

SELECTING *PINUS RADIATA* FOR RESISTANCE TO DOTHISTROMA NEEDLE BLIGHT

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ABSTRACT

Dothistroma needle blight caused by *Dothistroma pini* Hulbary was assessed on *Pinus radiata* D. Don in New Zealand in nine progeny trials ranging in age from 2 to 10 years. Resistant families could be identified from all assessments and rankings were consistent over sites and years. Heritabilities were moderately high, specific combining ability (SCA) was very small compared to general combining ability (GCA), and there was no indication of substantial genotype \times location interaction. The greatest net gain in volume from resistant progeny will result from placing as much selection emphasis on Dothistroma resistance as on improved growth rate and stem form. Genetic gain expected from seed orchard progeny from performance-tested first-generation parents is calculated from progeny test data to be about 11-12%. The actual reduction in disease with disease-resistant stock may be greater because of the epidemiological effect which occurs when all trees in a stand are resistant.

Keywords: Dothistroma needle blight; resistance; selection; heritability; predicted genetic gains; specific combining ability; general combining ability; selection index; economic weights; tree breeding; *Dothistroma pini*; *Pinus radiata*.

INTRODUCTION

Dothistroma needle-blight, caused by the fungus *Dothistroma pini*, affects large areas planted in *Pinus radiata* (Kershaw *et al.* 1988). The biology of the disease is well known (Gadgil 1977; Gilmour 1981). High disease levels appear to occur in 2 out of every 5 years. In these years about 20% of the stands in susceptible age-classes (1-15 years) in New Zealand have required aerial control measures (Carson & Carson 1986). Although extensive aerial control measures are carried out (Kershaw *et al.* 1988), they do not eradicate the disease.

About 6 years ago variability in resistance combined with a moderately high heritability estimate was demonstrated in a field trial (Wilcox 1982), and successful field screening for resistance was carried out on a limited scale. It was thought that a combination of aerial spraying and disease resistance of new plantations might further reduce levels of Dothistroma needle blight in *P. radiata* in New Zealand.

A disease resistance breeding programme was initiated in 1983 (Carson & Carson 1986), and seed from a *Dothistroma*-resistant breed is now available (Forest Research Institute 1987). Even though limited information was available at the time on the genetics of *Dothistroma* resistance, it was felt that it was important to begin the programme and initiate seed orchard establishment. The selection strategy developed (Carson & Carson 1986) involved (1) a very mild selection for *Dothistroma* resistance in the breeding population, and (2) creation of a seed-production population highly select for resistance, that is, a *Dothistroma*-resistant breed intended for use in high-hazard areas. Parents for the *Dothistroma*-resistant breed were selected using field progeny test data from among New Zealand selections for improved growth and form. Selection emphasised *Dothistroma* resistance as well as growth potential.

The selection strategy developed was based on several premises. They include:

- (1) Information from infected field progeny trials is effective in selection for *Dothistroma* resistance;
- (2) Selection of good general combiners for seed orchards will result in greater resistance than will selection and propagation of tested full-sib families;
- (3) Progeny perform consistently over years and sites, so only one set of resistant selections need be made for national use;
- (4) Selection for *Dothistroma* resistance of parent clones already selected for improved growth and form will yield as much gain as selection within an unimproved population;
- (5) The greatest net gain in volume from resistant progeny will result from placing as much selection emphasis on *Dothistroma* resistance as on improved growth and form.

Additional data have now been collected both from trials planted to develop the *Dothistroma*-resistant breed and from trials planted for other purposes. This allows a re-examination of selection strategy with the objective of designing a resistant breed for use on high-risk *Dothistroma* sites.

MATERIALS AND METHODS

Trial Data Used for Breed Development

Data on *Dothistroma* resistance were collected from eight North Island sites and one South Island site (Table 1). Progeny in the trials represent parents (approximately 350) which are all in the New Zealand *P. radiata* breeding population and are primarily from first-generation selections ("850" and "268" series) or from second-generation selections made in a "268" series wind-pollinated progeny test ("875" and "880" series). Further details about the origin of the breeding series are available in the "Radiata Pine Development Plan" (Shelbourne *et al.* 1987).

In addition, a number of control seedlots representing different select and non-select *P. radiata* populations were included in the NC-I and the "880" *Dothistroma* resistance trials (Table 1). The 1983 "880" *Dothistroma* trials were placed on high-hazard *Dothistroma* sites, but all other trials were established to performance-test parents for the Growth and Form breed (Vincent 1987).

TABLE 1—Description of trials used for development of a *Dothistroma*-resistant breed

Trial	Clonal series	Mating design	Field design	Year planted	Site	Age of assessment of <i>Dothistroma</i> symptoms
NC-II	"850"	NC-II (4 males, 23 females) (Comstock & Robinson 1952).	Row plots — 6 trees/row, 15 reps.	1972	Kaingaroa Forest, Cpt 905	10 (R.D. Burdon, unpubl. data).
"850" Diallels	"850"	Five five-parent disconnected half diallels (25 parents, 50 full-sib families) (Griffing 1956).	5 non-contiguous trees/rep, 6 reps.	1975	Kaingaroa Forest, Cpt 905 Mawhera Forest (South Island)	5 (Wilcox 1982), 7 (Carson & Carson 1986), 9, 9.
"875" Diallels	"875"	18 modified disconnected half-diallels (91 parents, 150 full-sib families) (Wilcox 1983).	Single-tree plots, 50 reps.	1980	Kaingaroa Forest, Cpt 327	4 (Carson 1986; Carson & Carson 1986).
NC-I	"268" (116 females) "850" (2 females, 47 males) "875" (130 males) Other series (12 males)	NC-I, random pair crosses (Comstock & Robinson 1952).	Single-tree plots, 50 reps.	1982	Mangaone (near Kawerau)	4.
"880" Growth and Form trials	"880"	Wind-pollinated, 166 parents.	Single-tree plots, 50 reps.	1981	Lake Taupo Forest Rotoehu Forest Moerewa Forest	4 (growth and form only, G.R. Johnson unpubl. data), 5. 4 (growth and form only, G.R. Johnson unpubl. data). 4 (growth and form only, G.R. Johnson unpubl. data).
"880" <i>Dothistroma</i> resistance trials	"880"	Wind-pollinated, 165 parents.	Single-tree plots, 33 reps.	1983	Kaingaroa Forest, Cpt 64 Mamaku Forest Atiamuri	3. 2, 3. 2, 3.

Assessment of Dothistroma Symptoms

Dothistroma infection resulted from naturally occurring inoculum. Crown infection was either uniformly distributed among trees or showed a slight gradient across the trial site. On most sites tree crowns were clearly visible for assessment, although the presence of weeds interfered with visibility on many trees at the Mamaku site. Assessments of trees at each site were made from a consistent compass bearing in order to standardise assessment conditions since on several sites trees appeared to be consistently more heavily infected on the north side than on the south side.

Disease levels (i.e., percentage of crown infected) were estimated in 5% steps using methods evaluated by van der Pas, Kimberley & Kershaw (1984). Assessment crews were trained originally by van der Pas and then received regular instruction and training sessions from other experienced observers. Observers were constant with replications, so that differences in assessment levels by different observers were confounded and could be partitioned as replication differences. The coefficient of variation of seedlot means was calculated for each assessment and tested against the criteria for research trials (CV < 10%) suggested by van der Pas, Kimberley & Kershaw (1984).

Analysis of Individual Assessment Data

Dothistroma levels were analysed primarily using SAS procedures on a VAX 780 computer. Analyses of variance were calculated for the "850" series NC-II experiment using Henderson's Method I in the FRI program "VARK" (written by M. O. Kimberley). Analyses of variance were calculated for the disconnected diallel experiments using program "DIALL" (Schaffer & Usanis 1969) and "PROC GLM" of SAS. Analyses of variance for all other experiments were calculated using "PROC GLM" of SAS. Variance components were calculated from analyses of variance by equating mean squares to their expectations.

For the diallel trials, analyses of variance included terms for replicates, diallels, general combining ability (GCA), and specific combining ability (SCA) within diallels, and all interactions. For the NC-II experiment, analyses of variance included replicates, testers (males), clones (females), and all interactions. For the NC-I experiment, analyses of variance included replicates, sets, females within sets, and males within females and sets. Parent breeding values for the diallel, NC-I, and NC-II trials were obtained using program "GSCA" (Snyder 1975).

For the wind-pollinated progeny tests ("880" series), terms for replicates, sets, families within sets, and interactions were included in the analyses of variance. Family means for Dothistroma infection were calculated as indicators of Dothistroma resistance.

Controls in the NC-I were analysed in an analysis of variance with terms for replicates, seedlots, and interaction. Controls in the Dothistroma resistance trials were analysed in an analysis of variance with sites, years within site, replicates within years and sites, seedlots, and interactions.

Comparison of Different Assessments

Pearson correlation coefficients were calculated between parent breeding values estimated from the various "850" series assessments (diallel, NC-II) and between family

means from the various "880" series assessments using SAS "PROC CORR". Genetic correlations between sites were calculated on the basis of the equation:

$$r_g = \frac{r_p}{h_a h_b} \quad (1)$$

where:

r_g = genetic correlation of parent breeding values or means for percentage crown infection from site a with site b,

r_p = phenotypic correlation of parent breeding values or means for percentage crown infection from site a with site b,

h_a = square-root of repeatability of half-sib family effects or means for site a, and

h_b = square-root of repeatability of half-sib family effects or means for site b.

Genetic correlations between assessment years within sites for "880" series progeny trials were calculated on the basis of the equation:

$$r_g = \text{Cov}_{xy} / (\sigma_x \sigma_y) \quad (2)$$

where:

r_g = genetic correlation for percentage crown infection between year x and year y.

Cov_{xy} = between-family component of covariance for percentage crown infection in year x with year y,

σ_x^2 = between-family variance in year x, and

σ_y^2 = corresponding variance in year y.

In addition, variance components for genotype and genotype \times environment interaction were estimated and compared for both the "850" and "880" series assessments. The 9-year assessments from the two sites of the "850" series diallel were subjected to analysis of variance with locations, replications within locations, diallels, crosses within diallels, and all interactions as sources of variation. The variance component estimate for genotype \times environment interaction was obtained by subtraction. SAS "PROC VARCOMP" was used to calculate variance components for Dothistroma symptoms from parent means of "880" series assessments using a model with sites, assessment years within sites, seedlots, and a seedlot \times sites interaction as sources of variation.

Expected Gains From a Dothistroma-resistant Breed

Differences in expected gains at different sites

Genetic gains in Dothistroma resistance were predicted for seed orchards of "880" series parents using data for each of the "880" series sites and assessments. A genetic selection index was constructed using data from all seven assessments, and was calculated using program "RESI" (Cotterill & Jackson 1981). Gains were predicted in two ways —

(1) using the genetic selection index and (2) choosing families based on the index and calculating expected gains from selection differentials on the basis of the equation:

$$\Delta g = 2Sh^2 \quad (3)$$

where:

Δg = predicted genetic gain in percentage crown infection,

S = selection differential, that is, mean of selected parents minus mean of all parents, and

h^2 = repeatability of half-sib family means.

The coefficient of 2 is included in the equation to account for both pollen parents and seed parents being selected. Genetic gain comparisons were constructed to represent 10-parent and 20-parent orchards with no pollen contamination selected out of a breeding population of 350 ($i = 2.15$ and 1.86 , respectively).

Effect of different selection strategies

The correlated response of selection for *Dothistroma* resistance on growth and form traits was calculated and compared for three different sets of selection criteria.

Selection for resistance only: Families were chosen based only on resistance using a three-site genetic selection index (Burdon 1979). The index included the second assessments of infection in the *Dothistroma* resistance trials at the Mamaku, Atiamuri, and Lake Taupo sites.

Selection for growth and form only: Selection for growth and form alone was based on the 4-year assessment of the three sites of "880" series progeny trials planted to assess performance for growth and form (and in which *Dothistroma* was essentially absent prior to the assessment). A genetic selection index which combined selection for volume and straightness was devised by G. R. Johnson (unpubl. data) and used in the New Zealand breeding programme, as volume and straightness were the best indication of worth for the Growth and Form breed (Forest Research Institute 1987).

Selection for resistance and growth: Selections for both resistance and growth were made using two methods.

Method 1: Selection for *Dothistroma* resistance was done using the three-site index constructed for selecting for resistance alone, but with an independent culling for volume. Families were culled if they were not rated in the top third for volume.

Method 2: A selection was made maximising gain in "relative stand volume" (R). R is a hypothetical measure constructed for comparative purposes only. It is defined here as "expected volume in the absence of *Dothistroma* minus expected volume loss due to *Dothistroma* infection, if the trees are grown in the presence of the disease". If a 1% volume loss is assumed to result from a 1% increase in *Dothistroma* infection (as was proposed by van der Pas (1981) for individual trees with less than 50% infection), and if stand volume and predicted volume gains from the

two sets of "880" series progeny test sites are assumed to be about the same, then R can be expressed for comparative purposes as:

$$R = (G_v + X_v) - ((X_d - G_d)/(100 (G_v + X_v))) \quad (4)$$

where: X_v = mean volume of all families in the absence of Dothistroma (that is, in trials planted to assess growth and form traits),

G_v = predicted genetic gain in volume in the absence of Dothistroma,

X_d = mean percentage crown infection for all families (that is, in trials planted to assess Dothistroma resistance), and

G_d = predicted reduction in crown infection (percentage of "full" crown) attributable to genetic gain in Dothistroma resistance.

Therefore:

$(G_v + X_v)$ = total expected volume of a stand produced from mating selected parents and grown in the absence of Dothistroma, and

$(X_d - G_d)$ = percentage crown infection of a stand produced from mating selected parents and grown in the presence of Dothistroma.

For each family G_v and G_d were calculated using Equation (3). Parents of families with the highest R values were selected.

As before, parents were selected at two selection intensities, representing 10- and 20-parent orchards without pollen contamination, chosen from a population of 350. Again, the "880" series was used as a model and sets of six parents and sets of 12 parents were chosen for each of the selection methods. Means of each set for volume, straightness, and malformation were calculated from the 4-year assessment for growth and form. The mean crown infection for each set was calculated from the three assessments of the Dothistroma resistance trials used in the index. Genetic gains were predicted for volume and resistance using Equation (3). "Relative stand volume" (R) was also calculated using Equation (4) for the parents selected using each strategy.

Economic weights for genetic selection index

The appropriate economic weights in a genetic selection index (Falconer 1960; Hazel & Lush 1942) for maximising stand volume when both volume and Dothistroma resistance are included as selection criteria were further examined by constructing two-trait genetic selection indices with a range of economic weights. Nine indices were constructed using "RESI" with economic weights varying from 8:1 to 1:8 for volume and Dothistroma resistance, respectively.

The indices were constructed using estimates of genetic parameters calculated from the "880" series trials. Repeatabilities of family means and phenotypic variances for both volume (G. R. Johnson, unpubl. data) and resistance were average site parameters over three sites. Estimates of phenotypic correlation were the correlation of parent mean volume over the three sites in the volume index with parent mean infection over the three assessments in the resistance index ($r_p = 0.29$). The genetic correlation was then estimated using Equation (1) ($r_g = 0.46$).

Predicted gains for a 10-parent orchard (assumed to have no pollen contamination) chosen from a breeding population of 350 were calculated for selections made using

each of the nine indices. The "880" series was again used as a model. Six "880" series parents were selected, selection differentials were calculated, and expected gains were estimated using Equation (3). The sets of parents selected using each of the nine indices were also compared with the parents selected using the two selection methods described above which combined selection for both resistance and growth, and also with the 15 parents selected in 1987 for propagation in control-pollinated *Dothistroma*-resistant orchards.

RESULTS

Analysis of Individual Assessments

Parent breeding values were significantly different for each assessment result involving full-sib crosses (Table 2), and half-sib family means were significantly different

TABLE 2—Genetic parameters for percentage of needles with *Dothistroma* symptoms in experiments involving control-pollinated families

Parent series:	"875"	"268"	"850"				
	Cpt 327, Kaingaroa	Mangaone	Cpt 905, Kaingaroa			Mawhera	
Expt design:	diallel*	NC-I	diallel		NC-II†	diallel	
Age:	4	4	5‡	7	9	10	9
σ^2_{GCA} §	8.4	6.9	0.048	9.2	9.17	24.00	18.89
σ^2_{SCA}	1.2	0	0.0083	4.1	1.46	0.45	0
σ^2_w	73	86	0.586	187	92	233	332
h^2	0.40	0.30	0.30	0.19	0.30	0.30	0.17
h^2_{hs}	0.79	0.76	0.83	0.73	0.76	0.91	0.67
Mean	12	16	1.88	40	30	42	34
Range of parent breeding values	0–28	8–30	0.97–2.9	23–58	13–43	31–50	18–52
CV of cross means	5.8%	3.9%	5.8%	3.2%	1.9%	2.6%	3.9%

* From Carson (1986)

† R.D. Burdon, unpubl. data.

‡ Data were a rating of *Dothistroma* severity on a 0–4 scale related to percentage of needles with symptoms (Wilcox 1982).

§ σ^2_{GCA} = estimated general combining ability variance. Parent breeding values are significantly different ($p < 0.01$) for all assessments.

σ^2_{SCA} = estimated specific combining ability variance.

σ^2_w = within-subclass variance (genetic variance within full-sib families + environmental or chance differences in infection from tree-to-tree within subclasses).

h^2 = estimated narrow-sense heritability

$$= \frac{4\sigma^2_{GCA}}{\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_p + \sigma^2_w}$$

where:

σ^2_p = estimated variance due to interaction between full-sib families and block replicates

h^2_{hs} = repeatability of half-sib family means

for each assessment result involving open-pollinated progeny trials (Table 3). The coefficients of variation of means for crosses or half-sib families were below 10% of the mean in every case except one (for which the mean infection was only 8%).

Heritability estimates for Dothistroma resistance were consistently high relative to those recorded for other important selection traits (Carson 1986). Narrow-sense heritability estimates averaged 0.24 over all assessments (range 0.13–0.37) and repeatabilities of half-sib family means averaged 0.71 (range 0.52–0.91) with apparently no

TABLE 3—Genetic parameters for percentage of crown with Dothistroma symptoms in progeny trials of wind-pollinated seedlots from “880” series parents

	Mamaku		Atiamuri		Kaingaroa Cpt 64	Lake Taupo	
	Age 2	Age 3	Age 2	Age 3	Age 3	Age 4	Age 5
σ_f^2 *	12.12	19.12	4.40	13.76	8.30	4.41	12.14
σ_w^2	238	265	123	247	244	74	148
h^2	0.19	0.27	0.14	0.21	0.13	0.22	0.30
h_{ha}^2	0.63	0.71	0.54	0.64	0.52	0.75	0.70
Mean	30	51	29	42	36	8	58
Range of family means	16–43	32–66	22–38	31–57	25–45	3–16	46–68
CV of seedlot means	8.7%	5.5%	6.8%	6.5%	7.7%	16.2%	4.0%

* σ_f^2 = estimated variance among open-pollinated families. Family differences are significant ($p < 0.01$) for all assessments.

σ_w^2 = within-subclass variance (genetic variance within open-pollinated families and environmental or chance differences in infection from tree to tree within subclasses).

h^2 = estimated narrow-sense heritability

$$= \frac{\sigma_f^2}{\sigma_f^2 + \sigma_w^2}$$

h_{ha}^2 = estimated repeatability of half-sib family means

$$= \frac{\sigma_f^2}{\sigma_f^2 + \sigma_w^2 / \text{number of replicates}}$$

relationship between these heritability estimates and stand mean infection or individual tree variability (σ_w^2). Heritabilities and repeatabilities did tend to be lower for assessments of very young trials (age 2). General combining ability (GCA) variance was much greater than specific combining ability (SCA) variance in all of the experiments in which SCA could be quantified (Table 2).

Comparisons among *P. radiata* populations revealed small differences in resistance among improved populations, and large differences between native provenances and New Zealand land races. Control seedlots were significantly different from one another ($p < 0.01$) in both the “880” series wind-pollinated progeny trial and in the “268”/“875”

series NC-I experiment (Table 4). Control seedlots representing parents from the "268", "875", and "880" clonal series had slightly and in some seedlots significantly less infection (about 4% fewer needles infected) than unselect or "850" series parents. Two of the three Californian provenances had substantially more infection than the other control lots (about 8% higher for Año Nuevo and about 14% higher for Cambria).

TABLE 4—Percentage of crown with *Dothistroma* symptoms for different *Pinus radiata* populations

Population	Trial	
	"880" series wind-pollinated <i>Dothistroma</i> -resistance progeny test (three sites)	"268"/"875" series NC-I experiment (one site)
Kaingaroa bulk	—	20.0
Kaingaroa climbing select	39.7	—
Gwavas orchard	42.5	19.2
Crosses of "875" series parents	39.0	20.6
Crosses of "268" series parents	39.0	16.3
Series being tested	36.0	16.3
California provenance		
Monterey	41.6	—
Año Nuevo	48.5	—
Cambria	54.5	—

Comparison of Different Assessments

Assessments of *Dothistroma* resistance ranked seedlots similarly at different forest sites, and for different years of assessment at the same site. Phenotypic correlations among "850" series breeding values from different sites (average $r = 0.54$) were all significantly different from zero ($p < 0.1$). Phenotypic correlation estimates of "880" series open-pollinated family means between different sites and different ages were also significant ($p < 0.0001$) with an average correlation of 0.52. Genetic correlation estimates derived from variance estimates were generally high (range 0.44–1.04). The average of estimated genetic correlations between assessments of the same trial of "880" series progeny at different ages was actually slightly lower ($r_g = 0.68$) than between assessments of trials at different locations ($r_g = 0.76$). The average genetic correlation across sites and ages for the "880" series parents ($r_g = 0.75$) was similar to that for the "850" series parents ($r_g = 0.72$).

There was little evidence for genotype \times environment interaction in *Dothistroma* resistance means for seedlots, indicating that seedlot rankings obtained at one site at a single age will be reliable for over-all ranking of parents for *Dothistroma* resistance. For the four locations of the "880" series trial assessed over 2 years, the variance attributable to the seedlot \times location interaction effect (4.29) was less than half the variance among seedlots (8.96). For the two locations of the "850" series trial assessed at the same age, the variance attributable to the full-sib family \times location interaction effect (2.29) was less than 15% of the variance among full-sib family crosses (15.58).

Expected Gains From a Dothistroma-resistant Breed

Differences in expected gains at different sites

When Dothistroma resistance was used as the only selection criterion, substantial gains in resistance were predicted for all sites using either the "selection index" or the "selection differential" prediction methods. The average predicted gain over seven assessments from using parents chosen with Dothistroma resistance as the only selection criterion, was 11% for a 20-parent orchard and 12% (of full crown) for a 10-parent orchard (Table 5). Predicted gains in Dothistroma resistance varied from 7% to 20% depending on site and year. Substantial gains were expected even on sites with relatively low infection levels. Average gain predicted from selection differentials was higher by about 1% infection than the average gain predicted from the genetic selection index.

TABLE 5—Predicted reduction in percentage of crown with Dothistroma symptoms for all sites and assessments of the "880" series progeny trials*

Number of parents selected	Method of prediction	Mamaku		Atiamuri		Kaingaroa	Lake Taupo		Av.
		Age 2	Age 3	Age 2	Age 3	Age 3	Age 4	Age 5	
10	Index	12.1	16.4	6.8	13.8	10.2	7.8	11.4	11.2
	Selection differential	16.4	19.6	6.8	13.4	10.4	7.2	11.7	12.2
20	Index	10.5	14.2	5.9	11.9	8.9	6.8	9.9	9.7
	Selection differential	13.2	18.3	6.8	13.2	6.8	6.6	11.1	10.9

* Assumes selections are made in the New Zealand *P. radiata* breeding population (350 parents), resistance is the only selection criterion, and parents are mated in a control-pollinated orchard.

Effect of different selection strategies

Although all the differing selection strategies predicted gains in both volume and resistance, gains in resistance were much higher and gains in volume were much lower when resistance was the only selection criterion than when volume and straightness were the only selection criteria. Means of the groups of parents selected using the three different sets of selection criteria were very close for straightness and malformation, but differed for volume and Dothistroma resistance (Table 6). However, when both resistance and volume were used together as selection criteria, predicted gains in each approached those calculated when the traits were considered separately. "Relative stand volume" (R) was higher when selection was for both resistance and volume than when either trait was considered alone (last column, Table 6).

Economic weights for volume and resistance

The best compromise for jointly selecting for volume growth and Dothistroma resistance occurs when these traits are given approximately equal weights. Varying economic weights in a two-trait (volume and crown infection) genetic selection index resulted in varied predicted gains in volume and resistance (Table 7). "Relative stand volume" (R) was maximised at a 1:1 ratio for volume and resistance. Gains in both

TABLE 6—Predicted genetic gains in growth, form, and *Dothistroma* resistance from selection in the New Zealand *radiata* pine breeding population

Number of parents selected	Selection criteria	Mean of selected families*				Predicted gain†			"Relative stand volume" (R)
		Volume (m ³)	Straightness‡	Malformation‡	Resistance (crown infected %)	Volume (m ³)	Resistance (percentage of mean)	Resistance (crown infected %)	
10	resistance§	67.9	5.7	7.5	41.3	7.1	11.1	16.4	46.9
	volume, straightness§	74.8	5.9	7.8	46.3	18.9	29.6	7.2	47.1
	resistance, volume(1)	69.6	5.7	7.5	41.4	10.0	15.7	16.2	48.7
	resistance, volume(2)	72.6	5.7	7.6	42.4	15.1	23.7	14.4	50.7
20	resistance§	66.4	5.5	7.5	42.3	4.6	7.2	14.5	44.0
	volume, straightness§	73.8	5.7	7.6	48.5	17.2	30.0	3.1	42.8
	resistance, volume(1)	69.4	5.5	7.5	42.7	9.6	15.0	13.8	46.7
	resistance, volume(2)	73.0	5.5	7.5	44.3	15.8	24.8	10.9	48.3
All families*		63.8	5.6	7.4	50.2				

* Mean of three essentially disease-free sites for growth traits, and mean of three diseased sites for percentage infection.

† Predicted from selection differentials using "880" series progeny test data.

‡ Measured on a 1–9 subjective scale.

§ Parents selected using three-site genetic selection index with traits specified included.

|| Parents selected for resistance using a three-site genetic selection index, then culled for poor volume.

¶ Parents selected for maximum "relative stand volume" (R).

TABLE 7—Predicted genetic gains from parents selected using selection indices with volume and Dothistroma resistance traits

Economic weight in selection index*		Mean of selected families†		Predicted gain‡			“Relative stand volume” (R)	Number of parents selected in common with those selected by other methods		
Volume	Resistance	Volume (m ³)	Resistance (crown infected %)	Volume (m ³)	Resistance (percentage of mean)	Resistance (crown infected %)		Resistance, volume(1)	Resistance, volume(2)	1987 propagation programme§
8	1	74.7	44.6	18.7	29.3	10.3	49.6	2	4	6
6	1	74.7	44.6	18.7	29.3	10.3	49.6	2	4	6
4	1	74.1	43.6	17.7	27.7	12.1	50.4	3	5	6
2	1	74.1	43.6	17.7	27.7	12.1	50.4	3	5	6
1	1	72.6	42.4	15.1	23.7	14.4	50.7	4	6	6
1	2	70.9	41.7	12.2	19.1	15.6	49.7	5	5	6
1	4	70.7	41.6	11.9	18.5	15.8	49.7	5	5	5
1	6	70.7	41.6	11.9	18.5	15.8	49.7	5	5	5
1	8	69.6	41.4	10.0	15.7	16.2	48.7	5	4	5
All families		63.8	50.2							

* Traits used in index are mean volume over three essentially disease-free sites, and mean percentage infection over three diseased sites.

† “880” series parents selected for 10-parent orchard with no pollen contamination.

‡ Predicted from selection differentials using “880” series progeny test data.

§ Fifteen parents selected for control-pollinated orchard. Selection was for Dothistroma resistance with culling for poor volume.

traits, however, did not drop off extremely sharply on either side of this ratio. More of the parents selected for resistance with independent culling for volume (Method 1) were in common with parents selected with indices heavily weighted for resistance. The parents selected for maximum R, however, were the same as those selected with a 1:1 ratio of economic weights for volume and resistance. The same set of parents were also selected by selecting for resistance with a culling of parents which were not outstanding for resistance and were not in the top 16% for volume. Almost all the parents chosen with selection using the nine indices were included in the group of 15 top parents selected in 1987 for propagation and planting in *Dothistroma*-resistant orchards.

DISCUSSION

The initial strategy formulated for development of *Dothistroma*-resistant orchards has been supported very strongly by the additional data now available. With this new information, the strategy for selecting resistant parents can be refined to maximise over-all volume production and minimise costs of disease control.

Selection in Infected Field Progeny Tests is Effective

Reliable rankings of seedlot means for *Dothistroma* resistance were obtained for assessments at all sites and ages. Heritability and variance estimates were consistently high, and family rankings of means for resistance were consistent over sites and years. Selection of parents for seed orchards was possible from all assessments of resistance. It appears that all that is required is a fairly uniform infection level across a progeny trial. Even with as little as 8% average infection at Lake Taupo and 12% at Kaingaroa Forest resistant families could be identified reliably.

Selection of Parents Better Than Selection of Full-sib Families

The strategy of testing and selecting parents for orchards rather than testing and selecting full-sib families is well supported by the lack of evidence of any kind for substantial SCA variance in this trait. Genetic variance in *Dothistroma* resistance appears to be almost entirely additive. The rationale for this "good general combiner" selection has been outlined elsewhere (Carson 1986).

Selection Does Not Need to be Regionalised

It appears that one set of resistant selections can be used to supply resistant seed for all New Zealand sites. Families appear to have performed consistently on different sites and in different assessments at the same sites. For example, "880" series families assessed on four North Island sites ranked consistently over sites as well as over 2 assessment years. Also, even in assessments of "850" families made in both North and South Islands, interaction between genotype and environment appeared to be unimportant. Therefore, one set of resistant selections for national use would result in the highest gains in disease resistance.

Regional sets of parents might be needed, however, if different races of *D. pini* existed in different frequencies throughout New Zealand, leading to different relative infection levels on the pine host families. Very little is known about pathogenic variation in *D. pini*. The only study on variability in this pathogen showed no difference

in mean infection between species (*Pseudotsuga menziesii* (Mirb.) Franco and *Pinus radiata*) inoculated with spores collected from *Ps. menziesii* and spores collected from *P. radiata* (Gadgil 1968). Despite this, it is unlikely that there is no pathogenic variation in this fungus as variation is the rule rather than the exception, even for asexually propagated fungi.

However, even if there are some as yet unmeasured differences in pathogenicity, regionalised selection for resistance is probably not necessary. Resistance of *P. radiata* to Dothistroma needle blight behaves very much like a polygenic trait – that is, one inherited through many genes, all with small additive effects. This suggests that the resistance incurred by selection should be durable even if pathogen populations are variable within regions.

Selection Within the New Zealand Breeding Population is Best Strategy

The parents used to produce the seed of the Dothistroma-resistant breed have been selected among parents already chosen for growth and form in New Zealand. Results of these trials as well as others (Burdon & Bannister 1973) suggest that the native Californian provenances have less resistance than the New Zealand breeding population and, indeed, even the unimproved New Zealand land races (as represented by bulk and climbing select seedlots). Thus, the New Zealand breeding population appears to be the most resistant population available. Selection within that population will, therefore, probably yield selections that are as resistant as any to be found while also yielding high growth rates. The slightly greater resistance of the New Zealand breeding population may be related to the positive but small genetic correlation between growth rate and Dothistroma resistance.

Resistance and Growth Rate Should Have Equal Selection Emphasis

Gains in straightness and lack of malformation can be expected to be similar for improved seedlots whether or not Dothistroma resistance is included as a selection trait. Selection with emphasis on Dothistroma resistance does involve acceptance of somewhat reduced predicted gains in growth potential. However, if selection for both resistance and volume is done so as to emphasise both about equally, the expected genetic gains in each trait are not much lower than if they were selected for individually – specifically, a 24% *v.* 30% gain in volume and a 14% *v.* 16% reduction in crown infection. (A reduction of 14% in the proportion of full crown infected represents a 28% gain relative to the average stand infection of 50.2%).

Crown infection by *D. pini* does result in growth loss. On individual trees with less than 50% infection in a recent study, a 1% increase in disease has been equated with a 1% loss in volume (van der Pas 1981), while volume loss was much greater for trees with more than 50% infection. On a stand basis, stand basal area (and therefore volume) has been shown to increase after disease reduction (van der Pas, Bulman & Horgan 1984; Woollons & Hayward 1984).

Therefore, it appears that substantial increases in volume can be obtained on high-risk Dothistroma sites through increases in genetic resistance, as well as through a genetic potential for increased growth rate. On such sites, the total realised volume gain

from a combination of genetically higher growth rate and genetically reduced infection is likely to be greatest if both traits are improved at the same time.

In addition, gains in growth potential predicted in this paper are made from stands which have not suffered significant *Dothistroma* infection. Growth rate gains measured in genetic gain trials vary greatly with site, and have generally been highest on sites where no environmental stresses occur and lowest where stress of some type is involved. It is, therefore, very probable that realised genetic gains from selection for increased growth potential will be smaller in stands with high infection. It is unlikely that a tree can realise its full genetic potential for growth rate when suffering from repeated needle loss due to *D. pini*. Thus it is possible that individuals highly select for increased growth rate may suffer greater growth losses from *D. pini* infection than unimproved populations.

Both of these factors suggest that high predicted gains in volume are likely to be realised on sites with potential for high disease levels only if they are combined with a high level of disease control. Forest sites are sprayed with fungicides to control *D. pini* when they have relatively high levels of needle blight symptoms (15–25% of the needles infected) (Kershaw *et al.* 1988). Spraying may prevent the disease increases for a period after the spray, but does not prevent the loss of needles already infected, and may not prevent the build-up of the disease in the following year. Thus growth loss will occur from the disease even if chemical control is 100% effective in the short term (which it often is not). Therefore, disease reduction by planting stock with *Dothistroma* resistance will result in disease decrease even with chemical control. Again, this suggests that the greatest realised gains in volume will occur with selection for substantial levels of both volume gain and disease resistance.

The provisional selection made for the 1987 propagation programme was successful in including all the parents identified in this study as achieving substantial gains in both growth and resistance. The strategy adopted allowed for a subsequent roguing of less-resistant clones based on the new information available.

Expected Gains From a *Dothistroma*-resistant Breed

Expected gains from a *Dothistroma*-resistant breed expressed as a reduction in average disease levels can now be calculated from progeny test data. Van der Pas, Kimberley & Kershaw (1984) identified the conditions important for accurate assessment of absolute disease levels as site conditions, observer skill, sample size, and sample structure. Trees assessed in this study were open grown, observers were trained and highly skilled, and sample sizes were very large (for example, excluding controls, "880" *Dothistroma*-resistance progeny trials had 5445 trees). Trials were planted with the structure of a randomised complete block experiment and assessments were assigned so that observer differences were removed in the analysis. In addition, for comparison of family performance identification of relative disease levels is important, rather than absolute levels. The high significance of family differences ($p < 0.01$) in every trial indicates that relative levels can be accurately identified and, thus, expected relative differences between select and base populations can also be calculated with confidence.

Predictions of gain from the "880" series progeny trials can be used as a model of the entire New Zealand breeding population. Estimates of heritability, variance components, and correlations are very similar for the different series, with no strong evidence that one series is, on average, more resistant than another. The "880" series is very suitable for estimating expected gains made from selection in the entire New Zealand breeding population (and for that matter examining the effect of different selection strategies) because of the extensive data set which has been built up for a large number of parents.

Genetic gain predictions are calculated from a statistical model based on quantitative genetic theory (Falconer 1960), itself developed from an extension of Mendelian genetics. Formulae used to predict gains relate only to a population of trees subjected to one specific method of selection. Gains can be predicted for selection in a genetic selection index combining single or multiple traits using data from one or more assessments (Hazel & Lush 1942). In general, when heritabilities and correlations are all similar, the more entries in the selection index (traits, sites, assessments, etc.) the less gain will be predicted for the average over all entries, and for the most part for any one entry.

With resistance as the only selection criterion, reduction in percentage of the crown infected was predicted for the "880" series to be 16% from a selection using a three-site genetic selection index (Table 6) and 12% from a selection index which considered data from seven assessments (Table 5). The difference is due solely to the inclusion of only the "best" selection sites and years in the three-site index. The three-site index was used for the comparison of volume gains with resistance gains in order to put predictions of resistance on the same footing as the three-site selection for volume. The selection index based on seven assessments is probably better for choosing parents for use at all sites, and it probably yields the more realistic prediction of genetic gain over all the progeny test sites.

The most realistic prediction of maximum possible reduction in disease from progeny test data, therefore, puts reduction in percentage crown infected from using a Dothistroma-resistant breed from a 10-parent orchard at about 12% on average. The prediction varies from site to site, with as little as 7% on some sites to as much as 20% on other sites. Combined selection for high growth rate as well as resistance modifies these estimates of reduced disease levels with resistant planting stock only slightly (to about 11% on average).

However, progeny-test-based estimates of reduction in Dothistroma symptoms are probably under-estimates of the reductions in disease which will actually occur in stands of resistant trees. The success of the fungus is highly influenced by environmental factors (Gadgil 1977; Gilmour 1981) which largely determine the size of the spore population and, in turn, the extent of disease development. The level of Dothistroma infection is thus closely related to the amount of viable inoculum present.

For some as yet unidentified reason, *D. pini* infects susceptible families more than resistant families. Susceptible and resistant trees were planted together in the progeny tests. This would result in a higher fungus spore population (and thus a higher mean infection) than for a stand which contains only resistant trees. When only resistant trees

are planted in a stand, the fungus population would be smaller, and inoculum pressure would be less, resulting in less disease. This epidemiological effect might be quite large and result in resistant stands with much less infection than predicted from progeny test data. An accurate evaluation of realised gains in resistance requires quantification of this effect in large plot genetic gain trials.

All of this suggests that volume gains are likely to result from planting *Dothistroma*-resistant stock on high-risk *Dothistroma* sites. The volume gains will come from both increased genetic growth rate and increased genetic resistance. Additional cost saving advantage will come from planting a *Dothistroma*-resistant breed through a reduction in the magnitude of the *Dothistroma* control operation. Reduced disease levels throughout the forest will mean more stands will be below the threshold that necessitates spraying control.

In conclusion, disease levels can be reduced by selecting and planting resistant stock. Any area which is likely to require control of *D. pini* should be planted with stock from a *Dothistroma*-resistant breed. Use of the breed maximises growth and minimises costs in the presence of repeated *D. pini* infection.

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