

From plus-tree to genomic selection – new developments in breeding strategy at the Radiata Pine Breeding Company (RPBC)

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Abstract

In genetic improvement programmes, breeding strategies are reviewed periodically as breeding populations advance, research gains new insight and the latest technologies are ready to be operationally implemented. The Radiata Pine Breeding Company (RPBC) strategy was reviewed in 2018 and this paper provides an update on the latest developments at the RPBC as the company begins to implement genomics to better inform tree selection decisions.

Introduction

From its origins in a relatively small geographical region in California and the islands of Cedros and Guadalupe off the coast of Mexico (Figure 1), *Pinus radiata* D. Don has proved remarkably well adapted to a range of growing conditions in temperate regions of New Zealand, Australia and Chile, producing a versatile general purpose timber.

The breeding programme for *Pinus radiata* in New Zealand began in the early 1950s and continued for several decades under the direction of the publicly funded New Zealand Forest Research Institute (NZFRI). The Radiata Pine Breeding Company (RPBC) was formed in 2001 and the programme became more commercially focused, developing a seed certification scheme with revenue generated by royalty collection. Today, the programme holds an integral place in the forestry value chain (Figure 2). There are 16 shareholder members from New Zealand, New South Wales and Tasmania who range from germplasm producers and growers through to wood processors.

The value of improved genetics on forest productivity has been demonstrated (e.g. Kimberley et al., 2015). Unlike many commercial breeding programmes, however, there is no vertical integration of the programme itself. The RPBC has limited control of germplasm deployment, suggesting that the transfer of genetic gain from the breeding population to the production forest may be sub-optimal.

With 1.7 million ha of stocked forest plantation area in New Zealand in 2020–21, 1.5 million ha were radiata pine alone, with 100,000 ha of Douglas-fir the next most important species (NZFOA, 2021). This inevitably raises concerns over a potential over-reliance on a single



Figure 1: *Pinus radiata* native to coastal California and Mexico (Guadalupe and Cedros Islands). Monterey and Año Nuevo provenances have been found to be best suited to NZ conditions. Source: Burdon et al., 1997

species for softwood production and therefore demands consideration of risk mitigation when developing selection strategies and future breeding goals for the RPBC breeding programme.

After years of promise, the use of genomics as a selection tool is starting to be implemented in the RPBC breeding programme, which is a significant milestone given the motivation of increasing the rate and delivery of genetic gain. It therefore seems an appropriate time to review the progress of the RPBC from a historical context, as well as outlining several recent developments to advance breeding strategies for radiata pine.

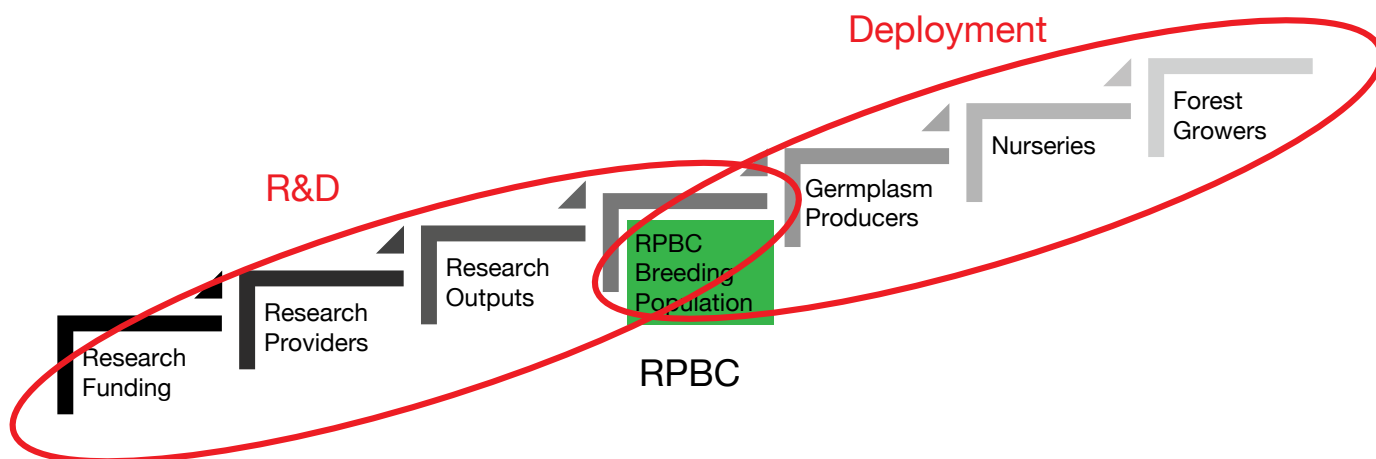


Figure 2: The RPBC's place in the NZ forestry chain

Breeding objectives

Genetic improvement is considered to be a technological development. Breeding programmes organised to drive these developments target the reduction of costs through new or improved breeding processes or increasing the value of the output. In tree breeding, for example, the objective might be to increase forest productivity in quantity or quality or improve system sustainability.

The perspective from which the objective is quantified will determine who benefits (e.g. the breeder, seed supplier, forest, sawmill, the industry or society in general). The RPBC's objective has been developed from the perspective of the forest industry as a whole. The breeding objective of the RPBC is reviewed periodically. The most recent was in 2019 (Woolaston, 2019) and places most emphasis on volume and timber stiffness. However, it also includes branching, and corewood density projected to rotation age, which for radiata pine in New Zealand is currently on average around 28 years (NZFOA, 2021).

For tree selection, it is generally considered ideal to include all traits that will contribute (directly or indirectly) to the breeding objective. In practice, a compromise must be met so traits are restricted to those that have potential for genetic change and those which are cost-effective to measure within a finite set of resources. Economic values for traits that directly contribute to the breeding objective (defined as the effect of a marginal unit change in the genetic level of a trait on the breeding objective when all other traits are kept constant) have been derived using a bio-economic model.

Each selection trait is weighted appropriately to maximise response in the objective, considering trait phenotypic and genetic parameter estimates. These weights are then combined with their estimated breeding values (EBVs), derived from trait measurements in field test trials, in a selection index (expressed in \$NPV (net present value)/ha), which is used to rank individual trees accordingly.

Traits that contribute to the selection index and are measured in test trials at selection age (five to eight years after trial establishment) include diameter at breast height (DBH), straightness of stem, branching frequency, corewood density and acoustic velocity to obtain a predicted modulus of elasticity (PME). All have low (~0.20 DBH) to moderate (~0.50 density) heritabilities. *Dothistroma septosporum*, a heritable trait, is also assessed. It is not currently included in the breeding objective but can be used as a threshold trait in parent selection.

Although the breeding population generally works with a single selection index, there are opportunities at the deployment step for seed/clonal providers to use deployment indices to emphasise other priorities for foresters (e.g. to put more influence on growth, or trade-off growth for improved log and wood properties, or target a particular end-use such as carbon capture biomass)).

Selection strategies

Early generations

At the start of the breeding programme, intensive selection of individuals from established forest stands to establish clonal seed orchards was based on observed phenotype ('plus-tree' selection). Subsequently, the screening of large numbers of progeny from less intensively selected trees by the establishment of test trials was used to identify open-pollinated (OP) progeny-tested parental candidates to form the next breeding generation.

Further collection, testing and selection took place over several decades, which has formed the genetic base for today's breeding population (for more details on these early developments see Shelbourne et al., 1986; Burdon, 1992; Burdon et al., 2008). For a comprehensive commentary, including a summary of publications and abstracts from tree breeding research in New Zealand, see Shelbourne and Carson (2019).

Stratification of the breeding population

The initial focus had been on the development of seed orchard parents and regionally adapted breeds. In a revised strategy by Shelbourne et al. (1986), the typical breeding population hierarchy was more clearly defined, with a production population underpinned by the breeding population (e.g. see Figure 3). The emphasis was still on progeny testing, but population structure had been refined and based on non-specialist 'Main' (non-regionalised) and specialised 'Elite' populations.

Selection emphasis up until now had been on growth and form, but by 1990 the importance of including wood properties was recognised. With the introduction of control-pollinated (CP) seed orchards from 1984, opportunities were identified to deliver specialist 'breeds' from elite parents and the production of deployment seedlots for specific end-uses (Carson, 1996; Jayawickrama & Carson, 2000). There were two key developments during these decades that form the basis of the RPBC breeding strategy as it is currently implemented:

- **Clonal testing**

The value of cloning of individuals within families was recognised, to improve selection precision and therefore to increase genetic gain (Shaw & Hood, 1985). Kumar (2006) demonstrated that clonal performance as cuttings appeared to be an adequate predictor of progeny seedling breeding values, and it was recommended that seed orchard selection could be made directly on this performance without recourse to progeny testing.

- **Forward selection**

Breeding strategy in tree breeding was initially based on backward selection of parents based on their progeny performance. Studies were indicating that there were advantages in trading off the longer generation intervals in backward selection, with lower selection accuracies in the forward selection of parents based on their own performance (as individuals or clones).

Based on these developments, the strategy evolved once again (Shelbourne et al., 2007; Dungey et al., 2009). The breeding population proposed was stratified further and was comprised of a large OP Main breeding population (MP) of two sublines to better manage genetic diversity (inbreeding that occurs is contained within sublines). The MP would be managed in discrete generations (i.e. all activities on the MP are completed once over a discrete phase, for example, crossing through to trial measurement and parent selection and no overlap of breeding activities).

A much smaller CP Elite production population (EP) was also proposed made up of two sublines, with clonal testing and selection implemented as a 'rolling front' (breeding activities carried out annually, for example, selection, pollination, test trial establishment

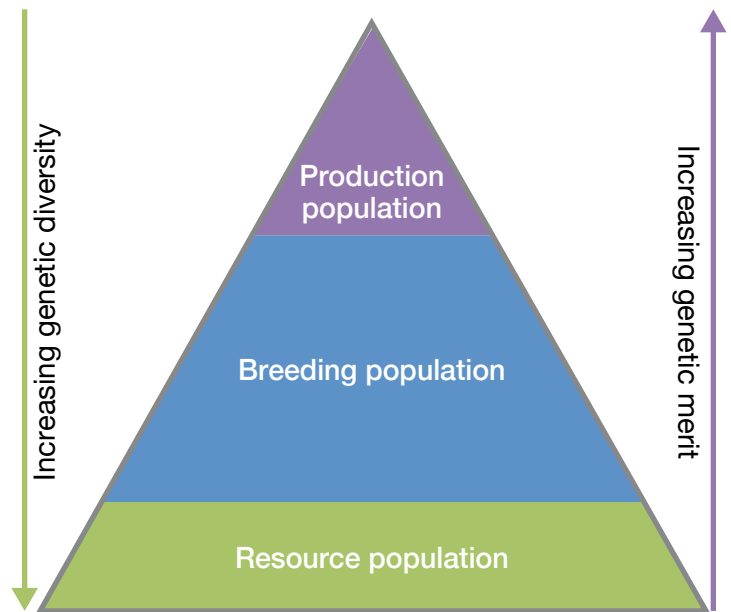


Figure 3: An illustration of breeding population structure with the production population as the top tier (including deployment genotypes), carried by the breeding population, with the genetic 'archive' conservation resource at the base

rather than as discrete generations). The best material from the EP could be propagated by grafting and being established into a seed orchard as seed deployment parents. The actual RPBC implementation is outlined in *The Breeding Management Plan* (Jefferson, 2016) and had some commonalities with what had been proposed but was not complete.

Simplifying the structure of the breeding population

After an RPBC review in 2018 (RPBC, 2018), it was decided to simplify the population structure and collapse the Elite and Mains into a single breeding population. Sublines are no longer maintained. Genetic diversity is maintained by selection algorithms, which maximise gain within certain constraints to control relatedness (e.g. Kinghorn, 2011). With the production of clones from juvenile cuttings becoming routine for nurseries, all testing is now based on vegetative clones as selection candidates.

Breeding trials are established annually in commercial forest stands on five to eight sites per year of 3–4 ha across New Zealand, NSW and Tasmania. An 'Individual Tree Model' calculates EBVs using BOLT software (Theta Solutions LLC, 2021) which also provides a platform to implement single-step genomic evaluations to obtain genomic estimated breeding values (GeBVs) for genomic selection (GS).

Breeding generations are overlapping, and new parental breeding and orchard candidates are selected from the top-performing clones based on their EBVs. These are retrieved from trial sites as scions (and pollen) and grafted for establishment into seed and/or breeding orchards.

Implementation of genomic selection

A 36k SNP (single-nucleotide polymorphism) genotyping array for radiata pine has been developed after several years of collaborative work between RPBC and Scion. It has already been used for parentage reconstruction and will be used operationally for GS (e.g. Grattapaglia & Resende, 2011) of seedlings in the nursery.

In validation studies, predictive abilities of tree performance using genotype information have been favourable, indicating the effectiveness of within-family selection of seedlings. The proposal is outlined in Figure 4. The CP orchard is producing ~10,000 seeds from selected parents to be sown in a nursery and grown to six-month-old seedlings. This material will include a proportion of somatic embryogenesis (SE) derived clones from the top parental crosses via green cones.

Needle samples are taken, and DNA extracted is and genotyped following the selection of 10%–15% of seedlings based on GeBVs and relatedness constraints. These are then entered into clonal test trials to be phenotyped and for re-training or validation of the GS model. Concurrently, a proportion of the top clonal

test trial entries will be archived. There will still be a four to five-year time lag before these are reproductively mature, but as soon as this is reached pollen can be collected and crosses made.

Archiving selections into an orchard is key if the generation interval of the breeding population is to be reduced to the target of nine years (Figure 5a), which compares with a current average generation interval of 17 years (Figure 5b). To meet the nine-year target, interventions may be required in the breeding orchard, such as top grafting.

Various scenarios of resource allocation under GS using stochastic simulation are currently being tested to compare rates of genetic gain and inbreeding. This includes alternative ways in which seed orchards could be structured under GS to enhance deployment gain. Options for various new genotyping platforms are also being considered to reduce genotyping costs. Even though SNP array genotyping costs are still considered high, an economic analysis (Evison, 2019) indicated that while the internal rate of return was sensitive to genotyping costs, the profitability of using GS was higher than for conventional selection under several current assumptions.

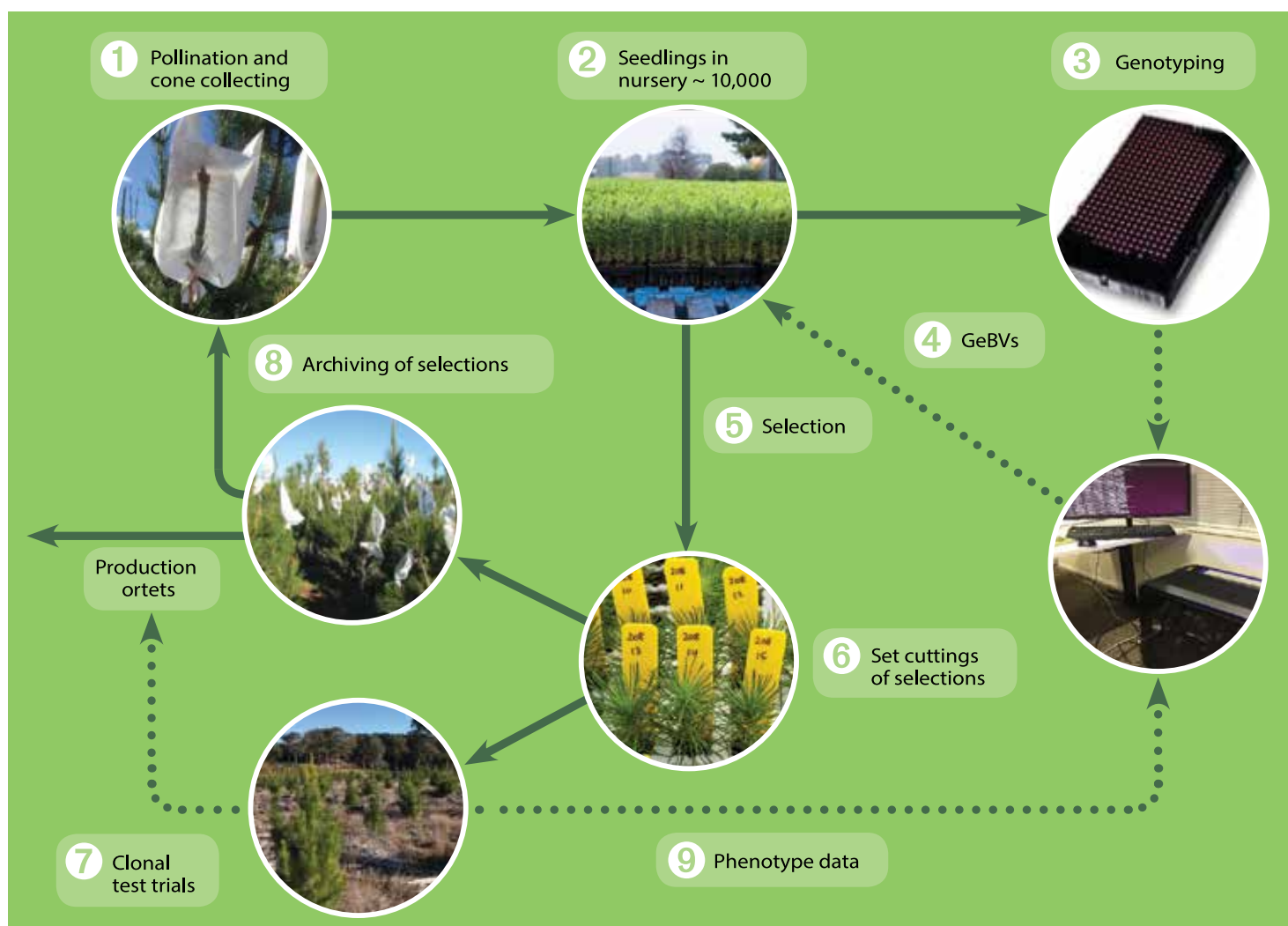


Figure 4: A proposed breeding cycle under genomic selection

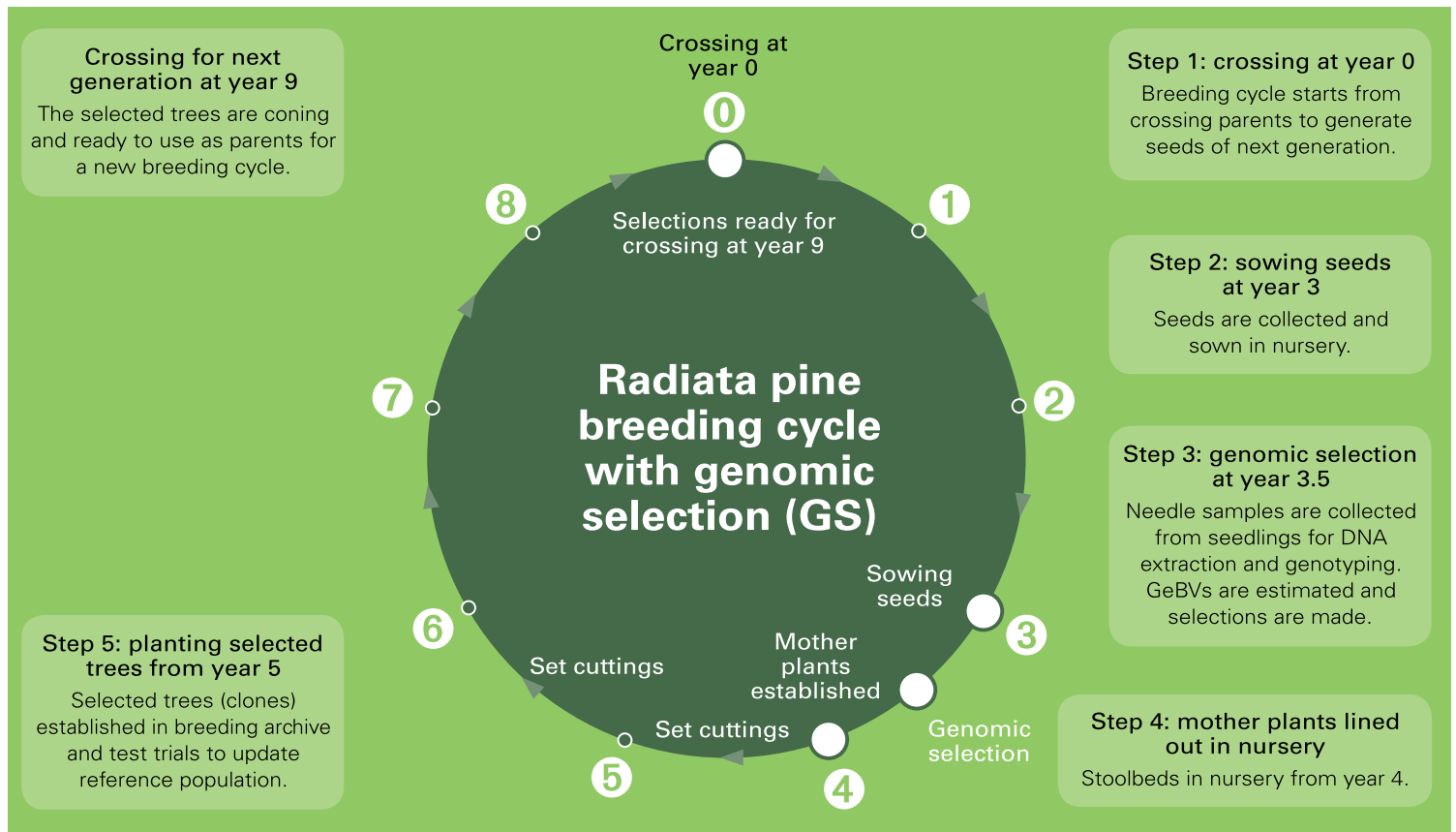


Figure 5a: Breeding cycle of nine years for radiata pine under genomic selection. Modified from Li, Y. & Dungey, H.S. 2018. PLOS ONE: doi.org/10.1371/journal.pone.0208232

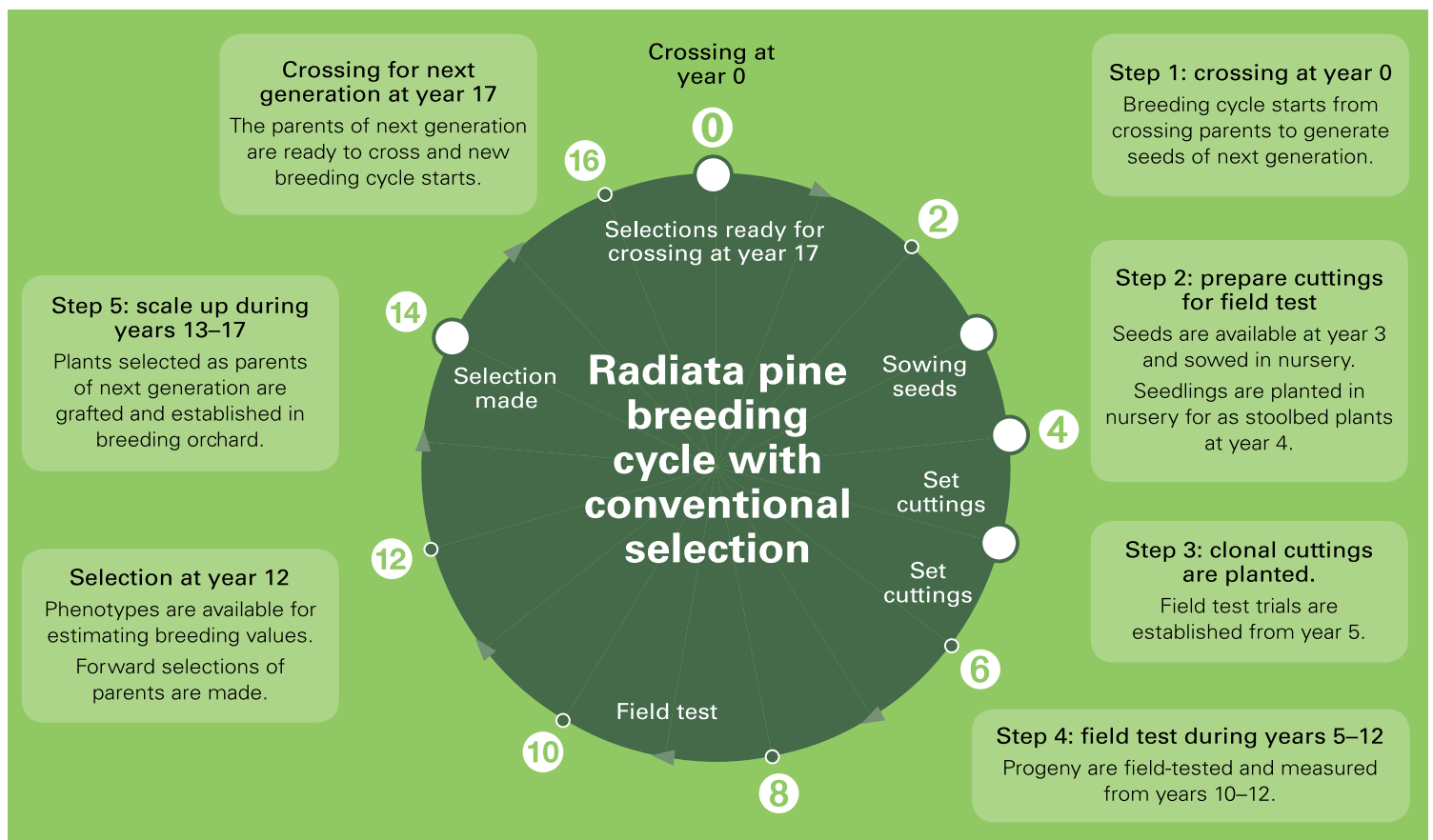


Figure 5b: Breeding cycle of 17 years for radiata pine under conventional selection. Modified from Li & Dungey (2018)

Genotype-by-environment interaction

The presence of qualitative genotype-by-environment interaction (G×E), where there is a re-ranking of genotype performance over different environments, can compromise genetic gain. Understanding the magnitude and type of G×E effects for traits helps to re-evaluate breeding strategies and improve selection efficiencies, as well as assisting in optimal deployment.

Carson (1991) found evidence of G×E effects for growth traits, but the magnitude was relatively small, and it was concluded that there was no justification in regionalising the breeding programme given the associated extra cost. In this study, testing on a small number of well-chosen sites accounted for over 90% of the predicted gain. Johnson et al. (1990) came to similar conclusions about regionalisation.

Although these studies were possibly limited in their scale, there is no convincing research to date to contradict these findings, and the RPBC multi-environment testing regime and selection strategy is built on this premise (i.e. the breeding population is non-regionalised and test trials are sited over a relatively small number (~5–8) of well-chosen and representative locations to ensure as clear a genetic signal as possible from the environmental noise and to obtain ‘average’ EBVs for all traits).

It is generally acknowledged, however, that there is a level of crossover G×E present for some traits, with growth characteristics being the most interactive. Elevation, precipitation, snow, temperature, underlying geology and prior land use have all been variously cited as important factors. A better understanding of this could be exploited at the deployment stage to improve productivity and rates of genetic gain in the production forest in addition to that achieved in the breeding population (e.g. better site matching of genotypes, particularly when deploying SE clones).

The opportunity for ‘regionalised’ breeding values for foresters is often discussed, but is not necessarily straightforward to implement, not least because ‘regions’ in New Zealand and Australia have been difficult to define. In any given arbitrary region, there can also be limited data to estimate breeding values with confidence, particularly if genetic connectedness is poor.

The approaches used by the RPBC previously have been analytical rather than descriptive in terms of environmental drivers, but there are opportunities to develop ‘envirotypes’ by grouping similar sites based on important climate and edaphic factors from principal component analysis or machine learning. Reaction norms can then be modelled to predict an individual’s breeding value as a function of the envirotype covariate. This gives a curve for each genotype and predictions in both tested and untested environments. The response curves can be used to identify high-performing and stable genotypes (general purpose) or to obtain EBVs at particular envirotypes.

Deployment lag

The RPBC has limited control over the deployment population. There is therefore a potential lag of genetic gain during translation from the breeding population to the production forest where its value is realised. Seed producers must understandably trade-off seed production considerations with the turnover of orchard parents (i.e. the lower the average age of the seed orchard, the higher the expected genetic merit, but this younger age class structure may reduce potential seed yield). This is not helped by the slow multiplication rate of orchard selections (as grafted scions) for establishment in CP seed orchards and the time radiata pine takes to reach reproductive maturity.

Operational GS in the tree breeding programme may require a re-think of the structure of seed orchards to maximise deployment gain. Breeding cycles (and genetic gain) in the breeding population will speed up under GS, but deployment gain will increasingly fall behind if turnover rate in seed orchards does not respond. For example, the rate of deployment gain could possibly be increased if there was a faster creation and turnover of smaller OP orchards based on GeBVs.

Various approaches are currently being tested using stochastic simulation of seed orchard composition. More informed decisions on selecting SE clones for production clone testing will also be made and this could, in turn, speed up deployment gains via clonal forestry (Carson et al., 2015). RPBC is currently targeting the entry of 5%–10% of the top parental crosses annually (as an ‘open nucleus’) into the SE pipeline and, alongside GS, aims to speed up deployment of improved germplasm in both New Zealand and Australia. A current industry-led research initiative overseen by the NZ Forest Growers Research aims to scale up the production of somatic clones in radiata pine.

Closing the genotype-phenotype gap

Genotyping technologies have made much progress in the last few years, and even though their transfer and application to breeding programmes has rarely matched the early promises, routine operational implementation in tree breeding programmes is now becoming a reality. Good phenotypic data is important for accurate breeding value estimation and the successful delivery of genomic technologies, but phenotyping in plant breeding has not kept up with advances in high-throughput genotyping.

Further, the lack of opportunities to feasibly measure standing trees routinely in test trials for a wider range of traits (such as height, resin pockets, spiral grain, browsing damage, timber strength, dimensional stability, fibre content, diseases and stress tolerance) at a scale required for genetic selection has been a constraint to the development of breeding objectives, targeted end-uses and GS involving new or novel traits. This phenotyping bottleneck can hinder the ability of a programme to change tack quickly if the need arises.

Tree breeders are still, for the most part, measuring the same limited number of traits using the same methods that were being used decades ago, including an over-reliance on subjective scoring for several form and disease characteristics. The collection of trial data is time-consuming and is one of the most costly operations in a tree breeding programme. New high-throughput phenotyping technologies with proximal and remote sensing using ground-based and unmanned aerial vehicle (UAV) approaches to measure growth, form, disease and physiological traits are showing promise in tree breeding.

The expectation is that these technologies, along with machine learning approaches to handle the vast amounts of data that will be collected on standing trees in single tree plots, large block trials and plantations, will develop rapidly for the scaling-up and regular capture of data. This will be an important research focus for RPBC in the next few years.

Threats from pests and diseases

There is a requirement to build resilience into the RPBC breeding programme given the uncertainties faced with a changing climate and other concerns, such as biosecurity threats. These include *Dothistroma* variants not currently found in New Zealand and Australia, *Fusarium circinatum* (pine pitch canker), *Lecanosticta acicola* (brown spot needle blight), as well as potentially invasive insects *Thaumetopoea pityocampa* (pine processionary moth) and *Lymantria dispar dispar* (European gypsy moth).

RPBC germplasm is currently being screened for some of these pests and diseases in Europe to better

understand the response. New screening methods are also required for red needle cast (*Phytophthora pluvialis*) and *Cyclaneusma* needle cast as field screening in breeding trials is unreliable. Despite these approaches to 'pre-emptive biosecurity', it is recognised that serious crop disease incursions in New Zealand in recent years have been largely caused by unforeseen agents (e.g. *Pseudomonas syringae* pv. *actinidiae* (psa) in kiwifruit and *Liberibacter* in *Solanaceae* crops).

Contingency and alternative species

There are opportunities to identify and develop potential radiata and other *Pinus* hybrids to build more resilience into the breeding programme. Unfortunately, there has been limited success in the hybridisation of *P. radiata* with other *Pinus* species to date, but *P. attenuata* x *P. radiata* is one of the few exceptions. Hybrid trials established in 1992 by NZFRI on 'semi-continental' sites have shown better growth, form and survival, largely attributed to better tolerance to snow load compared with radiata pine (Dungey et al., 2011; Paget, 2021).

RPBC is currently developing a breeding strategy for the *P. attenuata* x *P. radiata* hybrid. There is growing interest in establishing the hybrid at the margins of the radiata pine range where Douglas-fir has until recently been a preferred species on higher altitude sites. The hybrid is likely to contribute much less to wilding pine spread compared with Douglas-fir, which has had a detrimental environmental impact in some regions. The hybrid is considered as a contingency species and RPBC are currently reviewing opportunities to work with other potential contingency and alternative species, particularly radiata hybrids.

Average EBV – DBH (mm)

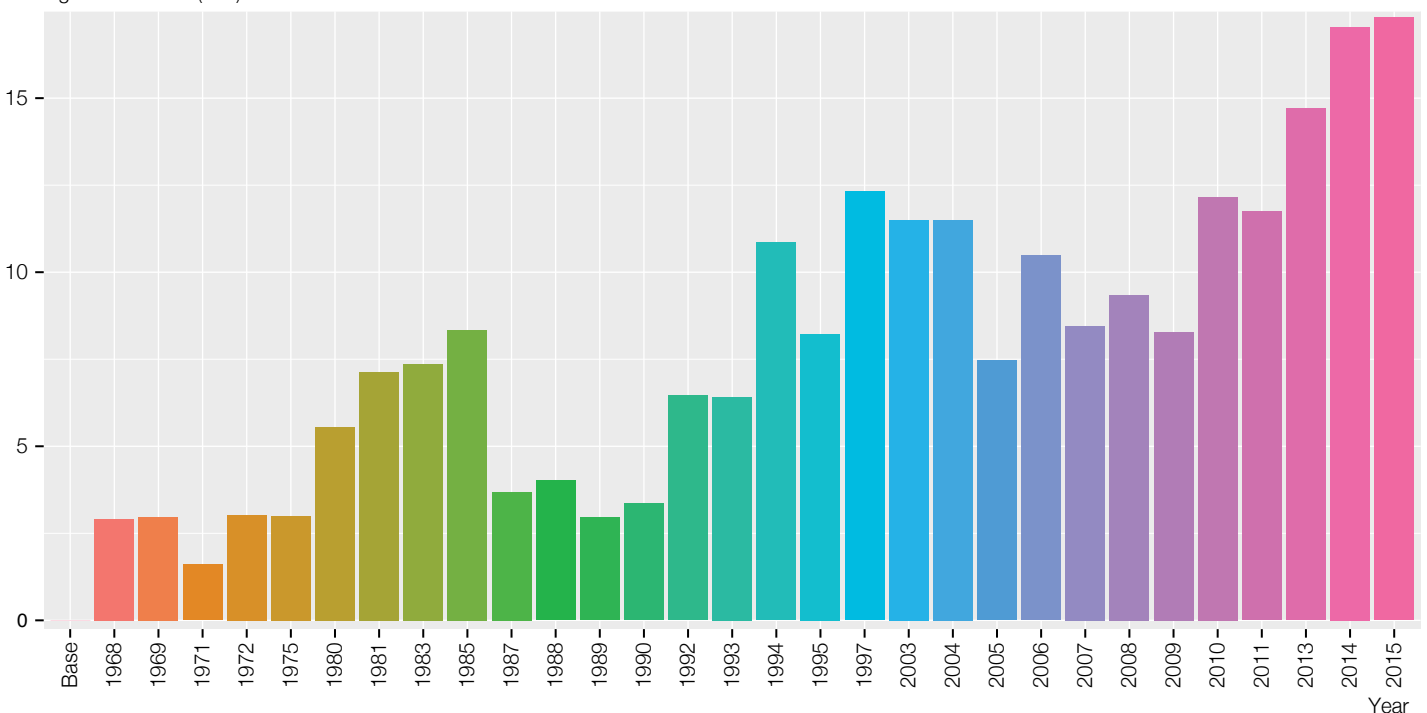


Figure 6: Trend in EBVs for diameter (mm) at breast height (DBH) in the RPBC breeding population

Proof of gain

Genetic trend in the breeding population

Improved tree form was quickly observed after the plus-tree selections of the earliest generations. With its low heritability, genetic gain in growth has been more difficult to demonstrate and wood properties did not become a focus until the 1990s. However, a positive genetic trend for DBH EBVs across years in the breeding population can be shown (Figure 6).

A trend in selection index (\$NPV/ha) can also be illustrated. Figure 7 shows the so-called 2003/04 RPBC breeding series and progenitors. This breeding series, which can be traced back to the very early plus-tree selections described earlier, forms an important part of the current breeding population.

Realised gains in large block trials

Genetic trends demonstrated in the breeding population are from breeding trial data (i.e. trials made up of small, non-contiguous single tree plots). Measuring gains from large block trials made up of commercially available seedlots, clones and unimproved seedlots is the preferred approach used to quantify realised gain. It is more comparable to a deployment setting and likely to be more meaningful for foresters.

A study of realised gain in large block trials made up of RPBC germplasm by Kimberley et al. (2015) found that a unit increase in GF Plus seed ratings, which are related to EBVs, was associated with a 1.5% increase in

volume growth rate. The magnitude of the increase, in absolute terms, was greater on more productive sites than less productive sites, but in percentage terms the increase varied little between sites or regions.

Conclusion

Breeding strategy in the RPBC programme is constantly evolving with a commitment to improving breeding efficiencies and delivering genetic gain to the New Zealand and Australian forestry sectors. Challenges such as a better understanding and exploitation of GxE effects and the routine use of new phenotyping technologies have yet to be resolved, but new opportunities (such as genomics) are now being implemented. Interested readers are also referred to Butcher (2015) for a previous, but recent, RPBC perspective.

Productivity gains from previous decades of the radiata pine breeding effort have been transferred to the production forest and the implementation of a genomic-led RPBC breeding strategy as an integral part of tree selection promises to deliver genetic gain more rapidly. Building resilience into the programme to face future market and climate challenges will require the RPBC to consider a greater range of traits, alternative species/hybrids, the development of new high-throughput measurement tools, and the implementation of new genomic applications.

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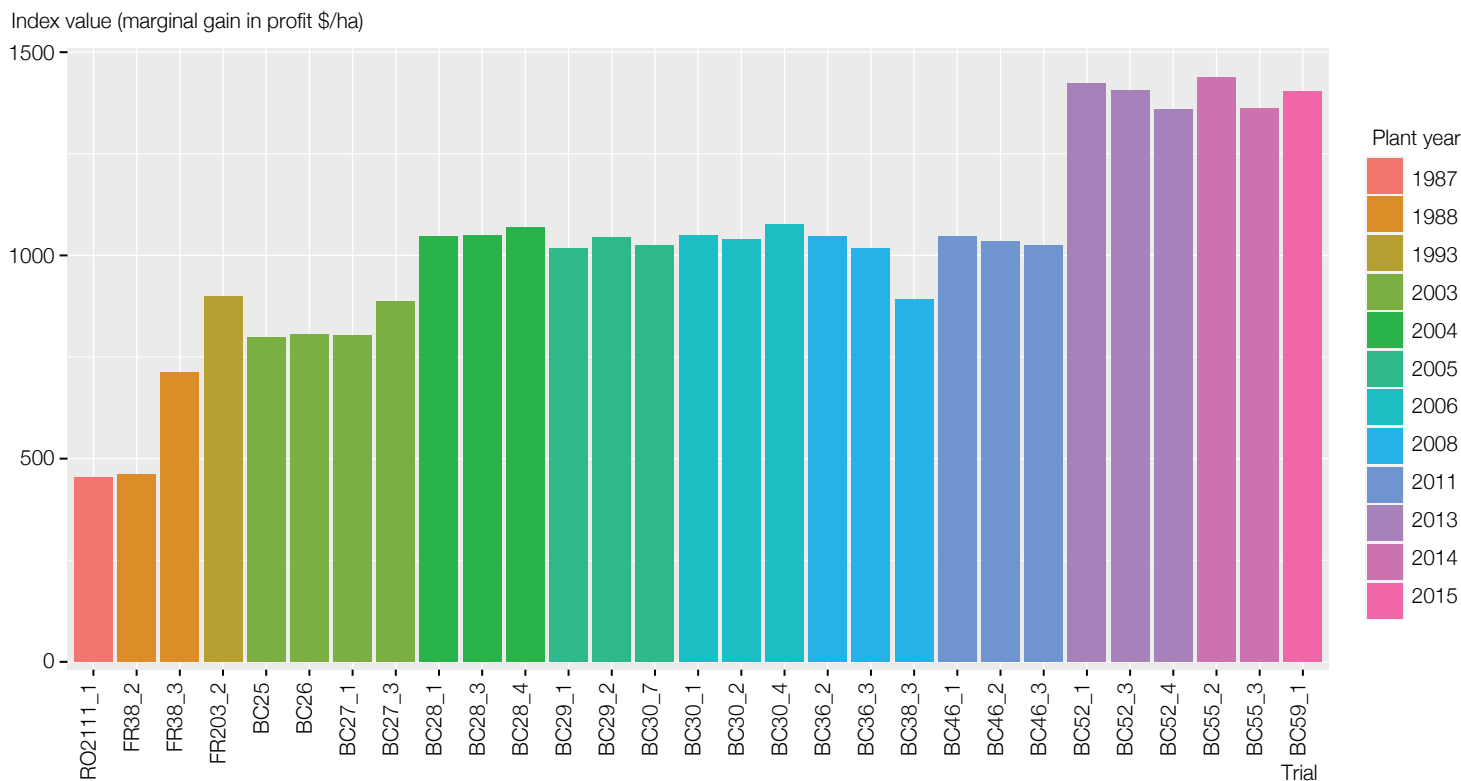


Figure 7: Trend in RPBC breeding index (\$NPV/ha) for '2003/04' series trials grouped by establishment year

years of involvement in radiata pine improvement. David Evison (University of Canterbury School of Forestry) and Jaroslav Klápště (Scion) are also gratefully acknowledged. The shareholders of the RPBC are also thanked for their ongoing support of the breeding programme.

References

- Burdon, R.D. 1992. Genetic Survey of *Pinus radiata*. 9: General Discussion and Implications for Genetic Management. *New Zealand Journal of Forestry Science*, 22 (2/3): 274–298.
- Burdon, R.D., Carson, M.J. and Shelbourne, C.J.A. 2008. Achievements in Forest Tree Genetic Improvement in Australia and New Zealand 10: *Pinus radiata* in New Zealand. *Australian Forestry*, 71(4): 263–279.
- Burdon, R.D., Firth A., Low C.B. and Miller M.A. 1997. Native Provenances of *Pinus radiata* in New Zealand: Performance and Potential. *New Zealand Forestry*, 41(4): 32–36.
- Butcher, J.A. 2015. A New Impetus for Radiata Pine Breeding – Identifying the Opportunities. *New Zealand Journal of Forestry*, 60(1): 3–7.
- Carson, M.J., Carson S.D. and Riini, C.T. 2015. Successful Varietal Forestry with Radiata Pine in New Zealand. *New Zealand Journal of Forestry*, 60(1): 8–11.
- Carson, S.D. 1991. Genotype x Environment Interaction and Optimal Number of Progeny Test Sites for Improving *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science*, 21(1): 32–49.
- Carson, S.D. 1996. Greater Specialization of Improved Seedlots in New Zealand: New Developments for Efficient Selection of Parents and Evaluation of Performance. *New Zealand Forestry*, 41: 12–17.
- Dungey, H.S., Brawner, J.T., Burger, F., Carson, M.J., Henson, M., Jefferson, P. and Matheson A.C. 2009. A New Breeding Strategy for *Pinus radiata* in New Zealand and New South Wales. *Silvae Genet*, 58(1-2): 28–38.
- Dungey, H.S., Low, C.B., Ledgard, N.J. and Stovold, G.T. 2011. Alternatives to *Pinus radiata* in the New Zealand High-Country: Early Growth and Survival of *P. radiata*, *P. attenuata* and Their F1 Hybrid. *New Zealand Journal of Forestry Science*, 41.
- Evison, D. 2019. *Scenario Analysis Under Genomic Selection. Radiata Pine Breeding Company (RPBC)*. RPBC Client Report (unpublished).
- Grattapaglia, D. and Resende, M.D.V. 2011. Genomic Selection in Forest Tree Breeding. *Tree Genetics & Genomes*, 7(2): 241–255.
- Jayawickrama, K.J.S. and Carson, M.J. 2000. A Breeding Strategy for the New Zealand Radiata Pine Breeding Cooperative. *Silvae Genetica*, 49(2): 82–89.
- Jefferson, P. 2016. *The Breeding Management Plan, Version 16-12*. RPBC Internal Report (unpublished).
- Johnson, G.R. and Burdon, R.D. 1990. Family-Site Interaction in *Pinus radiata*: Implications for Progeny Testing Strategy and Regionalised Breeding in New Zealand. *Silvae Genet*, 39(2): 55–62.
- Kimberley, M.O., Moore, J.R. and Dungey, H.S. 2015. Quantification of Realised Genetic Gain in Radiata Pine and Its Incorporation Into Growth and Yield Modelling Systems. *Canadian Journal of Forest Research*, 4(12): 1676–1687.
- Kinghorn, B.P. 2011. An Algorithm for Efficient Constrained Mate Selection. *Genetics Selection Evolution*, 43(1): 1–9.
- Kumar, S. 2006. Correlation Between Clonal Means and Open-Pollinated Seedling Progeny Means and Its Implications for Radiata Pine Breeding Strategy. *Canadian Journal of Forest Research*, 36(8): 1968–1975.
- New Zealand Forest Owners Association (NZFOA). 2021. *Facts and Figures 2020/21, NZ Plantation Forest Industry*. Retrieved from: www.nzfoa.org.nz
- Paget, M.F. 2021. *P. attenuata x P. radiata Hybrid Trial Analysis – Balmoral Station (FR352_2) and Ribbonwood Station (FR352_3)*. RPBC Internal Report (unpublished).
- Shaw, D.V. and Hood, J.V. 1985. Maximizing Gain Per Effort by Using Clonal Replicates in Genetic Tests. *Theoretical and Applied Genetics*, 71(3): 392–399.
- Shelbourne, C.J.A., Burdon, R.D., Carson, S.D., Firth, A. and Vincent, T.G. 1986. *Development Plan for Radiata Pine Breeding*. Rotorua, NZ: Forest Research Institute.
- Shelbourne, C.J.A. and Carson, M.J. 2019. *Tree Breeding and Genetics in New Zealand*. Springer International Publishing.
- Shelbourne, C.J.A., Kumar, S., Burdon, R.D., Gea, L.D. and Dungey, H.S. 2007. Deterministic Simulation of Gains for Seedling and Cloned Main and Elite Breeding Populations of *Pinus radiata* and Implications for Strategy. *Silvae Genetica*, 56(6): 259.
- Theta Solutions LLC. 2021. *An Introduction to BOLT Software for Genetic and Genomic Evaluations*. Retrieved from: www.thetasolutionsllc.com
- Radiata Pine Breeding Company (RPBC). 2018. *Radiata Pine Breeding Company (RPBC) Breeding and Deployment Strategy 2019–2024*. RPBC Client Report (unpublished).
- Woolaston, R. 2019. *RPBC Breeding Objective Review*. RPBC Client Report (unpublished).

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