RPBC®

Radiata Pine Breeding Co Ltd

Breeding and Deployment Strategy

2019 – 2024

The Radiata Pine Breeding Company Ltd

Breeding and Deployment Strategy 2019-2024

November 2018

Contact:

Brent Guild

CEO

Radiata Pine Breeding Company Ltd

Tel: 027 4453355

Email: brent.guild@rpbc.co.nz

Acknowledgements

The Board and Management of RPBC would like to express their deepest appreciation to all those who have given freely of their time to produce this document, with special thanks to those who stayed the course for the duration of the project.

Contents

Executive Summary

RPBC's Mission

"To breed elite genetic material, and provide knowledge, support and tools to continuously improve profitability for Australasian radiata pine forest owners."

- The Radiata Pine Breeding Company (RPBC) is New Zealand's only specialist radiata pine breeding company, and occupies a central position in the New Zealand forest industry's breeding supply chain.

- The RPBC is entering a new era, moving to capitalise on its strong foundations and access to unique genetic resources by embracing new breeding technologies and developing a more commercial approach to its operations.

- Our long-term aspiration is to deliver maximum genetic gain to the Australasian forest industry via well-characterised germplasm, as fast as possible and at least cost. Overall, we want to improve forest growers' profitability by increasing the rate of annual genetic gain in a cost-effective way.

- The present value of genetic improvement in trees planted from 1977-1994 in the New Zealand forest estate has been conservatively calculated at NZ$3.5billion, with further estimated gains of over NZ$5billion in trees planted since then.

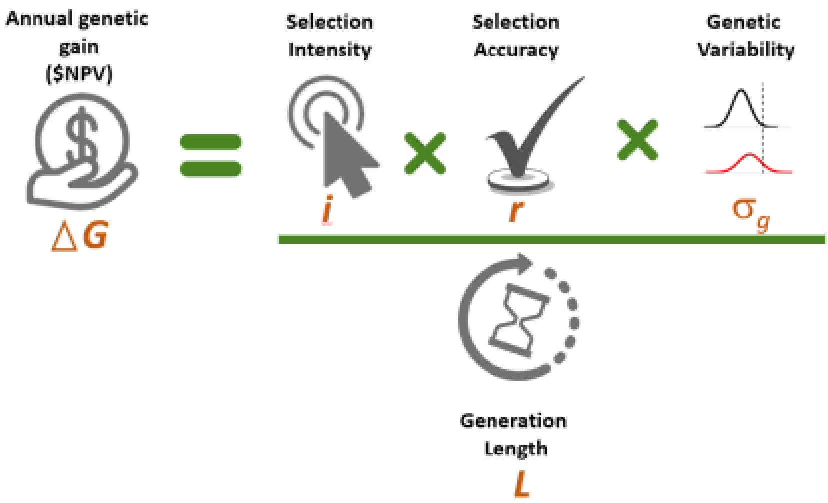
- This new Breeding and Deployment Strategy 2019-2024 describes how the RPBC plans to:

    - continue to make rapid genetic gains in the radiata pine breeding population
    - ensure that these gains are made available quickly for deployment.

- This Strategy will be complemented by Business and Operational Plans. The Breeding and Deployment Strategy focuses on our technical strategy for the next three to five years.

- Our fundamental long-term measure of success will be gains in the $NPV of material deployed to the industry. While we believe a target of a minimum of 1.5% genetic gain per annum is realistic, the key will be in ensuring that improved germplasm is deployed quickly and growers are educated in its use.

- The rate of improvement achievable in a breeding programme is determined by the 'breeder's equation', summarised as:



The breeder's equation.

- The components of the breeder's equation form the core of the RPBC's breeding strategy and are applicable whether selection is for an individual trait or combination of traits.

- Our first priority is to develop a clear understanding and definition of the breeding objective - the combination of trait changes that will lead to the greatest increase in profitability.

- Each of the other factors in the breeder's equation has an influence on the annual rate of gain in the breeding programme, and will define the RPBC's key areas of activity over the forthcoming three to five years. Through carefully planned workstreams we intend to:

    - enhance selection intensity
    - increase selection accuracy
    - manage genetic variability/diversity
    - reduce the breeding cycle, which in a tree breeding programme is comprised of the reproductive phase (selection to seedling) and the testing phase (seedling to selection)
    - ensure rapid deployment of improved germplasm.

- RPBC has invested heavily in developing genomic selection. Its application has the potential to profoundly impact on all of the elements of the breeder's equation, and genomics will form a significant component of RPBC's future focus.

- The speed of delivering genetic gain to growers is also a key factor in our strategic planning. The market must be informed about the genetic characteristics of the available material so that it can make rational deployment decisions. Hence market education is also an important part of this strategy.

- We have developed a comprehensive strategic timeline of activities, which will guide us and be regularly reviewed over the next three to five years (see page 12).

- In the short-term we propose to employ a second technical specialist, possibly on secondment, to overcome the current bottleneck which is slowing achievement of genetic gain. The intention is to create a permanent role if the secondment proves successful and finances allow.

- Recruitment of a full time person to manage the RPBC's education/marketing relationship with the deployment sector is also now deemed critical to the success of the organisation.

- In addition, we aim to collaborate with others working in the same field, and avoid overlap/duplication of effort. We intend to build and strengthen relationships with key partners in both New Zealand (for example with Scion, FGR and NZFOA) and Australia (SBTA and FWPA).

- The future RPBC will be the innovator and leader of radiata pine breeding in Australasia, by:
    - focusing our resources on enhanced breeding technologies
    - forging strong global research and development networks
    - formulating and demonstrating improved estate value
    - featuring a strong and sustainable revenue generation mechanism.

1. Introduction to the RPBC Breeding and Deployment Strategy

1.1 RPBC's Mission

"To breed elite genetic material, and provide knowledge, support and tools to continuously improve profitability for Australasian radiata pine forest owners."

Elite genetic material is improved germplasm that matches the forest regimes and end-product aspirations of both RPBC shareholders, and the broader New Zealand and Australian forest products sectors. The improved genetic material is developed and delivered through providers of seed and clonal varieties to forest owners as a result of the processes outlined in the Strategy.

RPBC's primary purpose is:

- to create and implement technological advances in genetics that will lead to greater competitiveness of the Australasian radiata pine industry. Our overall goal is to improve forest growers' profitability by increasing the rate of annual genetic gain.

We strive to do this through:

- maintaining and continually improving the radiata pine breeding population, underpinned by best-practice research and development along the tree breeding and deployment value chain.

Our mission includes:

- research and development related to propagation, deployment, and market education.

Our long-term aspiration

Our long-term aspiration is to deliver maximum genetic gain to the Australasian forest industry via well-characterised germplasm, as fast as possible and at least cost.

The future RPBC will be the innovator and leader of radiata pine breeding in Australasia, by:

- focusing our resources on enhanced breeding technologies
- forging strong global research and development networks
- formulating and demonstrating improved estate value
- featuring a strong and sustainable revenue generation mechanism.

1.2 Background to the RPBC Breeding and Deployment Strategy

RPBC's position in the radiata pine breeding supply chain

As New Zealand's only specialist radiata pine breeder, the RPBC occupies a central, critical space in the New Zealand and Australian forest industry's breeding supply chain. The company is responsible for the stewardship and ongoing improvement of some of the world's best-characterised radiata pine genetic resource. Australasian radiata pine has benefitted from some 70 years of genetic improvement, and the RPBC breeding population is now in its third and fourth cycles of selection.

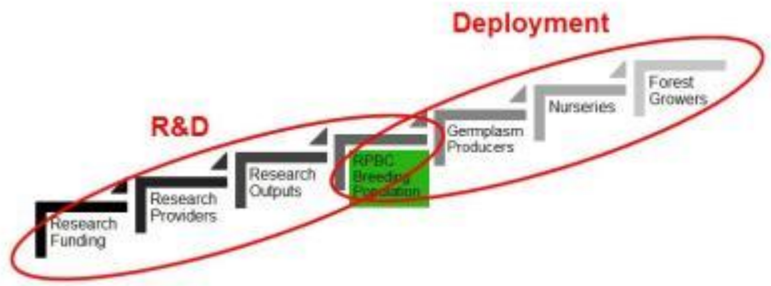


Fig 1. RPBC's central place in the breeding supply chain.

Our research and development is undertaken by a number of contracted research providers. Outputs include genetically improved germplasm (seeds, pollen or plant tissue) which are then deployed to four companies responsible for the mass scaling up of the resources e.g. in seed orchards or by propagation, and delivery to the tree nursery sector. Seedlings and clonal plants are then deployed from tree nurseries ready for planting.

The RPBC's structure means that the forest industry, represented by RPBC shareholders, plays a large part in determining the activities and outputs of the company. Improved germplasm produced is available to all radiata pine growers, not just shareholders, via commercial forestry nurseries. The RPBC operates on a not-for-profit basis, and royalties from sales of improved germplasm contribute directly to research and development costs.

1.3 The need for a new Breeding and Deployment Strategy

The RPBC has overseen major technological advancements over the past decade, with the development of genomic selection and cutting-edge data analysis methods, as well as the introduction of clonal testing. It is now time to harness these developments and focus more on the delivery of genetic gain to industry.

This new Breeding and Deployment Strategy describes how the RPBC plans to:

i. continue to make rapid genetic gains in the radiata pine breeding population
ii. ensure that these gains are made available quickly to the deployment population.

Relationship to other plans and documents

This document is one of a hierarchy of documents developed, or needing development, by RPBC as shown in Figure 2:

Fig 2. Relationship between the RPBC Business Plan, this strategy and operations plan.

Key Company Drivers: The RPBC Business Plan sets the platform for the business as a whole and takes a long-term view.

Strategic & Tactical: This Breeding and Deployment Strategy supports the Company's Business Plan with a high level technical strategy and medium-term time frame (3 – 5 years).

Operational: Implementation of the Strategy is supported by an Operational Plan. Usually developed annually, this provides details of the annual budget, trial establishment, the measurement program, and the crossing plan.

1.4 The RPBC: company description

- **Company structure**: the RPBC is a limited liability company, which operates on a not-for-profit basis.
- **Governance**: is provided by a board of directors (currently 6 members) some of whom are appointed by smaller growers, and some of whom have a board seat by virtue of the size of their organisations' plantation estate.
- **Shareholders**: the RPBC currently has 15 shareholders who represent companies throughout the value chain – from vertically-integrated forestry companies, forest management companies, and seed and planting stock producers.
- **Grower members**: are collectively responsible for over 1m ha of radiata plantations. Two of its members are based in Australia.
- **Staff**: the RPBC has a small professional team (a Chief Executive Officer and a Tree Improvement Manager).
- **Contractors**: the RPBC outsources most of its R&D, routine data storage and analysis and field operations to third party organisations, institutions and independent contractors.
- **Expert advice**: the RPBC maintains (1) a small external advisory board to provide independent science advice and guidance to the board and the CEO; and (2) a technical committee representing member organisations, supported by contractors and invited scientists.

1.5 RPBC strategic objectives

The RPBCs key strategic objective is to:

> *"Improve profitability by increasing the rate of the annual genetic gain delivered to industry"*

Our goal is to increase the annual genetic gain, expressed as Net Present Value (NPV) of our forests.

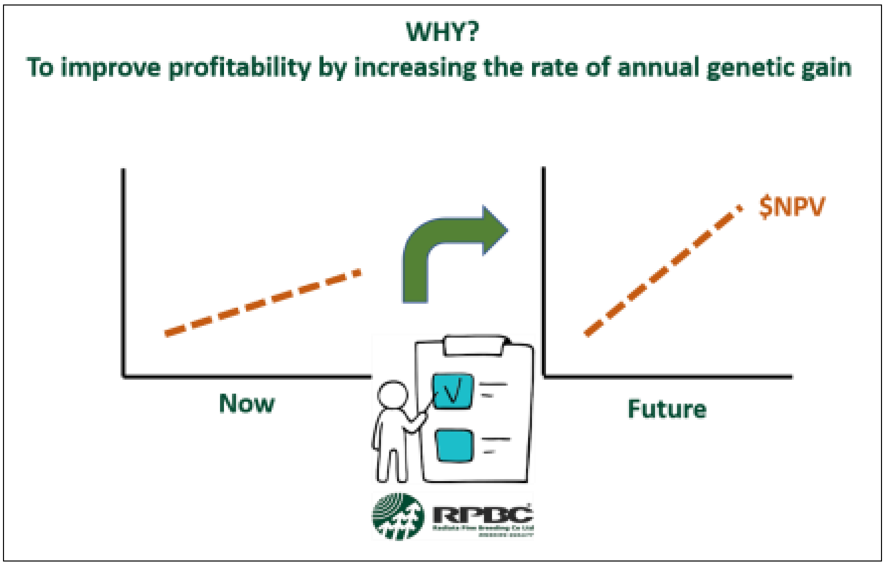


Fig 3. The aim: increasing the rate of annual genetic gain.

The value of genetic gain to the forest industry

RPBC has access to what is arguably one of the most comprehensive networks of large-plot genetic gain trials for a single species anywhere in the world. Results from these trials show that genetic gains have been impressive and compare very favourably with gains achieved in other species.

Recent studies of trial trees approaching rotation age and drawn from the RPBC breeding programme showed a realised gain for highly improved versus unimproved genotypes of 25% in stand volume, significant across all productivity site classes. Analyses involved plantings from 1977 to 1994. (Kimberley *et al*. 2015, Moore *et al.* 2017).

Using a 7% discount rate, their results indicated that:

> *"genetic improvement had increased the present value of the 1.57 million ha national radiata estate in New Zealand by NZ$3.5 billion."*

A further switch to highly improved stocks since the years in which these genotypes were developed should add an even greater increment. This could mean:

> *"the total gain in value for highly improved versus unimproved material is an estimated NZ$8.5 billion."*

These estimates were based purely on growth rate gains. Simultaneous improvements in stem form, disease resistance, wood properties and branching mean the estimated value of the gains is almost certainly too low.

Moore *et al*. (2017) estimated that the present value of the New Zealand radiata estate is predicted to increase by $NZ565m for each unit increase in GF Plus DBH rating. Kimberley *et al*. (2016) also found that wood density, which has been included in selected traits since the 1970s, had also increased significantly in improved genotypes when assessed at 20 years of age.

Compared with other species, genetic improvement programmes in trees are still in the early stages, with little evidence of decline in genetic variation. Consequently, the gains that have been achieved in the past can be expected to continue into the future at a similar rate.

> *"With the application of modern technology and with RPBC's investment in developing genomic selection methodology, projections indicate that rates of gain can potentially be more than doubled."* (Li et al. 2015).

Achieving genetic gain over time

The rate of improvement achievable in a breeding programme is determined by the 'breeder's equation', summarised as:

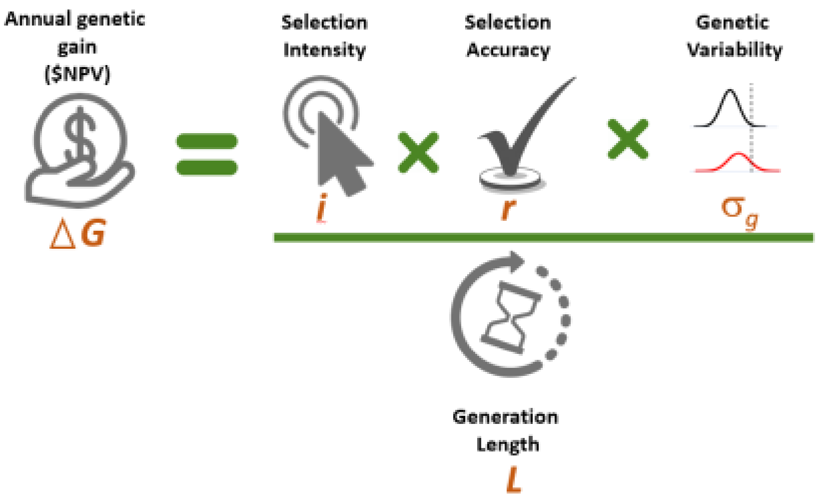


Fig 4. The breeder's equation.

This equation is applicable whether selection is for a single trait or a composite index of traits. The components of the breeder's equation form the core of the RPBC's breeding strategy; the speed of delivering genetic gain to growers is also a key factor in our strategic planning.

First and foremost, there must be clear understanding and definition of **the breeding objective** - the combination of trait changes that will lead to the greatest increase in profitability.

Each of the other factors has an influence on the annual rate of gain in the breeding programme, which can be increased by:

- Increasing **selection intensity**, which in turn is influenced by population size
- Increasing **accuracy of selection**, which can be influenced by the age and method of assessment, the ability to correct for environmental influences, and using all available information, which includes information from relatives and potentially, genotypic data
- Having access to a population with ample **genetic variability** / diversity
- Reducing the **generation length**, which in a tree breeding programme is comprised of the reproductive phase (selection to seedling) and the testing phase (seedling to selection). As the RPBC is operating in a commercial context, the deployment lag should also be as short as possible.

RPBC has invested heavily in developing **genomic selection**. Its application has the potential to profoundly impact on all of the above factors.

Finally, the market should be adequately informed about genetic characteristics of the available material so that it can make rational deployment decisions. Hence **market education** is also an important part of this strategy.

1.6 Measuring success

Success in the long-term

"Gains in the $NPV of material deployed to industry will be our long-term measure of success."

The key metric is the average $NPV of germplasm being made available to growers each year. We believe a target of a minimum 1.5% genetic gain per annum is realistic; however, it will also be essential to educate growers on options for deployment to ensure the full potential of the gains achieved by the RPBC are realised out in the forest.

The average potential $NPV of breeding material in seed orchards and clones is easy to calculate once the breeding objective has been determined.

Success in the short-term

Our short-term aspiration is:

"to become a fully self-funded business with a NZ$2m turn-over, undertaking collaborative research and managing an elite radiata pine breeding population."

There is a lot to be done over the next 24-36 months as RPBC embarks on as new era. The process for moving forward with the Breeding and Deployment Strategy is described in Section 1.7 below.

1.7 Implementation of the Breeding and Deployment Strategy

There are a number of commercial and organisational issues which will need to be addressed to ensure successful implementation of the BDS.

While the timeframes associated with delivery of various activities/projects (i.e. **WHAT** will be done, and **WHEN** it will be done by) are addressed elsewhere in this document, the question of implementation (i.e. **HOW** it will be done, and **WHO** it will be done by) is summarised here.

Funding

RPBC is currently self-funded to a level of $2.0M annually, of which $1.5M is funded by shareholders, and the balance sourced from royalties from seed and plant sales.

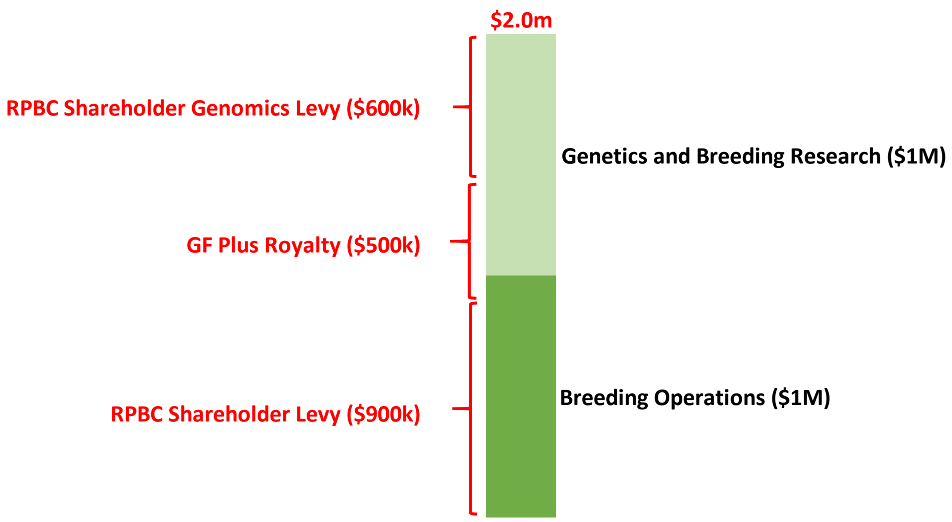


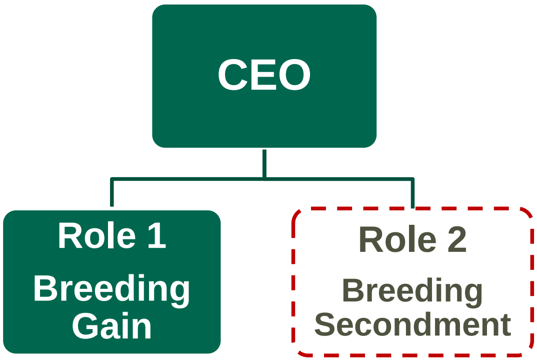
Fig 5. RPBC sources of annual income and expenditure.

While this is adequate to run a breeding operations programme alongside a modest research programme, it will not support significant investment in a new theme of research interest. That will require the support from, or partnering with, at least one other organisation. Consequently, RPBC is working now to rebuild its commercial relationships in New Zealand with Scion and Forest Growers

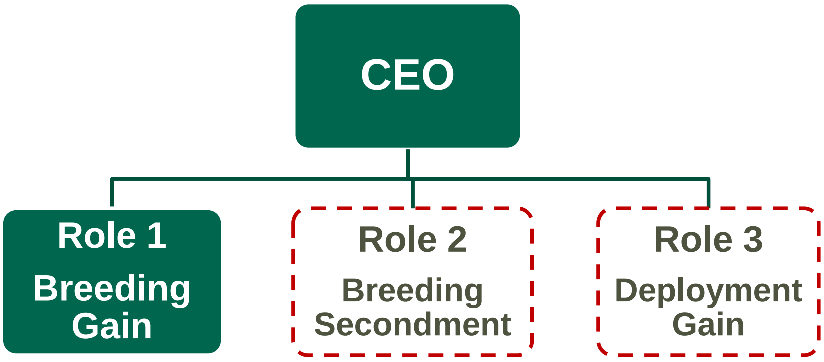
Research, as well as reaching out to prospective partners in Australia (Southern Tree Breeders Association, and Forest and Wood Products Australia).

Implementation activities: Months 1-6

Breeding Bottleneck: Many of the projects identified in the BDS are a consequence of a need to rework and strengthen the technical base at RPBC. Much of this work is constraining genetic gain at present, and so becomes an important near-term focus. It is not yet clear whether RPBC can sustain another full-time breeder resource to facilitate this work, however, an alternative is to make a short-term placement in the form of a well-managed secondment.



Market connectivity: Turning over the breeding population to deliver genetic gain, and then translating breeding gain into deployment gain (in the forest) is core business for RPBC. However, that connectivity with the forest/market has not been specifically resourced on the past. Recruitment of a full time equivalent resource to manage that relationship is now deemed critical to the success of the organisation.



Sector cohesion: Scion and NZFOA each have their own genetics strategy. Along with RPBC, these are the lead radiata pine research agencies in New Zealand and, together, need to quickly identify areas of commonality and difference, and align their various plans. A cohesive plan, with clearly identified points of linkage and demarcation, is a key gateway to leveraging third party funding in NZ. It is also represents the most efficient use of the scarce funding resources available to the sector.

Implementation activities: Months 6-24

Review progress. At the six-month mark we will reconcile progress against the project list, and will adjust the organisational structure accordingly. The secondment may have run its course, or require an extension.

In the event that the secondment is still running successfully at the 12-18 month mark, RPBC will consider recruiting for a full time role.

Implementation activities: Months 24-36

Update the Breeding and Deployment Strategy: In all likelihood RPBC will return within a two to three year timeframe to update the BDS. The rebuilt technical base will be a better platform from which to consider the future, and deployment of key workstreams, such as Genomics Selection, will be well advanced by that time.

1.8 Summary

RPBC aims to impact primarily on two parts of the breeding supply chain.

i. **On breeding and deployment populations, by:**

- reviewing the breeding objective, with a focus on quantifying the value of profit traits
- optimising selection intensity and selection accuracy
- carefully managing genetic diversity
- shortening the breeding cycle, with faster deployment.

ii. **On profitability of forest plantations, by delivering germplasm with:**

- increased productivity (more volume at same or younger age)
- improved wood quality
- reduced product variability
- enhanced disease resistance.

Ensuring that the market is better informed is a critical prerequisite to success. This strategy outlines the way in which RPBC will achieve these outcomes.

1.9 Timeline of high priority activities

The following timeline (p12) and Section 2 provide details of the proposed activities in the core areas of this strategic plan:

1. Defining the breeding objective
2. Enhancing selection intensity
3. Enhancing selection accuracy
4. Managing genetic variability
5. Shortening the breeding cycle and faster deployment
6. Genomic selection

In addition, this Strategy covers operational aspects, market education, mitigating risks, and ensuring the RPBC remains relevant to the Australasian forest industry.

Current status	Year	2019	2020	2021 » » » 2024	Future gains
GF Plus system. Economic assessment difficult. Selection process ill-defined	**Breeding objective**	Review the RPBC breeding objective	Monitor traits not included in breeding objective *(April)*	Monitor traits not included in breeding objective *(April each year)*	Gains expressed in $NPV. Value proposition defined. No unexpected correlated changes
		Ensure key genetic parameters are based on best available estimates	Collate & analyse data on disease incidence	Review need for objective to include diseases *(2021)*	
		Develop robust selection for deployment	Implement robust selection for deployment	Implement robust selection for deployment	
		Review procedures for monitoring genetic gain	Implement genetic gain monitoring procedures	Implement genetic gain monitoring procedures	
			Review the GFPlus system	Implement revised GFPlus system	
Population fragmented, loss of intensity; test trial regime not optimised	**Selection intensity**	Amalgamate sublines and remove distinction between 'Main' and 'Elite' sub-populations			Intensity/diversity trade-off optimised; optimum resource allocation in operations
		Review size of the breeding population	Review allocation of resources used in breeding operations	Implement new resource allocation for breeding operations	
		Evaluate available versions of mate selection software *(1st half 2019)*. Implement mate selection *(June)*	Implement mate selection *(June)*	Implement mate selection *(June)*	
		Review balance of seedling/clonal testing *(2nd half 2019)*	First genomic screening of seedlings	Routine genomic screening of seedlings	
Database fragmented; data wastage	**Selection accuracy**	Implement improved data collection protocols	Review trial designs, number and allocation	Implement new testing strategy	All available data used; advanced measurement techniques; genomic information used
		Refine genetic evaluation model	Implement changes in genetic evaluation model		
		Economic assessment of clonal testing and use of SE clones	Modify clonal/seedling test balance if necessary	Pedigree reconstruction	
		Evaluate parentage panels	Routine use of pedigree reconstruction		
			Review phenotyping technologies	Trial new phenotyping technologies	
Population closed; sub-optimum status number	**Genetic variability**		Validate pedigree of breeding population		Optimised selection processes; broader genetic base; archiving rationalised
			Evaluate DNA profiling for genetic grouping		
			Implement new archiving strategy		
		Develop an accession strategy	Implement new accession strategy		
			Review archiving strategy for breeding orchard and conservation		
Long generation interval; slow deployment; high OP usage	**Shorten breeding cycle and faster deployment**	Faster deployment of SO parents, CP crosses and clones	Promote deployment of CP crosses and somatic clones		Shorter generation interval with rolling front; CP seedlings and clones in common use
			Streamline delivery of new selections to seed orchards		
		Develop financially-based value proposition	Test & finalise decision support software (DSS)	Use DSS to guide deployment	
		Calculate mean $NPV of germplasm deployed to members *(2nd half 2019)*	Calculate mean $NPV of deployed germplasm *(annually)*		
			Rationalise processes for data receipt, storage and retrieval		
			Evaluate top-grafting options		
Under development	**Genomic Selection**	Evaluate SNP chip *(1st half 2019)*	Review additional SNPs for chip	Integrate genomic selection with breeding operations	GS used operationally (greatly reduced generation interval, faster deployment, higher accuracies, genetics better characterised)
		Commercialise parentage test *(1st half 2019)*			
		Training population to 12,000 individuals	Validate predictions for dothistroma, growth and form	Validate predictions for wood properties	
		Develop & test single step evaluation	Review selection accuracies	Review selection strategy for integration with GS	
				Support faster delivery of gain using genomic selection	
Exposed to trans-Tasman quarantine restrictions; disease threats not characterised	**Risk manage-ment**	Implement a strategy for managing pest and disease risks		Review role for new gene modification methods	Biosecurity issues addressed; Disease management strategies in place; Genetic diversity ensured
		Review trans-Tasman options for germplasm		Independent review of the BDS	
		Review trans-Tasman testing strategies	Implement trans-Tasman testing strategies	Implement trans-Tasman testing strategies	

2. Achieving the RPBC's objectives

2.1 The RPBC Breeding Objective

RPBC's core activity is about securing genetic improvement for industry benefit, so defining 'genetic improvement' is of central importance. Determining which traits will contribute to both ensuring plantation success and creating increased profits under future markets, and combining these in a 'breeding objective' that will achieve the desired outcome, is fundamental to implementation of the Strategy.

Actions – Breeding Objective	Priority
1. Review the RPBC breeding objective to ensure that it meets the needs of stakeholders and is technically sound, to be completed in the first half of 2019.	1
2. Ensure that the genetic parameters used to derive index coefficients and correlated responses to selection are based on the best available estimates, including the potential use of information from tree crop models.	1
3. Monitor traits that are not included in the breeding objective and apply corrective action if unfavourable changes occur.	2
4. Operationalise Robust Selection methods to support deployment decisions.	3
5. Continue to identify and support research of traits that are potentially important in certain situations	3

1. Essential 2. High priority 3. Desirable

When referring to commercially-deployed treestocks (or "germplasm"), the most appropriate descriptor of genetic merit is in units of an economic breeding objective, where aggregate genetic worth at harvest is described in discounted dollar terms. A breeding objective defines the mid-rotation and rotation-age traits that should be improved genetically because they have an important effect on economic returns; and the relative weightings that should be applied to those traits. Selection is the method by which improvement in those traits, including the agronomic traits required for growing a successful crop, is achieved.

The definition of genetic merit can vary along the production and processing chain. For example, Ivkovic *et al.* (2006) showed that the relative values of mean annual increment, sweep, branch size and modulus of elasticity vary between growers, sawmillers and integrated enterprises. Some companies also wish to see an emphasis placed on other traits, including those affecting dimensional stability of sawn timber, and corewood and other defects affecting timber appearance grades. However, James (1987) pointed out that in the long term, it is appropriate to adopt a whole of industry perspective, rather than consider any specific part of the chain in isolation. Furthermore, given the range of business models amongst RPBC's shareholders, a trait should be important for at least one of the main end uses of radiata pine (current and expected) for it to become incorporated into the breeding programme's objective.

The breeding objective should be directly identifiable as meeting the goal of an investor in a tree breeding programme. It should be able to, at least in principle, answer the question "if I invest in this breeding programme, these are the gains that I can expect, expressed as $/ha NPV for the improved material in question". The RPBC has access to a considerable amount of economic information for radiata pine in New Zealand and Australia, and is committed to using economic weights to guide breeding selection decisions.

The breeding objective has a strategic, as opposed to operational, focus. That is, it includes those traits that **will continue to be important for radiata pine for the foreseeable future**. The breeding objective reflects the idea that we want to breed for **more, better quality wood**, so it should take into account that a stand at rotation age is valued on the basis of the volume and the quality of the wood produced, accounting for associated costs.

Economic weights for radiata pine implicitly include a forecast of market conditions around 50 years in the future = 1 breeding cycle + 1 rotation (Evison and Apiolaza, 2013). Their derivation is based either on the assumption that future market requirements will be similar to those of today, and that similar quality characteristics will be required, or that they are the weighted average of all likely possibilities.

Economic weights were originally calculated for the RPBC in the mid-2000s by Ivkovic *et al*. (2006) and were reviewed by RPBC technical representatives in 2012 when it was agreed to include some emphasis on improving basic density. The draft Breeding Management Plan (Jefferson 2016) indicated that for much of this decade, the RPBC had taken the decision to: "*focus on the key traits of growth (dbh), wood density and [core]wood stiffness"*; although breeding values have also been computed for straightness. A focus on these traits remains the default position for the present – i.e. a focus on growth, corewood stiffness, density and tree form. However, the RPBC will move towards having a clearly-defined, linear economically-based breeding objective of the form:

RPBC Breeding Objective = w_1*volume + w_2*corewood stiffness + w_3*density + w_4*sweep

where the objective is expressed in dollar terms discounted to the present ($NPV), w_1, w_2, w_3, and w_4 represent the effect on profit for a unit change of the traits expressed at harvest age.

Currently, RPBC is using weighting coefficients relevant to an "average" forest grower and which were estimated from economic, tree growth and wood quality data. The assumptions made when estimating these values were most recently reviewed (Evison 2017) and were considered to still be fit for purpose; although further work is required to confirm that density should be included as a further contributor to biomass in addition to the contribution from volume.

There has also been some debate as to whether branch size and straightness (or sweep) require further selection pressure; and recently there has been a case made for including across-site stability in growth, which can now be readily quantified (Cullis *et al*. 2014, Smith and Cullis 2018).

Some shareholders have also expressed an interest in other traits not currently included in this objective (some of which are discussed below), so RPBC will aim to commission a review of the breeding objective in the first half of 2019, which will include input from relevant stakeholders and technical experts.

An important aim of that review will be to ensure that the breeding objective can be used to guide investment decisions. It must also be suitable for quantifying, in dollar terms, the mean values for any particular improved material, and therefore the expected difference (increase) in NPV compared with less-improved stock.

It is also important that RPBC is able to assess progress in the breeding programme by comparing average NPV estimates of those parents being crossed each year (or the expected merit of their progeny); and to assess progress in delivering genetic gain to industry by calculating the change in estimated NPV of the germplasm which is deployed each year. An economic breeding objective provides this capability.

Breeding objective versus deployment objective

Developing an objective that is all things to all people is not possible, so the RPBC has elected to focus on a general-purpose objective, or one that is applicable to an "average" end use. However, the RPBC recognises that shareholders have a variety of end uses in mind and consequently the RPBC breeding objective may not be perfectly aligned with the goals of some individual forest owners.

To resolve this potential misalignment, Individual companies can elect to develop and apply their own specific objective to help them identify a subset of genotypes from the breeding population that will meet their own unique deployment requirements. In other words, RPBC will focus on a single breeding objective for the breeding programme, but a variety of objectives may be used for deployment.

Breeding objective traits and selection criteria

In order to use "best bet" estimates of harvest-age economic weights for selection in the breeding population, weights for a different but related set of criteria, measured at time of selection, are used in the calculation of the selection index weights. Thus for selection decisions in the breeding population, economic weights must be translated into weights for selection criteria, measured at a younger age.

This requires the economic weights to be modified by young age – rotation age genetic correlations for each trait, as well as among-trait genetic correlations for different criteria used in the selection index (Figure 6). Although traditional tree breeding practice has been to use age-age correlations as estimated from tree breeding progeny trials, an alternative would be to use tree crop models (based on thousands of empirical measurements) to improve these estimates, and this option will be reviewed by the RPBC.

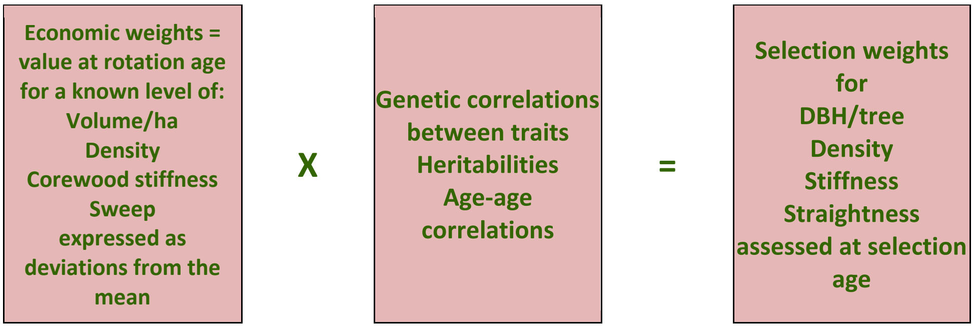


Fig 6. The implementation of multi-trait selection.

After the breeding objective is reviewed and revised as appropriate, a new selection index will be derived which can be applied to estimated breeding values for measurement criteria. This replaces the alternative used previously of applying arbitrary selection index weights, which does not utilise genetic and economic information in an optimal way.

Recognising other traits

While the current RPBC objective comprises only four traits, there needs to be continuing review of which other important traits should be included, and if not included, whether they are likely to change through correlated responses, and how they may be accounted for in the breeding programme. Common reasons for not including traits might be:

1. Current levels of expression of the trait may be acceptable, without a need for further improvement. Such traits may continue to be monitored, particularly if they are correlated with other key traits. Branching may be an example of such a trait in the RPBC programme, but this requires confirmation.

2. The trait is too hard (or too expensive) to assess. This alone is not a sufficient reason to ignore potential genetic changes in a trait resulting from selection. If reliable genetic parameters (or genomic predictions) exist, correlated changes can be predicted. If unfavourable changes are likely to occur, an appropriate economic weighting should be derived and added to the objective. Should reliable economic information not exist, an alternative is to include the trait in a “desired gains” selection index, which can effectively identify an implied economic weight. Compression wood and dimensional stability might be examples of traits worthy of future consideration in the RPBC programme.

3. The trait may also be either:
   a. Too highly variable or occurs in such low incidence across the range of growing environments that it doesn’t warrant being used in an overall breeding objective; or
   b. Expressed in a predictable manner across environments, but valued by only a small minority of growers.

   In both these cases, growers may select specific sub-sets of genotypes for deployment, based on their own requirements. Alternatively, if the traits are considered to be worthy of inclusion, further research into their economic impact and genetic characteristics may be warranted. The incidence of resin pockets or dimensional stability might fall into one of these categories.

Disease resistance

Radiata pine is susceptible to a number of diseases. Resistance to these might ultimately be considered sufficiently important to be included as traits in the overall breeding objective. These include: Dothistroma needle blight (Dothistroma), Red needle-cast (RNC), Cyclaneusma and Spring needle-cast (SNC). Of these, Dothistroma resistance is best-understood and is under strong genetic control and stable in expression across environments. However, since Dothistroma only reaches serious levels in moist environments, resistance to it is of regional importance rather than general importance across RPBC's targeted deployment plantations. (This is in fact an example of a trait in category 3, above). As a consequence and for the present at least, Dothistroma resistance will not be given an economic weight in the RPBC breeding objective, but can be included as a trait in specific deployment indexes. However, it will be monitored in the breeding programme and if it becomes apparent that resistance is deteriorating or that there aren't enough resistant genotypes becoming available for deployment, it may be necessary to add some selective pressure in the breeding programme. A similar rationale can be applied to decisions about resistance to the other important diseases, as and when their roles are sufficiently understood.

Branching and malformation

There is some evidence that branching habit and malformations (other than sweep) don't reach the threshold of importance to warrant being included in the breeding objective. Historically, the interest in branching habit has been to distinguish between uni-nodal, bi-nodal and multi-nodal trees with respect to clearcuttings grade potential. However, the RPBC has previously decided to allow the branching trait to 'float' (*i.e.* no emphasis either way), as there has been reduced interest in the long-internode habit over recent years (M. Carson, *pers comm*.). It is also worth noting that branching habit, which has been assessed in RPBC trials and ranges from uni-nodal to multi-nodal, is a different trait to branch size, which is not assessed by the RPBC, and which as a result of earlier work in NZ was rejected because of its low heritability.

Consequently, the roles of branching and malformation as components of the breeding objective and/or as selection traits are still to be clarified and will be considered in detail as part of the forthcoming review. It may be that malformation traits are be better managed by culling the worst genotypes either prior to or after ranking genotypes for potential deployment, since malformation traits tend to be poorly-inherited, and are expressed in a non-linear manner *i.e*. economic damage can be minimal for most trees, and much greater on only a minor proportion of a stand.

Dealing with uncertainty

An important consideration is that today's economic values might not adequately reflect those prevailing when harvest occurs several decades into the future. Furthermore, estimates of economic weights can vary markedly depending on the modelling assumptions used (whether a forest grower or an integrated industry is modelled, for example), and the silvicultural regime assumed. Evison and Apiolaza (2014) have outlined a method (termed "Robust Selection") for dealing with such market uncertainty when selecting trees for breeding. Essentially genotypes are ranked under a range of economic assumptions and those that consistently rank highly are chosen on the basis that they should perform well irrespective of changes in market conditions (or variations in the assumptions made during modelling). Robust selection can be carried out during breeding decisions or deployment decisions, but RPBC has elected to only apply the methodology at deployment, because in the breeding programme, the aim is to move population averages, and higher risks can be accommodated.

2.2 Enhancing Selection Intensity

Selection intensity is a function of the number of selections required as parents for the next generation, as well as the number of candidates available for selection. It cannot be considered in isolation from considerations about managing genetic diversity (which will be examined in a subsequent section). Suffice to say, however, that the RPBC has taken stock of the large, diverse and high quality genetic resource that it maintains, and has determined that a higher proportion of investment should be made on the subset of genotypes that offer the largest genetic gains in the short to medium term.

Actions - Selection Intensity	Priority
1. Amalgamate sublines and remove the distinction between "Main" and "Elite" sub-populations to create a single breeding population.	1
2. Review the allocation of resources used in breeding operations (test trials)	2
3. Evaluate available versions of mate selection software to ensure that breeding effort is concentrated on the highest-ranking genotypes while ensuring that genetic diversity is appropriately managed.	1
4. Review the concept of applying the SE Project and implement assimilation of somatic clones into the breeding population.	2
5. Implement genomic screening of candidate plants.	1

1. Essential; 2. High priority; 3. Desirable

Combining the Main and Elite populations

Historically, RPBC has used sub-lines in an attempt to delay any negative effects of increased relatedness. However, this reduces the available selection intensity and adds complexity to population management, as also has the partitioning of the population into "Main" and "Elite" sub-populations. The development of new decision-support algorithms has enabled the balance between genetic gain and genetic diversity to be managed more effectively in a single breeding population. Specialised software can design crosses in such a way that resources are focused more heavily on the best parents, without the need to explicitly stratify the population into "the best" and "the rest". Consequently, the distinction between sub-lines as well as between "Elite" and "Main" populations will be removed so that all parents are considered part of a single breeding population with a single objective.

Focussing investment on the best genetic material

The use of mate selection software will ensure that screening (or "phenotyping") and breeding effort is concentrated on the highest-ranking genotypes while ensuring that genetic diversity is appropriately managed. Once the desired population size has been determined, the challenge becomes one of optimising resource allocation across all the contributing breeding processes.

The RPBC will also continue to phenotype the best forward selections as clones. For deployment, the RPBC will give emphasis to and support delivery of genotypes that exhibit stable performance across sites, as well as options for deploying genotypes that perform well in specific regions.

Assimilating clones from the SE Project

Selections made from the set of somatic clones in the "Somatic Embryogenesis" (SE) Project will be assimilated into the breeding population, thereby expanding the cohort of candidates for selection. The SE Project was established to provide the RPBC with a rapid path to market for a portion of the Elite RPBC germplasm through the clonal providers Forest Genetics Ltd. and ArborGen Ltd. Approximately 2000 RPBC clones were propagated through somatic embryogenesis in order for them to be cryopreserved and potentially extracted and multiplied later to provide a rapid pathway to market, as well as assisting some RPBC operations. The SE Project concept will be reviewed re the potential benefits for it having a continuing role in the RPBC programme.

Genomic screening of seedlings

When genomic testing becomes fully operational, seedlings and/or clones will be screened on genotype prior to field testing (discussed later under Genomic Selection from page 28), thereby greatly increasing the selection intensity.

2.3 Enhancing Selection Accuracy

Selection accuracy is defined as the correlation between estimated breeding values and the (unknown) true breeding values. Clearly, higher accuracies are desirable provided they are not attained at the expense of other variables in the breeders' response equation.

Accuracies can be increased by good test designs, good choice of traits and data measurement and handling practices, by using information from relatives or information from correlated traits, using repeat measurements and/or through using genomic information.

Actions – Selection Accuracy	Priority
1. Ensure that trials and series are appropriately sited, well-designed and adequately connected genetically.	1
2. Implement improved data handling procedures.	1
3. Assign base ancestors to genetic groups if appropriate.	2
4. Quantify trade-off between MET models vs fitting multi-trait models with simplified GxE assumptions.	2
5. Continue using clonal testing, supported by B/C analyses	1
6. Review case for additional height measurements and the use of new phenotyping technologies	3
7. Use genomic information to increase accuracies at an early age and to enable parental reconstruction in OP crosses	1

1. Essential; 2. High priority; 3. Desirable

Data processes

A recent review of RPBC's databases has shown that there have been inconsistencies in recording of trait definitions, units of measurement and genotype identification. This is not unexpected for a data set which has been built over many decades with changing personnel. Consequently, the RPBC will improve data handling procedures by:

- Ensuring that trait definitions and best-practice data recording protocols are adequately documented and understood.
- Analysing each trial series when new data comes in.
- Checking for data errors and ensuring consistency of format.
- Estimating conventional genetic parameters (heritabilities, correlations, GxE) as well as indices for overall performance and stability.
- Checking spatial variation and other design aspects.
- Storing a clean copy of data in a single central database.

Connectedness

When candidates for selection are grown in different trials or different trial series, another important determinant of selection accuracy is the extent to which the trials are connected. If there are no common genotypes to act as a reference, environmental effects cannot be properly accounted for, thereby reducing true selection accuracies. Consequently, ensuring that linkage is established between disconnected sub-sets of the breeding population will remain a priority.

Genetic groups

Similarly, selection accuracies can be affected by whether or not ancestral genetic groups are accounted for in the pedigree structure, as these groups serve as the base(s) towards which phenotypic information is regressed during analysis. Thus pedigree structures which allocate base ancestors to different genetic groups will be investigated.

Information from correlated traits

Methods of analysis that include data from ancestors and co-lateral relatives will generally improve accuracies at virtually no additional cost if pedigree information is known, which is one of the reasons why the use of BLUP-based software to analyse multi-trait and multi-site trials has become standard practice. Similarly, multi-trait models can lift accuracies, but usually to a lesser extent, depending on the traits involved. The current method of genetic evaluation of RPBC data (Cullis *et al*. 2014) does not simultaneously use information from multiple traits, as priority is given to estimating genotype-environment interactions (in particular, for growth) at the individual trial level; and it is not computationally feasible to do both. In future, both multi-site and multi-trait models will be investigated for genetic evaluation.

Clonal testing

Shelbourne *et al*. (2007) simulated a range of breeding options using an additive genetic model and concluded that clonal testing led to greater gains than seedling testing (with equal numbers of test positions) for trait heritabilities up to 0.5. Consequently, by better exploiting the additive genetic variance that exists within families, superior gains were indicated from clone- within-family and among-family selection than by simply testing as seedlings. Apart from increasing breeding value accuracies, a major benefit of cloning an elite population is the ability to make clonally-tested forwards selections quickly available for use in orchards.

Clones also provide the potential to capture additional genetic variance from non-additive sources; although there is some evidence that the contribution of this component may decline with age, at least for growth (King *et al*. 1998). Baltunis *et al*. (2009) estimated genetic and clonal parameters using RPBC data and concluded that exploiting non-additive genetic effects in clonal varieties should generate greater gains than that typically obtainable from conventional family-based forestry of radiata pine. Similar conclusions have been reached in other tree breeding programmes.

Generating data from progeny as a means of increasing accuracies for “backwards” selection prior to deployment, is costly and time-consuming, adding substantially to the generation interval. An outcome of the previous revision of RPBC’s breeding strategy (Dungey *et al*. 2009) was the adoption of the process of clonally replicating forward selections and testing multiple ramets of the same genotype in RPBC's Elite sub-population.   After several years of experience with clonal testing, there is sufficient information available to review the benefits and costs of this approach versus seedling testing; and this will be carried out during 2019.

Using group averages

When considering accuracies, it is also worth noting that under current methods of genetic evaluation, estimated breeding values are, in theory at least, unbiased. This means that as extra information becomes available, either through progeny testing or some other means, those estimated BVs have an equal chance of either increasing or decreasing. Similarly, the average BV of a group of selections is also unbiased; but being an average, can have much higher accuracy than those of the individuals that it comprises (since the standard error of a mean is reduced according to the square root of the number of individuals contributing to that mean).   This property of group averages being more reliable has been exploited in so-called "Young Sire Programs" used by animal breeders and can be used in forestry when making deployment decisions, for example by constructing mixed-parent seedlots. It means that the additional effort and time required to achieve very high accuracies for parents is frequently not warranted.

Measuring additional heights

Rotation-age volume, a major component of the breeding objective, is a function of both tree height and stem diameter. However, diameter at breast height (DBH) is the main selection-age trait used to predict volume. DBH is known to be highly correlated with volume, but additional accuracy can be obtained by also measuring heights. Consequently, the case for measuring additional heights at selection age will be reviewed using all available information and taking into account the potential of new technologies for determine tree and stand heights.

Using genomic information

Genomic information, when supported by a sufficient quantity of calibration data, can be used to increase selection accuracies at a very young age. RPBC's strategy for implementing genomic selection will be discussed in more detail in a subsequent section (see page 28).

2.4 Managing Genetic Variability

Tree breeders have always found reasons for defending the maintenance of large breeding populations and, if costs are not an issue and everything else works as it should, it is difficult to argue against this. The advantages of a large breeding population include:

- Allows access to a larger proportion of the species' available genetic diversity/variability.
- Enables higher selection intensities to be used in each breeding and selection cycle, therefore potentially achieving higher gain.
- Reduces the risk of rare alleles being lost (e.g. for disease resistance).
- Delays the onset of relatedness among parents, and associated risks from inbreeding.

However, maintaining a large programme can reduce the focus on achieving gains/year from the 'sharp end' deployment population. Furthermore, as the RPBC's financial resources are constrained, affordability must be balanced against any risks associated with reducing population size. Management of the genetic risks is discussed in more depth below, and depends largely on optimising the pursuit of genetic gain (or more accurately, $NPV gains in the breeding objective) while ensuring that the breeding population retains sufficient genetic diversity to support further selection, and to reduce and/or delay the onset of inbreeding.

The way in which the breeding population is structured and managed is key to developing optimal gain in the heritable traits that determine forest profitability. Restructuring of the breeding population will be initiated to achieve increased gains/year and improved control of genetic diversity.

Actions – Genetic Variability	Priority
1. Combine Main and Elite sub-populations	1
2. Use mate selection software for mating decisions	1
3. Review archiving strategy for breeding orchard and conservation	1
4. Prioritise options for infusing new material and develop appropriate protocols.	3

1. Essential; 2. High priority; 3. Desirable

Combining Main & Elite Lines

The case for combining the Main and Elite lines has been outlined previously on page 19 when discussing selection intensity. As mentioned, the availability of decision-support algorithms enables the balance between genetic gain and genetic diversity to be managed more effectively in a single breeding population.

Evaluate options for infusions of new genetic material

Several of the recent changes in breeding strategy have arisen from the fact that the RPBC breeding population is now almost 'closed', in the sense that there are relatively few options for expanding genetic diversity without reverting to making selections in the relatively-unimproved native provenances. This, however, represents only one of several unexercised opportunities to access and utilise potentially-available genotypes. New accessions could come from at least four different sources, namely:

Other breeding programmes with radiata pine, including progeny-tested selections from the Forest New South Wales, Southern Tree Breeding Association and Chilean Tree Breeding Association programmes. In each case, there are potential biosecurity barriers to overcome, but these are probably resolvable with some creative planning and associated R&D investment. Accessions from these programmes are likely to provide substantial additional genetic diversity, since they will be largely unrelated to material already in the RPBC breeding population.

Other somatic clones Two NZ providers of somatic clones currently hold several thousand clonally-tested genotypes in their cryostorage facilities, archives and field trials. Although these clones represent progeny and siblings of breeding parents already in the RPBC breeding population, their introduction into the breeding population and provider seed orchards would undoubtedly create options for increasing gains/year in both the breeding and deployment populations.

Other material outside the breeding programme A similar potential exists within the NZ plantation resource, even although this resource is largely comprised of seed orchard progenies derived from the RPBC breeding programme. The NZ radiata pine estate covers 1.5 million hectares, and has been planted with over 1.2 billion individual genotypes, of which in the order of 400 million trees are expected to be present at harvest age. In terms of population genetics, this vast genetic resource will almost certainly contain a very large number of genotypes with new gene combinations and mutations, when compared to the concentrated sample of genotypes being progressed in the breeding programme. New plus-trees identified and sampled from this resource could be screened for their pedigree and performance using, for example, the new genomic SNP panel, thereby creating selection options for achieving additional gains and genetic diversity in both breeding and deployment.

Gene Resource Population As mentioned above, new selections can be made in various existing NZ and Australian trials and stands containing material from the five native provenances of radiata pine. To date this has been an unattractive option, since (with the possible exception of some genotypes from the Guadalupe provenance) these native populations have progressively fallen further behind the RPBC breeding population for their performance for the key target traits. This means that selections within them would likely need to be back-crossed with better parents for several breeding cycles before they could contribute to gains in deployment. However, these native populations offer potential contributions of valuable alleles not present in the breeding population, and such genetic variation could become critically important in combating any new serious threats from pests and diseases. Also, the new genomics tools should make it possible to short-cut the backcrossing process, such that these new alleles could be brought into play much more rapidly than otherwise.

2.5 Shortening the Breeding Cycle and Faster Deployment

The RPBC aims to deliver ongoing genetic improvement to forest owners in the shortest practicable timeframe, through multiplication of the superior genotypes, and facilitation of their rapid deployment to forest growers.

Actions – Generation Interval & Deployment Lag	Priority
1. Turn over breeding generations as quickly as possible such that annual genetic gains are maximised	1
2. Improve processes for rapid establishment of high-gain parents in orchards	1
3. Assist and incentivize seed and clonal producers to improve speed to delivery through:	
i. Providing decision support aids	2
ii. Developing a value proposition	1
iii. Utilising genomics in clonal applications	2

1. Essential; 2. High priority; 3. Desirable

The Strategy recognises genomic selection (GS) as the most important new technology capable of increasing gains/year, by increasing selection accuracy, increasing selection intensity and also reducing the generation interval. Cloning of forward selections has made an important contribution towards shortening the breeding cycle by providing more accurate breeding values at an earlier age. However, apart from GS, there has been relatively little success with early and indirect progeny screening of pines, despite numerous studies.

The quest to shorten the reproductive cycle for pines has proven equally challenging, although top-grafting offers some promise, and will be pilot tested in the RPBC breeding archive.

Given the imperative of making rapid genetic gain in the breeding population followed up by speedy deployment of improved material, the RPBC will support R&D directed at shortening the breeding and deployment processes.

Shortening the breeding cycle

Clonal testing of candidate forward selections using rooted cuttings is now accepted practice in the RPBC programme, providing benefits of higher heritability and associated greater confidence in estimated breeding values, leading to higher genetic gains/year. This increased confidence in BVs estimated from clonal testing also creates a strong case for further reduction in the progeny-testing stage of the breeding cycle, potentially from the current 8 years to 6 years from planting if the increased accuracy and shortened generation interval at the lower age more than compensate for an expected lower correlation between measurement age and harvest age. Evidence from other species and from preliminary work with radiata indicate that partial and/or full use of genomic selection will provide justification for reducing the progeny-testing cycle even further (refer to Genomic Selection from page 28).

The RPBC will consider all opportunities to shorten the breeding cycle. Apart from potentially reducing the selection age using conventional breeding with clonally-tested forward selections as parents until genomic evaluation becomes fully operational, all available information relevant to early selection will be reviewed. This includes the feasibility of wood property screening using genomic information.

Shortening the deployment lag

It can be argued that the industry has not fully capitalised on the substantial genetic gains that RPBC has made in recent years, as gains in the breeding programme have not been fully captured by the seed orchards. Further improvements in breeding strategy and operations will support better delivery, although there are still impediments to the current RPBC business model that can act to constrain the delivery of gains in deployed treestocks. Specifically, germplasm providers have insufficient incentives to upgrade the clones in their seed orchards.

The RPBC will investigate activities that will encourage seed and clonal providers to support more rapid deployment of genotypes to deliver higher gains to growers. Somatic clones represent an existing and proven technology offering the highest level of genetic gains that can be realised from the RPBC programme, with CP seedlings and cuttings the next highest option (M. Carson, *pers comm.*). Through provision of information and improved genetic material, the RPBC will support activities that increase the proportions of somatic clones and CP seedlots that are made available to its shareholders.

2.6 Genomic Selection

There are numerous examples in other plant crops of successful selection and breeding being carried out using Genomic Selection (GS). The RPBC plans to utilise genomic technologies principally for selection, and particularly, for earlier selection than can be achieved using current field and greenhouse screening methods. Such early selection is particularly valuable for economically-important traits that are either very expensive to measure using conventional methods (e.g. cell-wall galactans), and/or that take a long time to develop in field trials (e.g. heartwood development). However, earlier selection for more conventional, low-heritability traits like growth rate will also be feasible provided the genomic training population is sufficiently large.

Actions – Genomic Selection	Priority
1. Finalise details for implementation of genomic selection and incorporate these into the Breeding and Deployment Strategy by mid-2019. Essential steps include (*inter alia*): - Complete development of a commercially viable SNP (genotyping) chip - Ensure that a cost-effective parentage ascertainment process is in place - Finalise genotyping of an appropriate training population - Test and implement single step genetic evaluation processes - Complete a full benefit-cost analysis of alternative scenarios to identify the preferred implementation model, including an evaluation of clonal archiving and top-grafting.	1

1. Essential; 2. High priority; 3. Desirable

Understanding genotype-environment interactions

RPBC's ability to ramp up clonal testing has also boosted our understanding of genotype - environment interactions. Early clonal progeny trials were limited to 2 to 3 sites, but the 2003/04 elite cloned regional series is testing material across 12 different sites. This provides sufficient information to consider environmental stability as a new trait, which is also a promising candidate trait for GS.

Biosecurity implications

Importantly, GS will allow for a more rapid response to any future biosecurity or climatic threats. With the increased connectivity of existing RPBC trials, the assessment of risk and identification of tolerant or resilient germplasm will be accelerated through the use of GS.

Process for integrating GS

The integration of GS is expected to involve three stages, with the first offering immediate benefits:

1. **Improved breeding values** (BVs) through better connectivity and accurate pedigrees. Errors inherent in traditional pedigree recording will be greatly reduced or eliminated using genomic parentage testing. This will not only bring benefits for future parentage ascertainment but can be used to correct existing parentage errors. Genomic relationship matrices are also expected to improve our knowledge of connectedness across all RPBC selection series, by correcting pedigree

errors but also by revealing relationships which are not currently recognised. Importantly, it will enable open-pollinated material to be analysed in more detail.

2. Increased selection intensity through **two-step selection** and **more efficient progeny testing**. In the preliminary selection step, many thousands of progeny can be pre-screened using genomic information, ensuring that resources in the second step (progeny-testing) are focused on the very best. This offers the additional benefit of potentially reducing the deployment lag through forward selection of elite progeny based on the genomic profile and phenotypic information, not backward selection of parents based on the performance of their progeny.

3. All **selections based on GS alone** with periodic re-training. Ultimately, GS will be implemented to inform breeding decisions as well as deployment decisions (Figure 7). GS gains achieved from selection for the breeding population will ultimately flow through to the treestocks deployed in plantations, but (unless other supporting actions are taken) there will be delays in the order of 20+ years before seed and clonal producers will be able to deliver these gains. GS aimed directly at improving the deployment population can deliver gains much more quickly, but will require additional investment.

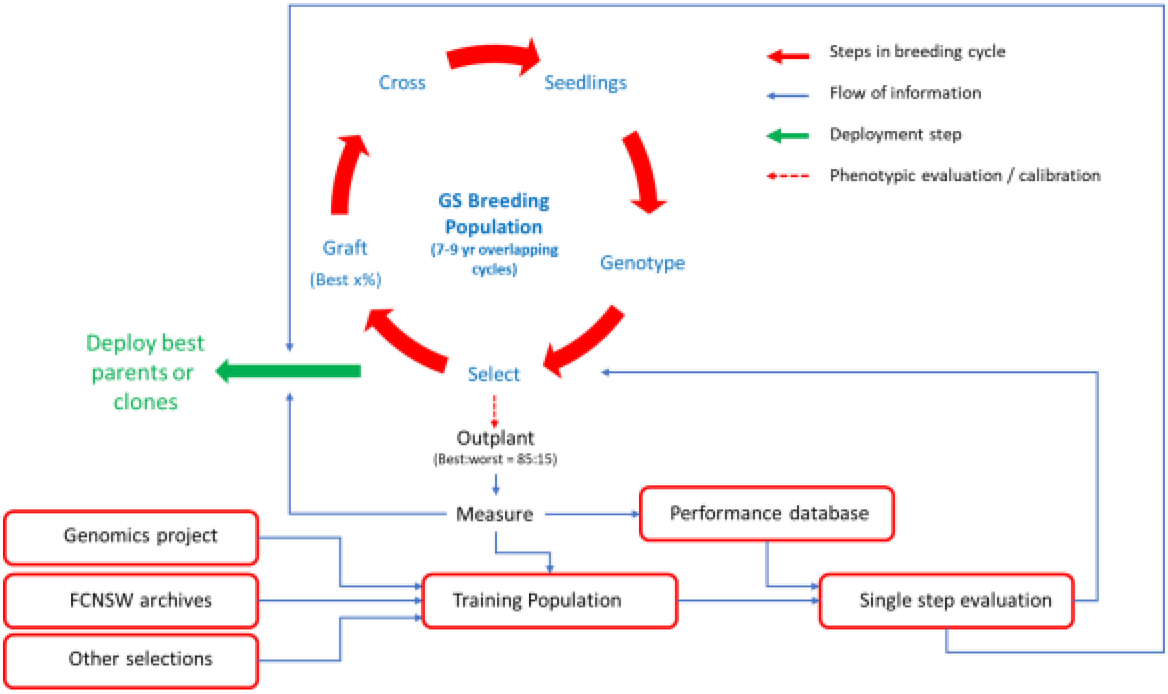


***Fig 7. Steps and flow of information in a genomic selection programme*.**

GS development is focused on the breeding population as opposed to separate training populations. The subset of genotypes used for calibration of genomic predictions will be added to each year and at this stage, it is envisaged that this will initially comprise about 16,000 genotypes. The intention is to add a further 8,000 genotypes each generation so that predictions remain current. Statistical methods for combining GS and field data are being developed and implemented (Single Step evaluation).

The RPBC is developing scenarios for resolving how to achieve the high selection intensities required for making genetic gain in the deployment population, while recognising the ‘per reaction’ costs of sampling large numbers of plants/genotypes (currently approximately NZ$37.00 and potentially as low as NZ$25.00 per DNA reaction, depending largely on scale). A recent study by Li and Dungey (2018) outlines some of these options and their benefits.

Opportunities to further accelerate the process

Breeding efforts with radiata pine in both NZ and Australia began in earnest in the 1950s and since that time a great deal has been learned about its reproductive and vegetative propagation.

In terms of sexual reproduction, radiata pine seedlings will typically produce pollen annually after about age 3-4 from seed, and viable seed annually after about age 6-7 from seed. Under some conditions pollen may be produced (or 'forced') a year or two earlier, and similarly, seed may be obtained a year or two earlier under controlled-environment conditions and/or by top-grafting of juvenile scions onto mature plants. Although applications of gibberellins have been used effectively to increase the amount of flowering and subsequent seed set, there is less evidence for this promoting earlier flowering. So in practical terms, the RPBC's ability to turn breeding generations over quickly is limited by a reproductive cycle of approx. 6-7 years, after which new selections can be crossed, possibly based on their BVs as determined using GS. If the new selections are crossed using controlled-pollination (CP) then there will be a further two-year delay before mature seed can be sown for ongoing trials and/or subjected to a further round of GS.

The expected benefit from using GS in a breeding programme is to be able to carry out a selection cycle without the delays inherent in field progeny testing. For the RPBC, this means that a new selection cycle/breeding generation might be accomplished using GS within the 7-10 year timeframe outlined above, instead of the current timeframe of up to 17 years using conventional field testing for multiple traits.

There will be obvious benefits, in terms of genetic gains/year, from the accelerating effects that will result from a reduction of around one-third of the time needed to cycle the breeding population. Such benefits will be most valuable, if the GS step can be accomplished for all the key target traits together (i.e. multi-trait selection), since any trait not selected for in the GS step will either lead to a shortfall in overall gain from that breeding cycle, or a delay in further breeding while performance for that trait is assessed in conventional screening trials. However, for rapid improvement of specific key traits and/or for a potential emergency response to a new pest or disease threat, GS may be used for single-trait breeding selection, enabling repeated generation cycles to be implemented, leading to increased breeding gains/year for that trait.

Genetic diversity

A reduction of the breeding cycle time will also introduce a more rapid approach to the onset of inbreeding in the breeding population, as well as the associated erosion of genetic diversity. However, knowing genomic relationships will facilitate better management of inbreeding by revealing relatedness which is currently hidden. Traditional management of inbreeding infers the degree of homozygosity (and therefore relatedness) by assessing the probability that two alleles at a locus are identical by descent, but genomics tools enable actual monitoring of homozygosity by assessing whether the alleles are identical by state. In other words, actual genetic architecture can be used to manage inbreeding rather than the architecture that is inferred by assumed pedigree relationships.

3. Operational Aspects

Breeding operations have been reviewed and a number of enhancements have been identified.

Resource allocation

It is essential that the RPBC allocates staff, provider, contractor and technical resources to maximise benefits. The efficiency of some operations can be improved (e.g. trial establishment and assessment, and trial designs), the intensity of others can be reduced (e.g. controlled-pollination, archiving, and trial numbers), thereby reducing costs, without incurring significant loss of benefits. Completing a resource allocation plan that achieves these efficiencies is a key Strategy recommendation.

An understanding of the costs and gains (or other benefits) associated with each breeding process and operation is a key requirement for planning resource allocation (RA). The RPBC will collate this information and simulate and compare a range of scenarios, leading to development and implementation of the RA Plan.

Rationalise trial establishment and assessment

The RA Plan will address and reduce the RPBC's exposure to financial risk. In particular, the RPBC will reduce such exposure by:

- Reducing the number of trial types by use of designs that meet multiple aims.
- Designing and siting trials to be consistent with deployment targets:
    i. Sites with poor growth will be avoided.
    ii. Flexible designs will be provided for sites with difficult terrain.
    iii. Compact, well-connected designs will be utilised for both BV and genetic gain estimation.
    iv. Investigate whether the physiological/mensurational model described by Mason *et al.* (2018) could be used to guide decisions on appropriate siting.
    v. Also investigate the use of LIDAR ('Light Detection And Ranging') for assisting decisions on appropriate siting. LIDAR datasets provide the opportunity to map field sites with unprecedented accuracy through digital terrain mapping, thus improving our picture of microsite environmental impact on GxE.

Review objectives for all current trial series & implement new trial designs

The RPBC will review and prioritise the objectives for the various types of trials that have been established in recent years, which include:

- Progeny trials using either seedlings or cuttings of cloned selections, used for advancing the breeding population.
- Production Population trials, used mainly for validating the performance of prospective seed orchard parents.
- Genetic Gain trials, used for gain validation and to enable inclusion of genetic information in tree crop models.

- Special-purpose R&D trials, used to test and/or to confirm new breeding options (e.g. Training Population trials for GS).

Some of these objectives will be addressed more efficiently and in combination in new trial designs. For example, the new 'sparse phenotyping' progeny trial designs promise to reduce costs of investment in trials, while also improving trial coverage and ensuring better connectedness across trials and trial series. 'Sparse phenotyping' in clonal trials shifts the emphasis of clonal replication within individual trials to testing replicate clones across environments in multi-environment trials (MET). This has a particular advantage when the between-location environmental variance is large relative to the local within-trial variance. This approach allows selection to be based on a broad screening of many genotypes rather than a more accurate assessment of a smaller number within the constraints of a fixed number of total test (single tree) plots. A higher rate of genetic gain can therefore be expected.

Refine genetic models

Currently the genetic models used in analysis assume that all unknown parents and ancestors are sampled from a single genetic base. The expected genetic characteristics of parents drawn from the various sources (different collections, improved vs unimproved pollen clouds) are likely to differ, and this assumption will be tested by assigning unknown parents to different genetic groups and comparing the group solutions and the impact on accuracies.

Implement annual Multi-Environment Trial (MET) analyses

Efficiency gains are coming from improved methods of breeding value estimation and improvements in progeny trial designs. University of Wollongong researchers have developed 'multiple environment trial' (MET) analysis methods for radiata pine, using the BLUP reduced animal model, combined with factor analysis. This work has provided new selection tools for separately characterising and selecting candidates for both their overall performance and stability of performance across sites, thereby offering opportunities to better manage GxE by identifying high performing and more broadly adapted genotypes. The RPBC will continue to strive towards a better understanding of G+E and improved interpretation of GxE to help identify and exploit more specifically-adapted genotypes. As described earlier, the effectiveness of these models will be compared with models similar to those currently used in TreePlan.

Use computer-based decision support tools

Tree breeding programmes have increased in complexity with increasing use of sophisticated trial designs and both multi-site and multi-trait analysis methods, and the extended pedigrees resulting from progressive breeding cycles. A recent review of RPBC's databases has revealed a number of inadequacies that have led to errors and inconsistencies in the data and pedigree files needed for multi-environment trial analysis. Furthermore, the performance database currently exists in several forms across multiple organisations. Various computer-based tools will enable the RPBC breeding programme to be managed more efficiently, including, for example, the Gemview and Katmandoo relational databases.

Develop and implement novel and cost-effective phenotyping methods

Remote sensing applications of tools like LIDAR and UAVs ('Unmanned Aerial Vehicles') are enabling more cost-efficient phenotyping of genotypes to be achieved in both trials and forest stands. This will see a transition from many of the qualitative (1 to 9 scalar) traits currently used for straightness, branching form and disease status, to more accurate quantitative data, resulting in increased accuracy in breeding for these traits.

LIDAR can already provide cost-effective data on trial plant survival and trial tree heights, as well as disease traits and nutritional status. Similar data collected on forest stands will enable tracking of the plantation performance of improved family and clonal treestocks, providing early feedback for guiding decision-making in both the RPBC Breeding and Deployment Populations. These tools will also provide early screening opportunities against new pest and disease incursions and, together with genomic pedigree reconstruction, early identification of already deployed resilient germplasm.

Implement early wood property screening

Recent work at the University of Canterbury's School of Forestry has demonstrated the potential for wood property screening of tree stem and core samples from trees as young as age two, using new laboratory techniques. Traits screened with these tools include wood basic density, grain spirality, resin content, and compression wood. These methods, if developed further, have the potential to enable earlier and more intensive screening of selection candidates, and will be reviewed for further study.

Trial assessment of corewood stiffness and wood density with new tools such as the Resistograph may prove cost-effective, and if effective will be used in combination with either the existing 'time-of-flight' Treetap tool, or its replacement.

Improve data handling procedures

This has been discussed earlier on page 21 under Selection Accuracy.

Improve QA and QC in breeding operations

The RPBC will improve quality assurance and quality control procedures by:

- Preparing standard operating procedures for its data pipeline and other key operations.
- Disseminating R script[1] used in estimating RPBC BVs for review, and store in an accessible form for RPBC administrators.
- Preparing a manual for routine genetic analyses.
- Implementing a stock management system that records and tracks all scion, pollen seed and crossing information for ready retrieval.
- Using genotyping to ascertain (and/or verify) parentage and for auditing chain of custody.
- LIDAR is also being developed for pre-screening and monitoring in nurseries, to capture accurate inventories and monitor the health of material pre-deployment.

---

[1] R is a programming language and free software environment for statistical computing and graphics that is supported by the R Foundation for Statistical Computing

4. Market Education

RPBC shareholders have identified the need for enhanced extension services to lift their capability, particularly for companies with limited staff resources to devote to tree improvement activities. The RPBC will provide information and education in support of any such extension services that may be developed within the sector.

New breeding objective

As indicated earlier, it is proposed to replace the current GF Plus™ system with an economics-based descriptor of merit, which should be more closely aligned with product outcomes. Thus in future, the emphasis will be on the contribution that improved germplasm can make on profitability at rotation age, expressed in NPV/ha. This will not only apply to informing selection decisions made in the breeding programme, but also to inform deployment. To support this, RPBC will publish estimated BVs for all stock types (i.e. OP seedlots, CP seedlots and somatic clones), where possible scaled to predict NPV gains per hectare, for use by all growers on a routine basis.

Technical backup

Assistance will also be given to growers regarding interpretation and utilisation of BVs and economic weights, as suited to their specific requirements and targeted deployment regions. Advice will be made available to growers on appropriate siting for mixed-parent seedlots, single families and somatic clones for achieving the highest returns. RPBC will also facilitate secondments for helping train members' technical staff and arranging technical workshops covering key extension topics. RPBC's extensive collection of reports, publications and bulletins will be made more accessible in a searchable on-line database.

Proof of profit

Proof of profit is an essential pre-requisite to market demand, and RPBC shareholders have identified that the quantification of genetic gain is essential to them. Forest growers use gain information in new crop investment, decisions as to what to plant, in yield tables and in determining woodflow and harvest levels.

As the result of a recent review, the RPBC has developed trial and plot-related activities that will help to validate the performance of improved mixed seedlots on a range of forest sites and regions. However, for individual somatic clones and crosses estimates of realised gains useful for validation can only be currently obtained in RPBC and company progeny trials.

Imbedding of inventory plots in trial designs could lead to improved validation. Remote sensing tools will also offer new opportunities to obtain (up to) 100% measurement samples from operational block plantings of both CP crosses and somatic clones, and these should be used by the RPBC and member companies to provide validation and feedback to the breeding selection and GF Plus™ processes. RPBC has a large number of genetic gain trials, with primarily a long-term focus. Assessment of these should be driven by a plan that optimises both the need for, and timing of information.

Computer-based decision support tools

Tree breeding programmes have increased in their complexity, with increasing use of sophisticated trial designs and both multi-site and multi-trait analysis methods, as well as the extended pedigrees resulting from progressive breeding cycles. Forest growers are being provided with decision support tools for optimising deployment of improved genotypes, with current examples including the RPBC's Genselector software and an application under development at the University of Wollongong for use with mobile devices. These will be further enhanced to suit members' requirements.

New genetic gain trial designs

The RPBC will examine and utilise benefits from new genetic gain trial designs by:

- Planting single crosses and somatic clones (vs mixed seedlots).
- Imbedding inventory plots within trials.
- Quantifying genetic gain in Dothistroma resistance, RNC and Spring Needle-cast resistance (SNC).
- Using remote and other sensing tools for both:
  1. Evaluating & validating realised gains in plantations, and
  2. Tracking plantation performance information on somatic clones and crosses to provide early feedback for breeding and deployment decision-making.

Tree crop models

Support will be given to the further development of tree crop models to properly account for overall genetic gains and for refinements such as estimation of gains from improved corewood stiffness. Growers will be assisted with relevant education, training and support for provision of improved information for valuers, that is consistent with NZIF valuation standards; and which should contribute towards recognising the value of genetic improvement of existing stands on balance sheets.

5. Financial, Biological, and Market Risk

Risk is defined as the effect of uncertainty on objectives and is scaled in terms of 'likelihood' and 'consequence'. The RPBC actively manages risk as they relate to financial, biological (e.g. disease risks) and market.

The RPBC maintains a breeding population that is sufficiently diverse to respond to future threats and opportunities in the face of market and environmental uncertainty.

Our typical process to evaluate risk is to use a Heat Map which maps likelihood (certainty) against consequence, as follows:

LIKELIHOOD	CONSEQUENCE: insignificant	minor	moderate	major	critical
almost certain	Moderate	Major	Critical	Critical	Critical
likely	Moderate	Major	Major	Critical	Critical
possible	Moderate	Moderate	Major	Major	Critical
unlikely	Minor	Moderate	Moderate	Major	Critical
rare	Minor	Minor	Moderate	Moderate	Major

Fig 8. The Likelihood-Consequence risk evaluation framework used for risk.

Once the full Operational Plan is developed, the RPBC will use that process to evaluate and manage the following risks:

Rationalise trial establishment and assessment

This is relevant to financial risk and has been discussed on page 31.

Disease risks

The RPBC will help reduce the threat posed by diseases by:

- Developing a reliable screening method to select for Red Needle Cast (RNC) resistance/tolerance.
- Obtaining assessment data for estimation of BVs for Dothistroma resistance for series not yet covered. - e.g. 397 series parents.

- Screening pre-emptively (where appropriate) for resistance to diseases not yet present in NZ, e.g. as for the IMPACT project (Devey *at al*. 1998) which used a Californian nursery and field trial study for screening RPBC seedlots for their resistance to pine pitch canker.
- Establishing protocols for rapidly screening somatic clones held in cryostorage for disease and other tolerances, so that they can be established in breeding archives, and deployed as seed from seed orchards, and/or as cuttings from clonal stoolbeds of bulked and single clones for deployment within 3-5 years of recognition of a crisis.
- Somatic clones also provide the necessary platform for deploying new genetic technologies whether responding to a threat or for making conventional breeding gains. These might include CRISPR-type gene editing and for gene transfer.

Biosecurity risks

Methods for overcoming quarantine restraints will be re-examined, in order to ensure that RPBC genetic material can be evaluated in both countries and that Australian material can contribute to the ongoing breeding population. Notably, shipping somatic clones *in vitro* from NZ to Australia should facilitate testing and deployment of exactly the same genotypes in both countries.

Loss of favourable allelles

The RPBC will make optimal use of its genetic resources by:

- Rationalising breeding and conservation archives.
- Reviewing and implementing alternative conservation strategies (e.g. seed storage of native provenances).
- Properly incorporating Australian genetic material into the breeding population.
- Continuing to assess and understand the interactions between genotype, environment and silviculture.

Possible changes in future market demand

The challenge of changing markets will be addressed by:

- Implementing robust selection in the deployment population.
- Utilising ongoing feedback obtained from Genetic Gain trials and mill studies to inform breeding decisions.

6. Maintaining Technical and Scientific Relevance

The Best Practice concept will also be applied to ensure that the RPBC continues to operate using relevant breeding technology through processes of regular review, benchmarking against other programmes and networking.

The RPBC will identify and maintain depth and breadth of research provision through:

Regular reviews

Regular reviews will be scheduled for the:

- Operational Plan (annual review, with 5-year time horizon)
- Breeding strategy (5-yearly review, with a 15-year time horizon), and
- Continued input from the External Advisory Board, with reviews scheduled every 3 years.

Benchmarking

RPBC genetic strategies will be benchmarked against other published strategies (e.g. The STBA breeding strategy, McRae *et al*. 2013).

Partnerships

RPBC will foster and further develop key working relationships with "winning" partners by:

- Supporting relationships with robust and clear contracts for technical and R&D services.
- Forging strong global R&D networks.
- Co-locating RPBC with the School of Forestry centre of learning and
    - Developing relationships with key staff
    - Utilising undergraduate and post-graduate resources
    - Coordinating guest lectures.

- Maintaining conference and network development by
    - Facilitating professional development for key staff and research stakeholders.

Appendix 1: Workstreams

Workstream 1. RPBC Breeding Objective

1.1 Review the RPBC breeding objective to ensure that it meets the needs of stakeholders and is technically sound, to be completed in the first half of 2019.

1.2 Ensure that the genetic parameters used to derive index coefficients and correlated responses to selection are based on the best available estimates, including the potential use of information from tree crop models.

1.3 Monitor traits that are not included in the breeding objective and apply corrective action if unfavourable changes occur.

1.4 Operationalise “Robust Selection” to support deployment decisions.

1.5 Continue to identify and support research of traits that are potentially important in certain situations.

Workstream 2. Increasing Selection Intensity

2.1 Amalgamate sub-lines and the remove the distinction between “Main” and “Elite” sub-populations to create a single breeding population.

2.2 Use mate selection software to ensure that breeding effort is concentrated on the highest-ranking genotypes while ensuring that genetic diversity is appropriately managed.

2.3 Assimilate clones from the “Somatic Embryogenesis” project into the breeding population.

2.4 Implement genomic screening of candidate genotypes.

Workstream 3. Improving Selection Accuracy

3.1 Ensure that trials and series are appropriately sited, well-designed and adequately connected genetically.

3.2 Improve data handling procedures.

3.3 Assign base ancestors to appropriate genetic groups.

3.4 Quantify the trade-off between fitting Multi-Environment Trial (MET) models taking full account of GxE but ignoring between-trait associations, versus fitting multi-trait models with simplified assumptions about GxE.

3.5 Continue use of clonal testing pending a review of benefits and costs.

3.6 Review the case for additional height measurements and new phenotyping technologies.

3.7 Use genomic information to increase accuracies for selection at a very young age and to enable parental reconstruction in open-pollinated crosses.

Workstream 4. Managing Genetic Diversity

4.1 Combine the Main and Elite sub-populations and use mate selection software to guide mating decisions.

4.2 Prioritise options for infusing new material and develop appropriate protocols.

4.3 Use genomic tools to characterise and help manage genetic diversity.

4.4 Review archiving strategy for breeding orchard and conservation.

Workstream 5. Shortening the Breeding Cycle and Faster Deployment

5.1 Turn over breeding generations as quickly as possible to maximise annual genetic gains.

5.2 Improve processes for rapid establishment of high-gain parents in orchards.

5.3 Identify and support research of traits not in the formal breeding objective but which affect deployment decisions.

5.4 Assist and incentivize seed and clonal producers to improve speed to delivery through providing decision support aids, developing a value proposition and utilising genomics in clonal applications.

Workstream 6. Genomics

RPBC has invested heavily in developing **Genomic Selection;** and its application has the potential to profoundly impact on Workstreams 2-5. The critical steps required for its roll-out are:

6.1 Finalise details for implementation and incorporate these into the strategy by mid-2019.

6.2 Complete development of a commercially viable SNP (genotyping) chip.

6.3 Ensure a cost-effective parentage ascertainment process is in place.

6.4 Finalise genotyping of an appropriate training population.

6.5 Test and implement single step genetic evaluation processes.

Appendix 2: Abbreviations and Acronyms

BDS	Breeding and Deployment Strategy
BLUP	Best Linear Unbiased Prediction
BV	Breeding Value
CEO	Chief Executive Officer
CP	Controlled Pollinated
CRISPR	Clustered Regularly Interspaced Short Palindromic Repeats
DBH	Diameter at Breast Height
DNA	Deoxyribonucleic Acid
GS	Genomic Selection
GxE	Genotype-environment interaction
LIDAR	Light Detection and Ranging
MET	Multi-Environment Trial(s)
NPV	Net Present Value (also appears as $NPV)
NZIF	New Zealand Institute of Forestry
OP	Open Pollinated
QA	Quality Assurance
QC	Quality Control
R&D	Research and Development
RNC	Red Needle-Cast
RPBC	Radiata Pine Breeding Company Ltd
SE	Somatic Embryogenesis
SNC	Spring Needle-Cast
SNP	Single Nucleotide Polymorphism
UAV	Unmanned Aerial Vehicles

Appendix 3: References

Baltunis, B.S., Wu, H.X., Dungey, H.S., Mullin, T.J. and Brawner, J.T. (2009) "Comparisons of genetic parameters and clonal value predictions from clonal trials and seedling base population trials of radiata pine." Tree Genetics & Genomes **5**:269–278

Burdon, R.D. and J.T. Miller (1992): Introduced forest trees in New Zealand: recognition, role and seed source. 12. Radiata pine (Pinus radiata D. Don). New Zealand Forest Research Institute Bulletin 124/12.

Butcher, J.A. (2015). "A new impetus for radiata pine breeding – identifying the opportunities." NZ Journal of Forestry, **60**: 3-7.

Cullis, B. R., Jefferson, P., Thompson, R. and Smith, A. (2014). "Factor analytic and reduced animal models for the investigation of additive genotype-by-environment interaction in outcrossing plant species with application to a Pinus radiata breeding programme." Theoretical and Applied Genetics **127**, 2193-2210.

Devey, M., Matheson, C.A. and Gordon, T.R. (1998). "Current and potential impacts of pitch canker in radiata pine: Proceedings of the IMPACT Monterey Workshop", Monterey, California, 30 November to 3 December 1998. CSIRO Forestry and Forest Products Technical Report 112

Dungey, H.S., Brawner, J.T., Burger, F., Carson, M., Henson, M., Jefferson, P. and Matheson, A.C. (2009). "A New Breeding Strategy for Pinus radiata in New Zealand and New South Wales". Silvae Genetica **58**: 28-38.

Evison, D.C. (2017). "Use of economic weights in RPBC for deployment of new germplasm." Radiata Pine Breeding Company Ltd. (RPBC) Report. August 2017.

Evison, D.C. and Apiolaza, L.A. (2013). "Specification and use of economic weights in breeding selection decisions." Radiata Pine Breeding Company Ltd. (RPBC) Report 20. January 2013.

Evison, D.C. and Apiolaza, L.A. (2014). "Field evaluation of individual trees identified using robust selection based on breeding values and economic information." Radiata Pine Breeding Company Ltd. (RPBC) Report 31. December 2014.

Evison, D.C. and Apiolaza, L.A. (2015). "Incorporating economic weights into radiata pine breeding selection decisions." Canadian Journal of Forest Research **45**: 135-140.

Ivkovic´, M., Kumar, S., and Wu, H. (2006). "Development of breeding objectives for structural and appearance products: bioeconomic model and economic weights for structure timber production in New Zealand." Radiata Pine Breeding Company Ltd. (RPBC) Client Report IO003 (unpublished).

James, J.W. (1987). "Breeding objectives for the Merino industry: an academic perspective." In: Merino Improvement Programs in Australia. Australian Wool Corporation. ed. B.J. McGuirk pp. 19-24.

Jefferson, P. (2016). “The Breeding Management Plan version 16-12.” Draft Radiata Pine Breeding Company Ltd. (RPBC) Report, December 5, 2016.

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 **45**: 1676–1687

Kimberley, M.O., Moore, J.R. and Dungey, H.S. (2016). “Modelling the effects of genetic improvement on radiata pine wood density”. New Zealand Journal of Forestry Science 46:8.

King, J.N., Carson, M.J. and Johnson, G.R. (1998). “Analysis of disconnected diallel mating designs II: results from a third generation progeny test of the New Zealand radiata pine improvement programme.” Silvae Genetica **47**: 80-87.

Li, Y. and Dungey, H.S. (2018). “Expected benefit of genomic selection over forward selection in conifer breeding and deployment.” [Submitted to PLOS One].

Li, Y., Dungey, H.S., Apiolaza, L.A. and Evison, D. (2015). “Expected benefit of genomic selection over forward selection in radiata pine breeding and deployment.” Report No. RPBC GS 7 30 May 2015.

Mason, E.G., Holmström, E. and Nilsson, U. (2018). “Using hybrid physiological/mensurational modelling to predict site index of *Pinus sylvestris* L. in Sweden: a pilot study.” Scandinavian Journal of Forest Research **33**: 147-154. http://dx.doi.org/10.1080/02827581.2017.1348539

Moore, J.R., Dungey, H.S., Kimberley, M.O., Stovold, T. and Buck, K. (2017). “Proof of genetic gain: an analysis for the RPBC.” Radiata Pine Breeding Company Ltd. (RPBC) Report. November 2017.

McRae, T.A., Buxton, P.A., Pilbeam, D.J., Dutkowski, G.W., Kerr, R.J., Ivkovic, M. Wu, H. (2013) “Breeding of radiata pine in Australia”. Forest Genetics 2013, Whistler, Canada. http://www.stba.com.au/cms/doc?id=5f8ecc1e. (Accessed 1 July 2018).

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**: 259-270.

Smith, A.B and Cullis, B.R. (2018). “Plant breeding selection tools built on factor analytic mixed models for multi-environment trial data”. Euphytica (2018):218-243. https://doi.org/10.1007/s10681-018-2220-5