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Progress in Breeding Pinus radiata Resistant to Dothistroma Needle Blight in East Africa

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Introduction

Dothistroma needle blight was first recorded in East Africa in the Western Usambara Mountains of Tanzania during 1958 (ETHERIDGE, 1965), although the identity of the causal organism was not determined until 1962 (GIBSON, 1963). The disease later spread to all Pinus radiata D. DON growing areas in Kenya, Tanzania and Uganda causing severe defoliation and even deaths where annual rainfall exceeds 60 inches (GIBSON, 1965). In areas with less thari 60 inches rainfall deaths did not occur but diameter and height growth were checked considerably (CHRISTENSEN and GIBSON, 1964).

After the preliminary experiments reported from Kenya (GIBSON et al., 1964) investigations were directed towards the development of control measures based on fungicide and shade treatments to the young susceptible crop in Kenya (GIBSON, 1965; GIBSON et al., 1966; GIBSON et al., 1967) and in Tanzania (HOCKING and ETHERIDGE, 1967). These have shown that control by shade treatment is impractical (GIBSON et al., 1967), but that aerial applications of copper-based fungicides are effective and practical (GIBSON et al., 1966). This has been confirmed by airspray trials in New Zealand (GILMOUR, 1967) and in small scale trials in the U.S.A. (THOMAS and LINDBERG, 1954; PETERSON, 1967).

It was realised at the onset of these trials that protective measures would be expensive relative to the income derived from a timber crop (DRAPER and GIBSON, 1964). Cheaper methods of control were therefore sought. Of those considered, the development of cultivars of P. radiata resistant to blight was thought to be most appropriate for East African conditions. However, as it takes a considerable time to select and build up cultivars from tree crops, it was thought desirable to continue with the development of protective control measures so that P. radiata might be grown during the interim period. The breeding Programme was begun in 1963 (GIBSON, 1965) and expanded during 1964 and 1965. The progress made up to June 1968 is reported in this paper.

Procedure and Results

(1) Selection of resistant trees

Tanganyika resistant selections (TR), Kimakia resistant 1 (KR1) and Kerita resistant selections (KR_{2-4}) were selected in 1963 and 1964 on the basis of resistance to needle blight alone. Kenya resistant selections (K. Res.) made during 1964—1965 were selected for blight resistance and certain desirable morphological characters such as vigour, good stem form, fine branches, low spiral grain and narrow crowns. This was completed in the same way as for normal plus tree selections (DYSON and PATERSON, 1966). Plus tree ramets (423, 935, 954 & R. from the capital territory of Australia) were used as controls because comparable grafted material was available at the time of setting up the field trials. The control trees (KUR) used in the later trials were chosen from E.A.A.F.R.O. estate as this was the nearest available source of trees of similar age to Kenya resistant selections. All were healthy so no estimate of their level of blight resistance could be made. Seedlings used as controls in one trial were taken at random from E.A.A.F.R.O. nursery stock.

A survey of 1,445 acres of P. radiata plantations made from 1964 to 1966 yielded 75 selections at a selection pressure of 1 resistant tree from 11,600 trees. Of these only 37 trees were considered acceptable for breeding work after eliminating those with severe stem defects and low production potential as described by PATERSON (1967). This gives a final selection intensity of 1 in 23,500.

(2) Assessments *of* select trees

In 1964 and 1965 thirteen resistant parent trees at Kerita forest station (K. Res.) were each compared with five random freegrowing neighbours using the criteria for selecting plus trees described by DYSON and PATERSON (1966) and PATERSON (1967). The results of this comparison are shown in Table *1.* It can be seen that the select trees are 4 times less affected by disease, and three times greater in volume, with less stem defects and slightly heavier branching than their random neighbours. This association of greater size and low level of disease attack was also found when 33 resistant selections from Nabkoi 2C were compared with their random neighbours. Fig. 1 shows that the resistant selections have a much lower degree of attack and a much greater volume than their neighbouring trees. A regres-

Table 1. — A comparison of 13 resistant selections with their 5 random neighbours at Kerita forest station.

Character	Mean of 13 selected trees	Mean of 65 random neighbour trees
Disease attack (%)	27.4	97.9**
Volume O.B. (cu. ft.)	15.5	5.2**
Ratio of stem to branch diameters	4.6	3.9**
Number of internodes	30.6	20.3**
Number of stem defects	3.2	3.9*
Internode length (ft.)	1.8	2.2N.S.
Grain angle B.H. (°)	2.2	3.1N.S.

** Significant at 1% level.
* Significant at 5% level.
N.S. Not significant.

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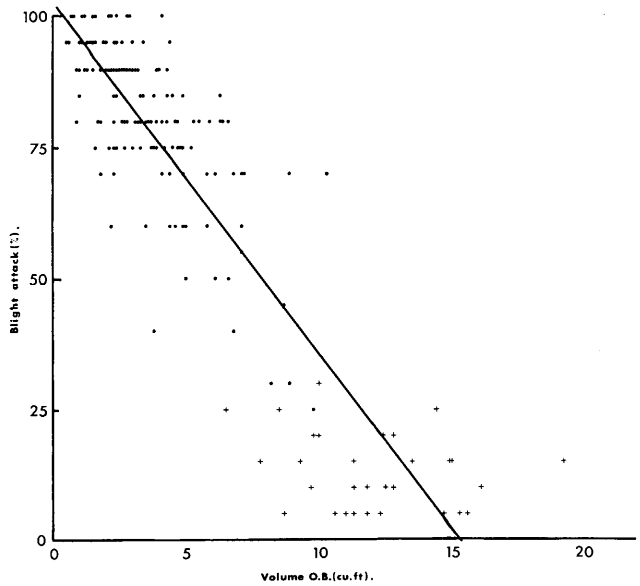

Fig. 1. — A comparison of 33 blight resistant selections in Nabkoi 2C with their 5 random neighbours 8 years after planting. + = resistant selections; ● = random neighbour trees.

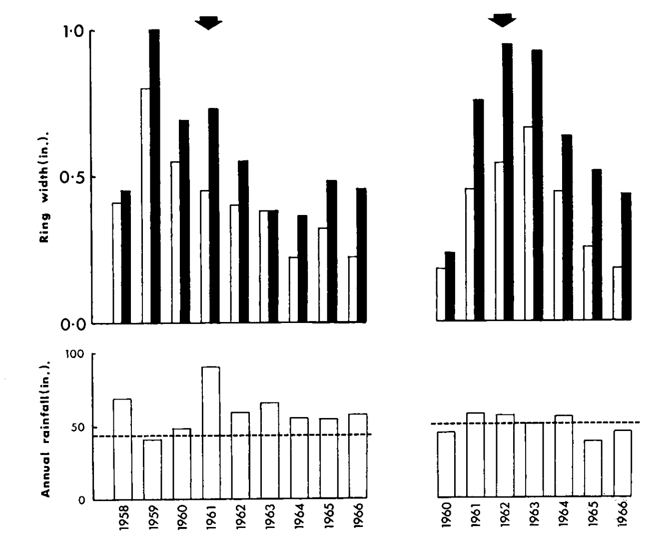

Fig. 2. — Ring width comparisons on blight resistant and random selections at Kerita and Nabkoi forest stations, ▬ resistant selections; □, random selections; ⬇, date of initial blight attack; - - - - - -, 19 year mean.

sion analysis of this data gives a line where Y = 102.7— 6.79X***.

In 1967, some wood quality studies were carried out on 30 select and 30 random trees, 13 pairs at Kerita forest station and 17 pairs at Nabkoi forest station. These were assessed for ring width, latewood percentage and wood density by analysis of single cores taken at breast height, and for grain angle by 4 measurements made at the same height. The density was found by measuring the specific gravity of the cores after the resine had been extracted. Only ring width differed consistently between the resistant and random selections, being about 0.2 in. greater in the resistant trees *(Fig. 2)*. It should be noted that in both cases the width of the rings was greater in the resistant trees before the onset of disease, indicating that the resistant trees were initially more vigorous and that this could be a factor in their ability to withstand the affects of the disease more readily than random *P. radiata* trees. It can also be seen that rainfall does not markedly affect the width of rings.

(3) Assessments of ramets from select trees

All scion material was grafted on to unselected seedling root-stocks using the top cleft graft. The scion and graft union were then enclosed in clear polythene to reduce moisture loss by transpiration. The same technique was used to interchange scion material on older trees. All ramets were assessed for performance in the field under conditions favourable to disease attack at Kimakia forest station (altitude 8,000 feet, rainfall 95 inches) or at Uplands forest station (altitude 7,900 feet, rainfall 55 inches). The assessment procedure was firstly a visual estimate of disease using the system described by Christensen and Gibson (1964), secondly a measurement of the length of the leading shoot from the tip to the point where > 90% of the needles are infected, and thirdly a measurement of the height increment.

In 1964 the first preliminary trial was laid out at Kimakia forest station using 4 Tanganyika resistant selections (TR), Kimakia resistant 1 (KR1), and 6 plus tree clones as controls. The results obtained after 2 years from this experiment are shown in *Table 2*. A second trial was begun in 1965, also at Kimakia forest station, using ramets from Kerita resistant (KR_{2-4}) selections and 4 plus tree clones as controls. *Table 3* shows the results obtained from this trial after 2 years. These two preliminary trials showed that ramets from the resistant selections are generally less susceptible to disease attack than those from plus tree parents, a result which is reflected in their greater height increment. It was therefore concluded that the resistant selections contain some factor which confers a slight degree of resistance to grafted progeny. It was also found that the vigour expected from plus trees does not wholly constitute resistance. In the absence of true control ramets no assessment of the effect of vigour can be made.

In April 1966 a larger field trial was laid out at Uplands forest station using ramets from 6 Kenya resistant clones (K. Res.) and from 6 control (KUR) clones together with unselected seedling controls. These were arranged in a randomized block design, each block consisting of one single plant plot of each selection and 6 seedlings, planted at an espacement of 12 feet by 12 feet. A single row of trees was used as a surround. *Table 4* shows the results, after adjustment for variation within blocks, from this trial after 22

Table 2. — The effect of needle blight on ramets from resistant and plus tree parents.

Scion Parent	Number of ramets	Mean amount of foliage affected (%)		Mean length of healthy leader (in.)		Mean height increment (in.) 14/12/65—31/5/66	
423	2	75.0		5.5		4.0	
935	2	62.5		6.0		5.5	
954	2	75.0	Mean	7.0	Mean	7.0	Mean
R5	2	62.5	66.7	3.0	5.0	2.5	4.0
R7	2	62.5		5.0		3.5	
R9	2	62.5		3.5		1.5	
TR1	1	75.0		3.0		2.0	
TR2	2	37.5		4.5		4.0	
TR22	1	50.0	Mean	10.0	Mean	7.0	Mean
TR30	2	62.5	59.0	11.0	6.3	10.0	5.6
KR1	5	64.6		5.2		4.8	

Table 3. — The effect of needle blight on ramets from resistant and plus tree parents.

Scion parent	Number of ramets	Mean amount of foliage affected (%)	Mean length of healthy leader (in.)	Mean height increment (in.) 14/12/65—31/5/66
R2	1	75.0	6.0	12.0
R5	1	75.0 Mean	2.0 Mean	4.0 Mean
R9	4	57.5 66.3	5.3 4.9	13.9 12.5
R11	2	75.0	5.0	14.1
KR2	19	45.0 Mean	6.8 Mean	30.4 Mean
KR3	3	50.0 44.4	6.0 7.4	34.4 31.6
KR4	4	37.5	11.0	35.5

months. An analysis of variance carried out on the adjusted data showed that the differences between selections were highly significant (0.1% level) for disease score and the length of healthy leader, but not for height increment. None of the resistant ramets have disease scores significantly lower than all the selected clones and only K. Res. 24 has a significantly longer healthy leader than all of the unselected clones. A less critical comparison, using a mean adjusted value for the 6 control clones, was therefore made. This showed that clones K. Res. 10, 24, and KUR 3 had disease scores significantly lower than the mean of the controls, and that K. Res. 10, 17, 23, and 24, had healthy leaders significantly longer than the mean of the controls. This trial would therefore seem to indicate that selections K. Res. 10, 17, 23, 24 and KUR 3 have a significant level of resistance.

To minimize the time lag for production of seed from resistant clones it was decided to set up a seed orchard at Uplands forest station using untested resistant clones. This was done with the proviso that poor clones would be removed after their level of disease resistance has been assessed. The orchard was therefore designed in two parts, in each of which 15 Kenya resistant clones (K. Res.) were replicated approximately 15 times according to an arrangement by the North Carolina State College, U.S.A. Espacement for the ramets was 18 feet by 18 feet. Superimposed on one half of the orchard were 14 control (KUR) clones, replicated 6 to 26 times. This half of the orchard has therefore been used to assess the resistance of the select clones. *Table 5* shows the results obtained 22 months after planting. An analysis of variance on the complete data showed that the differences between clones are highly significant (0.1% level) for disease score, length of healthy leader, and height increment. Using the calculated values for least significant difference (5%) no resistant clones are better than all the control clones in either disease score or length of healthy leader measurements. However, clones K. Res. 1, 10, 16, 17, 22, 23, 24, 25, 27, KUR 4, 10, and 14, had disease scores significantly lower than the mean of the controls, similarly clones K. Res. 1, 10, 16, 17, 23, 24, 25, 27, KUR 4, and 15, had healthy leaders longer than the mean of the controls. These results compare very favourably with those from the smaller resistance trial.

Table 4. — The effect of needle blight on ramets from resistant and random parents and on seedling plants.

Scion parent	Number of ramets	Mean disease score	Mean length of healthy leader (in.)	Mean height increment (in.) 16/9/66—19/2/68
K.Res.10	4	1.5	41.8	72.0
K.Res.17	3	2.3	39.3	75.3
K.Res.18	5	3.2	29.5	74.6
K.Res.23	5	2.8	38.5	79.0
K.Res.24	5	1.8	54.3	71.2
K.Res.25	5	2.6	28.3	57.8
KUR1	5	4.4	8.5	31.6
KUR2	3	5.2	9.9	54.6
KUR3	5	2.0 Mean	26.7 Mean	72.0
KUR9	5	4.4 3.67	26.1 21.03	76.0
KUR10	5	2.2	35.3	81.8
KUR14	4	3.8	19.7	61.6
Seedlings	24	5.0	17.5	67.6
Least significant difference at 5% for 5 replicates		1.59	16.22	25.7
at 5% for 5 and 24 replicates		1.24	12.60	20.0

Table 5. — The effect of needle blight on ramets from resistant and random parents.

Scion parent	No. of ramets	Mean disease score	Mean length of healthy leader (in.)	Mean height increment (in.) 16/9/66—19/2/68
K.Res.1	13	1.2	47.9	64.1
K.Res.10	13	1.8	42.4	81.4
K.Res.15	17	2.5	29.2	60.8
K.Res.16	15	1.7	42.6	76.5
K.Res.17	13	1.6	52.7	96.5
K.Res.18	13	3.3	25.9	85.2
K.Res.19	11	2.6	28.2	79.1
K.Res.20	14	2.6	27.8	74.4
K.Res.21	16	2.6	28.0	75.9
K.Res.22	13	2.2	27.5	70.9
K.Res.23	14	1.9	44.1	91.3
K.Res.24	15	1.2	52.1	77.8
K.Res.25	14	1.6	40.8	80.2
K.Res.26	10	2.6	19.0	47.5
K.Res.27	12	1.5	39.6	56.7
KUR1	16	3.5	19.7	69.8
KUR2	12	2.3	20.9	44.5
KUR3	16	2.5	28.8	83.4
KUR4	15	1.7	51.7	78.9
KUR5	20	4.4	14.7	63.4
KUR6	14	3.6	18.2	64.2
KUR7	15	3.6 Mean	21.9 Mean	84.6
KUR8	26	4.2 3.05	12.8 24.25	57.5
KUR9	12	3.8	21.4	74.5
KUR10	10	2.0	26.6	58.6
KUR12	6	3.7	20.7	72.8
KUR13	12	3.0	22.3	82.6
KUR14	16	2.6	21.0	43.8
KUR15	16	2.6	38.6	72.0
Least significant differences 5%		0.81	9.94	14.49

Calculations of the gross heritability estimates were made from the latter trial by analysing the data from the first 12 ramets of each selected and unselected clone. These were analysed as if they were in 3 blocks, each of 4 ramets, each character and clone type being analysed separately. The heritability values are shown in *Table 6*, together with the formula used. All the values are well above 0.5 indicating a high level of heritability for all characters in both selected and unselected clones.

Table 6. — Gross heritability estimates from Uplands *Pinus radiata* seed orchard.

Character	Unselected clones	Selected clones
Height increment	0.794	0.822
Length of healthy leader	0.717	0.797
Disease score	0.611	0.897

$$H^2 = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_e^2} \qquad \sigma_f^2 = \frac{\text{M.S. clones — M.S. error}}{\text{No. of blocks}}$$

$$\sigma_e^2 = \frac{\text{M.S. error}}{\text{No. of blocks}}$$

In all the previous trials scion material from resistant clones has been grafted on to unselected seedling stocks raised in E.A.A.F.R.O. nursery. This could have resulted in the dilution of the resistance by the stocks, all of which are likely to be very susceptible as shown by the performance of seedlings in *Table 4*, or in modification of the resistance due to the effect of grafting on the growth rate of the ramet. A small experiment was therefore set up in an highly infected plantation near Kimakia forest station in which scion material was interchanged between a resistant tree and a susceptible tree. This was repeated on seven pairs of trees, together with control grafts made between different branches of the same tree. Three pairs of trees were discarded due to the high failure rate of the grafting (50%). Results from the remaining 4 pairs of trees, with a failure rate of 9%, are summarized in *Table 7* together with calculated values for the three missing grafts. An analysis of variance of the data shows that the differences between treatments are highly significant (0.1% level) for disease score and length of healthy leader, but not for height increment. Using the calculated values for least significant difference at the 5% level the treatments can be split into 2 groups; those on resistant stocks and those on susceptible stocks. Differences between scions are not significant for any of the characters measured. The root-stock is therefore seen to play a very important part in the determination of disease expression of the scion, although this may have been exaggerated in this particular experiment by the inequality of size between the root-stock and the scion.

(4) Assessments of seedling progeny

In 1964 the wind pollinated progeny of several plus trees, unselected for disease resistance, were planted in a trial at E.A.A.F.R.O. estate. The 16 tree plots were replicated in

Table 7. — The effect of needle blight on scion material interchanged between resistant and susceptible *Pinus radiata* trees.

Stock type	Scion type	Number of replications	Mean disease score	Mean length of healthy leader (in.)	Mean height increment (in.) 18/11/66—28/2/68
R	R	8	1.63	20.38	31.44
R	S	7(+1)	2.08	13.33	24.94
R	Ungrafted	8	1.50	28.88	—
S	R	7(+1)	4.45	4.80	10.31
S	S	7(+1)	5.25	2.41	6.69
S	Ungrafted	8	5.50	2.38	—
Least significant difference (5%)			1.23	11.14	13.27

4 randomized blocks and planted at 8 feet × 8 feet espacement. The control plots were later established among trees in the surrounding guard rows in the form of 2 half plots at either end of each block. After 4 years it was noticed that certain plots were much healthier than their neighbours and the plots were therefore measured for disease score, (using the same technique as with the ramets) height and stem diameter. The results from these assessments are presented in *Table 8*. Analyses of variance show that the differences between clones are highly significant (0.1% level) for disease score, height and stem diameter, whereas the differences between blocks are significant at lower levels only, for height (1% level) and stem diameter (5% level), and insignificant for disease score.

In all 3 characters clone R11 is significantly better (5% level) than the control and all the other clones. Block 1 also differs significantly (5% level) from the other 3 blocks in height and stem diameter probably due to the effect of the sloping site on soil or climate. From the data in *Table 8* estimates of narrow-sense heritability have been calculated for all three characters. These are very high, being 0.952, 0.964 and 0.950 for disease score, height and stem diameter respectively.

This trial has also been assessed for the other characters used as breeding criteria by Dyson and Paterson (1966). These show that the increased level of disease resistance of clone R11 is likely to result in an improvement of tree form and timber quality. Further details will be given in later publications.

Table 8. — The effect of needle blight on 4 year old open pollinated progeny of 6 plus trees.

Clone	Disease Score I	II	III	IV	Mean	Height (ft.) I	II	III	IV	Mean	Stem Diameter (in.) I	II	III	IV	Mean
Control	4.7	4.6	5.2	4.5	4.74	17.3	19.4	18.5	21.0	19.1	2.6	2.9	3.0	3.3	2.95
R3	5.4	5.5	5.6	5.1	5.40	16.4	16.8	19.2	19.3	17.9	2.8	2.8	3.0	3.3	2.98
R5	6.1	5.1	5.6	5.6	5.60	15.4	20.4	20.2	18.5	18.6	2.2	3.4	2.9	3.0	2.88
R6	4.5	5.4	5.3	5.5	5.17	17.7	19.3	19.4	19.1	18.9	3.0	3.5	3.2	3.2	3.23
R7	5.3	4.5	5.4	5.0	5.05	15.3	19.6	19.6	20.1	18.7	2.4	3.2	2.9	2.8	2.83
R9	4.8	5.1	5.3	4.8	5.00	16.7	18.8	18.8	20.8	18.8	3.0	3.3	3.3	3.5	3.28
R11	3.4	3.8	3.6	4.3	3.78	22.6	23.8	23.9	24.4	23.6	3.9	3.6	4.2	4.2	3.98
Block mean	4.89	4.86	5.14	4.97	—	17.3	19.7	19.9	20.5	—	2.84	3.24	3.21	3.33	—
L.S.D. (5%)	0.40				0.54	1.1				1.5	0.28				0.36
Heritability (h^2)	0.952					0.964					0.950				

$$h^2 = \frac{2\sigma_f^2}{2\sigma_f^2 + \sigma_e^2} \qquad \sigma_f^2 = \frac{\text{M.S. clones — M.S. error}}{\text{No. of blocks}} \qquad \sigma_e^2 = \frac{\text{M.S. error}}{\text{No. of blocks}}$$

Discussion

The results obtained so far indicate that *P. radiata* trees, selected in the field for their apparent resistance to *Dothistroma* needle blight, are inherently resistant to the disease and not merely escapes due to site or climatic differences. This is shown by the comparative performance of scion material from selected and unselected trees in a randomized block trial at Uplands forest station. The level of resistance shown by scion material from selected resistant parents is rather low, although this is possibly to be expected under the severe disease conditions encountered at Uplands forest station. Since the last assessment date reported in this paper the health of the ramets has deteriorated considerably due to a very prolonged rainy season. However, in about 18 months, when the ramets are 4 years old all the surviving trees should begin to improve due to increasing resistance associated with increasing age (Ivory, 1968). It should then be possible to make more accurate comment on the effectiveness of the level of resistance.

A later experiment shows that the root-stock plays a very important part in the determination of the disease expression of the scion. Therefore it is probable that the level of resistance of the scion material has been considerably lowered by the use of root-stocks which are very disease susceptible. When this is taken into account the field performance of ramets is most promising, especially as the factors considered have fairly high gross heritability estimates. Unfortunately it has not been possible to eliminate this interaction between root-stock and scion as we have not been able to strike cuttings of *P. radiata* in Kenya.

The present series of trials also indicates that blight resistance can be transmitted, via open-pollinated seed, to seedling progeny, although in this case the parent trees had not been selected for resistance. The level of resistance obtained was reasonably high although the disease hazard level at Muguga is fairly low (Ivory, 1968). This also adds more weight to the theory that a non-resistant root-stock dilutes scion resistance because scion material from the same tree showed little evidence of blight resistance in an earlier trial at Kimakia *(Table 3).*

We can therefore conclude, firstly, that it is possible to select *P. radiata* with inherent blight resistance on the basis of the appearance of the phenotype; secondly, that we can test the selected trees by field-testing scion material, even though the effects are likely to be partially reduced by the use of non-resistant root-stock material; and thirdly, that the seedling progeny of selected trees will inherit a considerable proportion of the disease resistance of the parent, especially if the high heritability estimates are maintained. These estimates will probably decrease as the trees become older. However this will not be very serious as increased disease resistance is likely to be required for the first 6—10 years only. The wood quality studies also show that this selection for blight resistance will not lead to any deterioration of wood quality, but may in fact bring about considerable improvement. Future proposals for breeding *P. radiata* in East Africa should therefore include blight resistance as a major criterion for selection, but not to the exclusion or detriment of the other major criteria described by Dyson and Paterson (1966).

The study of ring width measurements of the parent trees also sheds some light on the relationship between vigour and resistance. It shows that the resistant trees were more vigorous than the random non-resistant trees even before the trees were affected by needle blight. This is supported by the fact that one exceptionally robust plus tree has given rise to blight resistant progeny even though it was not selected for blight resistance. Conversely, the performance of the progeny from 5 other plus trees included in the same trial, and the performance of scion material of plus trees used as controls in the preliminary trials, showed that not all vigorous trees are blight resistant. We can therefore conclude that blight resistant trees are generally more vigorous than random trees, but that vigorous trees are not usually any more blight resistant than random trees. A three way comparison is being made using scion material in an experiment in progress at Timboroa forest station.

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Summary

Results of preliminary trials and interim observations of more recent experiments show that it is possible to select *P. radiata* with inherent blight resistance on the basis of the appearance of the phenotype. Scion material from these select trees was also found to possess a greater degree of blight resistance than similar scion material from unselected trees, but the expression of this resistance was found to be influenced by the disease reaction of the root-stock used. Evidence is also presented which indicates that blight resistance is transmissible to seedling progeny and that its heritability is high.

A relationship between vigour and blight resistance is demonstrated, such that blight resistant trees are more vigorous than their random neighbours. However only one of six plus trees selected for vigour was found to possess enhanced blight resistance.

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