Breeding radiata pine - historical overview

Rowland D. Burdon[1]

Introduction

Genetic improvement has been one of the key planks of domesticating radiata pine. With the intensive plantation forestry that has been developed here, and the scale on which it has been planted as an exotic, radiata pine has become one of the most domesticated of all forest tree species. This historical review of the radiata pine breeding programme in New Zealand doubtless gives a personal viewpoint, but is intended as a backdrop for other articles in this issue of the Journal.

Quite remarkable was the degree to which radiata pine was the preferred species and yet posed obvious need and scope for genetic improvement. A high incidence of poor tree form, and certain adaptational problems, especially in the large pumiceland forests, proclaimed a need for genetic improvement. At the same time, patterns of tree-to-tree variation, especially in branching and stem straightness, strongly suggested the genetic variation that could be exploited by selective breeding. And the rapid growth and comparatively short rotations made breeding especially attractive.

Early breeding work

After some selection of outstanding trees by enthusiasts, serious operational breeding began in the early 1950s, based at the Forest Research Institute, Rotorua. It was led energetically by Ib Thulin, a pupil of the Danish tree breeding pioneer Syrach Larsen. Thulin organised very intensive selection of plus trees, outstanding looking individuals, which were documented in detail, and had seed and grafts collected. The grafts were used for controlled crossing, and establishing clonal seed orchards in the Scandinavian tradition.

After initial plus-tree selection, seed from both the original plus trees and controlled crosses made among the grafts was used for establishing progeny trials. The orchards were established with grafts of the very best-looking plus trees, which were left to interpollinate, with the idea that the orchards could be 'rogued' of the clones that failed in progeny tests to live up to their promise.

Evolving perceptions

The early breeding was based on some big assumptions. While some assumptions proved wrong, the decision to proceed without waiting to check the assumptions was basically correct. Even so, perceptions of the process of tree breeding evolved rapidly. It became appreciated that breeding was not going to end with roguing or reconstituting the fist generation of seed orchards. Rather, it was realised that breeding was going to be ongoing, with cumulative genetic improvement to be captured over successive generations. For that, and for providing for unanticipated changes in breeding goals, people came to realise that many hundreds of plus-tree selections would be needed, as would access to the full geographic range of the species.

Work on collecting and testing material from the full geographic range of the species was well underway by the mid-1960s (see Burdon 1992). In addition, a major expansion of the breeding programme took place in 1968 (Shelbourne *et al.* 1986) with selecting afresh around 600 plus trees, to provide a far broader genetic base. And, in the early 1970s the concept of a hierarchy of populations (Libby 1973) was fully and explicitly embraced (Shelbourne *et al.* 1986). At the top of the hierarchy are the seed orchards, or **production population**, with the most intensive genetic improvement but representing a comparatively limited genetic base. Underpinning that, representing slightly less genetic improvement but a considerably broader genetic base, is the **breeding population**, run on a recurrent cycle of selection, intermating, evaluation, selection, and so on; this is the main 'engine room' for providing cumulative genetic gain over generations. At the bottom of the hierarchy are the **gene resources**, representing the broadest genetic base but the lowest genetic merit. This schema is aimed at beating the typical trade-off between level of genetic improvement resulting from selection and the remaining breadth of genetic base. In effect it is a means of being able to eat one's cake, in terms of capturing genetic gain, and yet still having it in terms of genetic diversity.

These developments reflected tree breeding strategy becoming a discipline in its own right. It is easy for the unwary tree breeder to get 'painted into a corner' yet a slow and painful process to rectify that problem. The essence of a good breeding strategy is putting together a set of measures which, in conjunction, are designed to assure near-optimal outcomes in the face of various market- and biological uncertainties (Shelbourne *et al.* 1986).

Delivery of genetic gain

Getting the clonal orchards into full production was a steep and uncomfortable learning curve. Yet, by 1986 the orchards could meet all the country's needs (Shelbourne *et al.* 1986). The resulting stock had enhanced vigour, much straighter stems, far less malformation, and lighter, more regular branching, with an immediate benefit of much reducing the required planting density. Fortuitously, this self-sufficiency came when great institutional changes were afoot, calling for vigorous marketing of genetic improvement. For the marketing, demonstrating and monitoring genetic gain were very important, but had been brought well in hand by 1978 by the establishment of genetic-gain trials. These developments led to a system of

[1] *Scion Genetics, Private Bag 3020 Rotorua Mail Centre, Rotorua 3046*

seed certification whereby the seedlot numbering was both centrally coordinated and more descriptive of the properties of seedlots. This in turn led on to the *GF Plus* scheme.

Because of the demonstrated genetic gain, and the marketing, uptake of genetic improvement by industry has been extremely successful. The keen demand has been reflected in very strong price differentials according to the genetic merit of the seed. The prices for top-quality lots, however, have reflected a combination of scarcity value and the feasibility of extending such seed by multiplying the seedlings, mainly as nursery cuttings.

Breeding goals and the breed portfolio

Breeding goals have evolved over time. Initially the focus was on vigour and, above all, tree form. Selection was particularly stringent for straightness, freedom from malformation and light, wide-angled branching, which led to 'multinodal' or 'short-internode' trees. Choice of branching habit has been a major issue in the breeding programme, which does not appear to be finally settled (Burdon 2008). Selection for wood properties, however, was minimal, even though inheritance of wood properties was being researched from quite early on. Reasons for this were several. Industry personnel preferred to adapt to the available raw material (Burdon and Thulin 1966), rather than risking incorrect calls for avenues of improvement. The basic wood properties (as distinct from log quality and timber grades) of the 'old-crop' stands, planted during 1925-1935, were good. And indications of a trade-off between stem volume and wood density further inhibited any call for genetic improvement of wood properties. The appearance of *Dothistroma* in the early 1960s led to producing a *Dothistroma*-resistant breed.

A feature of the breeding programme has been the development of different breeds (Jayawickrama and Carson 2000), representing different breeding goals, in response to the range of sites where the species is grown, and the range of processes and products for which the wood is grown. Yet the original regionalisation of the breeding programme, with separate plus-tree selections and orchards for Southland and Canterbury in addition to the North Island *cum* Nelson, has proved basically unwarranted.

Wood properties to the fore

After the exhaustion of 'old crop' (1925-1935 plantings), and felling had begun in stands from the second planting boom beginning in the 1960s, wood properties came to the fore as an issue for genetic improvement (e.g. Sorensson *et al.* 1997). With major gains achieved in tree form there was scope for putting more effort into other avenues of improvement. Harvest ages have been drastically reduced, often to around 25 years, in the wake of aggressive thinning regimes, which has exposed major shortcomings in wood stiffness and stability during drying and in service. While wood properties are generally very heritable, addressing these shortcomings is not straightforward, and some active selection for wood properties is needed to avoid adverse correlated responses to selecting for growth rate. It is now appreciated that density is not the only important determinant of stiffness, microfibril angle (MfA) often being important (Walker and Butterfield 1996). Moreover, density has very little direct influence on dimensional stability which can be strongly influenced by both MfA and grain spirality. Also, the lignin chemistry of conifers in general makes chemical pulping expensive. Against these complications, however, assays for wood properties have been much refined.

Vegetative propagation and clonal forestry

The species is relatively easy to propagate vegetatively, as cuttings. Early efforts, during the 1960s, to exploit this feature focussed on trying to capture both the superior tree form of adult material and the theoretically greater genetic gains and uniformity of clonal material. However, they foundered on effects of maturation ('physiological ageing'), which made clones prohibitively difficult to mass-propagate. However, the easy propagation of young seedlings has been exploited by ***mass multiplying*** scarce seedlots of top genetic quality, in which slight maturation can be exploited to improve tree form. True clonal forestry, in which a limited number of intensively select and very well characterised clones are mass-propagated, has posed many challenges, even with the advent of in-vitro propagation systems, but it has now become operationally feasible and commercialised (Sorensson and Shelbourne 2005).

Hybridisation

The only species with which radiata pine hybridises readily is knobcone pine (*Pinus attenuata*). After promising early growth the hybrids showed extreme susceptibility to *Dothistroma*. However, hopes that they could be snow-resistant in central South Island have recently been vindicated (Dungey *et al.* in prep.).

Intraspeific hybrids of New Zealand and Guadalupe Island radiata pine have shown definite promise (Low and Smith 1997).

The rise of molecular biology

Integrating the development of molecular biology and tree breeding poses its own challenges, in allocation of resources and targeting of effort. Genetic fingerprinting is already well proven for verifying genetic identity of material, and may even obviate the need for controlled crossing. Functional genomics, and other types of '-omics', stand to inform breeding in various ways (Burdon and Wilcox 2007). Finally, genetic engineering is being pursued as both a research tool and as a means of conferring attributes that cannot readily be captured by conventional breeding. Currently its development is severely constrained by regulatory requirements, and its eventual application will doubtless need rigorous risk-management protocols.

Institutional changes

Various institutional changes have occurred since the inception of the breeding programme. An early separation within FRI into operational breeding and genetic research had come to an end by 1970. During the 1970s and early 1980s the radiata pine breeding had become a flagship programme, with several of its scientists having attained world standing, as contributors to research, methodology and breeding strategy. Inevitably, some of them moved on to other roles, but a landmark was still the publication of the Development Plan for Radiata Pine Breeding in New Zealand in 1956. The break-up of the Forest Service in 1987, and the advent of 'user pays' for research brought big changes - and tensions, especially as industry players were staking out their own Intellectual Property (IP) bases in tree improvement. At around that time the New Zealand Radiata Pine Breeding Cooperative (RPBC), involving FRI and industry, was formally constituted, and the Forest Service seed-orchard programme was vested in the newly created company, PROSEED. Further change came with privatisation of commercial State Forest during 1990-1996; FRI becoming a Crown Research Institute in 1992, with its own commercial stake in IP; the RPBC becoming a Limited Liability Company during 2000-2002; and the Foundation for Research, Science and Technology effectively imposing a consortium between FRI (now Scion) and the RPBC, in an evolving relationship. In the background, there has been the complication of ongoing changes in ownership and management of much of the plantation forest estate.

Concluding

Much has been achieved, operationally and scientifically by New Zealand's radiata pine breeding programme, but the task is necessarily ongoing. Other articles in this issue of the journal review various of the successes, and the challenges which will face future work on the genetic improvement.

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