Achievements in forest tree genetic improvement in Australia and New Zealand 5: Genetic improvement of Douglas-fir in New Zealand

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Summary

Douglas-fir is New Zealand's second most important plantation species and has been grown there since the late 1800s. Recently there has been increased commercial interest in the species, especially for higher-altitude, snow-prone sites in the southern South Island. Tree improvement began in 1957 with the establishment of extensive large-plot provenance trials. These have shown that coastal fogbelt provenances from California and southern Oregon are superior in growth to those of Washington coastal origin. The Washington provenances had been used for much of the afforestation up to 1980.

A first breeding program, started in 1969 from stands of Washington origin, became redundant following the provenance trial findings and, in 1988, selection of 186 plus trees in provenance trial plots of coastal Californian and Oregon provenances restarted the breeding program. In addition, open pollinated seed from 240 parents in 21 coastal Californian and Oregon populations was planted as a breeding population in 1994. An ambitious program of polycrossing and paircrossing of NZ selections failed to deliver sufficient crosses and seed, and recently a new breeding strategy based on open pollination in a clonal archive of the 1988 selections has been instituted.

The breeding objectives have also been recently revised to include volume yield, log quality and timber stiffness, selection criteria being diameter, bole straightness, light well-distributed branching and outerwood density and/or sound velocity.

Keywords: breeding programs; history; open pollination; wood properties; Douglas-fir; New Zealand

Introduction

Douglas-fir is New Zealand's second most important exotic conifer, though it falls a long way short of radiata pine in both area planted (104 000 ha) and the current annual planting rate of about 10 000 ha (Miller and Knowles 1994; Anon. 2002/2003). Douglas-fir has been grown in New Zealand since the end of the 19th century but the main establishment periods have been 1900–1935, 1950–1970 and from 1990 onwards. There was little interest in new planting of Douglas-fir during much of the 1970s and 1980s, as high establishment costs, long rotations (about twice those of radiata pine), modest value and low profitability discouraged expansion, as did Swiss needlecast disease (caused by the fungus *Phaeocryptopus gaeumannii*) (Anon. 1973).

Since around 1988, there has been renewed commercial interest in the species, owing to high values of Douglas-fir timber and the recognition that on some higher-altitude, snow-prone sites, especially in Otago and Southland, Douglas-fir performs better than radiata pine. This has been an important factor in the re-evaluation of Douglas-fir, as has the realisation that Californian and southern Oregon coastal fog-belt provenances were growing much faster than those of Washington origin. Also the superior stiffness of Douglas-fir, especially in the corewood zone, and the useful degree of natural durability of its early-forming heartwood, can produce timber much better suited to structural uses than radiata pine.

Historical development of tree improvement

A program of provenance research in Douglas-fir was started in 1955 by I.J. Thulin (Sweet 1965; Thulin 1967). Trials of 35 and 45 provenances were established in 1957 and 1959, with large 144-tree plots replicated on eight and 19 sites respectively. The first series was mostly of commercial seedlots from Washington and Oregon, and the second was from seedlots collected by NZ breeder Egon Larsen from Californian and Oregon coastal populations. Further provenance- and local seed-source trials were planted in 1974. Early results of these trials at age 6 y, and especially the 12-y results (M.D. Wilcox unpublished data) showed clearly that seedlots of coastal Washington origin were growing substantially slower than those from coastal provenances from southern Oregon and California (Thulin 1967; Sweet 1965). Recent studies based on 22 coastal fogbelt populations of California and Oregon (Low *et al*. 2007; Low and Shelbourne 2007) have confirmed results from the earlier trials.

Seed stands were initially developed to supply seed of known origin and to incorporate some genetic improvement from local land races of probable Washington and southern Oregon origins. Seed stands were also later developed from broadly-based native provenance seedlots from Fort Bragg and from Santa Cruz on the Californian coast.

A breeding program was initiated by M.D. Wilcox in 1969 before these provenance trial results became known. This was based on selection of 125 plus trees in stands aged 35–50 y of probable Washington origin. Trees were selected for superior diameter at breast height (dbh); stem straightness; freedom from malformation; and well-distributed, flat-angled and moderate-sized branches; and later wood density. Non-intensive phenotypic selection and open-pollinated (OP) progeny testing resulted in the planting of 125 OP progenies of the first series of selections in North and South Island forests in 1972, with a further 60 OP progenies planted in 1973, selected also for wood density.

By age 13 y the 1959 provenance trials were showing clearly that provenances from the fogbelt of the Californian and south Oregon coasts were growing appreciably faster in volume than the NZ landrace and Washington provenances (M.D. Wilcox unpublished data). This finding indicated that the 1969 and 1971 selections in Washington material were unsuitable as the sole basis for a breeding program. For this reason, and the lack of industry interest in the species at the time, the Douglas-fir breeding program was put on hold for the next 14 y.

The genetic improvement of Douglas-fir in NZ was reviewed in 1988 (C.J.A. Shelbourne unpublished data) when prices of Douglas-fir sawlogs from unpruned stands had risen rapidly and there was renewed interest by the industry in growing Douglas-fir. A new breeding program was initiated by making 186 new selections in the earlier provenance trials countrywide, mainly from provenances from the coastal fogbelt of California and Oregon. Selections were also made in seed stands of Fort Bragg, California provenance, and from stands of local land races of southern Oregon and Washington origin. A local seed company, Proseed NZ Ltd, funded the assessment of the provenance trials, the selection of plus trees ('Superline A' in the present breeding strategy), and collection and grafting of scion material. Grafts of the 186 clones were subsequently planted as a clonal archive at Proseed NZ Ltd's Waikuku site (near Christchurch, South Island). This greater confidence in Douglas-fir led to the formation of an FRI-Industry Douglas-fir Cooperative in April 1993, with base funding by the Ministry of Research, Science and Technology.

The restricted number of individuals and parentage of the coastal fog belt provenances in the earlier trials, and the possibility of some relatedness among the 186 selections from these, were of concern. Hence in 1993 an FRI expedition was organised which collected or acquired 240 OP progeny seedlots from 21 provenances in coastal Oregon and California (C.B. Low and M.A. Miller unpublished data). These progenies constitute Superline B (Fig. 1) and were planted in 1996 in three progeny/provenance trials at one North Island and two South Island sites at latitudes 38°, 41° and 45°S. These trials were first assessed at age 4 y (Low *et al*. 2007) and by 2008 should be ready for forward selection of the best trees for use in clonal seed orchards, and from which OP seed will be collected to establish a new generation of Superline B.

Breeding strategy

A strategy was formulated in 1995 (C.J.A. Shelbourne unpublished data) to include groups of selections from the NZ provenance trials and other stands (Superline A), and the OP seedlots collected in the USA (Superline B). The strategy was one of 'recurrent selection for general combining ability', with the creation of 15 sublines in Superlines A and B, each of around 27 families. Sublines systematically included a variety of provenance origins, within which future mating would take place for breeding-population turnover, and between which pollination would occur in clonal seed orchards. This would ensure that although inbreeding would build up slowly within sublines over generations, the production of seed from the seed orchard would be from unrelated parents.

The 1995 strategy involved complementary mating designs of polycrossing for estimation of breeding value and pair crossing to generate full-sib families for forward selection in Superline A. Superline B relied on OP mating, at least in the first generation, for advancement. The program for Superline A proved to be unachievable for a variety of biological and operational reasons, and after over a decade of effort sufficient seed of the projected crosses has not been produced, either of polycrosses or pair-crosses. This has necessitated the revision of the strategy in favour of a single open-pollinated design that fulfils breeding value and the requirements of forward selection, and is more rapidly and cheaply attainable. The two Superlines will be maintained in the new strategy, but the use of open-pollinated mating will disrupt the sublining. It is anticipated that control-pollinated orchards may be adopted in NZ in the longer term, which would make sublining unnecessary to achieve outcrossing in the orchards.

The most immediate deficiencies of Douglas-fir genetic improvement prior to the change of strategy were the lack of progeny tests of the NZ-derived Superline A parents to provide breeding values for selecting seed orchard clones, and the lack of a sufficient area of commercial seed orchards. The inability to extensively cross the NZ Superline A selections (originally from genetically-isolated populations) prevented the creation of an adapted NZ landrace and breeding population.

Selection criteria for Superline A candidates in the provenance trials in 1988 were diameter at breast height, bole straightness, absence of forking and ramicorn branching, and dense deep crowns. Selection of the parent trees of Superline B in the USA was for growth and form. Breeding objectives (the harvest-age traits to be improved) were yield and improved log quality. In a recent wood properties and sawing study of a stand of Douglas-fir of Fort Bragg, Californian origin, Knowles *et al*. (2003) have shown that lumber stiffness, the most important determinant of quality for structural lumber, shows high variability among trees of Douglas-fir. New data on sonic velocity from the 1969 progeny tests show moderately high heritability for sonic velocity and thus stiffness (L. Gea unpublished data). It was attempted in the early 1970s to choose the breeding objectives and plus tree selection criteria through two individual-tree wood property and sawing studies. These determined the amount of tree-to-tree variation in mean plank stiffness (by machine stress grading) and its relationship to tree form and wood properties (C.J.A. Shelbourne, J.M. Harris, J.R. Tustin, I.D. Whiteside unpublished data; M.D. Wilcox unpublished data). In both sawing studies tree-mean minimum stiffness as a 100 × 50 mm plank was well predicted through multiple stepwise regression on branch diameter, basic density and stem deviations ($R^2 = 0.62–0.79$). A recent study of eighteen 42-y-old trees from a densely-stocked

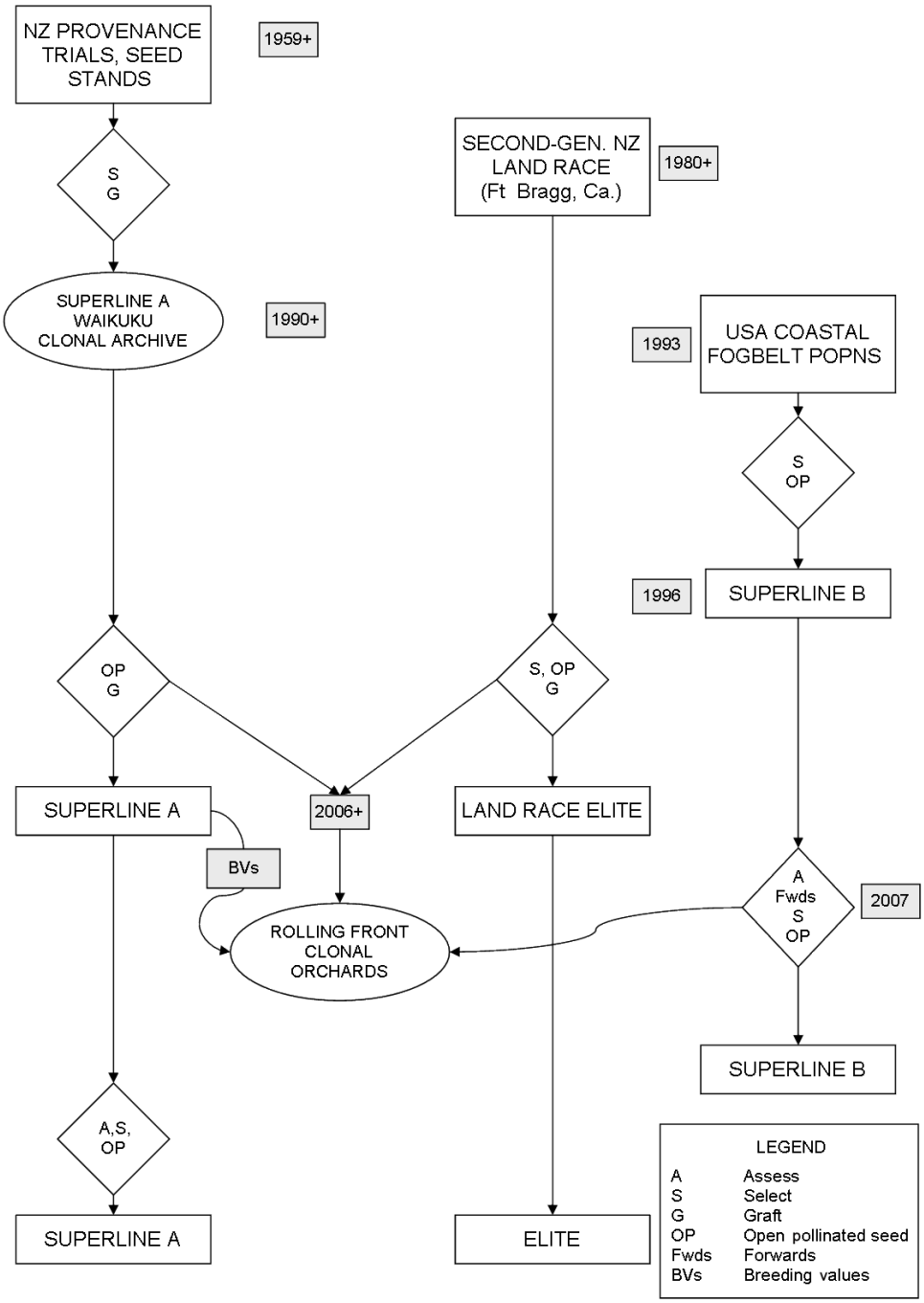

Figure 1. Douglas-fir breeding and seed production

stand of Californian origin (Knowles *et al*. 2003) showed that most tree variation in timber stiffness (as a joist) was explained by density ($r^2 = 0.75$), while branch diameter accounted for only 24% of the variation in log mean timber stiffness. Mean tree timber stiffness was also well predicted by microfibril angle, as measured by SilviScan.

Use of open-pollinated seed for tree improvement

The revised and simplified long-term breeding strategy (Fig. 1) will be effected through future use of OP seed for progeny testing as well as breeding-population advancement. This will first involve collection of OP seed from each of the 186 NZ Superline A clones in the Waikuku clonal archive, thus intermating and turning over the generation for this Superline. Later, after the 12-y assessment of the USA Superline B trials, collection of OP seed from about 200 selections will turn over the generation of this Superline.

Open-pollinated progeny testing is a practicable strategy to progress the Douglas-fir breeding population, and to realise gains from orchard seed either by backward or forward selection. Provided at least one or two sites of the breeding population progeny tests show early and good seed production, the mating

of selections by open pollination will reduce the length of the breeding cycle by avoiding the costly and time-consuming steps of grafted clonal archive establishment and control pollination. Provided balanced within-family selection is practiced, status number (*Ns*) (Lindgren *et al.* 1996) of the breeding population should be well conserved. This strategy utilises within-family genetic variance without the reduction in effective population size and status number that result from among-family selection, thus ensuring better sustainability of the breeding program over generations.

There is little disadvantage in using OP progenies of this species versus polycross progenies for estimating breeding values and for advancing a breeding population by balanced within-family selection (Shelbourne *et al*. 2007). The main disadvantages of OP half-sib progenies versus full-sibs as a breeding population are the loss of full control of parentage which may result in selection of half-sib relatives from different families, leading to increased inbreeding and reduced status number. In future, parental analysis through DNA markers might be used to avoid selecting siblings from different OP families (Lambeth *et al*. 2001). The same approach has been successfully used in a recent study of (insect) open-pollinated breeding in a *Eucalyptus nitens* clonal archive (Gea *et al*. 2007).

There are opportunities for gain from intensive phenotypic selection for stiffness in 15-y or older stands of second-generation Fort Bragg, Californian origin. These stands were established using seed collected in seed stands planted at the same time as the 1959 provenance trials, and are of a top-performing provenance for growth. They form a resource from which intensive phenotypic selection for growth, form and sonic velocity can realise higher gains than from other elements of the program. Conceptually, selections from this developed land race can form a small 'Elite' breeding population that can be managed by intensive among- and within-family selection for immediate gains, especially in stiffness, to supply seed orchard parents. Selection may run down status number of the Elite population quickly without jeopardising the status number of the 'Main' breeding population.

Future seed orchards

Open-pollinated clonal seed orchards of grafts are the most efficient means of producing genetically-improved seed of Douglas-fir in quantity, and they use technologies that are well developed. They have not been without problems in British Columbia and the Pacific Northwest; graft incompatibility has been serious in North America. However, compatible-rootstock families have been successfully developed there, and these should be accessed for orchard establishment in NZ.

The immediate establishment of 'Rolling Front' clonal orchards with the better Superline A clones and the new 'stiffness' Elite selections is a key component of the new strategy. These will be progressively rogued of poorer clones and extended with grafts of the best, as indicated by assessment of the OP progeny tests. By 2008, forward selection within Superline B will add further fast-growing, high-stiffness selections to the clonal orchards.

Predicted genetic gain in the breeding population and from seed orchards

On average, basal area of offspring of unselected parents from the Californian fogbelt provenances near harvest age will show 18% superiority over NZ seed sources originally of Washington origin (Kimberley and Knowles 2002). This was demonstrated at age 29 y in replicated provenance trials with large plots on six widely-scattered sites with one to three plots per provenance.

As a part of research towards devising a new breeding strategy for radiata pine in NZ, genetic gains were deterministically simulated over a range of trait heritabilities for selection in large Main and small Elite breeding populations and from seed orchards (Shelbourne *et al*. 2007). Gains from Main populations derived from open pollination, pollen mix crosses and full-sib crossing using balanced within-family selection were highest for polycross families (equivalent to open pollination in an isolated clonal archive, e.g. Waikuku), somewhat lower from open-pollinated families in a thinned test and lowest for full-sib families. Gains from forward-selected orchards from OP, polycross and full-sib breeding populations were all very similar at different heritabilities, and gains for backward selection of the parents of the forward selections were always less than from forward selection. Results of these simulations in large Main populations support the use of open pollination that forms the basis of the new Douglas-fir strategy.

The gene resources of coastal fogbelt populations of Douglas-fir have been well utilised to select a breeding population of about 400 parent trees that will eventually recombine the adaptation and variability of a wide variety of coastal populations. There are preliminary indications from the performance of a few controlled crosses between Oregon and Californian parents that this outcrossing could generate some 'hybrid vigour'.

Conclusions

The Douglas-fir breeding program stalled because an ambitious program of polycross mating for estimation of breeding values, and pair crossing for generation turnover, in NZ-selected clones from provenance trials failed to deliver sufficient crosses and seed. The new strategy uses open pollination in the breeding population for both generation turnover and for forward and backward selection of orchard parents.

The selections of Superline A from coastal fogbelt provenances in the 1957 and 1959 provenance trials, archived at Waikuku, have recently provided seed from open pollination within the archive from natural crossing amongst a variety of coastal fogbelt populations, with some potential release of heterosis. Field trials of these families will rank the parents for roguing seed orchards and will eventually provide another generation of the breeding population from mainly within-family selection.

USA Superline B of OP families from seed collected in the native populations of coastal California and Oregon is an unrelated set of the same sort of material as in the 1959 provenance trials. Seed collected from selections in these trials will recombine

genotypes of 21 different native populations, following some selection in the NZ environment. Selection of the best parents by about 2008 and then open pollination within these progeny trials after thinning will parallel the collection of seed from the archive of Superline A, both of which will generate an improved provenance hybrid swarm. The propagation of the best of these forward selections in a clonal seed orchard, along with those of Superline A, will produce commercial seed with a greatly increased potential for growth, log quality and stiffness.

These two superlines form a solid and diverse basis for ongoing and sustainable improvement of Douglas-fir in the long term, provided they are managed skilfully through open pollinated mating and within-family selection, moderated by parentage reconstruction by DNA markers.

The new Elite population will derive largely from an adapted, advanced-generation NZ land-race, originally of Fort Bragg, California, origin that has been a top performer for growth in all trials. The intensive selection of plus trees that is possible in these extensive stands will enable substantial gains in stiffness as well as growth and form to be quickly realised from orchards. In future, intensive among- and within-family selection will provide a pre-production population from which to select orchard clones. Rolling-front establishment of seed orchards of the best clones from these three populations will provide progressively-improved seed for industry planting.

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