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Breeding Radiata Pine to Maximise Profits by Incorporating Risk Traits

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Breeding Radiata Pine to Maximise Profits by Incorporating Risk Traits

Prepared for

Forest & Wood Products Australia

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Executive Summary

Objective

The main objectives of this project were to drive the economic weights for drought, Essigella pine aphid, Dothistroma needle blight and Fusarium pitch canker resistance, to estimate quantitative genetic parameters including heritabilities and correlations, and to derive selection indices according to site hazard ratings that can be used for selection of radiata pine genotypes with superior resistance to current and potential risks.

Key Results

Drought resistance and early growth Climate data from 134 radiata pine progeny trials, covering a significant range of radiata pine plantations were collated, and drought prone sites were identified based on the climate variables and bio-climatic indices. Narrow-sense heritability for survival on drought prone sites was low to moderate (median $h^2 = 0.12$). Dominance proportion parameter was higher than heritability (median $d^2 = 0.18$). When survival was included as an early selection trait and a breeding objective trait there was an improvement in early age survival (<5 years) of 4.7%, 5.4% and 6.6%, for low, medium and high drought hazard rating, respectively. The drought resistant genotypes could form a basis for molecular genetic studies aiming to improve water use efficiency. Data should be obtained from assessments of more recently planted trials targeting dry sites.

Essigella resistance Impact of defoliation caused by Essigella on profitability through deployment of resistant crop was similar between the production systems in Green Triangle region (1.6%-31.2% NPV) and in north-eastern Victoria (1.3%-54.2% NPV) depending on severity of upper crown defoliation. A linear relationship (r^2=0.44) between the aphid score and an eco-climatic index was estimated from available data. Narrow-sense heritability for assessments of defoliation scores in a 12-year-old trial was 0.18±0.04. Genetic correlations with early selection criteria traits were statistically significant for growth (DBH) (-0.37±0.15), stem straightness (-0.55 ±0.16), fork count (0.50±0.16) and wood density (0.34±0.15). Under a selection index in which Essigella defoliation was included as a breeding objective trait, there was a reduction in defoliation of -5.2%, -5.9% and -6.5% for low, medium and high hazard rating sites, respectively. Biological control and insecticide applications impacted significantly on economic weight estimates for Essigella caused defoliation. However, biological control alone may not be sufficient and an integrated pest management approach including genetic resistance may be necessary.

Dothistroma resistance Generally, volume growth reduction of 15% due to defoliation at an early age (4-10 years) had a relatively small effect on subsequent yield reduction (Thinning1: 2%-3%, Thinning2: 2%-5% and ClearFall: 0.6%-1.5%). However, at high infection sites, the percent effect of resistance to Dothistroma (31%) was comparable to the effect of improvement in MAI on uninfected sites. For Dothistroma infection in sixteen progeny trials in north-eastern Victoria non-additive genetic variance was statistically insignificant in most sites. Estimated narrow-sense heritability had median value of $h^2 = 0.29$. Phenotypic and genetic correlations between Dothistroma infection at early age and DBH at late age were negative (median values -0.35 and -0.39, respectively). Also, correlations of Dothistroma infection and growth traits assessed before or in the same growing season were generally negative, possibly indicating that less vigorous trees were more susceptible to Dothistroma infection.

Fusarium resistance Combining probability of entry and establishment, a disease exlusion benefit was NPV/y of $303,000. Previous studies indicated there were substantial resistance to *Fusarium* pitch canker in radiata pine. The level of genetic control reported in four studies

is moderate (median $h^2 = 0.25$). It is recommended that a thorough genetics study should be implemented to identify host genes and alleles that confer pitch canker resistance.

Application of Results

The results indicate that the four risk resistance traits studied are moderately inherited and that significant genetic gains can be obtained from selection and breeding, especially for sites with high hazard rating. Genetic parameters obtained here, together with economic weights can be used in the TREEPLAN® system to develop selection indices for breeding and deployment of resistant genotypes.

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1. Introduction

Risk can be defined as the product of probability of an adverse outcome and its severity or seriousness. However, the probabilities are rarely precisely known and we have to deal with uncertainty (Vose 2000). Generally, risk management consists of active countermeasures against known risks, forward preparation for prospective risks and risk spread against poorly quantifiable or currently unknown risks (Burdon and Aimers-Halliday 2003, Burdon and Aimers-Halliday 2006). In plantation forestry, climatic (*e.g.* drought) and biotic (*e.g.* insect and disease) risks are usually site-specific. Generally, the importance of risks increases with extent of damage and/or mortality at a given planting site (Chambers and Borralho 1997). Selection of genotypes, which can perform well on sites with high hazard rating, is the main goal of resistance/tolerance breeding.

1.1 Climatic and Biotic Risks

Climatic and biotic risks are usually related. For example, risks from pests and diseases usually become higher if trees are growing under stress. Climatic risks such as drought are present on many sites in Australia, especially on sites with low winter rainfall, where soil water is easily depleted by vigorous growth in early establishment stages. Soil moisture deficiency in the spring, summer and beginning of autumn was recognised to be the most limiting factor for plantation growth and survival in dry areas (Boardman 1988). Due to shortage of land for plantations in high rainfall areas, new plantations may expand into drier areas (Ken Nethercott pers. comm.). In Australia, there are sufficiently large areas of low rainfall zones (400-600 mm/y) for new plantation establishment to justify investment for breeding radiata pine for drought tolerance (Spencer 2001, Matheson *et al.* 2007).

There are few serious insect pests affecting radiata pine in Australia. European bark beetles *(Hylastes ater* and *Hylurgus ligniperda*) can kill natural regeneration and seedlings, but normally do not affect healthy nursery stock. Wood wasp (*Syrex noctilo*) is an important pest of mature radiata pine, but vigorous trees are unlikely to be affected and the most serious attacks have been in closed unthinned and underthinned stands (Lewis and Ferguson 1993). More recently, there has been considerable defoliation of mid-rotation radiata pine plantations in Australia by *Essigella californica* which was identified in 1998. An extrapolation of estimates of defoliation and associated growth losses indicates a significant national cost in terms of lost wood production (May and Carlyle 2003, May 2004). There are more potential pest risks for radiata pine. For example, in New Zealand there have been a few outbreaks of pests such as the bag moth (*Liothula omnivora*), the forest semi looper (*Declana floccosa*) and lucerne looper (*Zermizinga indocilisaria*) (Cooley 2005).

All significant diseases of radiata pine in Australia are caused by fungi. *Dothistroma septosporum* is the most serious disease affecting radiata pine both in Australia and New Zealand. Severe infections by needle blight have been mainly confined to parts of northern humid New South Wales and moist protected valleys in north-eastern Victoria. In New Zealand the disease is wide spread and losses in growth and spraying costs are currently considered to be approximately NZ$ 24 million a year (Bulman 2004). Needle cast (*Cyclaneusma minus*) causes defoliation due to spring casting, and significant reductions in growth in Tasmania and New Zealand have been observed (Podger and Wardlaw 1990). Other widespread needle cast fungi such as

Lophodermium pinastri and *Naemacyclus niveus* are present in the eastern states of Australia but rarely resulted in significant loss of growth. *Sphareopsis sapinea* can cause damage in warm and humid microsites such as shoot dieback, whorl cankers in heavily pruned trees, degrade of logs, and death of the crown. Trees under moisture stress are more conducive to fungal development in the stem. *Phytophthora* (root rot) causes scattered mortality in the radiata pine plantations in Western Australia (Lewis and Ferguson 1993). There are also many potentially dangerous fungi for radiata pine offshore. For example, in Papua New Guinea, *Ceroseptoria* is a close relative of *Dothistroma,* potentially more dangerous for Australia because it favours drier sites (Ades *et al*. 1992). In USA, western gall rust *Endocronartium harknessii* and *Fusarium circinatum* pitch canker are known to infect native radiata pine trees (Old and Dudzinski 1999). It is a major challenge to predict what the future impact of such varied and complex diseases would be if they became established in Australia (Ganley 2007).

1.2 Site Hazard Ratings and Effects of Climate Change

In general, risk mitigation involves specific breed development and site-specific deployment. Development of specific breeds and/or multiple breeding populations involves *"genetic risk spread"* with specific attention to *"functional diversity"* or variation in "risk traits" of adaptive and economic significance (Burdon and Aimers-Halladay 2006). The first step in breed development is to formally define breeding objectives including the so called "risk traits" with consideration of their impacts on growth, form and wood quality, and consequential economic importance. Determining site hazard ratings involves defining risks in terms of eco-climatic indices for current and future climate (Sutherst *et al.* 2007). The importance (economic weight) for resistance traits defined according to site hazard rating is used both for deployment and breeding. Breeding for resistance on high risk sites is important as well as understanding of genotype by environment (site) interactions for different site risk ratings.

CSIRO projects an annual average warming of 0.4 to 2°C over most of Australia by 2030 (relative to 1990), and the warming is likely to be 1 to 6°C by 2070 (CSIRO 2001). The greatest warming occurs in spring and least in winter. Annual average rainfall is predicted to decrease in parts of the south-east (–10% to +5% by 2030 and –35% to +10% by 2070). Decreases are most pronounced in winter and spring. Contributing to these climate changes is an increase in carbon dioxide concentration from about 350 parts per million (ppm) in 1990 to 430–455 ppm by 2030, and 525–705 ppm by 2070 (CSIRO 2001). Such climatic change would leave a large proportion of the current radiata pine estate outside the optimal range for growth.

Development of a drought resistant breed of radiata pine would help avoid this effect, but would also enable expansion of plantations into new areas. Drier and warmer climate may be also more conducive to various pests and diseases.

1.3 Economic Importance of Risks and Economic Weights

Breeding objective and associated economic weights for risk related traits have not yet been formally defined in radiata pine (Ivković *et al.* 2006). This is in spite of the fact that those traits may have estimated breeding values at selection age (Chambers *et al.* 2000). Economic evaluations of risks can be done on the national, regional, stand or per hectare basis. For example, Moore (2000) used general assumptions regarding impact of Essigella aphid and subdivided radiata pine national estate into regions according to National Plantation Inventory (1999). Each region was categorized into three susceptibility classes: currently affected, highly likely and less likely to be affected. Annual increment was estimated at 20 m^3/ha/year, with an assumed loss of growth at 5%, and average value of wood at $30 per m^3. The estimated value of loss due to Essigella to the Australian radiata pine plantation industry was 17 million dollars per annum. Similarly, May (2004) concluded that if stands continue to be defoliated at 2004 levels the potential reduction in volume was expected to increase from around 5.7 m^3/ha/year to 17.8 m^3/ha/year by year 2024. The NPV (i=7.5%) of losses from 2004 to 2033 is estimated to be $107 million or $274/ha. Based on those studies, Essigella pine aphid emerges as the most important pest attacking Australian pine plantations.

Economic impact of *Dothistroma* in New Zealand has been estimated at about NZ $24 million per year, comprising growth loss cost and chemical control cost of about NZ $2.5 million per year (Bulman *et al.* 2004). Growth losses are directly proportional to the amount of the crown that is infected. For example, approximately 50% increment loss is estimated from an average disease level of 50% (Whyte 1976). Similar results have been obtained in Australia (Old and Dudzinski 1999). The disease is managed by aerial spraying with copper oxychloride. Such spraying can be costly and may have environmental implications.

Economic impact of drought resistance on production system is less well defined. Better survival or less drought related mortality would allow expansion of pine plantations into more marginal areas with low rainfall (*e.g.* north of Mt Gambier) which could potentially bring benefits in form of secure timber supply and lower land rental costs. At a threshold level of mortality, replanting is needed, but there is only a limited time frame to do so after initial planting. Better weed control is another option for increasing survival and early growth. There is little literature on these subjects. Therefore, various scenarios of economic impact on drought resistance were considered.

1.4 Genetics of "Risk Traits" and Breeding to Minimise Risks

Two mechanisms of drought resistance have been reported in pines: drought avoidance and drought tolerance. Drought avoidance is achieved mostly through stomatal control, while drought tolerance is achieved through maintenance of photosynthetic activity and growth under drought conditions. Both mechanisms are reported in various pine species (Dean and Sands 1983, Leburgeois *et al.* 1998). The first step toward creating stress-resistant varieties (by marker-assisted selection) is identification and characterization of water-stress-resistance genes in selections already made by classical breeding techniques.

Similarly, varying tolerance or resistance to insect attack may be based on genetic differences in ability to cope with soil and atmospheric water deficit in the first place and ability to fight off attack in the second. A resistance mechanism based on secondary metabolites was proposed for green spruce aphid (*Elatobium abietinum*), where more vigorous trees probably sequester more effective surface deterrents (Day *et al.* 1997). Two resistance mechanisms have been proposed for Dothistroma needle blight resistance, a hypersensitive response to toxin dothistromin, by accumulation of the phytoalexin and benzoic acid (Franich *et al.* 1986), and a response involving fungistatic fatty acid and resin acid derivatives on the needle surface (Franich *et al.* 1983). However, it is likely that a number of different mechanisms are acting under different conditions. Defence responses to *Fusarium* pitch canker correspond to disease progression of a necrotrophic pathogen. They may include physical barriers to the pathogen and may also include the rapid production of antimicrobial compounds and proteins.

Like almost all other traits of economic significance disease resistance is expressed quantitatively. Resistance is amenable to recurrent selection since it is additively inherited with little expression of dominance variance and little genotype by environment interaction (Carson 1989). Recurrent selection will increase frequency of resistance genes for a range of response mechanisms, so there will not be unidirectional selection on the pathogen. An improved population would then be expected to have durable resistance (Carson and Carson 1989). Quantitative genetic parameters are of importance if resistance is comprised of cumulative effects of many different independently inherited mechanisms.

1.5 Selection Indices, Genetic Gain and Sensitivity Analyses

Selection index theory

Selection indices are used for improving multiple traits simultaneously through breeding (Cotterill and Dean 1990, Flakenhagen 1988). Selection index is a composite (a linear combination) of several traits evaluated in economic and genetic terms. The aggregated genetic worth (H) of several traits for an individual tree can be expressed as:

[1.1] $$H = a_1g_1 + a_2g_2 + \dots a_ng_n$$

where g_i (i =1 to n) is the genetic merit (breeding value) and a_i is the economic weight (or value) for the ith trait. In practice, selection of an individual tree for use in breeding is based on a selection index, which is expressed as:

[1.2] $$I = b_1x_1 + b_2x_2 + \dots b_nx_n$$

where x_i is the phenotypic values of the ith trait and b_i are index coefficients (*i.e.* multiple regression coefficients derived by maximizing the correlation between H and I). Expressed in matrix notation, the correlation between the index value and the aggregated genetic worth is maximized when:

[1.3] $$\boldsymbol{Xb} = \boldsymbol{Ga}$$

and the solution for the vector of index coefficients $\boldsymbol{b}$ is:

[1.4] $$\boldsymbol{b} = \boldsymbol{X}^{-1}\boldsymbol{Ga}$$

where $\boldsymbol{X}$ is the phenotypic and $\boldsymbol{G}$ is the genetic variance-covariance matrix for trait vector $\boldsymbol{X}$, and $\boldsymbol{a}$ is the vector of economic weights.

Traits in H could be the same as or different from traits in I. In tree breeding, due to the long generation interval, selection is usually conducted at an early age (4 or 12 years), while the breeding objective traits are defined at the final harvest age (25-35 years). The early selection traits are often referred to as selection criteria in contrast to breeding objective traits. In such circumstances the appropriate index coefficients can be obtained as:

[1.5] $$\boldsymbol{b} = \boldsymbol{X}_{11}^{-1}\boldsymbol{G}_{12}\boldsymbol{a}$$

where $\boldsymbol{X}_{11}$ is the phenotypic variance-covariance matrix for selection criteria traits and $\boldsymbol{G}_{12}$ is the genetic variance-covariance matrix between selection criteria and breeding objective traits, and $\boldsymbol{a}$ is the vector of economic weights for breeding objective traits.

Expected genetic gains or mean response in breeding objective traits expressed per standardised selection differential (*i*) can be calculated as:

[1.6]

$$\Delta\mu = i\frac{Gb}{\sqrt{b'Xb}}$$

Sensitivity analyses

Sensitivity of relative economic weights and selection index weights can be tested against various assumptions related to typical plantation production systems, using the approach of (Ivković *et al.* 2006b). Different sets of economic weights are derived from different assumptions and tested in what-if and Monte Carlo analyses. The analyses show how production system input parameters affect variation of the estimated economic weights. The model input parameters that have the highest rank-order correlations with the relative economic values are identified. The Spearman rank-order correlation coefficient are calculated between the rank of model input values and the rank of generated economic weights for each combination of production system inputs, and relative economic weights for each breeding objective trait. A certain distribution is assumed around the means of relative economic weights, the elements of the genetic variance-covariance matrices and heritabilities and predicted genetic gain for selection and breeding objective traits is calculated. Sensitivity of the derived solutions (*i.e.* predicted gains and/or selected trees) can be tested using different sets of economic weights and genetic parameters.

2 Drought Related Mortality and Early Growth

2.1 Introduction

Because of land shortage in high rainfall areas in south-eastern Australia and predictions of reduction in rainfall caused by climate change, it is important to study genetic variation in survival and early growth on drought prone sites (Matheson *et al.* 2007). However, there are only a few radiata pine provenance/progeny trials established in the low rainfall (<700mm) areas (Matheson *et al.* 2007). Provenance variation was found at a dry site (Wirrabara - 660mm rainfall and 1900mm pan evaporation) where the most commonly planted inland Monterey provenance, which performs best on optimal sites, was inferior to Guadalupe Island provenance in height growth and to Cedros Island provenance in resistance to *Ips* beetle attack (Boardman and McGuire 1997). There is only anecdotal information about families that perform better relative to other families when weeds were not controlled and soil had low water potential (D. Spencer, CSIRO, pers. comm.).

Climatic data for the year before planting and the first few years after planting are particularly important for survival. The climate data can be used to calculate soil moisture status using actual and potential evapo-transpiration, which showed significant correlation with survival in other pines (McKinley *et al.* 1988). If there is a relationship between those variables and survival, site hazard ratings can be defined in terms of climatic conditions. For the drought prone sites we performed genetic analyses on survival to determine heritability, but large environmental and nursery effects are expected. Assuming that the mortality was most likely caused by drought conditions, such analyses should provide a first approximation for heritability of drought tolerance.

2.2 Materials and Methods

Definition of site hazard ratings

Climate variables for 134 sites of Southern Tree Breeding Association (STBA) progeny trials were obtained using ESOCLIM module of ANUCLIM program (Hutchinson *et al.* 1999). Drought stress was considered to be likely correlated to intensity, duration and seasonality of extreme climatic conditions. Climate data on temperature, precipitation and radiation (Tom Jovanovic pers. comm.) were used to calculate bio-climatic indices, and aridity indices. Climate variables and derived indices included:

1. Max Temperature of Driest Month (*MTDM*)
2. Max Temperature of Warmest Month (*MTWM*)
3. Mean Temperature of Driest Quarter (*MTDQ*)
4. Annual Precipitation (*AP*)
5. Precipitation of Driest Month (*PDM*)
6. Min Monthly Raindays (*MMRD*)
7. Precipitation of Driest Quarter (*PDQ*)
8. Precipitation of Warmest Quarter (*PWQ*)
9. A xerothermic index (*XIX*) was defined as an integral area under curve where p<4t during consecutively dry months. It was based on the Ombrothermic diagram (Lebourgeois and Piedallu 2005) and takes into account monthly averages of precipitation (p in mm) and temperature (t in ˚C) and provides a relative measure of duration and intensity of summer drought.
10. A simple monthly aridity index *(AIX)* was calculated as a ratio of monthly mean daily pan evaporation rate to the total monthly rainfall. Monthly minimum *AIX* value for the most arid quarter was used to rank the sites in terms of aridity (Eamus *et al.* 2000). Aridity indices can also be based on precipitation and potential evapo-transpiration (PET) and are related to water balance.

For sites that had the most extreme climate according to the above 10 indices (*i.e.* the most drought prone sites), we performed genetic analyses on survival and early growth variables.

Effect of change in average survival on production system

Various production systems in Australian radiata pine industry were modeled in our previous study on breeding objectives (Ivkovic *et al.* 2006a). Two generic production systems with different productivity levels: MAI 15 m^3/ha/year and MAI 20 m^3/ha/year (Appendix: Tables A1 and A2) were simulated to evaluate the impact of drought on plantation establishment. Plantation growers had cost structures including land rental, growing of plantations, which included establishment costs and maintenance costs (fertilisation, weed control, *etc.*), and harvesting and transportation costs. The incomes for the growers were derived from the sale of sawlogs to saw-mills, and pulplogs or chips to pulpmills. A simplified economic model was designed for the two generic production systems. Low growth rate (MAI 15 m^3/ha/year) model is assumed profitable at 6% discount rate and at land rental costs of $71 per ha per year, while the higher growth rate model (MAI 20 m^3/ha/year) model was assumed profitable at 7% discount rate and at land rental costs of $158 per ha per year.

Effect of reduced land rental costs for marginal sites was examined under the assumption that survival and early growth can be kept at acceptable levels. The profitability of the two described production systems is compared at different levels of land rental cost. The effect of lower land rental price for marginal site with lower productivity was evaluated relative to the higher productivity site but with a higher land rental cost.

A scenario was generated for examining effects of survival on the two production systems. Weibull distribution was assumed to approximate distribution of survival across the radiata pine plantation estate. Average mortality on marginal sites was assumed to be 30%. The distribution was evaluated over the limits of survival. Effect of changes in average survival was obtained as a product of cumulative probability of each survival class and the corresponding loss of net present value (NPV) due to mortality, which necessitates replanting and causes reduction in volume. The linearity of the effect of a trait change in terms of NPV was examined over a range of average trait values.

To adjust mortality at different sites assessed at different ages, the survival at a given age T (S_T) was estimated according to formula of Mason (1997):

[2.1]

$$S_T = e^{-\alpha T^{\beta}}$$

As the mortality decreases over time the constant $\beta < 1$ and parameter α can be related to factors describing site quality, site preparation and/or climatic variables.

Genetic analyses of survival and early growth on drought affected sites

Mortality data from progeny trials in the data management system (DATAPLAN®) of STBA or status code (A-Alive, B-Blank, D-Dead, N-Not Assessed, V/Y-Fork) at different ages were obtained for the sites with high drought hazard (Table 2.1).

Table 2.1 Progeny trials assessed for survival score and early growth. The number of full-sib (FS), half-sib (HS) families, check lots (Ch.), individual trees, latitude (Lat), longitude (Long), altitude (Alt) and planting date for the trials.

Trial ID – Trial Name	FS	HS (Ch.)	Trees	Lat	Long	Alt	Plant. date
BR0503 - Bundaleer Progeny Trial	46	80 (1)	2240	-33˚17’	138˚34’	414	8/2005
BR0603 - Bundaleer Progeny Trial	64	25 (8)	2160	-36˚40’	146˚53’	268	8/2006
RAD116 - Myrtleford CP	29	4	1818	-36˚39’	146˚39’	305	7/1968
RAD134 - Rennick, Comp. 085	0	23 (3)	1560	-37˚59’	141˚03’	20	7/1970
RAD165 - Warrenbayne CP Trials	23	5 (20)	1800	-36˚43’	145˚50’	325	6/1975
RAD179 - Basin Ck NZ880 Trial	62	4 (3)	1771	-36˚29’	146˚45’	350	6/1984
RAD194 - Myrtleford Diallels	44	0 (3)	2016	-36˚43’	146˚40’	305	7/1985
RAD195 - Myrtleford Other Families	10	20 (3)	1344	-36˚42’	146˚40’	305	7/1985
RAD196 - Lake Buffalo Guadalupe	0	46	896	-36˚42’	146˚40’	295	7/1985
RAD222 - Clemens Block 4x4 Factorial	20	1 (3)	720	-36˚42’	146˚39’	285	6/1989
RAD223 - Clemens 3x4 Factorial, Topcrosses	16	11 (1)	932	-36˚42’	146˚39’	280	6/1989

RAD225 - Rennick, 4x4 Factorial	22	(3)	845	-37°51’	141°58’	60	6/1991
RAD226 - Rennick, 4x4 Factorial	12	(3)	845	-37°51’	141°58’	60	6/1991
RAD228 - Dandongadale Factorial	43	3 (2)	1449	-36°47’	146°40’	290	7/1990
RAD230 - 2G and OPSO Families	0	48 (1)	1530	-36°47’	146°40’	290	7/1990
RAD231 - Dandongadale OPBA Families	0	37 (2)	1291	-36°49’	146°39’	290	7/1990
RAD236 - Dandongadale Factorials	55	18 (3)	2508	-36°47’	146°39’	290	7/1991
RAD237 - Dandongadale NZ Families (APM)	3	107 (3)	3538	-36°47’	146°39’	290	7/1991
VRC070 - Factorial Crosses Saxton's Block Glencoe	51	0 (1)	1089	-38°15’	147°06’	55	7/1990

Binomial (present or absent) survival score data were analysed using generalised linear mixed models (GLMM) in ASREML (Gilmour *et al.* 2006) on a transformed scale using a link function and distribution specific weights:

[2.2] $$\mathbf{y} = \mathbf{X}b + \mathbf{Z}u + D(O - E)$$

where $\mathbf{Z}u$ is the incidence matrix relating to the u vector of random effects; *D* is derivative of link function, *O* is the observed value and *E* is *g(Xt + Zu)*, the expected value, weights are a function of *D* and *E*. The quasi-likelihood technique (Gilmour *et al.* 2006) based on a first order Taylor series approximation to the likelihood was used for GLMM analyses. The binomial analysis has a reasonable base for genetics because the probit link functions implies an underlying residual normal distribution (Littell *et al.* 2002).

Estimates of variance components for a single trait at a single site were obtained according to the following linear mixed model for diallel and factorial crossing designs:

[2.3] $$\mathbf{y} = \mathbf{X}b + \mathbf{Z}_R r + \mathbf{Z}_P p + \mathbf{Z}_T t + \mathbf{Z}_S s + \mathbf{e}$$

where $\mathbf{y}$ is the vector of observations and $\mathbf{X}$ is the incidence matrix relating the observations in $\mathbf{y}_i$ to the b vector of fixed effects (*i.e.*, overall mean); $\mathbf{Z}_R$ is the incidence matrix relating to the r vector of random replicate effects; $\mathbf{Z}_P$ is the incidence matrix relating to the p vector of random plot effects; $\mathbf{Z}_T$ is the incidence matrix relating to the t vector of individual tree (additive genetic) effects; $\mathbf{Z}_S$ is the incidence matrix relating to the s vector of specific combining ability (full-sib family) effects; *e* is the vector of residuals. For half-sib design only general combining ability was estimated.

The estimate of individual-tree narrow-sense heritability (on underlying scale) was obtained as:

[2.4] $$h^2 = \frac{\sigma_a^2}{\sigma_P^2}$$

Where σ_a^2 is the estimate of additive genetic variance,

$\sigma_P^2 = \sigma_a^2 + \sigma_f^2 + \sigma_p^2 + \sigma_e^2$ is the estimate of phenotypic variance, where σ_f^2 is the estimate of full-sib family variance (specific combining ability), σ_e^2 is the plot variance and σ_e^2 is the model error variance.

Dominance variance proportion (Costa e Silva *et al.* 2004) was estimated as:

[2.5] $$d^2 = \frac{4 \times \sigma_f^2}{\sigma_P^2}$$

A multivariate (individual site) analysis was used to estimate variance components in order to obtain genetic correlations among the selection criteria and risk traits. A multivariate mixed model REML analysis using ASREML (Gilmour *et al.* 2006) was used for the analyses:

[2.6] $$\mathbf{y}_j = \mathbf{X}_j\mathbf{b}_j + \mathbf{Z}_{a_j}\mathbf{a}_j + \mathbf{Z}_{f_j}\mathbf{f}_j + \mathbf{Z}_{p_j}\mathbf{p}_j + \varepsilon_j$$

Where y_j is the vector of individual tree observations for trait j (j = 1 to n), b_j is the vector of fixed effects and X_j is the known incidence matrix relating the individual tree observations in y_j to the fixed effects in b_j where

[2.7] $$\mathbf{X}_j\mathbf{b}_j = \begin{bmatrix} X_1 & 0 & 0 & 0 \\ 0 & X_2 & 0 & 0 \\ 0 & 0 & X_{...} & 0 \\ 0 & 0 & 0 & X_n \end{bmatrix} \times \begin{bmatrix} b_1 \\ b_2 \\ b_{...} \\ b_n \end{bmatrix}$$

Z_{a_j} is the known incidence matrix relating observations in y_j to additive genetic effects in $\boldsymbol{a}_j$; $\boldsymbol{a}_j$ is a vector of random additive genetic effects of individual genotypes ~MVN $(0, G \otimes A)$

[2.8] $$G = \begin{bmatrix} \sigma^2_{a_1} & \sigma_{a_1a_2} & \sigma_{a_1a_{...}} & \sigma_{a_1a_n} \\ \sigma_{a_2a_1} & \sigma^2_{a_2} & \sigma_{a_2a_{...}} & \sigma_{a_2a_n} \\ \sigma_{a_{...}a_1} & \sigma_{a_{...}a_2} & \sigma^2_{a_{...}} & \sigma_{a_{...}a_n} \\ \sigma_{a_na_1} & \sigma_{a_na_2} & \sigma_{a_na_{...}} & \sigma^2_{a_n} \end{bmatrix}$$

A is the additive relationship matrix, $\sigma^2{}_{a_j}$ is the estimated additive genetic variance, $\sigma_{a_xa_y}$ is the estimated genetic covariance between additive effects of the two traits.

Z_{f_j} is the known incidence matrix relating observations in y_j to random effects in f_j; f_j is a vector of random effects of full-sib families ~MVN$(0, F \otimes I_f$ where diagonal elements of F are $\sigma^2{}_{f_j}$ are the estimated variance attributed to full-sib families (specific combining ability), and off-diagonal elements ($\sigma^2{}_{f_xf_y}$) are the estimated covariance between full-sib family effects of two traits; and I_f is an identity matrix diagonal elements equal to the number of full-sib families.

Similarly, Z_{p_j} is the known incidence matrix relating observations in y_j to genetic effects in p_j; p_j is a vector of random effects of plots within replications

~MVN(0,$P \otimes I_p$) where, diagonal elements of P are $\sigma^2{}_{f_j}$ the estimated variance attributed to plots within replications, and $\sigma^2{}_{f_x f_y}$ is the estimated covariance between plot effects of two traits, and I_f is an identity matrix diagonal elements equal to the number of plots.

[2.9]
$$R = \begin{bmatrix} \sigma^2_{e_1} & \sigma_{e_1e_2} & \sigma_{e_1e_{...}} & \sigma_{e_1e_n} \\ \sigma_{e_2e_1} & \sigma^2_{e_2} & \sigma_{e_2e_{...}} & \sigma_{e_2e_n} \\ \sigma_{e_{...}e_1} & \sigma_{e_{...}e_2} & \sigma^2_{e_{...}} & \sigma_{e_{...}e_n} \\ \sigma_{e_ne_1} & \sigma_{e_ne_2} & \sigma_{e_ne_{...}} & \sigma^2_{e_n} \end{bmatrix}$$

ε_j is a random vector of residual terms ~MVN (0, $R \otimes I_j$) and $\sigma^2{}_{e_j}$ is the estimated residual variance for each trait and $\sigma^2{}_{e_x e_y}$ is the estimated residual covariance between two traits.

The genetic correlation r_G between two traits was estimated within the ASREML software as:

[2.10]
$$r_g = \frac{\sigma_{a_x a_y}}{\sqrt{\sigma^2{}_{a_x}\sigma^2{}_{a_y}}}$$

where:

$\sigma_{a_x a_y}$ = additive genetic covariance component between traits x and y;

$\sigma^2{}_{a_x}$ = additive genetic variance component for trait x;

$\sigma^2{}_{a_y}$ = additive genetic variance component for trait y

Standard errors for each of the correlations were calculated using a truncated Taylor series in ASREML (Gilmour *et al.* 2006).

Selection indices and genetic gain

In radiata pine, the breeding objective and target traits to achieve the objective are defined at harvest age (usually between 28-35 years). However selection of genotypes for breeding purposes is usually done at an earlier age (6-8 years) based on the measurement of young- age traits. These early traits are often referred to as selection criteria in contrast to breeding-objective traits at rotation age. The early selection criteria were: diameter at breast height (DBH), stem straightness score (STS), branch size score (BSS), wood density (DEN) and modulus of elasticity (MOE). The breeding objective traits were: mean annual increment (MAI), stem sweep (SWE), branch size (BSO) and wood stiffness (MoE). To link selection criteria to breeding objective traits for selection purposes, genetic correlations between traits at selection and rotation ages are used.

The parameters used for derivation of selection index were economic weights (vector **a**), the phenotypic variance-covariance matrix ($\mathbf{V}_X$) for selection criterion traits and the genetic variance-covariance matrix between selection criterion traits and breeding objective traits ($\mathbf{V}_{XG}$). The vector of selection index coefficients was derived using formula 1.5. The phenotypic and genetic variance–covariance matrices used for selection index sensitivity analyses were taken from Wu *et al.* (2008). Expected genetic gains or mean response in breeding objective traits, expressed per standardised selection differential, was calculated according to formula 1.6.

Currently, the STBA *P. radiata* pine breeding objective and selection index does not include survival as a breeding objective trait or as selection criteria (Powell *et al.* 2005, Ivković *et al.* 2006). We introduced survival as a selection and a breeding objective trait and examined the potential genetic gain for sites with different levels of productivity and survival (70% to 95%).

Sensitivity of selection index weights to relative economic values and genetic parameter estimates

Parameters that influence selection index coefficients were the estimated economic weights, genetic correlations for selection criterion traits, genetic correlations between selection criterion traits and breeding objective traits (formula 1.5), and trait heritabilities (h^2). For the analyses of sensitivity of the selection index to various inputs, we assumed a triangular distribution around the means of genetic correlations and normal distribution around the means of heritabilities and economic weights (1.2). Changes of sign for some genetic correlations were also included (Wu *et al.* 2008). Sensitivity of the solutions (*i.e.* selected parents and predicted gains) was tested using selected sets of genetic parameters and REVs.

Table 2.2. Inputs used for Monte Carlo sensitivity analyses of selection index weights. EW_ is economic weight for a trait, h^2_ is heritability for a trait, and trait / trait denotes genetic correlation.

Input	Distribution parameters
EW_MAI	Normal(300, 600)
EW_SWE	Normal(-62, 124)
EW_BIX	Normal(-340, 680)
EW_SVS	Normal(34, 68
h^2_DBH	Normal(0.2, 0.054)
h^2_STS	Normal(0.32, 0.075)
h^2_BSS	Normal(0.35, 0.105)
h^2_DEN	Normal(0.63, 0.195, Truncate(1))
h^2_SVS	Normal(0.12, 0.09, Truncate(0))
h^2_MAI	Normal(0.25, 0.075)
h^2_SWE	Normal(0.14, 0.042)
h^2_BIX	Normal(0.15, 0.045)
h^2_SVO	Normal(0.1, 0.03)
DBH / SVS	Triang(0.15, 0.35, 0.45)
DBH / STS	Triang(-0.15, 0.05, 0.25)
DBH / BSS	Triang(-0.49, -0.29, -0.09)
DBH / DEN	Triang(-0.45, -0.25, -0.05)
DBH / MAI	Triang(0.5, 0.7, 0.9)
DBH / SVO	Triang(0.1, 0.3, 0.6)
DBH / BIX	Triang(0.25, 0.45, 0.65)
DBH / SWE	Triang(-0.3, -0.1, 0.1)
STS / BSS	Triang(-0.05, 0.15, 0.35)
STS / DEN	Triang(-0.25, -0.05, 0.15)
STS / SVS	Triang(-0.6, -0.4, -0.2)
STR / MAI	Triang(-0.06, 0.14, 0.34)
STS / SWE	Triang(-0.9, -0.7, -0.5)
STS / BIX	Triang(-0.25, -0.05, 0.15)
BSS / DBH	Triang(-0.49, -0.29, -0.09)
BSS / STS	Triang(-0.05, 0.15, 0.35)
BSS / DEN	Triang(-0.15, 0.05, 0.25)
BSS / SVS	Triang(0.0, 0.2, 0.4)
BSS / MAI	Triang(-0.05, 0.15, 0.35)
BSS / SWE	Triang(-0.25, -0.05, 0.15)
BSS / BIX	Triang(-0.9, -0.7, -0.5)
DEN /SVS	Triang(-0.2, 0, 0.2)
DEN / MAI	Triang(-0.39, -0.19, 0.01)
DEN / SWE	Triang(-0.11, 0.09, 0.29)
DEN / BIX	Triang(-0.31, -0.11, 0.09)

DEN / SVO	Triang(-0.2, 0, 0.2)

The results of Monte Carlo simulations were used to calculate Spearman rank-order correlations (r_S) as a measure of association between the estimated economic weight and each input parameter. Rank-orders were used rather than the actual values because the method does not require the normality assumption and some of the inputs were assumed to have either uniform or triangular distributions (Table 2.2). The coefficient r_s is calculated according to the formula (Vose 2000):

$$r_s = 1-(6\sum D_i^2 / N(N^2-1)) \qquad [2.11]$$

where D_i is the rank difference between i^{th} pair in the N ranks.

What-if analyses

For the input parameters that were influencing economic weights the most (*i.e.* site productivity, land rental cost, planting costs we also performed what-if analyses. What-if scenarios were conducted by varying the model input parameters widely (± 15% with a 5% incremental level) while keeping all other parameters constant. The analyses were conducted for both site productivity levels (management regimes).

2.3 Results and Discussion

Site hazard ratings

The Southern Tree Breeding Association's progeny trial sites were ranked based on climate variables and ecoclimatic indices. Sites with the highest rankings for the climate variables and indices (*i.e.* drought prone sites) were selected in Table 2.3.

Table 2.3. Ranking (high temperature, low precipitation) of sites based on climate variables and derived bioclimatic indices: Max Temperature of Warmest Month (*MTWM*), Max Temperature of Driest Month (*MTDM*), Mean Temperature of Driest Quarter (*MTDQ*), Annual Precipitation (*AP*), Min Monthly Raindays (*MMRD*), Precipitation of Driest Month (*PDM*), Precipitation of Driest Quarter (*PDQ*), xerothermic index (*XIX*), and aridity index (*AIX*). Data on survival are currently available only for site ID codes indicated in bold face.

Rank	*MTWM*	*MTDM*	*MTDQ*	*AP*	*MMRD*	*PDM*	*PDQ*	*XIX*	*AIX*
1	**BR0503**	**BR503**	**BR0503**	**BR0503**	**BR0503**	**BR0503**	**BR0503**	**BR0503**	**BR0503**
2	**BR0603**	**RAD194**	**RAD223**	**VRC070**	**RAD165**	BR0702	BR0702	BR0702	BR0702
3	**RAD222**	**BR0603**	**RAD222**	VRC094	**RAD179**	BR0502	**BR0602**	BR0502	BR0502
4	**RAD223**	**RAD239**	**RAD165**	VRC040	RAD180	**BR0602**	BR0502	**BR0602**	**BR0602**
5	**RAD116**	**RAD237**	**BR0603**	VRC041	RAD181	BR0703	BR0703	RAD134	RAD134
6	**RAD196**	**RAD236**	**RAD116**	BR9709	GT9508	BR9601	BR9705	BR0703	RAD218
7	RAD216	**RAD230**	RAD216	BR0702	RAD116	BR9602	BR9706	BR9705	**RAD225**
8	**RAD179**	RAD229	GT9508	GT0002	RAD216	BR9603	BR9706$_G$	BR9706	**RAD226**
9	RAD180	**RAD228**	**RAD196**	BR0704	**RAD222**	BR9705	RAD134	BR9706$_G$	GT0001

10	RAD181	**RAD231**	**RAD194**	BR0502	**RAD223**	**BR9706**	RAD218	RAD218	BR9705

The basic climatic requirements for growing radiata pine are mean annual rainfall between 650 and 1800 mm, with a uniform rainfall regime and a winter rainfall regime with dry season not over 5 months, mean maximum temperature of the hottest month at 18 – 30°C, mean minimum temperature of the coldest month at -2 – 12°C, and mean annual temperature between 10 and 18°C. Radiata pine does not tolerate severe summer droughts (Jovanovic and Booth 2002, Lavery 1986). Evapo-transpiration indices showed significant correlation with survival and early growth in other pines (*e.g.* McKinley *et al.* 1988).

Site BR0503 - Bundaleer progeny trial site had the highest aridity index (*AIX*=12.4) and was ranked first for all other drought related climate indices. It was followed by BR0702 - Dr Goodes, BR0502 - Nangeela East and BR0602 - Nangeela Central progeny trials in relative ranking for *AIX* (Table 2.4). However, data from site BR0702 were not available for analysis, and Trial BR0502, assessed at 4 months after planting, had mortality less than 2%. More recent assessments are needed for meaningful genetic analyses of these highly vulnerable sites. We obtained survival and early growth data from STBA's DATAPLAN® for available highest ranked sites in terms of extreme climate variables and aridity indices (Table 2.4). BR0602 - Nangeela Central has suffered losses since the 4 month assessment and it is now standing at 87% survival.

Table 2.4. Climate variables and bioclimatic indices for drought prone sites: Max Temperature of Warmest Month (*MTWM*), Max Temperature of Driest Month (*MTDM*), Mean Temperature of Driest Quarter (*MTDQ*), Annual Precipitation (*AP*), Min Monthly Raindays (*MMRD*), Precipitation of Driest Month (*PDM*), Precipitation of Driest Quarter (*PDQ*), xerothermic index (*XIX*), and aridity index (*AIX*).

Trial	*MTWM* (˚C)	*MTDM* (˚C)	*MTDQ* (˚C)	*AP* (mm)	*PDQ* (mm)	*PDM* (mm)	*MMRD*	*XIX*	*AIX*
BR0503	30.1	29.6	20.2	465	70	22	3.8	319	12.4
VRC070	24.1	24.1	17.3	595	142	42	7.9	97.2	4.1
BR0702	26.7	26.7	17.7	652	86	25	6.3	193	8.8
BR0502	25.9	25.9	17.1	689	97	28	6.6	158	7.7
BR0602	25.8	25.8	17.2	696	96	28	6.7	120	7.7
RAD134	23.7	23.7	16.8	746	98	29	7.7	144	7.1
RAD225	23.9	23.9	16.6	754	99	29	7.7	138.6	7.1
RAD226	23.9	23.9	16.6	754	99	29	7.7	138.6	7.1
RAD165	28.5	28.5	18.9	840	133	39	5.0	126.8	4.7
RAD165	28.8	28.8	18.7	983	160	48	5.3	89.4	4.3
RAD116	29.2	28.8	18.8	1061	170	53	5.4	76.8	4.0
RAD223	29.3	28.9	18.9	1094	174	54	5.4	72.4	3.9
RAD222	29.3	28.8	18.9	1100	174	54	5.4	71.8	3.9
BR0603	29.3	29.1	18.9	1102	182	55	5.5	64	3.6
RAD196	29.2	28.8	18.8	1126	177	55	5.5	65.4	3.8
RAD194	29.1	29.1	18.8	1133	179	56	5.5	62.6	3.8
RAD195	29.1	29.1	18.8	1133	179	56	5.5	62.6	3.8
RAD228	29	29	18.7	1183	184	57	5.6	54.2	3.6

RAD229	29	29	18.7	1183	184	57	5.6	54.2	3.6
RAD230	29	29	18.7	1183	184	57	5.6	54.2	3.6
RAD236	29	29	18.7	1183	184	57	5.6	54.2	3.6
RAD237	29	29	18.7	1186	184	57	5.6	54.2	3.6
RAD231	28.9	28.9	18.7	1204	186	58	5.7	50.4	3.5

Effect of land cost and mortality on production system

Using production system assumptions given in the Appendix (Tables A1 and A2) the internal rate of return (IRR) on an investment in radiata pine for production system in Table A1 (based on MAI 15 m^3/ha/y) was 7.01% per annum at land lease cost 25 $/ha/y. For production system in Table A2 (based on MAI 20 m^3/ha/y) IRR was 7.13% per annum at land cost of 150 $/ha/y. The land rental cost (assuming land is leased) had a substantial impact on returns, and decreasing the rental from $150/ha/y to only $25/ha/y increases returns to the grower so that a marginal site with the low productivity (MAI 15) can have similar profitability as a higher productivity site (MAI 20). Table 2.5 shows a range of land holding cost for the two sites classes of different productivity. Analyses clearly show the benefit from choosing high productivity and high rainfall sites. At the higher productivity site, even with land rent as high as $150/ha/y, the IRR return exceeds 7.1%. However, planting on relatively low productivity sites (15 m^3/ha/y) which normally produces poor returns, can achieve a rate of return of 7.01% if the land rental is sufficiently lower, *i.e.* <$ 25/ha/y.

Table 2.5 Internal Rate of Return (%) for two production systems for different values of land holding cost.

Land holding cost ($/ha/y)	**150**	**125**	**100**	**75**	**50**	**25**
MAI 15 (m^3/ha.a)	4.44	4.92	5.42	5.93	6.46	7.01
MAI 20 (m^3/ha.a)	7.13	7.51	7.91	8.32	8.75	9.2

With known replanting cost and losses in volume due to mortality, the production system models can be used to predict the effects of different levels of mortality. Assuming Weibull distribution of mortality with a mean 30%, 20%, 10%, and 5%, replanting costs were calculated as: $376, $251, $126 and $62 per ha, respectively (Table 2.6). If mortality levels are high, significant reduction in profitability is expected due to cost of replanting and volume losses. If mortality exceeds 20%, higher productivity site is no more profitable at 7% IRR, and lower productivity site is no more profitable at 6% IRR.

Table 2.6. Net Present Value loss for four levels of mortality for two production systems (discount rate *d*=6.0% for MAI 15 and *d*=7% for MAI 20).

	d	NPV Loss	Mortality			
			30%	20%	10%	5%
MAI 15	6.0%	Replanting	-$376	-$151	-$126	-$62
		Vol. loss	-$1535	-$904	-$335	-$35
MAI 20	7.0%	Replanting	-$376	-$151	-$126	-$62
		Vol. loss	-$1853	-$1138	-$536	-$246

Quantitative genetics of survival and early growth

Quantitative genetic analyses were performed on survival and early growth data for selected sites based on climatic indices. Binomial survival scores (0 or 1) were analysed to obtain mean survival (%), variance of specific combining ability (σ^2_{SCA}), additive genetic variance (σ^2_a) or four times the general combining ability (*GCA*), narrow-sense heritability (h^2), dominance proportion (d^2) (*e.g.* Costa e Silva *et al.* 2004) and standard errors of h^2 *and* d^2 (Table 2.7)

Table 2.7. Analysis of survival scores: site code, age of assessment (YYMM), mean survival (%), variance of specific combining ability (σ^2_{SCA}), additive genetic variance(σ^2_a) narrow-sense heritability (h^2), proportion of dominance variance (d^2) and standard errors (SE).

Site	**Age** (yymm)	**Mean** (%)	σ^2_{SCA}	σ^2_a	$h^2(d^2)$	**SE** $h^2(d^2)$
BR0503	0010	0.96	ns[1]	0.159	0.15	0.09
BR0602	0109	0.87	0.083	0.055	0.04 (0.29)	0.03 (0.12)
BR0603	0000	1.00	-	-	-	-
	0003	0.95	0.107	ns	(0.39)	(0.19)
	0004	0.92	ns	ns	-	-
	0005	0.70	ns	0.07	0.06	0.03
RAD116	0710	0.97	ns	ns	-	-
	1307	0.93	0.034	ns	(0.15)	(0.13)
RAD165	0904	0.95	ns	ns	-	-
RAD165	1700	0.80	ns	0.166	0.14	0.05
RAD194	0300	0.93	0.115	ns	(0.31)	(0.09)
	0400	0.92	0.115	ns	(0.30)	(0.09)
	1400	0.88	0.083	ns	(0.25)	(0.08)
RAD195	0200	0.96	0.032[1]	ns	(0.12)	(0.28)
	1400	0.90	0.035[1]	ns	(0.13)	(0.19)
RAD196	0207	0.78	-	0.562	0.35	0.09
RAD222	1200	0.80	ns	0.045[1]	0.04	0.06
RAD223	0400	0.88	0.197	ns	(0.66)	(0.30)
	1509	0.76	0.156	ns	(0.56)	(0.32)
RAD225	1104	0.84	ns	ns	-	-
RAD226	1104	0.98	ns	ns	-	-
RAD228	1007	0.70	ns	0.134	0.12	0.05
	1011	0.69	ns	0.158	0.14	0.05
RAD230	1408	0.73	-	0.031	0.03	0.03
RAD231	0300	0.87	-	0.082	0.08	0.06
RAD236	0907	0.94	0.029	ns	(0.12)	(0.12)
RAD237	0300	0.81	-	0.146	0.13	0.05
VRC070	1502	0.83	0.012ns	0.107	0.10	0.05

[1] statistical significance based on variance component to standard error ratio, if the ratio <1.5 the components was considered not significantly different from zero (ns), if variance ratio was >1 and <1.5 log-likelihood deviance was tested against the chi-square distribution with one degree of freedom.

Generally, the variance components obtained from binomial distribution using PROBIT link analyses were similar to analyses assuming normal distribution. In all trials, either σ^2_a or σ^2_{SCA} were significant, except in three relatively small trials with a high level of survival (*e.g.* RAD165 - 23 full-sib families, 95% survival; RAD225 22 full-sib families, 84% survival; and RAD226 12 full-sib families, 98% survival).

Narrow-sense heritability was generally lower (median h^2=0.12) than the proportion of dominance variance (median d^2=0.18). In a number of trials, where σ^2_a was not significant, while σ^2_{SCA} was significant (*i.e.* RAD194 and RAD195) we re-analysed data using plot means instead of individual tree values. Nevertheless, d^2 on those sites was still more significant than h^2. In other words, in those trials there were no statistically significant differences between parents, but specific parental combinations (full-sib families) were significantly different. One example is the trial RAD223 (Clemens 3×4 Factorial design) with a particularly high dominance variance proportion (d^2 = 0.55, equation 2.5) (Table 2.8). Such full-sib family differences may be purely genetically based, but may also be due to differences in nursery environment or planting technique for different full-sib families (Ken Eldridge pers. comm.). On the other hand, in BR0603 there was a change from significant σ^2_{SCA} at age 3 to significant σ^2_a at age 5, which may indicate that additive genetic differences become more obvious as mortality increases, and/or non-genetic effects (C effects) tend to decrease with age.

Table 2.8. Survival percentage for different crosses at RAD223

Mum\Dad	**10271**	**10277**	**11107**	**41957**	**42146**	**81482**	**277831**	**277833**	**Total**
10238	83%								**83%**
10425		47%	63%			80%		47%	**59%**
11108		37%	77%						**57%**
36069		73%							**73%**
41687				90%			93%		**92%**
42198								73%	**73%**
42613					80%				**80%**
42656				93%			90%		**92%**
42658				77%			73%		**75%**
Total	**83%**	**52%**	**70%**	**87%**	**80%**	**80%**	**85%**	**60%**	**73%**

At plot mean level there was no significant genetic correlation between survival scores and early growth measurements (at RAD194, BR0503). Design features such as incomplete blocks were significant (BR0503- Sc_0010, BR0603-Sc_0003-5). In some cases (*e.g.* BR0603, RAD165 and RAD179) plot term (*i.e.* family by replication interaction) was highly significant. More detailed spatial analyses could elucidate this problem, and contribute to more precise estimates of genetic parameters (Dutkowski *et al*. 2002).

Variance components were also obtained for growth traits (diameter at breast height and tree height) measured at an early (<5) age. Generally, σ^2_a was statistically significant, although heritability was low (median h^2=0.16). However, σ^2_{SCA} was also significant at RAD223 and RAD236 (Table 2.9). As with survival score this variance may also be due to nursery (tray) effects. The specific full-sib family effect σ^2_{SCA} for a later measurement Dbh_1509 at RAD223 was not significant. The issue needs further investigation.

Table 2.9. Analysis of early growth: Site code, age of assessment, *i.e.* _YYMM (Age), mean, minimum and maximum (in cm or mm), variance of specific combining ability

(σ^2_{SCA}), additive genetic variance (σ^2_a), narrow-sense heritability (h^2), dominance proportion (d^2) and standard errors (*SE*).

Site	*Age*	*Mean*	*Min*	*Max*	σ^2_{SCA}	σ^2_a	$h^2(d^2)$	$SE\ h^2(d^2)$
BR0503	Ht_0010	61.6 (cm)	22.0	100.0	ns[1]	25.5	0.15	0.05
RAD194	Ht_0300	31.3 (dm)	12.0	47.0	ns	4.04	0.17	0.07
RAD196	Ht_0207	35.1 (dm)	19.0	52.0	-	13.4	0.35	0.09
RAD223	Dbh_0400	105 (mm)	50	150	41.7	33.1	0.14(0.72)	0.09(0.34)
RAD228	Ht_0300	42.8 (dm)	20.9	62.0	ns	1.88	0.040	0.027
RAD230	Ht_0300	43.3 (dm)	20.0	60.0	-	3.16	0.081	0.046
RAD231	Ht_0300	42.2 (dm)	18.0	59.0	-	9.11	0.23	0.08
RAD236	Ht_0300	42.5 (dm)	19.0	65.0	1.70	7.1	0.16(0.15)	0.05(0.07)
RAD237	Ht_0300	44.6 (dm)	10.0	67.0	-	7.5	0.15	0.04

[1] statistical significance based on variance component to standard error ratio, if the ratio <1 the components was considered not significantly different from zero (ns), if variance ratio was >1 and <1.5 log likelihood deviance was tested against the chi-square distribution.

Genetic correlations

Genetic correlations between survival scores and other selection criteria were generally imprecisely estimated (Table 2.10), and thus weighted average was calculated (using ratio of estimate to its standard error or “t” values as weights). All the estimates were less than their standard errors (estimate/s.e. ratio < 1) and not statistically different from zero (Table 2.10). Nevertheless, the patterns of positive genetic relationship between survival and growth and a negative correlation of survival with *Dothistroma* resistance appeared to be consistent (Tables A3 and A4).

Recently, genetic variation in drought hardiness traits (foliage damage, cavitation of xylem tracheids, xylem hydraulic conductivity) and their genetic correlations with growth potential and recovery traits were investigated in full-sib families of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) by Anekonda *et al.* (2002). Most hardiness traits were strongly inter-correlated (genetic correlations often exceeded |0.80|) indicating that these traits are controlled largely by the same set of genes and that selection for hardiness based on one trait will increase hardiness as reflected in the other traits as well. Growth potential under favourable moisture regimes was nearly uncorrelated with drought hardiness, suggesting that drought hardiness could be improved without negatively impacting growth potential in favourable moisture conditions. Only one Australian study on stomatal resistance and needle water potential, involving a limited number of families from Californian radiata pine provenances and one Australian landrace family, reported correlations with seedling growth (Dean and Sands 1983).

Further studies are needed into genetics of drought resistance and survival. A more recent series of trials (BR series) has been planted targeting dry sites and the data on survival and early growth from those plantations are now being included into DATAPLAN®. Those large trials will present us with an opportunity to evaluate the correlations with more precision, and provide genetic material for physiological and molecular genetics studies.

Table 2.10. Average genetic correlations (r_G) and estimate to standard error ratios (*t*) in parentheses between survival scores and other selection criteria traits (DBH), branch size score (BSS); branch angle score (BAS); stem straightness score (SSS); fork count (FKC); and *Dothistroma* defoliation score (DOTHI).

SEL. TRAIT	DBH _06-12	DBH _13-24	BSS _06-12	BAS _06-12	SSS _06-12	FKC _06-12	DOTHI _06-12
r_g (estimate/s.e)	0.33 (0.60)	0.35 (0.72)	0.21 (0.38)	-0.14 (0.30)	-0.40 (0.95)	0.40 (0.52)	-0.37 (0.71)

Genetic gain and selection indices

Expected genetic gains based on preliminary estimates of correlations and economic weights are presented in Table 2.11. Under the base index (BI) survival was not included as a selection or breeding objective trait, but there was some positive expected response for selection trait SVS (R=4.1%), presumably due to positive genetic correlation with growth. When survival was included as a breeding objective and as a selection trait, there was an improvement in survival SVO of 0.8%, 1.1% and 1.5% over whole rotation and early selection trait SVS of 4.7%, 5.4% and 6.6% for low, medium and high drought hazard rating, respectively. At the low level of mortality (<10%) there was some opportunity cost in MAI response (*R*=14.8%) compared to base index (*R*=17.5%). However, at mortality >20% the improvement in MAI was greater than that obtained by base index (17.4%-22.7% vs. 17.5%), similar to that obtained by Chambers and Borralho (1997). There was an improvement in all other breeding objective traits except in MoE at medium (M) and high (H) and some trade offs with magnitude of improvement in other breeding objective and selection traits, as a consequence of including survival into breeding objective (Table 2.11).

Chambers and Borralho (1997) proposed use of restricted (desired gain) indices where gain in volume per hectare was determined according to site hazard rating for survival. The authors used an empirical growth function relating individual tree growth and survival (spacing) to predict the importance of including survival as a selection trait. The results clearly showed that survival is a generally important selection trait. The importance of including survival increased with increasing mortality within a stand, and with adverse genetic correlations between volume per tree and survival. Index selections combining volume per tree and survival resulted in 10% to 90% greater gains in volume per hectare than selection based on an index including only volume per tree alone. The desired gain in survival may be set as high as 15% before any substantial gains in volume per tree are foregone, even though mortality in plantations was zero.

Table 2.11 Response to selection (genetic gain with 10% selection intensity) in objective and selection traits under four indices: BI index assumes adequate survival and does not involve survival as selection score (SVS) or breeding objective trait (SVO). The economic weight on survival percent differed according to site hazard rating to mortality: low (L) <10%, medium (M) 10%-20% and high (H) >20%.

OBJECTIVE TRAITS						SELECTION TRAITS						
Trait	MAI	MOE	SWE	BSO	SVO	DBH	DEN	MFA	STS	BRA	BRS	SVS

Mean unit	20 m^3/ha/y	11.5 GPa	10.5 mm	5.5 cm	80 %	145 mm	400 Kg/m^3	25 Deg	3.5 score	3.5 score	3.5 score	0.86 score
BI	17.5%	-1.2%	-3.5%	-4.4%	-	4.1%	-3.7%	-5.1%	9.4%	5.1%	7.1%	4.1%
L	14.8%	1.5%	-2.9%	-3.0%	0.8%	3.7%	-3.4%	-8.5%	7.2%	3.5%	5.0%	4.7%
M	17.5%	-0.3%	-3.2%	-2.9%	1.1%	4.1%	-3.9%	-7.1%	8.2%	3.5%	4.7%	5.4%
H	22.7%	-4.2%	-3.7%	-2.2%	1.5%	5.0%	-4.8%	-3.8%	9.8%	3.3%	3.6%	6.6%

What-if analyses

Initial level of survival varied with site productivity from 70%-85% for MAI 15 and from 70%-85% for MAI 20 and land rental cost (from A$25 to A$150). Economic weight on survival varied proportionally to replanting costs irrespective of MAI or land rental costs. However, because relative volume losses were higher at higher levels of mortality, the economic weights were higher at the site with lower productivity and higher level of mortality ($27.5-$99.9 vs. $21.9 vs. $46.8). Economic weight on SVO changed non-linearly relative to economic weights on other breeding objective traits MAI, SWE, BRS according to level of survival (75% to 95%) (Table 2.12).

Table 2.12. Economic weight on survival (SVO) relative to mean annual increment (MAI), survival level, land rental costs and replanting costs (Low=$250/ha and High=$500/ha).

MAI	Survival (%)	Land rental cost ($)	Replanting cost ($)	Economic Weights ($ NPV/year)
				SVO
15	70	25	Low	87.4
			High	99.9
	75	50	Low	40.6
			High	53.1
	80	75	Low	27.5
			High	40.0
20	85	100	Low	34.3
			High	46.8
	90	125	Low	26.2
			High	38.7
	95	150	Low	21.9
			High	34.4

Selection index sensitivity

Using rank-order correlations (r_s) between the input parameters and selection index value, we identified the most important parameters influencing selection index estimation. For an average stand with 20 m^3/ha/y these parameters were: the economic weight for MAI (EW_MAI, r_s= 0.92), phenotypic correlation DBH/SVS (r_s=0.09) heritability of MAI (h^2_MAI, r_s= 0.09). The results suggested that parameters for the two traits related to growth (DBH and MAI) were the most important determinants of the selection index value. The index weight on selection trait SVS was also influenced the most by the EW_MAI, but having a rank order correlation of lesser magnitude (r_s=-0.36), phenotypic correlations DBH/SVS (r_s=-0.25) and SVS/BSS (r_s=-0.11) (Figure 2.2).

It has been previously reported that errors in economic value estimates had a relatively small influence on selection index estimation (*e.g.* Cotterill and Dean 1990). However, we found that under the current assumptions economic values were indeed one of the most important factors influencing the selection index weights for individual selection trait SVS and for selection index value. The economic weight of EW_MAI was the single most important factor influencing index values for current management regimes in an integrated production system. When the profit is predominantly determined by the positive economic weights for two or more genetically negatively correlated traits, the selection index is generally more sensitive to the economic weights (King and Hansen 1997, Kinghorn 2002). However, the relative importance of economic weights for selection index estimation diminished as the errors of genetic parameters increased (Ivković *et al.* 2006b). This was reflected in a decline of the correlation between economic weights and selection index weights as the errors on genetic parameters increased. The errors in estimating genetic parameters depend on several factors such as the quality of data, field design and size of sample. Therefore, in developing the selection index, minimising errors in both economic weights and genetic parameters is of vital importance.

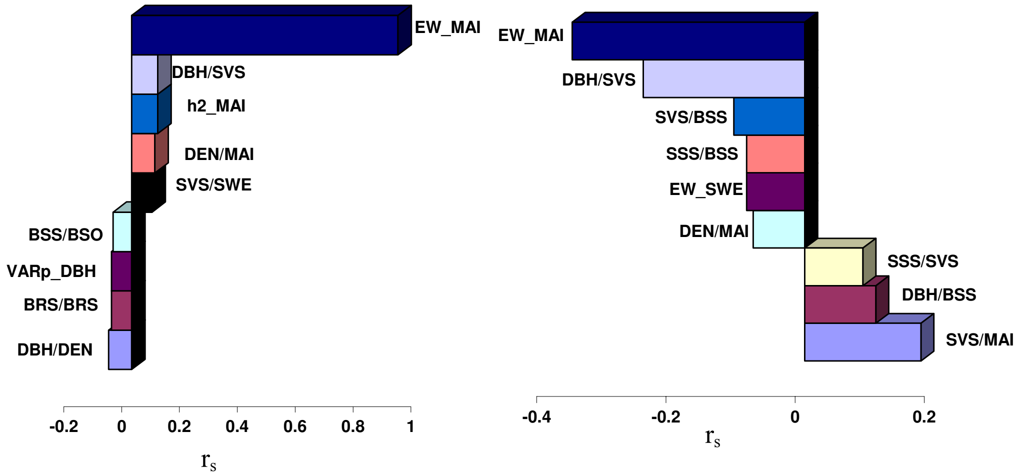

Figure 2.1. Rank order correlation (r_S) of selection index input parameters (Table 2.2) and selection index value (left) and selection index coefficient for survival (right).

2.4 Conclusions

- Climate data from 134 radiata pine progeny trials, covering a significant range of radiata pine plantation were collated, and drought prone sites were identified based on the climate variables and ecoclimatic indices. However, most of the trials that have been planted on drought prone sites (STBA’s BR series) are yet to be assessed for survival and early growth.
- A low productivity site (MAI 15) can achieve 7% IRR only if land holding cost is sufficiently low (A$25), and a higher productivity site can achieve the same IRR at a high land holding cost of up to A$150. However, if mortality levels are high significant reduction in profitability are expected due to cost of replanting and volume losses. If mortality exceeds 20% higher productivity site is no longer profitable at 7% IRR, and lower productivity site is no longer profitable at 6% IRR. More realistic scenarios can be simulated if actual parameters of the

mortality distribution are determined from field data. Such information on production system would assist a more realistic estimate of economic weight for drought resistance.

- Narrow-sense heritability for survival on drought prone sites was low to moderate, but the proportion of dominance variance (d^2, a full-sib family effect) was often higher than narrow-sense heritability. In the case of survival and early growth this may be due to the so called "nursery effect", especially because the effect seemed to diminish over time. More measurements consecutive over time are needed to precisely quantify the additive variance and the nursery effect, especially in trials with higher mortality levels.
- Genetic correlation between survival and early growth at plot level was not significant, but there was a positive phenotypic correlation. Genetic correlations for binomial trait such as survival were typically difficult to estimate. Further studies are needed into genetics of drought resistance and survival. A more recent series of STBA trials (BR series) has been planted targeting dry sites and the data on survival and early growth from those plantations are now being included into DATAPLAN®. Those large trials will present us with an opportunity to evaluate the correlations with more precision, and provide genetic material for physiological and molecular genetics studies.
- When survival was included as a selection trait and in breeding objective, there was an improvement in survival over rotation (SVO) of 0.8%, 1.1% and 1.5% and early survival score (SVS) of 4.7%, 5.4% and 6.6% for low, medium and high drought hazard rating, respectively. At the low level of mortality (<10%) there was some opportunity cost for including survival as objective trait in MAI response (14.8% vs. 17.5%). However, at mortality >20% the improvement in MAI (17.4%-22.7%) was greater if survival was in the objective.
- Parameters related to growth (DBH and MAI) were the most important determinants of the selection index value. The index weight on selection trait SVS was also influenced the most by the EW_MAI. Under the current assumptions economic values were indeed one of the most important factors influencing the selection index weights for individual selection trait SVS and for selection index value. The economic weight of MAI was the single most important factor influencing index values for current management regimes in an integrated production system;
- Economic weight on survival SVO changed relative to economic weights on other breeding objective traits MAI, SWE, BSO according to level of survival and planting cost level. MAI and land cost were fixed at initial level of mortality, replanting costs were proportional to mortality, while volume losses were assumed to increase at higher rate at higher levels of mortality. Therefore economic weights used in the gain calculation increased non-linearly according to level of mortality.

3 Essigella Pine Aphid

3.1 Introduction

The co-evolution between Norway spruce (*Picea abies*) and the green spruce aphid *Elatobium* in Europe has reached equilibrium, where the host is tolerating quite dense populations without serious needle loss. However, on introduced North American spruce species such as *P. sitchensis, P. glauca* and *P. pungens,* the aphid is causing severe needle loss. In Sitka spruce (*P. sitchensis*), heritability of aphid resistance was estimated to be 0.26, and was consistent over successive attacks (Sokov and Wellendorf 2000, Harding *et al.* 2003). Simpson and Ades (1990) reported variation in susceptibility of provenances of *P. radiata* and *P. muricata* to the woolly aphid *Pineus pini* and the needle aphid *Eulachnus thunbergia* in Australia.

Little is known about the mechanisms of resistance and genetics of Essigella aphid. Mechanisms of resistance may act on the pest's potential for reproduction and aphid number build-up, or ability to damage foliage. There is evidence of clonal and/or family differences in aphid damage in older radiata pine thinned stands (Sasse *et al.* 2009). We present additional evidence of genetic variation for Essigella aphid resistance in younger (*i.e.* less than13 years old) progeny trials. We present additional information on relationship between site ecoclimatic index and aphid numbers that can be used to determine site hazard ratings. We also present the effects of Essigella defoliation on production system and relative economic weight for defoliation on low to high hazard rating sites. The economic weights can be used in selection indices for selecting more resistant and profitable genotypes.

3.2 Materials and Methods

Effect of Essigella pine aphid on radiata pine production system

Two production systems with different productivity levels but similar cost-income structures (Tables A5 and A6) were created for studying effect of the pine aphid representing two regions: north-eastern (NE) Victoria and the Green Triangle. Plantation growing was profitable at 11% discount rate in Green Triangle and at 7.4% discount rate in NE Victoria.

The observed effects of Monterey pine aphid on defoliation and losses of volume were generally linear (Smith *et al.*1999). May (2004) quantified the linear relationship at the individual tree level and at stand level for NSW, Victoria and the Green Triangle regions. At the stand level, the relationship between defoliation and reduction in growth for years 1999, 2000, and 2001 did not differ significantly, and the overall regression formula was GR=0.739×DF, R^2=0.918. Percent defoliation and growth reduction increased more rapidly earlier in the rotation, from age 10 up to age 17 years, and reached maximum percent defoliation of 17% at ages 26-30 years (May 2004). Relationship between defoliation and wood quality is unknown, but presumably similar to that of Dothistroma (Harris and McConchie 1978).

In our analyses the pine aphid is assumed to have a cumulative effect on volume reduction in harvested trees. Based on the assumptions by May (2004), we used Atlas Forecaster to simulate growth and yield under several disease control scenarios: removal of defoliated trees at thinning, fertilizer application, insecticide spraying and biological control. However, implementation costs of these measures and their potential benefits in terms of reduction of defoliation have not been properly quantified.

Site hazard ratings

According to May (2004) the most significant defoliation and largest aphid populations were found in southern NSW, northern and central Victoria and the Green Triangle region. A CLIMEX model has been produced for pine aphid by Wharton and Kriticos (2004) which provides an ecoclimatic Index (EI) an index of climatic suitability for all locations in which pine aphid can occur. A high resolution risk map showing damage function for Monterey pine aphid is still needed for pine plantations in South Australia, specifically the Green Triangle and in Victoria.

Location and basic climate characteristics for six sites monitored in major Essigella defoliation areas are given in Table 3.1. The number of aphids increased during the summer as the temperature reached between 22 -25˚C and peaked before the temperature falls below 20˚C in May. Relative humidity has been found to correlate with the aphid numbers in south-eastern Australia, where high humidity often associated with rainfall and wet cool conditions inhibit development of Essigella. Significant correlation between crown damage and relative humidity and rainfall during late summer and fall (February to May) has been observed (May 2004).

Table 3.1. Location and basic climate characteristics for six sites where Essigella defoliation was monitored. Mean annual temperature (*MAT*), mean annual rainfall (MAR), mean summer temperature (MST) and Mean summer rainfall (MSR).

Trial ID – Trial Name	**Lat**	**Long**	**Alt**	***MAT***	***MAR***	***MST***	***MSR***
RAD168 - Warrenbayne CP	-36˚49’	145˚52’	625	11.4	1113	17.7	160
RAD117 - Warrenbayne CP	-36˚44’	145˚53’	605	11.6	983	17.9	156
RAD148 - Narbethong 1972	-37˚29’	145˚37’	430	11.9	1351	17.2	225
RAD170 - Toorour Factorial	-36˚51’	145˚52’	670	11.1	1046	17.3	164
RAD195 - Lake Buffalo Myrtleford	-36˚42’	146˚40’	305	13.3	1133	19.7	179
RAD225 - Rennick, 4x4 Factorial	-37˚51’	141˚58’	60	13.0	754	16.9	99

We obtained data for South Australia (Charlma Phillips, PIRSA Forestry, pers. comm.) for various locations of pine plantations, and damage level used was the aphid-number score in accordance with the monitoring protocol (Kent and Carnegie 2000). The mean number of aphids per site as estimated using the aphid-number score. The aphid density score was a scale of 1-4, where 1=0 aphids, 2=1-10 aphids, 3=10-100 aphids and 4=>100 aphids. Sites that did not record an aphid score of 4 were eliminated from the analyses. Victorian Aphid data was used to see if the damage parameters used are consistent with the South Australian data and the data for other states. The relationship between the damage parameter and EI will then be determined and a risk map for the specific areas, showing where the greatest risk of damage will be produced.

Quantitative genetics of Essigella aphid defoliation

Test sites and data sets Sasse *et al.* (2009) assessed 18 progeny trials for Dothistroma defoliation between 2001 and 2005. Summary of trial establishment and design are given in Table 3.2a (for further details see Sasse *et al.* 2009). In addition, a younger progeny trial was assessed over two growing seasons (2008 and 2009) for upper crown damage. The trial consists of 254 entries of genetically connected (full- and half-sib) progeny for use in advanced generation selections and breeding. Trial design is row-column, incomplete block, 5 replications, 4 trees per plot, a total of 5120 trees planted at 3m by 3m spacing. It was established in 1996 near the Mt. Gambier Airport at altitude 60m on sandy soil. The trial was assessed for survival and diameter at breast height (DBH) growth at age 3, and for growth (DBH), branching (BRS, BRA), form (stem straightness, malformation, ramicorn and fork count) at age 5 and for wood quality (core density, acoustic velocity, spiral grain) at age 6.

Table 3.2a (Table 1 from Sasse *et al.* 2009*) S*ummary of trials assessed from 2001 to 2005 for defoliation by aphids, Table 3.2b and summary of a trial assessed in 2008-2009 for defoliation in the upper crown.

a) Trial	Year established	Location	Trial type	Number of trees assessed	Number of families	Average trees per family	Year assessed
VRC025	1979	Flynn 268	Provenance trial	1348	16	84.3	2005
RAD114	1967	Warrenbayne 011	CP families	354	52	6.9	2001
RAD117	1967	Warrenbayne 026	CP families	237	36	8.9	2001, 03, 04
RAD148	1972	Narbethong 240	Heritability trial, NC1 design CP families	425	48	9.0	2004
RAD150	1972	Narbethong 240	NSW OP SO families	154	20	8.1	2004
RAD151	1972	Narbethong 240	Vic & Tas OP SO families	176	20	9.3	2004
RAD152	1972	Narbethong 240	CP families, density x spiral grain	118	23	5.4	2004
RAD153	1972	Narbethong 240	SA IGP OP families	172	42	4.2	2004
RAD154	1972	Narbethong 240	ACT IGP OP families	82	32	2.6	2004
RAD155	1972	Narbethong 240	QLD IGP OP families and Vic OP SO families	154	26	6.2	2004
RAD156	1972	Narbethong 240	NSW IGP OP families	360	61	6.0	2004
RAD157	1972	Narbethong 240	Guadalupe, Cedros, Cambria OP families ex ACT	79	19	4.4	2004
RAD162	1973	Narbethong 245	CP families	376	62	6.2	2002
RAD168	1976	Warrenbayne 084	Heritability trial, NC1 design CP families	600	54	12.2	2001, 03, 04
RAD170	1978	Toorour	12 × 3 CP factorial	216	34	6.5	2001
RAD195	1985	Myrtleford Lake Buffalo	CP families	1344	36	28.6	2003
RAD205	1986	Rennick 006	4 × 4 2G CP factorial	129	14	9.9	2001
RAD225	1989	Rennick 013	4 × 4 CP factorial	442	26	17.7	2001
RAD226	1989	Rennick 013	3 × 4 CP factorial	233	16	15.5	2001
Lal Lal SO	various	Lal Lal	Clonal seed orchard	254	12 clones	21	2002

b) BR9601	1996	Mt. Gambier Airport	Half and full-sib families	5120	254	20	2008, 09

Defoliation by aphids is assessed using a standard technique where the level of defoliation in the upper crown of individual trees is scored on a scale of 1–10, where 10 represents 91–100% lost foliage and 1 represents 0–10% lost foliage (*i.e.* little or no defoliation due to aphids). Assessments were done by two assessors within blocks, and the assessor's identity was recorded. Defoliation was assessed in winter, when needles were in an advanced stage of chlorosis or have been already shed.

Exploratory data analyses revealed that the defoliation scores followed a multinomial distribution, and because the within-class variance of the distribution depends on mean, the assumption of homogeneity of variance required for the computation of statistical tests was violated (SAS Institute Inc. 2008). For the scores (expressed as proportion $0 > p < 1$) the arcsin(sqrt(p)) transformation made the variance essentially free of the mean value (Sokal and Rohlf 1995). Furthermore the distribution of defoliation scores was in some cases skewed and the transformation made the distribution nearly normal.

Genetic analyses

For analyses of 18 trials in NE Victoria see Sasse et al. (2009). For BR9601, estimates of variance components for a single trait were obtained according to the following linear mixed model:

[3.1] $$\mathbf{y} = \mathbf{X}b + \mathbf{Z}_R r + \mathbf{Z}_P p + \mathbf{Z}_T t + \mathbf{Z}_S s + \mathbf{e}$$

where $\mathbf{y}$ is the vector of observations and $\mathbf{X}$ is the incidence matrix relating the observations in $\mathbf{y}_i$ to the b vector of fixed effects (*i.e.*, overall mean); $\mathbf{Z}_R$ is the incidence matrix relating to the r vector of random replicate effects; $\mathbf{Z}_P$ is the incidence matrix relating to the p vector of random plot effects (or replicate by family interaction); $\mathbf{Z}_T$ is the incidence matrix relating to the t vector of individual tree (additive genetic) effects; $\mathbf{Z}_S$ is the incidence matrix relating to the s vector of specific combining ability (full-sib family) effects; e is the vector of residuals. For half-sib design only general combining ability was estimated. Check seedlots were excluded from these analyses.

For the multivariate case including Essigella, growth, form and survival variables:

[3.2] $$\mathbf{y}_j = \mathbf{X}_j\mathbf{b}_j + \mathbf{Z}_{a_j}\mathbf{a}_j + \mathbf{Z}_{f_j}\mathbf{f}_j + \mathbf{Z}_{p_j}\mathbf{p}_j + \varepsilon_j$$

Where y_j is the vector of individual tree observations for trait j (j = 1 to n), b_j is the vector of fixed effects and X_j is the known incidence matrix relating the individual tree observations in y_j to the fixed effects in b_j where

[3.3] $$\mathbf{X}_j\mathbf{b}_j = \begin{bmatrix} X_1 & 0 & 0 & 0 \\ 0 & X_2 & 0 & 0 \\ 0 & 0 & X_{\dots} & 0 \\ 0 & 0 & 0 & X_n \end{bmatrix} \times \begin{bmatrix} b_1 \\ b_2 \\ b_{\dots} \\ b_n \end{bmatrix}$$

Z_{a_j} is the known incidence matrix relating observations in y_j to additive genetic effects in $\boldsymbol{a}_j$; $\boldsymbol{a}_j$ is a vector of random additive genetic effects of individual genotypes ~MVN $(0, G \otimes A)$

[3.4] $$G = \begin{bmatrix} \sigma^2_{a_1} & \sigma_{a_1a_2} & \sigma_{a_1a_{\dots}} & \sigma_{a_1a_n} \\ \sigma_{a_2a_1} & \sigma^2_{a_2} & \sigma_{a_2a_{\dots}} & \sigma_{a_2a_n} \\ \sigma_{a_{\dots}a_1} & \sigma_{a_{\dots}a_2} & \sigma^2_{a_{\dots}} & \sigma_{a_{\dots}a_n} \\ \sigma_{a_na_1} & \sigma_{a_na_2} & \sigma_{a_na_{\dots}} & \sigma^2_{a_n} \end{bmatrix}$$

A is the additive relationship matrix, $\sigma^2{}_{a_j}$ is the estimated additive genetic variance, $\sigma_{a_xa_y}$ is the estimated genetic covariance between additive effects of the two traits.

Z_{f_j} is the known incidence matrix relating observations in y_j to random effects in f_j; f_j is a vector of random effects of full-sib families ~MVN(0,$F \otimes I_f$ where diagonal elements of F are $\sigma^2{}_{f_j}$ are the estimated variance attributed to full-sib families (specific combining ability), and off-diagonal elements ($\sigma^2{}_{f_xf_y}$) are the estimated covariances between full-sib family effects of two traits; and I_f is an identity matrix diagonal elements equal to the number of full-sib families.

Similarly, Z_{p_j} is the known incidence matrix relating observations in y_j to genetic effects in p_j; p_j is a vector of random effects of plots within replications ~MVN(0,$P \otimes I_p$) where, diagonal elements of P are $\sigma^2{}_{p_j}$ the estimated variance attributed to plots within reps, and $\sigma^2{}_{p_xp_y}$ is the estimated covariance between plot effects of two traits, and I_f is an identity matrix diagonal elements equal to the number of plots.

[3.5]

$$R = \begin{bmatrix} \sigma^2_{e\,1} & \sigma_{e_1e_2} & \sigma_{e_1e_{\dots}} & \sigma_{e_1e_n} \\ \sigma_{e_2e_1} & \sigma^2_{e\,2} & \sigma_{e_2e\dots} & \sigma_{e_2e_n} \\ \sigma_{e_{\dots}e_1} & \sigma_{e_{\dots}e_2} & \sigma^2_{e\,\dots} & \sigma_{e_{\dots}e_n} \\ \sigma_{e_ne_1} & \sigma_{e_ne_2} & \sigma_{e_ne_{\dots}} & \sigma^2_{e\,n} \end{bmatrix}$$

ε_j is a random vector of residual terms ~MVN (0, $R \otimes I_j$) and $\sigma^2{}_{e_j}$ is the estimated residual variance for each trait and $\sigma^2{}_{e_xe_y}$ is the estimated residual covariance between two traits.

Spatial adjustment partitioned the residual variance into an independent component and a two-dimensional separable spatially auto-correlated component (ASREML®, Gilmour *et al.* 2005). The model specifies a first order autoregressive correlation model (AR1) for columns and rows of the tree positions within a trial. The R matrix structure is a direct product of two autoregressive correlation matrices giving a two-dimensional, first-order separable autoregressive spatial structure for variance:

[3.6]

$$R = \sigma^2_e \Sigma_c(\rho_c) \otimes \sigma^2_e \Sigma_r(\rho_r)$$

where σ^2_e is the spatial variance, $\otimes$ is the Kronecker product, and $\Sigma_c(\rho_c)$ is a first-order autoregressive correlation matrix with an autocorrelation ρ:

$$\Sigma(\rho) = \begin{bmatrix} 1 & \rho & \rho^2 & \cdots & \rho^{n-1} \\ \rho & 1 & \rho & \cdots & \vdots \\ \rho^2 & \rho & 1 & \cdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \rho^{n-1} & \cdots & \cdots & \cdots & 1 \end{bmatrix}$$

[3.7]

An additional random term with one level for each experimental unit was used so that a second (independent) error term could be fitted. The “units” term was fitted to allow for the so-called “nugget” effect and represents unstructured environmental correlation (Dutkowski *et al.* 2006):

[3.8] $$R = \sigma_e^2 I_{nr} I_{nc} + \sigma_\varepsilon^2 \Sigma_r(\rho_r)\Sigma_c(\rho_c)$$

The spatial component best models widespread continuous trends, rather than discontinuous effects such as assessor effects. Variograms, plots of spatial residuals (Gilmour *et al.* 2006) and colour intensity maps of spatial residuals (Dutkowski *et al.* 2002) were used to detect extraneous effects. All terms were fitted in a single model, where the spatial, extraneous, and treatment effects are estimated simultaneously.

The estimate of individual-tree narrow-sense heritability was obtained as

[3.9] $$h^2 = \frac{\sigma_a^2}{\sigma_P^2}$$

Where σ_a^2 is the estimate of additive genetic variance,

$\sigma_P^2 = \sigma_a^2 + \sigma_f^2 + \sigma_p^2 + \sigma_e^2$ is the estimate of phenotypic variance, where σ_f^2 is the estimate of full-sib family variance (specific combining ability), σ_e^2 is the plot variance and σ_e^2 is the model error variance.

The genetic correlation r_G between two traits was estimated within the ASREML software as:

[3.10] $$r_g = \frac{\sigma_{a_x a_y}}{\sqrt{\sigma^2{}_{a_x}\sigma^2{}_{a_y}}}$$

where:

$\sigma_{a_x a_y}$ = additive genetic covariance component between traits x and y;

$\sigma^2{}_{a_x}$ = additive genetic variance component for trait x;

$\sigma^2{}_{a_y}$ = additive genetic variance component for trait y

Standard errors for each of the correlations were calculated using a truncated Taylor series in ASREML (Gilmour *et al.* 2006).

Selection indices and genetic gain

The early age selection criteria were: diameter at breast height (DBH), stem straightness score (STS), branch size score (BSS), wood density (DEN) and modulus of elasticity (MoE). The breeding objective traits were: mean annual increment (MAI), stem sweep (SWE), branch size (BSO) and wood stiffness (MoE). Essigella defoliation scores at ages over 12 years were linked to selection criteria and to breeding objective traits through estimated and assumed genetic correlations. The parameters used for derivation of selection index were economic weights (vector *a*), the phenotypic variance-covariance matrix for selection criterion traits and the genetic variance-covariance matrix between selection criterion traits and breeding objective traits. The formula [1.5] for deriving the vector of selection index coefficients was used.

The phenotypic and genetic variance–covariance matrices used for selection index sensitivity analyses were taken from Wu *et al*. (2008). Expected genetic gains or mean response in breeding objective traits, expressed per standardised selection differential, was calculated using formula [1.6]. We introduced Essigella defoliation as a selection and a breeding objective trait and examined the potential genetic gain for sites with different levels of productivity and survival (70% to 95%).

Sensitivity analyses

What-if analyses Different levels of MAI, growth reduction due to upper crown defoliation (ESSI) and the value relative to stem form, branch size and wood stiffness economic weights were calculated. Bio-control assumed to be effective in reduction of defoliation and growth loss ½ of the level in untreated stands. One spray cost was assumed to be A$25/ha, but it was assumed to be reduce defoliation and growth loss ¼ relative to untreated stand. Based on those assumptions economic weights were calculated for two sites with different productivity levels.

Monte Carlo simulations Parameters that determine selection index coefficients were the estimated economic weights, the genetic correlation matrix for selection criterion traits and the genetic correlation matrix between selection criterion traits and breeding objective traits, and trait heritabilities (h^2). For the analyses of sensitivity of the selection index to economic weights and other inputs, we assumed a triangular distribution with parameters maximum and minimum of around the means of genetic correlations and normal distribution around the mean of heritabilities and economic weights.

The results of Monte Carlo simulations were used to calculate Spearman rank-order correlations (r_S) as a measure of association between the estimated economic weight and each input parameter. Rank-orders were used rather than the actual values because the method does not require the normality assumption and some of the inputs were assumed to have either uniform or triangular distributions.

3.3 Results and Discussion

Effect of Essigella Pine Aphid on Radiata Pine Production System

Economic evaluations of the pest impact have been done on the regional and country-wide level, under some general assumptions (Moore 1999, May 2004). Our simulations using Forecaster® were based on the assumption that percent defoliation and growth reduction increases more rapidly early in rotation, from age 10 up to age 17 years, and reaches maximum percent defoliation at ages 26-30. An average defoliation of 13.5% could cause approximately 10% growth reduction over rotation. We assumed that the shape of growth curve does not change significantly, and that the volume decreases due to attack after age 17 is a linear function of growth on unaffected site (Figure 3.1).

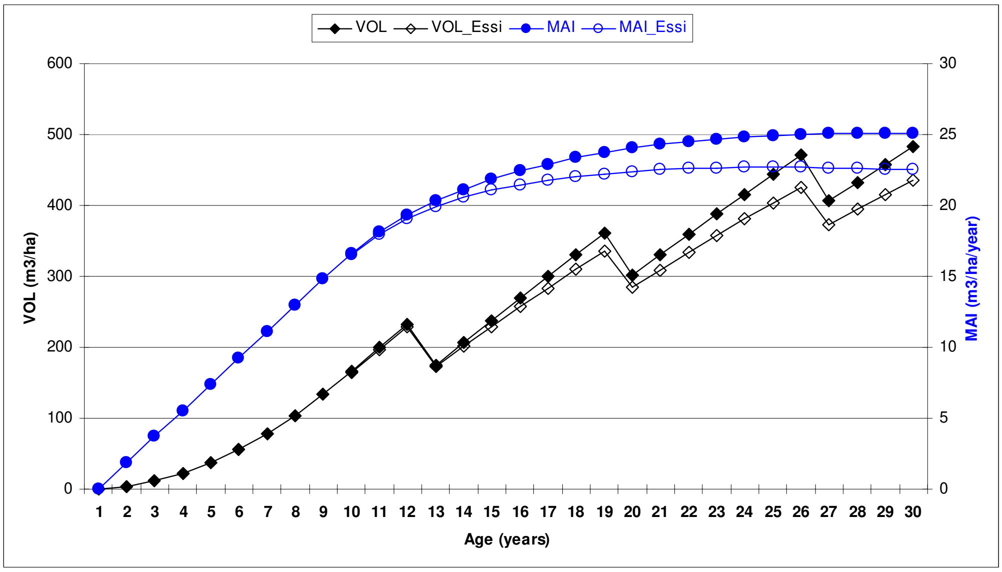

Figure 3.1. Modelled volume and mean annual increment for sites unaffected (VOL and MAI) and affected (VOL_Essi and MAI_Essi) by Essigella aphid in the Green Triangle region.

Based on the modelled volume loss in Figure 3.1 the NPV over a rotation are estimated for trait change (10% reduction of average infection rate) and differential change in profitability in NE Victoria (1.6%-31% NPV change) and the Green Triangle (1.3%-54.2% change) (Tables 3.3. and 3.4.).

Table 3.3. The effects of 10% trait change at three levels of Essigella caused defoliation on plantation production system in NE Victoria and derived economic weights @ 6% discount rate. (For comparison economic weight on MAI was A$ 225 ha^{-1}y^{-1})

		Essigella defoliation rate			
		Very Low	Low	Medium	High
		5.5%	11%	22.0%	44.0%
Base	*NPV $/ha*	1148	977	580	-293
10% change	*NPV$/ha*	1163	1009	652	-134
	ΔNPV%	1.3%	3.2%	12.3	54.2%
Economic Weights for Essigella *(NPV change per % infection rate)*					
	NPV $/ha	26.7	28.9	32.6	36.2

Table 3.4. The effects of 10% reduction in Essigella caused defoliation on plantation production system in Green Triangle region and derived economic weights @ 7% discount rate. (For comparison economic weight on MAI was A$ 298 ha^{-1}y^{-1}).

		Essigella defoliation rate			
		Very Low	Low	Medium	High
		5.7%	11.4%	22.0%	44.0%
Base	*NPV $/ha*	1912	1560	743	-1055
10% change	*NPV$/ha*	1942	1625	810	-728
	ΔNPV%	1.6%	4.2%	19.8%	31.0%

Economic Weights for Essigella *(NPV change per % infection rate)*				
NPV $/ha	52.8	57.2	64.3	71.5

The average defoliation rate (22%) chosen here may represent a relatively low level of insect attack. In the future, the average defoliation rate in different regions can be quantified using field monitoring data. The pattern of Essigella aphid attacks is usually from the younger (top) to the older needles, while *Dothistroma* tends to remove older needles first and progresses up the tree to the younger needles. Since younger needles contribute more to growth then older needles (Rook and Whyte 1976), it appears that the effect of Essigella on growth could be greater then that of *Dothistroma* at same infection rates (Smith *et al.* 2000). The economic weights were estimated for objective traits growth rate and defoliation resistance separately, which is conceptually different from the approach adopted by Chambers *et al.* (2000) who defined a single objective trait as "growth on affected site".

The weight of MAI relative to stem form, branch size and wood stiffness may change. Effects of the insect defoliation on stem form and wood quality have not yet been quantified. As a guide relative economic weights for sites with reduced MAI productivity (-5%; -10%; and -20%) based on a generic production system model (Ivković *et al.* 2006b) are given in Table 3.5 and Table A5.

Table 3.5. Economic weights (NPV$ per trait unit, at discount rate = 7%) and relative weights for breeding objective traits: mean annual increment (MAI), sweep (SWP), branch size (BRS), and modulus of elasticity (MoE) at four base levels of traits MAI and MoE.

Base MAI & MoE	***Objective traits***			
	MAI	***SWP***	***BRS***	***MoE***
	m^3/ha/y	mm/m	cm	GPa
MAI 24.0 & MoE 10.7	$255	$-308	$-872	$765
	1	-1.21	-3.42	3.00
MAI 22.8 &	$283	$-274	$-799	$694
MoE 10.7	1	-0.97	-2.82	2.45
MAI 21.6 &	$300	$-258	$-762	$658
MoE 10.7	1	-0.86	-2.54	2.20
MAI 19.2 &	$363	$-261	$-761	$478
MoE 11.5	1	-0.72	-2.10	1.32

As site productivity decreased, the economic weight for growth rate (MAI) increased relative to other traits, which could be result of defoliation by pine aphid. The economic weight for MAI relative to MoE increased relative to MoE, especially when the base value of MoE was increased, which can be expected on sites affected by defoliation (Harris and McConchie 1978).

Different pest control scenarios have been explored. May (2004) suggested that biological control is the most viable control method. Introduction of a parasitic wasp (*Diaeretus essigellae*) can potentially reduce the aphid numbers and reduce defoliation up to 50% with almost insignificant implementation costs. That would significantly reduce the risk and economic weight on defoliation as a resistance trait. The reduction of economic weight may not be directly proportional to the reduction of defoliation. However, more detailed information on the bio-control application and effectiveness is needed, before a more practical scenario can be created.

Site hazard ratings for Essigella attack

A CLIMEX model has been produced for Essigella aphid (Wharton and Kriticos 2004) which provides an index of climatic suitability or ecoclimatic index (EI) for all locations where that the aphid can occur. The relationship between the aphid score and mean aphid numbers has been established by an equation $y=0.1261e^{2.0787x}$ (Wharton 2005), where x is aphid score and y is mean aphid numbers. Mean aphid number estimates are plotted against the EI obtained from the CLIMEX model for *E. californica*. The relationship between the mean aphid number and the EI (r^2=0.44) was obtained from the data collected so far (Figure 3.2).

A risk map showing damage function for Essigella is still needed for specific pine plantations in the Green Triangle region and Victoria.

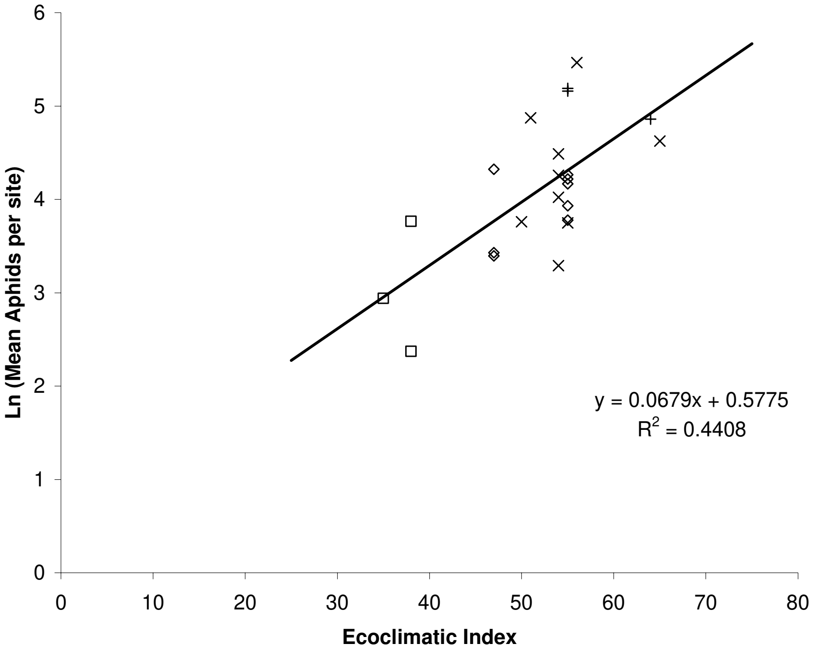

Figure 3.2. The relationship between the aphid score and Ecoclimatic Index (**x**) South Australia, (+) Australian Capital Territory, (◊) New South Wales, (□) Western Australia (T. Wharton unpublished data)

Genetics of Essigella resistance

Hancock Victorian Plantations assessed, between 2001 and 2005, defoliation in a radiata pine provenance trial, a subset of clones within a seed orchard, and 18 progeny trials (Sasse *et al.* 2009). There were significant differences in retained foliage between provenances, and populations within provenances. The inland northern population of Ano Nuevo provenance had the highest level of retained foliage in the upper crown (mean score of 8.3), and the northern population of the Cambrian provenance had the least retained foliage (5.0). Estimates of heritability from progeny trials ranged from 0–0.9, and averaged about 0.5 in trials where there was a significant family (maternal) effect (Table 3.6 - Table 5 of Sasse *et al.* (2009). Cross-site analysis using a family model resulted in an overall heritability of 0.45. Genetic correlations between assessments across two trials in 2004 and those in 2001 and 2003 were high

(0.9). In addition to the observed differences between provenances and families, there were significant differences between clones, and average levels of retained foliage within a clone ranged from 19% to 94%.

Table 3.6 a) (Table 5. of Sasse *et al.*). Variance components and heritability (***h^2***) for trials assessed for aphid defoliation in the winter 2004. b) Trials assessed for aphid defoliation in winters of 2008 and 2009.

a)

Trial	Year assessed	Mean defoliation	σ^2_{mother} (se)	σ^2_{father} (se)	$\sigma^2_{mother.father}$ (se)	σ^2_{resid} (se)	h^2 (se)
RAD114	2001	33%	0.243 (0.264)	0.296 (0.272)	0.133 (0.266)	2.725 (0.225)	0.32 (0.21)
RAD117	2001	31%	0.936 (0.596)	1.231 (1.092)	0.348 (0.397)	2.440 (0.229)	0.88 (0.32)
RAD117[b]	2003	29%	0.770 (0.457)	1.920 (1.571)	~0	2.984 (0.318)	0.95 (0.31)
RAD117	2004	34%	0.226 (0.547)	0.748 (0.895)	0.742 (0.611)	2.028 (0.218)	0.52 (0.47)
RAD148[b]	2004	39%	0.389 (0.216)	0.454 (0.306)	~0	4.075 (0.301)	0.34 (0.12)
RAD152[a]	2004	47%	0.864 (0.575)	-	-	3.462 (0.528)	0.80 (0.45)
RAD153[a]	2004	26%	0.544 (0.308)	-	-	2.579 (0.341)	0.70 (0.36)
RAD162[a]	2002	33%	0.260 (0.126)	-	-	1.747 (0.159)	0.52 (0.23)
RAD168	2001	31%	0.743 (0.321)	0.340 (0.250)	0.044 (0.206)	2.586 (0.158)	0.58 (0.17)
RAD168[b]	2003	25%	0.344 (0.150)	0.121 (0.093)	-	2.026 (0.125)	0.37 (0.10)
RAD168	2004	31%	0.343 (0.207)	0.178 (0.183)	0.098 (0.192)	2.492 (0.154)	0.33 (0.16)
RAD225	2001	33%	0.175 (0.135)	0.154 (0.130)	0.036 (0.044)	1.115 (0.089)	0.45 (0.20)

b)

Trial	Year assessed	Mean defoliation	-	$\sigma^2_{additive}$ [c] (se)	σ^2_{SCA} [c] (se)	σ^2_{resid} [c] (se)	h^2 (se)
BR906	2008	51%	-	$0.756*10^{-2}$ $(0.195*10^{-2})$	$0.111*10^{-3}$ NS $(0.854*10^{-3})$	$0.464*10^{-1}$ $(0.185*10^{-2})$	0.18 (0.04)
	2009	24%	-	$0.521*10^{-2}$ $(0.164*10^{-2})$	0.000 NS (0.000)	$0.350*10^{-1}$ $(0.175*10^{-2})$	0.10 (0.03)

a OP trial

b mother.father variance estimated to be negative or close to 0, or completely aliased with other terms, and therefore excluded from model

c ARCSIN(SQRT) transformed data

For BR9601 trial, the percent defoliation in the upper crown decreased from winter 2008 (51.4%) to winter 2009 (24.4%). Narrow-sense heritability for assessments of upper crown defoliation scores also decreased from 0.18±0.04 to 0.10±0.03. Nevertheless, genetic year to year (winter 2008 to winter 2009) correlation between assessments was high 0.88 ±0.09. Specific combining ability was not significant in either year (Table 3.6b). Arcsine square root transformed scores showed strong assessor effect, however, the correlation between assessors was high (>0.90). Genetic correlations between Essigella upper crown defoliation scores at age 12 years and early (<7 years) selection criteria traits were obtained for growth DBH (-0.37±0.15), branch size BRS (0.29±0.19), stem straightness STS (-0.55±0.16), fork count FKC (0.50±0.16) and wood density DEN (0.34±0.15) (Table 3.7).

Table 3.7. Genetic correlations (r_G) and estimate to standard errors ratios in brackets between Essigella upper crown defoliation scores at age 12 years and early (<7 years) age selection criteria traits: growth measured as DBH; branch size (BRS); branch angle (BRA); stem straightness (STEMST); fork count (FKC); and wood density (DEN).

SEL. TRAIT	DBH _0307	DBH _0510	BRS _0510	BRA _0510	STS _0510	FKC _0510	DEN _0609

r_G **(estimate/s.e)**	-0.18 (1.15)	-0.37 (2.45)	0.29 (1.53)	-0.29 (1.15)	-0.55 (3.37)	0.50 (2.60)	0.34 (2.3)

Selection index and genetic gain

Genetic and phenotypic correlations given in Tables A3 and A4 are only preliminary estimations because there is little information on genetic parameters available apart from those of ESSI_12 four-level score at the Mount Gambier BR9601 “Airport” trial and correlations with growth reported by Sasse *et al.* (2009). Because Essigella caused defoliation occurs at a later age (>12 years) than *Dothistroma* caused defoliation, correlations with growth and wood quality are assumed to be higher in magnitude. On the other hand, correlations with stem form and branch size were assumed to be lower in magnitude than those correlations with DOTHI. Genetic correlations between selection criteria and breeding objective traits were also assumed to be high. However, a biological control program involving the importation of a wasp parasitic from North America is currently underway, which can make estimation of genetic (and economic) parameters even more complex.
Essigella is affecting mostly the older trees (>12 years) and defoliation would affect mature age traits more directly than *Dothistroma*. Therefore, it was assumed that the magnitude of the correlation with the mature objective traits would be stronger for Essigella caused defoliation than for *Dothistroma* caused defoliation. Based on these data, it is not clear if correlations would have a regional correlation based on the regional infestation rates, *i.e.* the negative correlation with growth may be stronger in highly affected areas. It is likely that the genetic correlation may be non-linear, *i.e.* the correlation increases with intensity of damage (*e.g*. May 2004, Hopmans *et al.* 2008).

The expected genetic gain based on current correlation estimates and economic weights is presented in Table 3.8. For a base selection index (BI), where Essigella defoliation (ESSI) was not included either as an objective nor as selection trait, there was very little correlated response (R=-0.2%). Using the alternative index, ESSI was included as a selection and breeding objective trait. There was a reduction in ESSI$_{\text{O}}$ defoliation of 5.2%, 5.9% and -6.5% over whole rotation and a reduction in selection trait ESSI of -6.5%, -6.9 and 6.9% for medium and high hazard rating sites, respectively. There was an improvement in breeding objective traits, except in MoE at higher defoliation sites. There was a favorable response in all selection traits except in DEN. However, there were some trade offs as a consequence of including ESSI into breeding objective (*i.e.* reduced magnitude of favorable response in some breeding objective and selection traits if the defoliation is low).

Table 3.8 Response to selection (genetic gain) under 10% selection intensity and different selection indices: Base index (BI) does not involve Essigella upper crown defoliation (ESSI). The response in objective trait ESSI$_{\text{O}}$ and selection trait ESSI included in selection indices according to site hazard rating low (L), medium (M) and high (H), respectively.

OBJECTIVE TRAITS						**SELECTION TRAITS**						
Trait	**MAI**	**MOE**	**SWE**	**BRS$_{\text{O}}$**	**ESSI$_{\text{O}}$**	**DBH**	**DEN**	**MFA**	**STS**	**BRA**	**BRS**	ESSI
Mean unit	20 m^3/ha/y	11.5 GPa	10.5 mm	5.5 cm	22.0 %	145 mm	400 Kg/m^3	25 Deg	3.5 score	3.5 score	3.5 score	3.1 score

BI	17.5%	-1.2%	-3.5%	-4.4%	-	4.1%	-3.7%	-5.1%	9.4%	5.1%	7.1%	-0.2%
L	15.6%	0.8%	-3.0%	-3.1%	-5.2%	4.0%	-3.7%	-7.6%	7.2%	3.5%	5.3%	-6.5%
M	17.9%	-0.8%	-3.2%	-2.9%	-5.9%	4.4%	-4.1%	-6.3%	7.9%	3.5%	5.0%	-6.9%
H	22.7%	-4.2%	-3.5%	-2.2%	-6.5%	5.2%	-5.0%	-3.3%	9.2%	3.1%	3.9%	-6.9%

What-if analyses

At initial levels of upper crown defoliation (ESSI) ranging from 11%-44% and assuming application of biological control and one or two applications of insecticide spray, economic weight on ESSI varied according to stand productivity level (MAI15 and from MAI 20). The economic weights were higher at the site with higher productivity, and volume losses were higher at higher levels of defoliation. Spray application had higher effect of economic weight for ESSI at higher defoliation levels (Table 3.9).

Table 3.9 Economic weight on Essigella defoliation relative to mean annual increment (MAI), defoliation percent (ESSI), bio-control and spray costs.

ESSI (%)	Bio-control	Spray Cost (A$)	Economic Weights ($ NPV/year)	
			MAI 20	MAI 24
44	Yes	25	28.9	57.2
		0	32.6	64.3
44	No	50	32.6	64.3
		0	36.2	71.5
22	Yes	25	26.7	52.8
		0	28.9	57.2
22	No	25	28.9	57.2
		0	32.6	64.3
11	Yes	0	26.7	52.8
11	No	25	26.7	52.8
		0	28.9	57.2

Sensitivity analyses of selection index

Using rank-order correlations (r_s) between the input parameters and selection index value, we identified the most important parameters influencing selection index estimation. For an average stand the most important parameter influencing selection index value and selection index coefficient for ESSI was the economic weight for MAI (EW_MAI, $r_s > 0.90$) (Figure X). All other genetic parameters (correlations and heritability) and economic weights had much less influence on selection index value and coefficients. The results suggested that special attention should be given to estimation precision of parameter EW_ MAI.

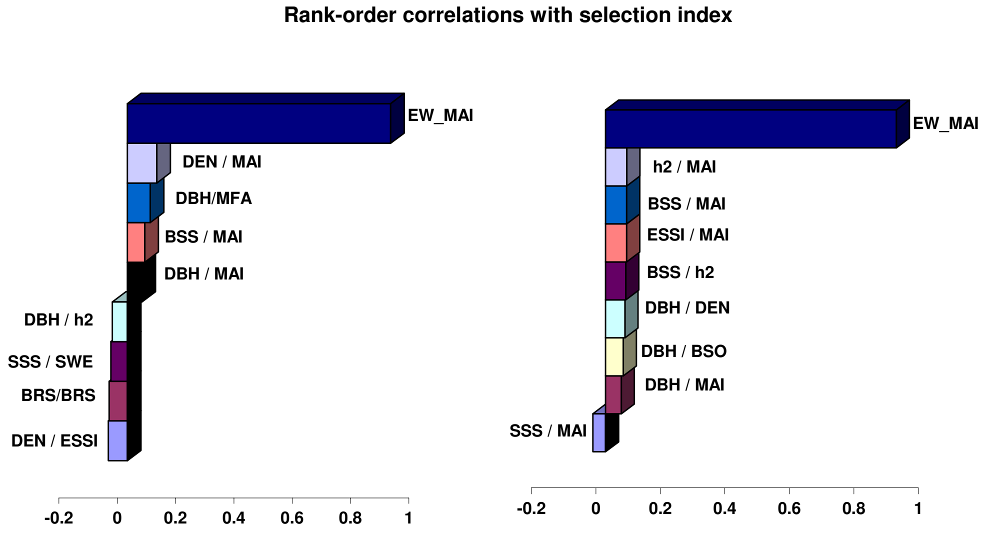

Figure 3.3. Rank-order correlations (r_s) of input parameters (*i.e.* economic weights Table 3.4 and genetic parameters Tables A3 and A4) and selection index value (left) and selection index coefficient for Essigella upper crown defoliation (right).

3.4 Conclusions

- The shape of growth curve did not change significantly, but the volume decreased due to defoliation caused by Essigella as a liner function of growth on unaffected site, at a given defoliation level
- Deployment of resistant crop impacted on profitability at a higher rate as the defoliation was increased. For example, at a high defoliation level (44%) reducing defoliation 10% increased NPV profitability more than 30% and 54%, for a typical stand in NE Victoria and Green Triangle region, respectively
- A significant linear relationship was established between estimated mean aphid number and the Ecoclimatic Index obtained from the CLIMEX model for *E. californica* data available data from South Australia, Victoria and New South Wales
- For the BR9601 trial, the percent defoliation in the upper crown was reduced to one half from winter 2008 (51.4%) to winter 2009 (24.4%), (possibly because of very high rainfall in December 2008 wettest on record). Narrow sense heritability for assessments of upper crown defoliation scores in also decreased from 0.18 to 0.10. Nevertheless, genetic year to year (winter 2008 to winter 2009) correlation between assessments was high (0.88)
- Genetic correlations between Essigella upper crown defoliation scores (ESSI) at age 12 years and early (<7 years) age selection criteria traits were statistically significant for diameter at breast height (-0.37), branch size (0.29), stem straightness (-0.55), fork count (0.50) and wood density (0.34)
- For a base selection index where Essigella upper crown defoliation was not included as an objective or as selection trait, there was very little correlated response (-0.2%). Under a selection index in which $ESSI_O$ was included as a breeding objective trait, there was a reduction in defoliation of -5.2%, -5.9% and -

6.5% over rotation and a reduction in early selection trait ESSI of -6.5%, -6.9 and -6.9% for low, medium and high hazard rating sites, respectively

- Biological control and insecticide applications impacted significantly on economic weight estimates for ESSI, however, the factor that influenced the selection index coefficients the most was the economic weight on mean annual increment.

4 Dothistroma Needle Blight

4.1 Introduction

Dothistroma needle blight is one of the most serious foliar diseases of *Pinus* spp., and is caused by *Dothistroma septosporum* (Dorog.) Morelet (formerly *D. septospora* and *D. pini*) in the anamorph (asexual) stage. The teleomorph (sexual) stage of the pathogen, *Mycosphaerella pini* (formerly *Scirrhia pini*), has rarely been observed. Recently, a second distinct species, *Dothistroma pini*, has been found to be responsible for red-band needle blight in north-central America and the Ukraine (Brown and Webber 2008). Dothistroma needle blight is the most serious disease affecting *P. radiata* D. Don. in both Australia and New Zealand.

The disease is characterised by needle necrosis, resulting in defoliation of up to 80% of the tree crown, and a consequent loss of growth. In Australia, severe infections of needle blight have been mainly confined to the humid parts of northern New South Wales and moist protected valleys in north-eastern Victoria. In New Zealand, Dothistroma is widespread, resulting in growth losses and significant fungicide spraying costs (Bulman *et al.* 2004).

In temperate forests of the northern hemisphere, from where both the pathogen and host species originate, damage levels have historically been low. However, Dothistroma is currently causing extensive defoliation and mortality in plantations of lodgepole pine (*P. contorta var. latifolia* Dougl. ex Loud.) in north-western British Columbia, Canada. A local increase in summer precipitation appears to be responsible (Woods *et al.* 2005) suggesting that climate change may result in the spread of the disease as environmental thresholds that have previously restricted the pathogen's development are surpassed.

4.2 Methods and Materials

Definition of site hazard ratings

If a relationship can be established between climate variables and infection level in progeny trials, (rough) site hazard ratings can be defined in terms of climate conditions. Climate variables for sites of 134 progeny trials in the database (DATAPLAN®) of Southern Tree Breeding Association (STBA) were obtained using the ESOCLIM module of ANUCLIM program (Hutchinson *et al.* 1999, Jovanovic and Booth 2002). Climatic data on temperature, precipitation and radiation were used to calculate climate indices: mean annual temperature (*MAT*), mean temperature November to February (*MTNF*), mean temperature of the warmest month (*MTWM*), annual precipitation (*AP*), precipitation November to February (*PNF*), precipitation warmest month (*PWM*), and rain days November to February (*RNF*). STBA trial sites were ranked according to those climatic indices in order to determine which ones discriminate the sites affected by Dothistroma the best.

Economic impact of Dothistroma needle blight on production systems and economic weights

A plantation model for an average site in north-eastern Victoria was used to evaluate the effect of Dothistroma needle blight on the production system (Ivković *et al*. 2006). For a site unaffected by the disease with a mean annual increment (MAI) of 20 m^3 ha^{-1} y^{-1} cost structures included land rental, establishment costs and maintenance costs (fertilisation, weed control, etc.), and harvesting and transportation costs, while income was from sales of sawlogs to saw-mills, and pulplogs or chip to pulpmills (Table A7).

Evaluation of the effect of Dothistroma needle blight on the production system required making assumptions about the expected frequency of infection over a rotation, the severity of infection and degree of defoliation, the number and dose of spray applications, the effect of defoliation on growth in each season, and projecting those growth losses to harvest age.

We used simplified scenarios to estimate the effect of Dothistroma on a stand basis. For a low hazard site, we assumed a single disease outbreak during the first 15 years of the rotation with an average defoliation up to age 15 of 8.9% (the outbreak lasted 3 years, starting at age 7 with 14% of the stand defoliated in the first year, 35% defoliated at age 8, and 20% defoliated at age 9) and an average of 1.8 spray applications. On a moderate hazard site, we assumed 2 disease outbreaks with an average defoliation up to age 15 of 22.4% and an average of 5.4 spray applications; and at a high hazard site, we assumed 3 disease outbreaks with an average defoliation of 45.7% and 10.8 spray applications. Overall growth loss was about 5.6%, 9.5%, and 27.1% for the low, medium and high hazard sites, respectively. At the high hazard site, the effect of 3 outbreaks over a rotation was also evaluated in terms of lost time before harvest (up to 5.7 years over rotation period). Temporary loss of volume growth at ages 5 and 10 years to rotation age for an average site was modelled by simulation, using ATLAS Forecaster® model (Atlas Technology 2008). Spraying followed Dick's (1989) schedule, where if less than 15% of the crown is infected, the stand is not sprayed; if 15–30% of the crown is infected, a single spray is applied in the early summer; and if >30% of the crown is infected two sprays are applied, one in early summer and the second in late summer. The cost of a single spray application was assumed to be \$25 ha^{-1} (Bulman *et al.* 2004) and spraying was assumed to reduce the absolute infection level by 15%.

Genetic analyses

Test sites, genotypes and data sets

Sixteen progeny trials at different sites in north-eastern Victoria were used for analysis of Dothistroma infection scores (Table 4.1). All 16 trials are in the Buffalo River valley, within about a 12 km range from Blades (furthest south) to Clemens (furthest north), and were established in 5 planting seasons from 1985 to 1991. The trials can be grouped into 5 distinct locations: Lake Buffalo (194–196); Blades (199–203), Yarrarabula Ck, Clemens Block (219), and Dandongadale (Osborne's) (228–237).

Most families were from control-pollinated (CP) first-generation Victorian selections, with other material from South Australia, Tasmania, Queensland, NSW, and New Zealand. Open-pollinated material (HS) from seed orchards was also present, together with other routine material and used in check lots (Table 4.1).

Table 4.1. Progeny trials in north-eastern Victoria assessed for defoliation due to Dothistroma infection: number of full-sib (FS), half-sib (HS) families, check lots (Ch.) and individual trees, latitude (Lat), longitude (Long), altitude (Alt) and planting date for the trials.

Trial ID – Trial Name	FS	HS (Ch.)	Trees	Lat	Long	Alt	Planted

194 - Myrtleford Diallels	44	(3)	2016	-36°43’	146°40’	305	7/1985
195 - Myrtleford Other Families	10	20(3)	1344	-36°42’	146°40’	305	7/1985
196 - Lake Buffalo Guadalupe	-	46	896	-36°42’	146°40’	295	7/1985
199 - RWG1 Diallel Dandongadale	99	(3)	1609	-36°49’	146°39’	315	6/1986
200 – Dandongadale, Blades 4x4 Factorial	16	-	480	-36°49’	146°39’	320	6/1986
201 - Dandongadale, Blades - APP Diallel	16	-	672	-36°49’	146°39’	315	6/1986
202 - Dandongadale, Blades - APP Diallel	25	(3)	840	-36°49’	146°39’	320	6/1986
203 - Dandongadale, Blades - CSIRO Diallel	35	-	400	-36°49’	146°39’	320	6/1986
219 - Yarrarabula Ck 4x4 Factorial	21	(3)	721	-36°42’	146°42’	320	6/1989
222 - Clemens Block 4x4 Factorial	20	1(3)	720	-36°42’	146°39’	285	6/1989
223 - Clemens 3x4 Factorial, Topcrosses	16	11(1)	932	-36°42’	146°39’	280	6/1989
228 - Dandongadale Factorial	43	3(2)	1449	-36°47’	146°40’	290	7/1990
230 - 2G and OPSO Families	-	48 (1)	1530	-36°47’	146°40’	290	7/1990
231 - Dandongadale OPBA Families	-	37(2)	1291	-36°49’	146°39’	290	7/1990
236 - Dandongadale Factorials	55	18(3)	2508	-36°47’	146°39’	290	7/1991
237 - Dandongadale NZ Families (APM)	3	107(3)	3538	-36°47’	146°39’	290	7/1991

Dothistroma infection (DOTHI) was assessed based on defoliation, using a score from 0 to 10, defined as a percentage of the total crown infected: <5%=0; 5%-14%=1; 15%-24%=2; … 85%-94%=9; and >95%=10. Stem straightness (StS) was scored on a 1-6 scale (with 6 representing the best stems in the trial). Exploratory data analyses revealed that the untransformed Dothistroma scores followed a multinomial distribution, and because the within-class variance of the distribution depends on mean, the assumption of homogeneity of variance required for the computation of statistical tests was violated (SAS Institute 2008). For the scores (expressed as proportion $0 > p < 1$) the arcsin(sqrt(p)) transformation made the variance essentially free of the mean value (Sokal and Rohlf 1995). Furthermore the distribution of Dothistroma scores was in some cases skewed and the transformation made the distribution nearly normal.

Data analyses and genetic parameters

Estimates of variance components for a single trait at a single site were obtained according to the following linear mixed model for diallel and factorial crossing designs:

$$[4.1] \qquad \mathbf{y} = \mathbf{X}b + \mathbf{Z}_R r + \mathbf{Z}_P p + \mathbf{Z}_T t + \mathbf{Z}_S s + \mathbf{e}$$

where $\mathbf{y}$ is the vector of observations and $\mathbf{X}$ is the incidence matrix relating the observations in $\mathbf{y}$ to the b vector of fixed effects, $\mathbf{Z}_R$ is the incidence matrix relating to the r vector of random replicate effects; $\mathbf{Z}_P$ is the incidence matrix relating to the vector of random plot effects (p); $\mathbf{Z}_T$ is the incidence matrix relating to the t vector of individual tree (additive genetic) effects; $\mathbf{Z}_S$ is the incidence matrix relating to the s vector of specific combining ability (full-sib family) effects; and e is the vector of residuals. For half-sib designs only, the general combining ability was estimated. Routine and check seedlots were excluded from these analyses.

For the multivariate case including Dothistroma, growth, form and survival variables:

[4.2] $$\mathbf{y}_j = \mathbf{X}_j b_j + \mathbf{Z}_{Rj} r_j + \mathbf{Z}_{Pj} p_j + \mathbf{Z}_{T_j} t_j + \mathbf{Z}_{S_j} s_j + \mathbf{e}_j$$

$\boldsymbol{y_j} = (y_{Dothi}, y_{Growth}, y_{Form}, y_{Surv})$; $\boldsymbol{b_j} = (b_{Dothi}, b_{Growth}, b_{Form}, b_{Surv})$; $\boldsymbol{r_j} = (r_{Dothi}, r_{Growth}, r_{Form}, r_{Surv})$; $\boldsymbol{p_j} = (p_{Dothi}, p_{Growth}, p_{Form}, p_{Surv})$; $\boldsymbol{t_j} = (t_{Dothi}, t_{Growth}, t_{Form}, t_{Surv})$ ~$\mathrm{MVN}(\mathbf{0}, \mathbf{G} \otimes \mathbf{A})$ where **G** is additive variance-covariance matrix (equation 3) and **A** is the additive relationship matrix; $\boldsymbol{s_j} = (s_{Dothi}, s_{Growth}, s_{Form}, s_{Surv})$ ~$\mathrm{MVN}(\mathbf{0}, \mathbf{S} \otimes \mathbf{I})$ where **S** is full-sib variance-covariance matrix and I is an identity matrix, $\boldsymbol{e_j} = (e_{Dothi}, e_{Growth}, e_{Form}, e_{Surv})$ ~$\mathrm{MVN}(\mathbf{0}, R \otimes \mathbf{I})$ where **R** is variance-covariance matrix for the residuals and the model terms were the same as in equation (2).

[4.3] $$G = \begin{bmatrix} \sigma^2_{A_{Dothi}} & \sigma_{A_{Dothi}A_{Growth}} & \sigma_{A_{Dothi}A_{Form}} & \sigma_{A_{Dothi}A_{Surv}} \\ \sigma_{A_{Growth}A_{Dothi}} & \sigma^2_{A_{Growth}} & \sigma_{A_{Growth}A_{Form}} & \sigma_{A_{Growth}A_{Surv}} \\ \sigma_{A_{Form}A_{Dothi}} & \sigma_{A_{Form}A_{Growth}} & \sigma^2_{A_{Form}} & \sigma_{A_{Form}A_{Surv}} \\ \sigma_{A_{Surv}A_{Dothi}} & \sigma_{A_{Surv}A_{Growth}} & \sigma_{A_{Surv}A_{Form}} & \sigma^2_{A_{Surv}} \end{bmatrix}$$

Spatial adjustment partitioned the residual variance into an independent component and a two-dimensional separable spatially auto-correlated component (ASREML®, Gilmour *et al.* 2005). The model specifies a first order autoregressive correlation model (AR1) for columns and rows of the tree positions within a trial. The R matrix structure is a direct product of two autoregressive correlation matrices giving a two-dimensional, first-order separable autoregressive spatial structure for variance:

[4.4] $$R = \sigma_e^2 \Sigma_c(\rho_c) \otimes \sigma_e^2 \Sigma_r(\rho_r)$$

where σ_e^2 is the spatial variance, $\otimes$ is the Kronecker product, and $\Sigma_c(\rho_c)$ is a first-order autoregressive correlation matrix with an autocorrelation ρ:

[4.5] $$\Sigma(\rho) = \begin{bmatrix} 1 & \rho & \rho^2 & \cdots & \rho^{n-1} \\ \rho & 1 & \rho & \cdots & \vdots \\ \rho^2 & \rho & 1 & \cdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \rho^{n-1} & \cdots & \cdots & \cdots & 1 \end{bmatrix}$$

An additional random term with one level for each experimental unit was used so that a second (independent) error term could be fitted. The "units" term was fitted to allow for the so-called "nugget" effect and represents unstructured environmental correlation (Dutkowski *et al.* 2006):

[4.6] $$R = \sigma_e^2 I_{nr} I_{nc} + \sigma_\varepsilon^2 \Sigma_r(\rho_r) \Sigma_c(\rho_c)$$

The spatial component best models widespread continuous trends, rather than discontinuous effects such as assessor effects. Variograms, plots of spatial residuals (Gilmour *et al.* 2005) and colour intensity maps of spatial residuals (Dutkowski 2002) were used to detect extraneous effects. All terms were fitted in a single model, where the spatial, extraneous, and treatment effects are estimated simultaneously.

In addition to spatial linear mixed model analyses on arcsin(sqrt(p)) transformed data, raw defoliation scores were analysed using generalised linear mixed models (GLMM) in ASREML® (Gilmour *et al.* 2006) using a probit link function and distribution specific weights:

[4.7] $$\mathbf{y} = \mathbf{X}b + \mathbf{Z}u + D(O - E)$$

where $\mathbf{y}$, $\mathbf{X}$ and b are as defined as above, $\mathbf{Z}$ is the incidence matrix relating the data to the vector of random effects (u); D is derivative of link function, O is the observed value and E is the expected value. The quasi-likelihood technique (Gilmour *et al.* 2005) based on a first-order Taylor series approximation to the likelihood and was used for GLMM analyses. The analysis has a reasonable base for quantitative genetics because the probit link functions imply underlying normal residual distribution (Littell *et al.* 2002).

The estimate of individual-tree narrow-sense heritability was obtained as

[4.8] $$\hat{h}^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_P^2}$$

where $\hat{\sigma}_a^2$ is the estimate of additive genetic variance and $\hat{\sigma}_P^2 =$ is the estimate of phenotypic variance, and $\hat{\sigma}_P^2 = \hat{\sigma}_a^2 + \hat{\sigma}_f^2 + \hat{\sigma}_p^2 + \hat{\sigma}_e^2$, where $\hat{\sigma}_f^2$ is the estimate of full-sib family variance, $\hat{\sigma}_p^2$ is the plot variance and $\hat{\sigma}_e^2$ is the model (non-spatial) error variance.

The genetic correlation between two traits, r_G, was estimated within ASREML® as:

[4.9] $$\hat{r}_g = \frac{\hat{\sigma}_{a_x a_y}}{\sqrt{\hat{\sigma}^2{}_{a_x}\hat{\sigma}^2{}_{a_y}}}$$

where:

$\hat{\sigma}_{a_x a_y}$ = additive genetic covariance between traits x and y;

$\hat{\sigma}^2{}_{a_x}$ = additive genetic variance for trait x;

$\hat{\sigma}^2{}_{a_y}$ = additive genetic variance for trait y

Selection indices and genetic gain

Selection indices can be used in breeding to improve multiple traits simultaneously (Cotterill and Dean 1990). Expressed in matrix notation, the correlation between the index value and the aggregated genetic worth is maximized when:

[4.10] $$Xb = Ga$$

and the solution for the vector of index coefficients b is:

[4.11] $$b = X^{-1}Ga$$

where X is the phenotypic and G is the genetic variance-covariance matrix for trait vector X, and a is the vector of economic weights.

Traits in a breeding objective could be the same as, or different from, traits in the index. In radiata pine, selection is usually conducted at an early age (6 or 7 years), and the breeding objective traits are defined for final harvest age (25–35 years). The early selection traits are often referred to as selection criteria in contrast to breeding objective traits. Selection criteria are defined according to the measurement year range (*i.e.* _00-05, _06-12, _13-24 and _24+), and are continually revised whenever there is a measurement. In such circumstances the appropriate index coefficients can be obtained as:

[4.12]
$$b = X_{11}^{-1} G_{12} a$$

where X_{11} is the phenotypic variance-covariance matrix for selection criteria traits, G_{12} is the genetic variance-covariance matrix between selection criteria and breeding objective traits, and a is the vector of economic weights for breeding objective traits. Expected genetic gains or mean response in breeding objective traits, expressed per standardised selection differential (i), can be calculated as:

[4.13]
$$\Delta\mu = i \frac{Gb}{\sqrt{b' Xb}}$$

Currently, the STBA *P. radiata* breeding objective (BO1) does not include either Dothistroma defoliation or growth on defoliated sites as breeding objective traits, but only as selection criteria. Defoliation (Dothi) is selected against via its negative correlation with growth on defoliated sites (Growth_Dothi), which is in turn correlated with the other selection criteria and breeding objective traits (Powell *et al.* 2004, Ivković *et al.* 2006). For example, the genetic correlations of Dothi_00-05 with Growth_Dothi _00-05 and Growth_Dothi_ 06-12, are assumed to be -0.1 and -0.4, respectively. These correlations would not differ in sign, but they would likely differ in their magnitude depending on the site hazard rating.

We defined a breeding objective (BO2) for sites with high risk level that includes Dothistroma defoliation and growth on defoliated sites both as selection criteria and breeding objective traits. Correlation between selection criteria Dothi and Growth_Dothi was assumed to be -0.5. Both selection criteria were also correlated with objective traits average Dothistroma defoliation over rotation (Dothi_o) and MAI with correlations of 0.9 and 0.8, respectively. Both variance-covariance matrices and economic weights changed depending on site hazard rating.

4.3 Results and Discussion

Site hazard ratings

Compared to all 134 trials in the STBA's progeny trial database, the 16 progeny tests affected by Dothistroma infection in north-eastern Victoria were 1.51 SD above average for mean temperature between November and February (*MTNF*), 1.57 SD above average for mean temperature warmest month (*MTWM*), and 0.38 SD above average for mean precipitation November to February (*MPNF*) (Table 4.2). When all the STBA trials were ranked on mean annual temperature and mean annual precipitation, sites in the north-eastern Victoria, Murray Valley in NSW and Victoria, and the Central Victoria (Narbethong) appear to be susceptible to Dothistroma (Figure 4.1).

Table 4.2 Climate variables for 16 progeny tests in north-eastern Victoria: precipitation November to February (PNF), precipitation warmest month (PWM), annual precipitation (AP), mean temperature November to February (MTNF), mean temperature of warmest month (MTWM), mean annual temperature (MAT), raindays November to February (RDNF), and raindays warmest month (RDWM). Average ± standard deviation for all 134 STBA trials is given in the bottom row.

Trial	**PNF** (mm)	**PWM** (mm)	**AP** (mm)	**MTNF** (˚C)	**MTWM** (˚C)	**MAT** (˚C)	**RDNF** (num.)	**RDWM** (num.)
194	252	56	1133	18.6	20.4	13.3	29.8	6.5
195	252	56	1133	18.6	20.4	13.3	29.8	6.5
196	250	55	1126	18.6	20.5	13.4	29.7	6.4
199	268	58	1234	18.4	20.2	13.2	30.9	6.7
200	268	58	1239	18.4	20.2	13.2	31.0	6.7
201	268	58	1234	18.4	20.2	13.2	30.9	6.7
202	268	58	1240	18.4	20.2	13.2	31.0	6.7
203	268	58	1240	18.4	20.2	13.2	31.0	6.7
219	265	58	1205	18.4	20.2	13.0	30.7	6.6
222	245	54	1100	18.7	20.6	13.5	29.5	6.4
223	245	54	1094	18.8	20.6	13.5	29.5	6.4
228	260	57	1183	18.6	20.4	13.4	30.4	6.6
230	260	57	1183	18.6	20.4	13.4	30.4	6.6
231	263	58	1204	18.5	20.3	13.4	30.9	6.7
236	260	57	1183	18.6	20.4	13.4	30.4	6.6
237	260	57	1186	18.6	20.4	13.4	30.4	6.6
ALL_134	**234±67**	**51±18**	**951±229**	**16.9±1.07**	**18.3±1.30**	**12.8±0.72**	**38.2±6.2**	**8.3±1.6**

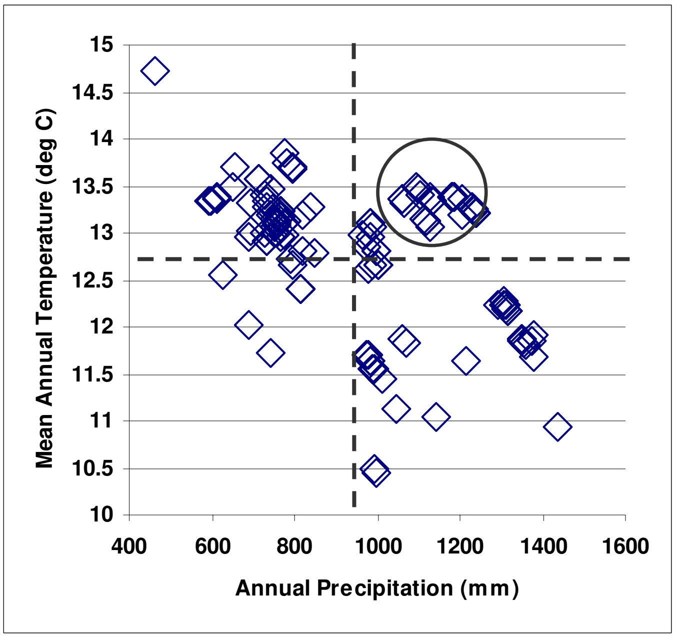

Figure 4.1. Climate envelope for 16 Dothistroma defoliated sites (circled) compared to all 134 progeny trial sites from the STBA database. Climatic variable means are represented as dashed lines.

The basic climatic requirements for Dothistroma infection may not be sufficient to predict site hazard ratings. More sophisticated models such as CLIMEX® have been used to predict potential Dothistroma spread in Australia (Sutherst *et al.* 2007, Watt *et al.* 2009). The CLIMEX simulation model mimics the mechanisms that limit geographical distributions and determine seasonal phenology and relative abundance of a pathogen species. Growth and stress indices are combined into an eco-climatic index, to give an overall measure of suitability of a location for development of a population. However, with such predictions there was a trade off between the precision of the eco-climatic index estimate and the resolution on the geographic scale (Darren Kritikos, CSIRO, pers. comm. 2008). High resolution predictions for planting sites are still needed.

Effect of Dothistroma on the radiata pine production system

Based on simulation (ATLAS Forecaster®) the effect on subsequent yield of a 15% reduction in volume growth at an early age (4-10 years) was relatively small: first thinning volume was decreased by 2–3%; second thinning volume by 2–5%; and clear-fell volume by 0.6–1.5%. The simulation results were in general agreement with the results obtained by Pas *et al.* (1984), although they used a threshold of 25% defoliation before growth losses were incurred. It is likely that growth losses (of up to 5%) can still accrue at lower levels of infection. Overall growth loss was about 5.6%, 9.5%, and 27.1% for the low, medium and high hazard sites, respectively (Table 4.3). Experiments on the relationship between infection level and growth clearly showed that the relationship was not linear over the full range of defoliation levels (New 1989, Bulman *et al.* 2004). Thus, more precise assessments of the effect of defoliation on growth, and precise extrapolations of growth losses to harvest age, are still needed (Richardson *et al.* 2006).

Table 4.3 Effects of reduction in defoliation due to Dothistroma needle blight at low, medium and high hazard sites on present value (NPV) at 6% discount rate for a plantation growing enterprise in north-eastern Victoria. Economic weights (value of unit trait change) for Dothistroma resistance and for Mean Annual Increment (MAI)

	Dothistroma defoliation rate		
	Low	Medium	High
Base Infection Rate %	8.9%	22.4%	45.7%
NPV$	1255	1112	695
Reduced Infection Rate	8.0%	20.2%	41.1%
NPV$	1276	1214	914
Economic weights for a % reduction in Dothistroma defoliation			
NPV$ / ha / %	23.3	45.5	47.9

The economic consequences of defoliation by Dothistroma on plantation growing in north-eastern Victoria are dependent on the cost of lost volume and spray applications. At the high hazard site, the effect of 3 outbreaks over a rotation evaluated in terms of lost time before harvest was up to 5.7 years over rotation period. There are several studies evaluating the economics of spraying to control disease and alleviate growth losses (Woollons and Haywood 1984, Pas *et al.* 1984, Dick 1989, Alzamora 2004), but their assumptions vary widely, with most studies adopting a 15% infection rate as a threshold for spraying. Economic weights were calculated as the difference between the NPV of the base production system and the NPV after a reduction in defoliation. For example, under the medium risk scenario, the economic weight (EW) in NPV$ per percent reduction in defoliation ($1214-$1112)/2.24%=$45.5 per 1%. However, the change in economic weight between the different risk scenarios was not linear. On sites with a high risk of infection, a reduction in defoliation had the greatest effect of $47.9.

The proportional change in the production system profitability was similar to the change in profitability resulting from improvement in mean annual increment on an uninfected site (around 30% change in NPV). Based on analysis of 9 unsprayed genetic trials, Carson (1989) also concluded that the resistance and volume have similar importance in terms of relative stand volume. Relative stand volume was defined as “expected volume in the absence of Dothistroma minus expected volume loss due to infection, if the trees were grown in the presence of the disease”.

Genetics of Dothistroma defoliation

The average infection score varied widely among the 16 sites and ranged from <5% to 65% crown infected. Generally, full-sib family genetic variance (or specific combining ability) ($\hat{\sigma}^2_{SCA}$) was not significantly different from zero. Estimates of narrow-sense heritability (h^2) of Dothistroma infection ranged from being non-significant (zero additive genetic variance) to 0.69, with a median of 0.36. Overall, the estimates of narrow-sense heritability were moderate and similar to those obtained in previous studies (Table 4.4).

Table 4.4 Genetic analysis of Dothistroma infection scores on 16 sites in north-eastern Victoria: trial code, age of assessment (YYMM), score (0–10), variance of specific combining ability (σ^2_{SCA}), additive genetic variance (σ^2_A), narrow sense heritability (h^2), and standard errors ($SE\ h^2$).

Trial	Age	Mean	Min	Max	σ^2_{SCA}[a]	σ^2_{A}[a]	h^2	SE h^2
194	0300	0.92	0	5	0.000^{ns}	$0.631^{x}10^{-2}$	0.43	0.13
	0400	6.12	1	10	$0.596^{x}10^{-3ns}$	$0.739^{x}10^{-2}$	0.34	0.12
195	0300	1.51	1	5	0.000^{ns}	$0.716^{x}10^{-2}$	0.56	0.14
	0400	6.12	1	10	$0.379^{x}10^{-2ns}$	$0.964^{x}10^{-2}$	0.42	0.21
196	0303	1.44	1	6	-	0.012	0.63	0.09
	0403	6.34	1	10	-	0.011	0.61	0.07
199	0404	2.23	1	8	$0.306E^{-2}$	0.014	0.42	0.18
200	0406	1.20[b]	0	4	$0.306^{x}10^{-2ns}$	0.000	-	-
201	0207	1.84	1	7	0.000	$0.554^{x}10^{-2}$	0.55	0.20
202	0207	2.42	1	8	0.002^{ns}	0.025	0.63	0.18
203	0405	1.70	1	6	$0.136^{x}10^{-2,ns}$	$0.672^{x}10^{-2}$	0.29	0.16
219	0309	2.35	1	7	0.000^{ns}	$0.355^{x}10^{-2}$	0.27	0.16
222	0308	1.78	1	7	0.000	$0.403^{x}10^{-2}$	0.18	0.10
223	0400	2.37	1	6	0.023^{ns}	0.081^{ns}	-	-
228	0300	3.96	1	8	$0.265^{x}10^{-3}$	$0.164^{x}10^{-2}$	0.13	0.06
230	0300	3.62	1	7	$0.619^{x}10^{-3}$	$0.120^{x}10^{-2}$	0.10	0.11
231	0300	4.19	1	8	-	$0.581^{x}10^{-2}$	0.31	0.09
236	0300	5.17	2	8	0.007^{ns}	$0.106^{x}10^{-2}$	0.19	0.05

237	0300	5.83	1	10	-	0.230×10^{-2}	0.15	0.04

[a] SQRT(ARCSIN) transformed data; [b] 0-4 score, [ns] –non-significant likelihood ratio test at $p = 0.005$

Additive genetic variance ($\hat{\sigma}_A^2$) increased as the level of Dothistroma infection increased from 10% to 60% between ages 3 and 4, at sites 194, 195 and 196. However, there was no apparent correlation between infection rate and heritability (Table 4.4). Estimates of heritability obtained at consecutive years (ages 3 and 4 years) seemed to decrease as the infection rate became more severe (*e.g.* at 194 $h^2_{\mathrm{Dothi\_3000}} = 0.51$ vs. $h^2_{\mathrm{Dothi\_4000}} = 0.36$; or at 195 $h^2_{\mathrm{Dothi\_3000}} = 0.56$ vs. $h^2_{\mathrm{Dothi\_4000}} = 0.37$). This may be because when infection levels pass a certain level the genetic component of resistance may become overloaded (Chambers *et al.* 2000, Pederick *et al.* 1993).

Estimates of heritability based on multivariate analyses were similar to univariate estimates (not shown). However, generalised linear mixed model (GLM_PROBIT) analyses using ASREML® (Gilmour *et al.* 2006) produced somewhat different heritability estimates than linear mixed model analysis at sites 228, 230, 231 and 236. We prefer using linear mixed models when analysing categorical variables with more than two levels. The models are robust to implement, with solid statistical foundations, and the results are easy to interpret. In tree breeding programs, we deal with a large amount of data, so assumptions of normality for mixed models are usually not an issue (Fikret Isik, NC State University, pers. comm.). Therefore in the Table 4.4 we report the results of the linear mixed model analyses.

The spatial component of defoliation represented a significant proportion of the total residual variance on most sites (*e.g.* 194, 195, 196, 199, 201, 202), but the spatial models showed no significant likelihood improvement for some trials (*e.g.* 228, 230). For example, at 202 spatial variance represented 56% of the total residual variance, and at 201 it accounted for 22% of total residual variance. Removing the spatial component of the residual variance increased heritability estimates proportionally. High variance due to plots or intermediate autocorrelations in the spatial model indicated the presence of small patches or local trends in the data. High autocorrelations indicated that there were large patches traversing multiple plots, or more global trends. Global trends and effects aligned with rows or columns can inflate autocorrelations, which in turn may mask local trends (Dutkowski *et al.* 2002, 2006). In our analyses there were detectable global trends and effects aligned with rows or columns at some sites (*i.e.* row at 199 and 231, column within replications at 222). In these cases, fitting of smooth global trends, presumably representing “assessor effects”, as random row/column effects, had similar log likelihood deviance as autocorrelation modelling.

For early Dothistroma defoliation score, assessed at age less than 4 years, and diameter at breast height (DBH), assessed at age greater than 9 years, phenotypic correlations (r_p) were all negative, ranging between –0.14 and –0.49, with a median value of –0.35. Genetic correlations (r_g) were also all negative, ranging between –0.03 and –0.69, with a median value of –0.39. The genetic correlation estimates were more variable and had higher standard errors than the phenotypic correlation estimates (Table 4.5). We also evaluated the correlation of Dothistroma defoliation and growth traits assessed before or in the same growing season. The correlations were generally negative suggesting that less vigorous trees may be more susceptible to Dothistroma infection (Table 4.5).

Table 4.5 Additive genetic (r_g) and phenotypic (r_p) correlations between early-age assessment of Dothistroma infection and later-age assessments of growth as diameter at breast height (DBH), form as stem straightness and survival (dead or alive) survival score.

Trial code	**Dothi. Score**	**DBH**	r_g (r_p)	**Stem straight.**	r_g (r_p)	**Survival score**	r_g (r_p)
194	0400	1400	-0.66 ± 0.17 (-0.37 ± 0.02)	-	-	1400	-034± 0.30 (-0.14 ± 0.02)
195	0400	1400	-0.39±0.22 (-0.49 ± 0.02)	-	-	1400	- (-0.18 ± 0.02)
219	0309	1108	-0.10±0.08 (-0.26±0.06)	1200	- (0.06±0.06)	1200	- (-0.11±0.05)
222	0308	1108	-0.03±0.43 (-0.29±0.04)	1200	0.08±0.29 (0.03±0.05)	1200	0.56±0.45 (-0.12±0.04)
223	0400	1509	-0.35±0.30 (-0.14±0.04)	1200	-0.46±0.35 (-0.07±0.04)	1200	-0.14±0.47 (-0.08±0.04)
228	0300	1007	-0.69±0.16 (-0.21±0.02)	1011	-0.13±0.27 (-0.03±0.02)	1011	-0.01±0.05 (-0.03±0.02)
230	0300	1408	-0.49±0.19 (-0.39±0.03)	1408	-0.06±0.21 (-0.08±0.03)	1408	-0.28±0.42 (-0.11±0.03)
231	0300	1408	-0.40±0.21 (-0.40±0.03)	1409	0.32±0.27 (-0.04±0.03)	1409	-0.45±0.37 (-0.09±0.03)
236	0300	0907	-0.39±0.19 (-0.32±0.02)	0907	0.32±0.27 (-0.04±0.03)	0907	- (-0.07±0.03)
237	0300	0907	-0.29±0.17 (-0.40±0.02)	0910	0.21±0.17 (-0.10±0.02)	0910	-0.22±0.19 (-0.15±0.02)

Table 4.6 Additive genetic (r_g) and phenotypic (r_p) correlations between Dothistroma infection score and diameter at breast height (DBH) and height (Ht), at an early age.

Trial code	**Dothi. score**	**Growth trait**	r_g (r_p)
196	Dothi_0403	Ht_0200	-0.33±0.23 (-0.20 ± 0.04)
200	Dothi_0406	DBH_0406	-0.20±0.19 (-0.24 ± 0.05)
201	Dothi_0207	Ht_0207	- (-0.04 ± 0.04)
202	Dothi_0207	DBH_0406	-0.26±0.27 (-0.13±0.04)
203	Dothi_0405	DBH_0405	0.10±0.27 (-0.14±0.05)

For early Dothistroma infection scores (Dothi) and later age assessments of stem straightness (Sts), both phenotypic and genetic correlations were low and statistically not significant (Table 4.6). The phenotypic correlations between Dothistroma infection and survival scores were negative and generally low, ranging from –0.03 to –0.18, with a median value of –0.11. Genetic correlations with survival were also mostly negative and generally low, but values ranged from –0.45 to +0.56, with a median value of –0.07. However, the high positive value for 222 had a very high standard error ($r_g = 0.56 \pm 0.45$). Thus, higher rates of defoliation are correlated both phenotypically and genetically with poorer survival (Table 4.6).

A possible consequence of Dothistroma infection is an increase in wood density due to reduced growth rate, as was found in New Zealand (Harris and McConchie 1978). In trials 228, 236, 237 there was only a weak positive phenotypic correlation between early Dothi_0300 measurement and later age (9 to 11 years old) measures of full core density. There were no significant genetic correlations between the two traits in the three trials (not shown).

Selection indices and genetic gain

A correlated response in Dothistroma defoliation score to selection on a selection index that does not include Dothi as a selection would result in mean predicted defoliation increasing 2.7%. Dothistroma defoliation score and growth on infected sites (Dothi, and DBH_Dothi) are currently included only as selection traits in the national breeding program (Powell *et al.* 2004). The selection intensity for these traits is derived solely through correlations with other selection and breeding objective traits. Under the current breeding objective (BO1, Table 4.7), there was very little expected genetic response (*R*) in the selection criteria Dothi (0.01%) and Growth_Dothi (0.1%) on both low and medium risk sites.

Table 4.7. Response to selection (genetic gain) under 10% selection intensity and different selection indices: Base Index (BI) that does not involve *Dothistroma* defoliation (DOTHI); BO1 index in which DOTHI and growth on defoliated sites (DBH_DOTHI) are included only as selection traits; and BO2 index where DOTHI$_O$ and GROWTH_DOTHI are included as breeding objective traits. The percent response differs according to site hazard rating low (L), medium (M) and high (H).

		OBJECTIVE TRAITS					**SELECTION TRAITS**							
Trait		**MAI**	**MOE**	**SWE**	**BRS$_O$**	**DOTHI$_O$**	**DBH**	**DEN**	**MFA**	**STS**	**BRA**	**BRS**	**DOTHI**	**DBH _DOTHI**
Mean unit		20 m^3/ha/y	11.5 GPa	10.5 mm	5.5 cm	33.4 %	145 mm	400 Kg/m3	25 Deg	3.5 score	3.5 score	3.5 score	3.1 score	100 mm
BI		17.5%	-1.2%	-3.5%	-4.4%	-	4.1%	-3.7%	-5.1%	9.4%	5.1%	7.1%	2.7%	
BO1	**L**	14.6%	1.5%	-3.0%	-3.2%	-	3.7%	-3.4%	-8.5%	7.3%	3.7%	5.3%	0.01%	0.1%
	M	17.0%	-0.1%	-3.2%	-3.0%	-	4.1%	-3.9%	-7.2%	8.1%	3.7%	5.0%	0.01%	0.1%
BO2	**M**	16.5%	0.1%	-3.2%	-3.5%	-4.2%	4.2%	-3.9%	-7.1%	8.1%	4.2%	5.5%	-7.1%	4.2%
	H	22.0%	-3.7%	-3.6%	-2.5%	-4.2%	5.0%	-4.8%	-4.0%	9.5%	3.6%	4.1%	-6.2%	5.0%

We proposed a selection index, BO2, that can be used to target sites with medium to high risk of defoliation by Dothistroma. Under the BO2 index, average defoliation over rotation Dothi_{O} was reduced by 4.2% and the selection criterion Dothi was reduced by 7.1% and 6.2% for medium and high hazard sites, respectively. There was only a slight trade-off in response to selection for MAI between BO1 and BO2 (17.0% vs. 16.5% on medium risk sites). The response in the other objectives (stem sweep, branch size, and modulus of elasticity) and selection traits (DBH, wood density, microfibril angle, stem straightness score, branch angle score, branch size score) was favorable under the BO2 index (Table 4.7). Thus, the STBA should consider including Dothistroma defoliation and growth on defoliated sites as traits in breeding and deployment objectives for sites with a medium or high risk of Dothistroma defoliation.

Sensitivity of selection index

Using rank-order correlations (r_s) between the input parameters and selection index value, we identified the most important parameters influencing selection index estimation. For an average stand the most important parameter influencing selection index value and selection index coefficient for DOTHI was the economic weight for MAI (EW_MAI, r_s= 0.79) (Figure 4.2). The second most important parameter was the genetic correlation between DOTHI and MAI. All other genetic parameters (correlations and heritability) and economic weights had lesser influence on selection index value and coefficients. The results suggested that special attention should be given to estimation precision of parameter EW_ MAI.

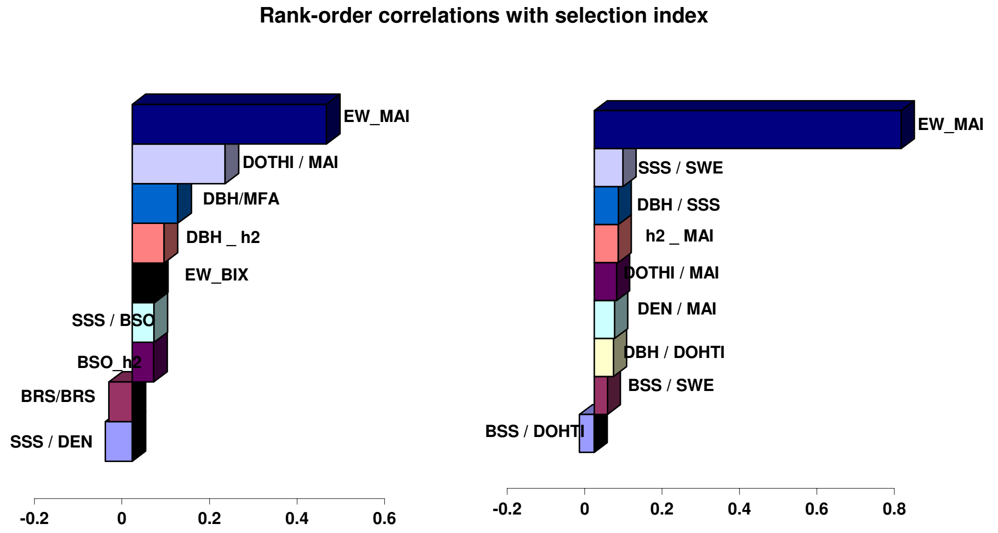

Figure 4.2. Rank order correlations (r_s) of input parameters and selection index value (left) and selection index coefficient for Dothistroma defoliation (right).

4.4 Conclusions

Optimal conditions for the growth of Dothistroma are a mild, humid climate with a high rainfall during the warmer summer months. Sixteen progeny tests in north-eastern Victoria affected by Dothistroma infection were the highest ranked among 134 STBA trials for combined site temperature and rainfall between November to February. Severe infections by needle blight have been mainly confined to moist protected valleys in north-eastern Victoria and parts of northern humid New South

Wales (Neumann and Marks 1990). Higher resolution climate modelling using tools such as CLIMEX can provide more accurate site hazard assessments.

Economic analyses indicate that defoliation due to Dothistroma needle blight has a potentially important impact on productivity, especially for sites with a high risk of infection. On these sites, reducing defoliation was, in terms of profitability, comparable to increasing MAI on a site free from infection. Generally, risk traits have higher relative economic weights in the breeding and deployment objectives on high-risk sites. Thus, the magnitude of the economic weight for a risk trait depends on the effect of the risk on the production system and the hazard rating of a given site. The economic weights we derived can be used in a specific breeding objective for risk resistance/tolerance. Specific breeds for risk traits can be developed using multiple index selection within multiple breeding populations (Namkoong 1976). The weights for sites with different hazard ratings can be used for site-specific deployment.

Dothistroma defoliation was moderately quantitatively heritable (median heritability of $h^2 = 0.36$), suggesting that substantial gains can be obtained from breeding. There was no apparent correlation between percent infection and heritability value across sites, indicating that reliable estimates of heritability can be obtained from well-designed trials even at relatively low infection levels. Estimates of heritability obtained in consecutive years decreased somewhat as the infection level increased. Spatial analysis removed spatial autocorrelations and further improved estimates of genetic parameters for Dothistroma, which is probably because the disease spreads by raindrop splash.

Correlations between Dothistroma defoliation and growth traits assessed before or in the same growing season were generally negative, suggesting that less vigorous trees may be more susceptible to Dothistroma infection. Conversely, the negative correlation indicates that selection of genotypes with vigorous early growth may, in effect, have lower infection rates. A negative correlation between defoliation and survival indicates that selection of vigorous genotypes for planting may also improve survival on sites with a high risk of Dothistroma.

The issue of genotype by environment interactions should be pursued further. The data on resistance in north-eastern Victoria could be combined with the results from trials in other regions in Australia (*e.g.* NSW Northern Tablelands) and/or New Zealand in order to form universally more resistant breeds.

Dothistroma defoliation is currently not included as a breeding objective trait, partly because the risk varies among companies, regions, yearly weather patterns and other environmental factors. Inclusion of risk traits as objective traits would increase selection pressure on those traits. Furthermore, if Dothi is selected directly rather than indirectly by correlation with growth on infected sites, the genes responsible for resistance would be targeted directly. Sufficient data on economic weights and genetic parameters for Dothistroma defoliation are now available and allow the trait to be included in breeding objective and to derive selection indices.

Finally, this analysis was based on visible differences between trees in needle loss. Defoliation may reflect a range of mechanisms and responses, and they have the advantage of being an integrated response to disease. However, mechanisms behind differences in needle loss may be due to either disease resistance or tolerance. The risk trait could be dissected into initial vigour, resistance to attack and tolerance to the disease, by specifically designed experiments. Further physiological and genetic studies are needed to elucidate these mechanisms and the best strategy for developing vigorous, resistant and/or tolerant trees. Complex genetic segregation analyses could reveal the mechanism of inheritance of resistance (*e.g.* Li *et al.* 2006). Also early screening methods (molecular and otherwise) would allow efficient early selection for breeding and deployment.

5 Genetics of Fusarium

Resistance to *Fusarium* pitch canker has been identified in *P. radiata* (Gordon *et al.* 1998; Storer *et al.* 1999). It is generally characterised by a reduced rate of lesion development, relative to more susceptible phenotypes. Resistance to pitch canker that has been characterised in radiata pine appears to be quantitative, with a nearly continuous range of variation in lesion lengths (Gordon *et al.* 1998). The presence of genetic-based resistance in radiata pine and other conifers has been reported (*eg*. Correll *et al.* 1992; Hodge and Dvorak 2000; Kayihan *et al.* 2005; Matheson *et al.* 2006) (Table 5.1). For example, Matheson *et al*. (2006) reported moderate levels of genetic control in pitch canker resistance in Australia, New Zealand and Chile breeding materials. A study by Hodge and Dvorak (2000) reported evidence of the presence of additive genetic control in resistance to pitch canker of radiata pine seedlings. Similarly, Blackslee and Rockwood (1998) reported moderate levels of genetic control in loblolly and slash pine (family and individual-tree heritability of 0.65 and 0.25, respectively). Kayihan *et al*. (2005) reported moderate to high levels of genetic control for pitch canker resistance in loblolly pine at individual tree, clonal, and family level. There have also been molecular studies that have sought to identify genes that are associated with resistance, and compared gene expression levels that are associated with resistance or susceptibility. For example, genes cesA3 and SODchl were found to have significant associations with pitch canker lesion length in loblolly pine (*eg*. Morse *et al.* 2004).

From literature review, we conclude that there are substantial levels of resistance to pitch canker in radiata pine and other conifers tested to date. Evidently, the level of genetic control reported in most studies suggests that possibility for selecting against pitch canker is good. As suggested by Aegerter and Gordon (2006), heritability of pitch canker disease resistance in radiata pine will be a critical determinant of the rate at which the frequency of resistant genotypes increases over time. Others have suggested the use of hybrids as a way to reduce the risk of pitch canker (*eg*. Hodge and Dvorak, 2000). For example, there are published reports of successful crosses of *P. radiata* and *Pinus tecunumanii* (Hodge and Dvorak, 2000). Lastly, it is anticipated that association genetics will identify host genes and alleles that condition pitch canker resistance (*eg*. Kayihan *et al.* 2005).

Table 5.1 Summary of narrow-sense heritability estimates in pitch canker resistance in some conifer species.

Species	Trait	Heritability	Reference
P. radiata	lesion length	0.21	Matheson *et al*. 2006
P. elliottii	lesion length	0.25	Blackslee and Rockwood 1998
P. teada	lesion length	0.25	Blackslee and Rockwood 1998
P. teada	lesion length	0.27	Kayihan *et al.* 2005

6 Conclusion and Recommendations

6.1 Drought Resistance

STBA has progeny trials covering the whole range of climatic conditions from dry to humid sites. Prediction of site hazard ratings (*i.e.* expected survival and early growth) based on the ecoclimatic indices using ESOCLIM module of ANUCLIM program (Hutchinson *et al.* 1999) is possible. Climate data are useful to define site hazard ratings, but soil characteristics are also important for survival. A sandy soil will hold only one or two centimetres of rainfall in a soil of 30 cm depth while a silt or clay may hold five or more centimetres of rainfall with the same depth. Furthermore roots penetrate to different depths in different types of soil and the root system tends to compensate somewhat for different water holding capacities of soils. The amount of water in the root zone is highly variable and is usually estimated based on soil type and vegetation cover (Thorntwhite and Mather 1957). However, site hazard ratings based on climate and soil characteristics have not yet been established for potential expansion of radiata pine plantations.

Generally, narrow-sense heritability for survival and early growth on dry sites was low to moderate. Plot level variation in survival was statistically significant in some cases, but detecting significant additive genetic variance for survival requires large data sets. Our study represented only a first attempt to estimate the degree of inheritance for survival and early growth. More detailed spatial analyses could elucidate the questions about the influence of micro-climate on survival, and contribute to more precise estimates of genetic parameters. The identified drought resistant genotypes will form a basis for physiological and molecular genetic studies aiming to improve water use efficiency.

6.2 Essigella Resistance

Our simulations confirmed that Essigella pine aphid is the most serious pest currently affecting Australian radiata pine plantations. Introduction of a parasitic wasp (*Diaeretus essigellae*) can potentially reduce the aphid numbers and reduce defoliation up to 50% with almost insignificant implementation costs. That would significantly reduce the risk and economic weight on resistance defoliation as a breeding objective trait. However, the reduction of economic weight may not be directly proportional to the reduction of defoliation. An integrated pest management approach involving development of genetic resistance is the most viable risk management option. This study is a first step towards formal inclusion of Essigella resistance into the breeding objective for the STBA's national radiata pine breeding program.

Sasse *et al.* (2008) analysed 18 progeny and provenance trials for Essigella upper crown defoliation. The inland northern population of Ano Nuevo provenance had the highest and the Cambrian provenance lowest level of retained foliage in the upper crown. Estimates of narrow-sense heritability from progeny trials was very variable, but averaged about 0.5. There were also significant differences between clones. However, the pedigree of the aphid resistant deployment breed used by HVPP was limited and needed expansion. Therefore, we assessed a second generation STBA progeny trial BR9601 with the material relevant to the current breeding and deployment populations. Significant but lower (0.18) heritability was found.

Identification of trials in aphid-affected districts that have already been thinned and possibly fertilised with high levels of nitrogen should be considered.

Although there is strong evidence of an association between Essigella and defoliation, there is still no explanation of a causal relationship. Unequivocal information on causality is required to help develop an appropriate breeding strategy for building resistance. Investigating the feeding preferences of the aphids and/or defence mechanisms of the trees may provide clues to possible resistance mechanism. Complex segregation genetic analyses could reveal the mechanism of inheritance of resistance. Screening methods (molecular and otherwise) are needed to enable efficient early selection for breeding and deployment.

6.3 Dothistroma Resistance

Optimal conditions for the growth of *Dothistroma* are a mild, humid climate with a high rainfall during the warmer summer months. Sixteen progeny tests in north-eastern Victoria affected by *Dothistroma* infection were the highest ranked among 134 STBA trials for combined site temperature and rainfall between November to February. Severe infections by needle blight have been mainly confined to moist protected valleys in north-eastern Victoria and parts of northern humid New South Wales (Neumann and Marks 1990). Higher resolution climate modelling can be used for more detailed site hazard assessments.

Moderate quantitative inheritance (median heritability of $h^2 = 0.29$) indicates that substantial gains can be obtained from breeding for resistance. There was no apparent correlation between infection rate and heritability value and its standard error. This indicates that even at relatively low infection rate reliable estimates of heritability can be obtained from sufficiently large trials. Estimates of heritability obtained in consecutive years were also generally similar. Considering that that the fungal disease spreads by rain drop splash, spatial analysis could probably remove spatial autocorrelations and further improve genetic parameter estimates for *Dothistroma* infection rates.

Correlations of *Dothistroma* infection and growth traits assessed before or in the same growing season were generally negative possibly indicating that less vigorous trees were more susceptible to *Dothistroma* infection. The positive correlation indicates that selection of genotypes with vigorous early growth may in effect reduce infection rates. A negative correlation between infection rate and survival indicates that selection of vigorous trees for planting may possibly improve survival on sites with high *Dothistroma* risk.

Initial evidence of significant genotype by environment interactions should be pursued further. Results on resistance in north-eastern Victoria could be combined with the results from trials in other regions (*eg.* NSW Northern Tablelands, and/or New Zealand) in order to form a *Dothistroma* resistant breed. Highly significant quantitative genetic differences could be used in complex segregation analyses to further dissect the mechanism of inheritance of resistance.

6.4 Fusarium Resistance

There are substantial levels of resistance to Fusarium pitch canker in radiata pine. The level of genetic control reported in four studies is moderate (median $h^2 = 0.25$). Design and planting of trials representative of STBA's breeding population so that breeding values for pitch canker resistance can be obtained using TREEPLAN® is recommended. It is anticipated that association genetics will identify host genes and alleles that condition pitch canker resistance.

6.5 Overall Effects of Risk Resistance Improvement

Overall economic importance of biotic risks was calculated over the entire radiata pine plantation estate as the product of the average damage level and the total area affected. This comparison can be used to determine how much effort should go into breeding for resistance for different risk traits (Table 6.1). A generic production system of a plantation grower with MAI = 20/m^3/ha/y was assumed, and net present value (NPV profitability was calculated at 6% discount rate). Value of 10% improvement in resistance to *Essigella* aphid was obtained based on the effect on production system presented in Table A5, a total area affected of 392,000 ha of mature radiata pine plantation, and volume loss realised at harvest on 16,000 ha per year. Similarly the value of 10% improvement in resistance to *Dothistroma* needle blight was obtained based on the effect on production system presented in Table A7, a total area potentially affected of 46,000 ha young radiata pine plantation, and volume loss realised at harvest on 1,840 ha per year. The potential cost of invasion of radiata pine plantations in Australia by pitch canker was calculated under the assumptions of annual planting of 40,000 ha per year and 15% infection rate (Cook and Matheson 2008). The relative economic importance of breeding for improved risk traits relative to breeding for growth rate (MAI) was generally low (*i.e.* 4.0% for pine aphid, 0.6% for needle blight, and 1.3% for pitch canker resistance. However, there was a high degree of uncertainty about these estimates and the results should be interpreted with caution.

Table 6.1 Overall economic importance of breeding for risk traits: *Essigella* aphid, *Dothistroma* needle blight and *Fusarium* pitch canker resistance. The net present value (NPV) at 6% discount rate of 10% improvement in mean annual increment (MAI) was used for comparison.

		Overall effects of 10% trait improvement			
		MAI	*Essigella*	*Dothistroma*	*Fusarium*
Base Infection Rate %			*11%*	*22.4%*	*15%*
min	*$ NPV/y*		450,000	38,600	33,000
mean	*$ NPV/y*	23,300,000	944,000	138,000	303,000
max	*$ NPV/y*		1,888,000	314,640	1,235,000

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Appendix

Table A1: Summary of production system components for plantation growing at a site with productivity of 15 m^3/ha/y, at discount rate of 6% and survival of 70%.

Wood Flows		
total harvested volume	*m3/ha*	318
WTC&pulplog	*m3/ha*	175
preservation	*m3/ha*	0
sawlog :	*m3/ha*	143
- small sawlog <20 cm SED	*m3/ha*	10
- prime sawlog 20-45 cm SED	*m3/ha*	121
- large log >45 cm SED	*m3/ha*	12
Costs		
establishment & growing costs	*$/ha*	-2986
ann. maintenance costs	*$/ha*	-688
harvest costs	*$/ha*	-975
transport costs	*$/ha*	-629
Total costs NPV/ha	*$/ha*	***-5278***
Income		
delivered roundwood		
WTC&pulplog	*$/ha*	1749
preservation	*$/ha*	0
sawlog :	*$/ha*	**2110**
- small sawlog <20 cm SED	*$/ha*	109
- prime sawlog 20-45 cm SED	*$/ha*	1773
- large log >45 cm SED	*$/ha*	228
Total income NPV/ha	*$/ha*	***3859***

Table A2: Summary of production system components for plantation growing on a site with productivity of 20 m^3/ha/y, at discount rate of 7% and survival of 80%.

Wood Flows		
total harvested volume	*m3/ha*	499
WTC&pulplog	*m3/ha*	122
preservation	*m3/ha*	0
sawlog :	*m3/ha*	**377**
- small sawlog <20 cm SED	*m3/ha*	57
- prime sawlog 20-45 cm SED	*m3/ha*	304
- large log >45 cm SED	*m3/ha*	15
Costs		
establishment & growing costs	*$/ha*	-2590
ann. maintenance costs	*$/ha*	-1961
harvest costs	*$/ha*	-1105
transport costs	*$/ha*	-646
Total costs NPV/ha	*$/ha*	***-6302***
Table A2 continued		
Income		
delivered roundwood		
WTC&pulplog	*$/ha*	1243
preservation	*$/ha*	0
sawlog :	*$/ha*	**4053**
- small sawlog <20 cm SED	*$/ha*	561
- prime sawlog 20-45 cm SED	*$/ha*	3271
- large log >45 cm SED	*$/ha*	221
Total income NPV/ha	*$/ha*	***5296***

Table A3. Trait means (μ), heritabilities (h^2), phenotypic variance (Vp), genetic variance (on diagonal), genetic (above diagonal) and phenotypic (below diagonal) correlations between selection criteria: diameter at breast height (DBH), wood density (DEN), microfibril angle (MFA), branch size score (BSS); branch angle score (BAS); stem straightness score (STS); *Dothistroma* defoliation score (DOTHI), Essigella defoliation score (ESSI) and survival score (SVS).

		μ	**unit**	**h^2**	**V_p**	**DBH**	**DEN**	**MFA**	**STS**	**BRA**	**BRS**	**_BO1**		**_BO2**	**ESSI[3]**	**SVS[4]**
												DBH_DOT[1]	**DOTHI**	**DOHTI[2]**		
	DBH	145	mm	0.20	680	**136**	-0.48	0.26	0.22	0.05	-0.21	0.5	0.00	-0.39	-0.37	0.34
	DEN	400	Kg/m^3	0.65	851	-0.46	**553**	-0.14	-0.17	0.01	0.01	-0.10	0.00	0.1	0.34	-0.20
	MFA	25	degº	0.75	12.0	0.29	-0.06	**9**	0.11	0.00	-0.07	0.10	0.00	-0.1	-0.20	0.15
	SSS	3.5	score	0.32	1.06	0.20	-0.19	0.03	**0.34**	0.24	0.42	0.10[1]	0.00	0.0	-0.55	0.10
	BRA	3.5	score	0.25	1.24	0.00	0.00	0.00	0.10	**0.31**	0.33	0.05	0.00	-0.37	-0.29	0.00
	BSS	3.5	score	0.33	1.00	-0.29	0.04	-0.02	0.36	0.37	**0.33**	-0.15[1]	0.00	0.44	0.29	-015
BO1	**DBH _DOTHI**	100	mm	0.20	450	0.33	-0.09	0.09	0.09	0.05	-0.13	**90**	-0.50	-	0.00	0.30
	DOTHI	3.1	score	0.30	2.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.50	**0.6**	-	0.00	-0.30
	BO2_DOTHI	3.1	score	0.30	2.00	-0.35	0.05	-0.05	0.00	-0.34	0.57	-	-	**0.6**	0.00	-0.20
	ESSI	2.0	score	0.25	1.20	-0.33	0.18	-0.18	0.05	-0.05	0.04	0.00	0.00	0.00	**0.30**	0.00
	SVS	0.86	score	0.15	1.00	0.33	-0.13	0.00	0.00	0.0	-0.19	0.30	-0.30	-0.11	0.00	**0.14**

[1] Correlations of DBH_DOTHI with other selection traits in a defoliated stand were assumed to be ½ in magnitude than the ones of DBH.
[2] Correlations of DOTHI with other selection traits based on milestone report 4
[3] Based on 2008 assessment BR9601 trial
[4] Correlations of SVS with other selection traits not statistically significant but were assumed to be ½ in magnitude than the ones of DBH

Table A4. Objective trait means (μ), heritabilities (h^2), phenotypic variance (Vp), genetic variance (on diagonal), and genetic (above diagonal) correlations between breeding objective traits mean annual increment (MAI), modulus of elasticity (MoE), stem sweep (SWE), branch size (BSO), *Dothistroma* defoliation percent (DOHTI$_O$), Essigella defoliation percent (ESSI$_O$) and survival percent (SVO) and selection criteria traits: diameter at breast height (DBH), wood density (DEN), microfibril angle (MFA), branch size (BRS); branch angle (BRA), stem straightness (STS); *Dothistroma* defoliation score (DOTHI), Essigella defoliation score (ESSI) and survival score (SVS).

OBJECTIVE TRAITS					**SELECTION TRAITS[1,2]**								
	μ	**unit**	**h^2**	**V_p**	**DBH**	**DEN**	**MFA**	**STS**	**BRA**	**BRS**	**DOTHI**	**ESSI**	**SVS**
MAI	20	m3/ha/y	0.23	66	0.69	-0.49	0.24	0.53	-0.02	-0.11	-0.20	-0.20	0.15
MOE	15	GPa	0.45	1.6	-0.54	0.54	-0.77	-0.74	0.22	0.17	0.10	0.10	-0.10
SWE	10	mm	0.25	33	-0.27	0.25	-0.05	-0.90	-0.14	-0.42	0.00	0.05	-0.05
BSO	5.5	cm	0.26	32	0.28	-0.05	0.04	-0.42	-0.46	-0.9	-0.20	-0.20	0.08
DOHTI$_O$	22%	%	0.25	77	-0.35	0.20	-0.12	-005	-0.01	-0.05	0.80	0.00	-0.30
ESSI$_O$	22%	%	0.25	100	0.00	0.20	-0.12	-0.06	-0.01	-0.05	0.00	0.90	0.00
SVO	80	%	0.15	88	0.33	-0.13	0.00	0.36	-0.13	-0.19	-0.30	0.00	0.90

[1] The correlations between selection traits (DBH, DEN, MFA, STS, BRA, BRS) and objective traits was assumed to be the same on defoliation free sites and on sites affected by defoliation

[2] Correlations involving DBH, DEN, MFA, STS, BRA, BRS obtained from STBA DATAPLAN® the ones involving DOTHI, ESSI and SVS assumed 50% lover in magnitude than for selection traits

Table A5: Summary of production system components for forest growing in Green Triangle region with site productivity of 24 m^3/ha/y and discount rate of 7%, used for assessment of defoliation by Essigella pine aphid.

Wood Flows		
total harvested volume	*m3/ha*	721
WTC&pulplog	*m3/ha*	166
preservation	*m3/ha*	0
sawlog :	*m3/ha*	555
- small sawlog <20 cm SED	*m3/ha*	50
- prime sawlog 20-45 cm SED	*m3/ha*	481
- large log >45 cm SED	*m3/ha*	24
Costs		
establishment & growing costs	*$/ha*	-2047
ann. maintenance costs	*$/ha*	-1241
harvest costs	*$/ha*	-1628
transport costs	*$/ha*	-973
Total costs NPV/ha	*$/ha*	***-5890***
Income		
delivered roundwood		
WTC&pulplog	*$/ha*	1952
preservation	*$/ha*	0
sawlog :	*$/ha*	6151
- small sawlog <20 cm SED	*$/ha*	473
- prime sawlog 20-45 cm SED	*$/ha*	5331
- large log >45 cm SED	*$/ha*	347
Total income	*$/ha*	***8103***
Profit NPV/ha	*$/ha*	***2214***

Table A6: Summary of production system components for forest growing in North-East Victoria with site productivity of 20 m^3/ha/y and discount rate of 6%, used for assessment of defoliation by Essigella pine aphid.

Wood Flows		
total harvested volume	*m3/ha*	589
WTC&pulplog	*m3/ha*	146
preservation	*m3/ha*	0
sawlog :	*m3/ha*	**443**
- small sawlog <20 cm SED	*m3/ha*	67
- prime sawlog 20-45 cm SED	*m3/ha*	358
- large log >45 cm SED	*m3/ha*	18
Costs		
establishment & growing costs	*$/ha*	-2389
ann. maintenance costs	*$/ha*	0
harvest costs	*$/ha*	-2125
transport costs	*$/ha*	-1468
Total costs NPV/ha	*$/ha*	***-5982***
Income		
delivered roundwood		
WTC&pulplog	*$/ha*	1657
preservation	*$/ha*	0
sawlog :	*$/ha*	**5620**
- small sawlog <20 cm SED	*$/ha*	877
- prime sawlog 20-45 cm SED	*$/ha*	4461
- large log >45 cm SED	*$/ha*	282
Total income NPV/ha	*$/ha*	***7277***
Profit NPV/ha	*$/ha*	***1295***

Table A7. Summary of the production system components for a forest growing enterprise in north-eastern Victoria, on a site with productivity of 20 m^3 ha^{-1} y^{-1} evaluated at a discount rate of 6%.

Wood Flows		
total harvested volume	m3/ha	587
WTC&pulplog	m3/ha	145
preservation	m3/ha	0
sawlog :	m3/ha	**442**
- small sawlog <20 cm SED	m3/ha	67
- prime sawlog 20-45 cm SED	m3/ha	357
- large log >45 cm SED	m3/ha	18
Costs		
establishment & growing costs	$/ha	-2414
harvest costs	$/ha	-2114
transport costs	$/ha	-1461
Total costs NPV/ha	$/ha	***-5989***
Income		
delivered roundwood		
WTC&pulplog	$/ha	1646
preservation	$/ha	0
sawlog :	$/ha	**5599**
- small sawlog <20 cm SED	$/ha	873
- prime sawlog 20-45 cm SED	$/ha	4486
- large log >45 cm SED	$/ha	281
Total income NPV/ha	$/ha	***7285***