.*, 1991). Recent work with loblolly pine has suggested that even under well controlled conditions, the poorest families can be identified and eliminated from progeny tests, thereby reducing progeny test establishment costs (Lowe and van Buijtenen, 1989).

Flower Stimulation

The long time required for some conifers to begin flowering has encouraged basic research into the flowering process in trees. Stress has been known for many years to stimulate flowering and seed production. More recently studies on plant growth regulators have led to the recognition that certain forms of gibberellic acid can stimulate flowering in many members of the pine family (pines, spruces, hemlocks, Douglas-fir). Treatment with gibberellins, either applied as foliar sprays of more effectively as stem injections combined with water stress, induced by root pruning, warm temperatures or stem girdling, will stimulate flowering in conifers. It can be useful in making seed production more reliable, especially in young orchards. In some species even sexually immature seedlings can be induced to flower. Work on flower stimulation in Sitka spruce has been summarized by Philipson (1987).

These methods have been applied to both potted grafts as well as large field grown trees in seed orchards. Flower stimulation techniques are now at the stage where we can consider the development of indoor or potted seed orchards in regions, like Ireland, where climatic conditions are not conducive to regular flowering (Figure 1).

Depending on the species, large quantities of genetically improved seed will generally not be available from these indoor orchards, because trees must be of a limited size to fit in a greenhouse. Regular production of small quantities, multiplied through vegetative propagation, will, however, supply improved plants in commercial quantities.

Vegetative Propagation

Man has been vegetatively propagating horticultural plants since Roman times. Only through vegetative propagation is it possible to faithfully reproduce selected individuals with desired characteristics. Reproduction by sexual means results in segregation of genes and creates variation in the offspring.

Vegetative propagation can be accomplished by grafting, air layering, the rooting of cuttings or by tissue culture. Grafting, air layering and rooting of cuttings are together known as "macropropagation" because a relative large (macro) piece of the plant is used in propagation. In contrast, tissue culture or "micropropagation" involves the removal of a small piece of the plant, anything from a small piece of the stem or bud down to, at least in theory, a single cell and placing it into culture under controlled conditions of nutrition, temperature and light. Micropropagation will be discussed in more detail in Part II of this review.

Vegetative propagation of forest trees is not a new idea. Japanese cedar (*Cryptomeria japonica*) has been propagated by cuttings in Japan since the 1400's. One of the earliest reports of the vegetative propagation of a forest tree species in Europe was Norway spruce (*Picea abies*) propagated by cuttings in Germany in the 1840's.

Currently it is estimated that worldwide as many as 65 million conifer

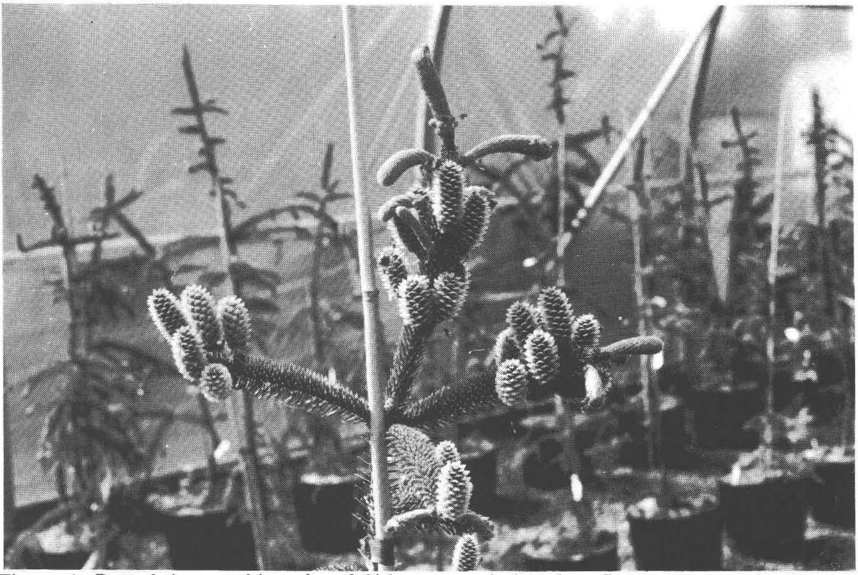

Figure 1. Potted 4 year-old grafts of Sitka spruce induced to flower as a result of warm temperatures, water stress and injection with gibberellic acid.

propagules are produced by rooted cutting production systems (Ritchie, 1991). Presently between 150,000 and 170,000 rooted cuttings of selected clones of Sitka spruce are rooted for clonal testing in Ireland by Coillte's genetics research section each year. Plans call for this to increase to about one million rooted Sitka cuttings per year in the next several years (Figure 2). Probably the most well developed commercial programme is the Forestry Commission's Sitka spruce programme. Because only limited amounts of "the best" genetically improved material are available as seed, vegetative propagation is used as a way to multiply this limited supply. In Sitka spruce one seed can produce 500 rooted cuttings in 2 cutting steps spread over 6 years (John and Mason, 1987). Because of the amount of time and labour involved, rooted cuttings typically costs 2 to 3 times the price of seedlings (Mason, 1989). The selling price of genetically improved rooted cuttings in 1990 was UK£ 190/1000 compared with UK£ 75/1000 for unimproved bare-root seedlings. Current production rates of Sitka rooted cuttings in the U.K. are between 2 to 3 million per year.

The rooting of conifer cuttings depends to a great extent on the age of the plant from which the cutting is taken. The older the donor plant, the more difficult it will be to root. Different species lose the ability to root at different rates. Douglas-fir cuttings, for example, can be rooted quite easily from a 1 year-old seedling, but beyond that age the rooting frequency decreases rapidly. Sitka spruce cuttings can be rooted from donor trees up until about

Figure 2. Plastic tunnel containing 100,000 Sitka spruce cuttings under mist during the rooting process.

6 or 8 years old. After this, not only does the rooting percentage decline, but the incidence of plagiotropism (growth as a branch rather than as an upright shoot) increases. The propagation of "tested" genotypes offers the greatest genetic gain, but testing requires 6 to 8 years which increases the chance of problems with poor rooting and plagiotropism. This has led to an interest in techniques to slow, or delay, aging in woody plants.

The position on the crown from which the cutting is collected may be important in rooting success, with cuttings from the lower part of the crown tending to root best. Several techniques such as pruning close to the ground (hedging) or the repeated use rooting of cuttings as donor plants (serial propagation) may have the effect of slowing aging of the donor plant or clone. These treatments do not stop aging, they only delay it. Repeated grafting of scions of mature trees onto seedling rootstock has been suggested was a way to return a mature individual to its juvenile (high rooting frequency and no plagiotropism) state which is known as "rejuvenation". The effectiveness of this process varies with the species studied and requires further proof of "rejuvenation". For example if tissue from a selected superior individual could be returned to the juvenile state (high rooting percentage) but it continued to grow at the slower mature growth rate, it would not be of very great commercial interest. In vitro techniques rejuvenation (discussed in Part II of this review) are also reported to return mature genotypes to their "juvenile" state.

Crop Ideotype

In the past, the main focus of tree improvement was on growth and wood production. Other factors such as dry matter accumulation/stem unit, cell wall thickness, fibre length and ratio of spring to summerwood have been mostly neglected. Faulkner (1981) likens this to cattle breeders who selected for the width of the forehead and symmetry of horns while they neglected milk production and butterfat content. Tree breeding has demonstrated that it can make improvements in the growth and form of forest trees, but is this really what is needed? Now is probably a good time to devote some time to thinking about the concept of crop ideotypes and what type of trees we actually want to breed. The idea of selecting for generally adapted progeny to grow well on a variety of sites, under a range of climates, using current site preparation and forest management techniques of fertilisation and thinning may need rethinking. A limited number of small sub-lines should be considered for special purposes (disease resistance, high wood densities, water and nutrient use efficiency, etc.) but only if they are economically viable.

The concept of identifying the "ideal" tree form is not new, but it is an idea that has probably not received the attention it deserves. Gordon (1975) suggested three approaches for increasing forest tree yields. The first approach would be to change the nature of the photosynthetic process in trees. The only way this would be possible would be with the techniques of "genetic engineering' (discussed in Part II). The second approach is to change the shape of individuals so that they would efficiently occupy the space allocated to them and be less competitive under intensive cultural conditions. Cannell (1982) argued that progeny testing methods actually select for genotypes that are either "isolation" ideotypes that grow well as widely spaced individuals or as "competition" genotypes that grow at the expense of their neighbours. Whether selection for either of one of these two ideotypes seriously affects stand productivity over the rotation has yet to be studied. The idea of establishing a forest with a type of tree that will be able to be grown to full rotation with minimal or no thinnings has been developed in Finland. This is the ideotype of the narrow crowned spruce. This tree has long, pendulous branches that concentrate their photosynthate into the main stem rather than branch wood. Its narrow crown also allows for more trees to be planted per hectare, thus producing more wood per unit area (Figure 3). This ideotype is selected to produce a tree with improved stem quality in a shorter period of time with reduced thinning or pruning costs (Pulkkinen *et al.*, 1989: Pulkkinen and Poykko, 1990). It is also supposed to be better at resisting wind damage, an idea that might be useful in Irish forests. In Sitka spruce sparsely branched clones were found to allocate high proportions of their dry weight matter to stems (Cannell *et al.*, 1983). The authors suggested selecting for tallness and sparse branching as a way of selecting for efficient stemwood producers.

Gordon's third option for increasing forest yields is selection for optimal internal allocation and utilization of photosynthate, nitrogen and nutrients. Evidence exists that such genotypes are possible in Sitka spruce (Cannell *et al.*, 1983). Sheppard and Cannell (1985) reported clonal differences of 10 to 30% in the amount of dry matter accumulated per unit of nutrient taken up. Since publication of these observations, little further work seem to have been done in this area.

Future of Tree Improvement

Tree improvement is a collection of techniques that are used to accomplish an overall strategy. Some of the techniques have been around for some time while others are relatively new. The techniques are like pieces of a puzzle. Their position in the puzzle will allow us to reach the overall strategy to improve a forest tree species. The "classical" methods of tree improvement such as selection, testing, breeding and seed orchard establishment are well established and understood. They have served us well and resulted in the development of a successful seed orchard system.

Conventional seed orchard methods initially appeared to satisfy the demand for genetically improved material in amounts large enough to supply commercial demands. This has proven to be true, especially for pine species. Similar work with northern non-pine species were not so successful, mainly because of the long time required for flowering. With increased interest in genetically improved material, together with demands for reducing costs and time required by conventional tree improvement programmes, new strategies have been developed.

An initial attempt was made to try and reduce the size, and thus the cost, of seed orchards. The bi clomal and meadow orchard were attempts at this (Sweet and Krugman, 1978). Flower stimulation, originally developed for use on large trees was adapted for use on potted, grafted trees. Unfortunately the amounts of seeds produced by the miniaturized and potted orchards was not enough for commercial use. Some means of multiplying the seed was needed.

Shortly afterwards, in a paper by Smith *et al.*, (1981), the use of micropropagation was proposed as a way to "vegetatively amplify" the small amounts of seed produced by the meadow orchard. However, at that time the technique was unable to produce the required number of plants at a competitive price.

At about the same time, the use of cuttings collected from seedling stock plants as a way to avoid problems in trying to root cuttings from mature, tested individuals led to the development of efficient seedling rooted cutting propagation systems (Gill 1983).

The combination of flower stimulation methods applied to potted, grafted material for the production of controlled crosses of superior families,

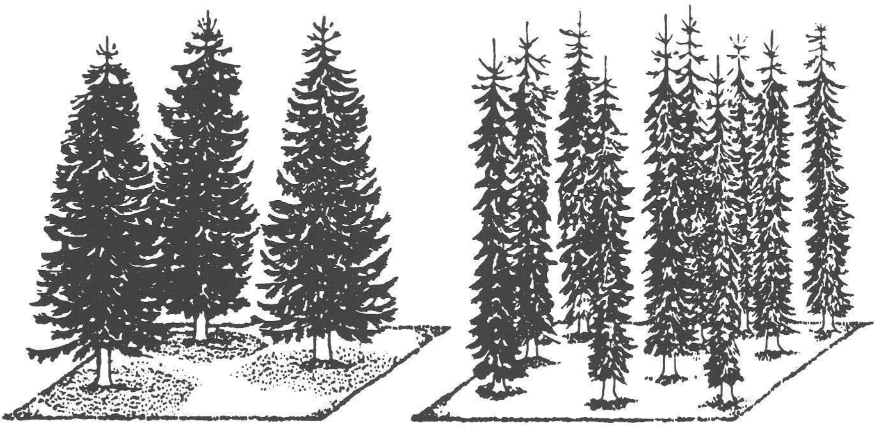

Figure 3. Hypothetical comparison of narrow crowned trees (right) with a stand of normal crown form. Individual tree yield of narrow crowned trees may be smaller, but because more trees occupy the same land area yields are higher than normal crowned trees (From Pulkkinen et al., 1989).

followed by vegetative propagation may be the solution to large-scale production of improved material without a large, expensive, slow to produce seed orchard. It also allows for a large amount of flexibility because material in a potted orchard can be added and deleted more easily than in a conventional orchard. Rooted cutting methods might be replaced by micropropagation, specifically somatic embryogenesis once it has been tested and improved. Micropropagation may be used as a first stage of multiplication for the production of stock plants so that the high production costs of micropropagation can be spread over a large number of rooted cuttings.

Early selection methods will allow a way to reduce costs in another expensive component of the tree improvement process, progeny testing. These techniques will not replace field testing, but will permit the early elimination of poor genotypes from progeny testing.

A combination of early selection, flower induction and vegetative propagation by rooted cuttings would be able to reduce the time required to produce genetically improved material.

Conclusions

It is inevitable that due to current world economics, much of the world's wood in the future will come from plantations of pure species or more productive exotic species. Thus more wood must be produced on less land. Not only will it be necessary to use the best silvicultural management practices but it is also essential to use the most appropriate species, selected and bred for the required end uses.

Calculations of theoretical production rates provide evidence that there are opportunities for continued improvement in most forest tree species. Selection and breeding will continue to provide a powerful tool in the continued improvement in production rates in a species. We will not be limited by ideas and techniques because geneticists working with agricultural and horticultural crops face the same problems. Fortunately for them, they do not have to work under the long periods necessary for breeding and testing woody species. Undoubtedly some of the technology developed for non-woody species will be inapplicable to forest species, but of the technology that is relevant it will certainly require a much longer period for the fruits of this work to reach commercial fruition.

Perhaps tree improvement has reached the first plateau in its development. As Faulkner (1981) described it" ...the use of the broadsword to crudely reduce the breeding base to a manageable size, then to use a scalpel to refine existing and develop new techniques..." for continued improvement.

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