determined. Larch conelets should be pollinated as soon as possible after they have curved upwards at a 90° angle in respect to the short snoot axis. An increase of seed yield (up to 50 percent in the mid-portion of the seed cone has been observed after artificial pollination during the days defined as "receptive" (SAID, unpublished data). Nevertheless, this method requires daily monitoring of the trees. Moreover, repeated pollination is necessary because the stage of female cone development is variable between clones and even between ramets of the same clones

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# Variation in Susceptibility to Dothistroma Needle Blight among Provenances of Pinus radiata var. radiata

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## Summary

Considerable variation in susceptibility to *Dothistroma* needle blight was found among provenances of *Pinus radiata* var. *radiata*. Cambria was the most susceptible. Monterey and Ano Nuevo were very similar; both were

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significantly more resistant than Cambria, but Monterey appeared to be the slightly less susceptible of the two. There was statistically significant variation between subpopulations within these populations but the magnitude of this variation was much smaller than between populations. The ranking of the provenances was stable from ages three to nine years and across two contrasting experimental sites. A representative seedlot from an Australian seed-orchard was much less susceptible than any of the natural populations although the Australian population is probably derived from Monterey and Ano Nuevo and had not been selected for resistance to Dothistroma septospora.

Key words: Pinus radiata provenances, Dothistroma needle blight, disease susceptibility.

#### Introduction

Needle blight caused by Dothistroma septospora (Dorog.) Morelet var. septospora (= D. pini Hulbary) is a severe problem in plantations of Pinus radiata D. Don in parts of south-eastern Australia. The pathogen was first recorded in Australia in 1975 (EDWARDS and WALKER, 1978) and subsequently it has spread throughout the tablelands of New South Wales and north-eastern Victoria where P. radiata is grown commercially. D. septospora is dispersed by splash-distributed conidia. Warm temperatures combined with prolonged periods of high humidity or the existence of free water films on needle surfaces have been observed to favour serious disease outbreaks (Hocking and Etheridge, 1967; Gadgil, 1977; Gibson, 1979). Plantations at high altitude on the eastern edge of the northern tablelands of New South Wales are at a particularly high risk from Dothistroma needle blight because of the plentiful summer rainfall and the frequent occurrence of mist. Additionally many of these plantations are situated on soils low or deficient in boron or sulphur (LAMBERT and TURNER, 1977). These deficiencies, which are common in plantations growing on soils derived from basalt, have been associated with increased susceptibility to D. septospora (Eldridge et al., 1981). In other parts of its current range there is typically severe summer drought and outbreaks of needle blight are usually confined to protected gullies or valley bottoms (MARKS and HEPWORTH, 1986). More extensive disease outbreaks occur only in those years when there is unusually high summer rainfall.

D. septospora seldom directly kills trees. Its main economic effect is to reduce increment with the loss being proportional to the percentage of needles infected. In New Zealand stands with infection levels of less than forty percent, a loss of one percent of volume increment was observed for each percentage increase in the proportion of needles infected (van der Pas, 1981). In stands in northeastern New South Wales, where the severity of defoliation often exceeds 50% of the green crown, a loss of 0.9% of basal area increment for each percentage increase in needles infected has been observed (R. H. Eldridge and J. A. Simpson, unpubl. data). The disease may be controlled in plantations by aerial spraying with copper-based fungicides. This approach has been very successful in New Zealand where a single application can reduce disease severity for several years (Gilmour et al., 1973). However, in more severely infected stands in New South Wales annual spraying is necessary to achieve a similar degree of control.

A second approach is to use more resistant planting stock, either as an alternative to chemical control or complementing it in an integrated control programme. Ge-

netic variation in susceptibility within the cultivated populations of P. radiata has been reported by researchers in East Africa (Ivory and Paterson, 1970), California (LIBBY, Bannister and Linhart, 1968), New Zealand (Wilcox, 1982) and Australia (Ades and Simpson, 1990). Variation in susceptibility also exists between the natural populations of the species (Cobb and Libby, 1968; Burdon and Bannister, 1973). Pinus radiata var. radiata occurs at three separate localities on the central coast of mainland California: Cambria, Monterey and near Ano Nuevo Point. Two further varieties occur on Cedros Island and Guadalupe Island off the coast of Mexico (MILLAR, 1986). Despite this small natural range, considerable variation between the varieties and populations in silvicultural characteristics has been demonstrated in trials in California (Guinon et al., 1982), Australia (Fielding, 1961) and New Zealand (Burdon and Bannister, 1973; Shelbourne et al., 1979). There are also significant differences between provenances in bark and wood characteristics (Nicholls and Eldrige, 1980), frost resistance (Hood and Libby, 1980) and tolerance of low soil boron levels (Burdon and Bannister, 1973). Provenances have been shown to differ in their susceptibility to D. septospora in New Zealand (Burdon and Bannister, 1973) and California (Совв and Libby, 1968) but no similar comparison has been reported in Australia.

This paper reports the relative susceptibilities to *D*. septospora of provenances of *P. radiata var. radiata* in two trials in north-eastern New South Wales, the consistency of these differences between the two sites and between ages three and nine years.

# Methods

A series of *P. radiata* provenance trials was planted in New South Wales in 1979. Two of these trials subsequently became significantly infected by *Dothistroma* needle blight. They are located in Nundle State Forest (latitude 31°25'S, longitude 151°15'E), and Riamukka State Forest (latitude 31°22'S, longitude 151°40'E). The trials are situated 43 km apart, both on the southern edge of the New England Tableland. The Riamukka trial is situated at 1300 m altitude on soil derived from Tertiary basalt while the trial at Nundle is at 1200 m on a soil derived from shale and sandstone.

Each trial contains seedlots from the three mainland Californian populations of *P. radiata* as well as a representative local seed orchard seedlot. The three populations, Ano Nuevo, Monterey and Cambria were divided on a geographic and ecological basis into a total of 13 subpopulations (Eldridge, 1978a, b). Details of these 13 seedlots are given in *Table 1*.

Both trials are randomised complete block designs with 14 treatments, ten replicates and five-tree row plots. All seedlings were planted as one year old stock. They were raised at the CSIRO Division of Forestry and Forest Products nursery in Canberra.

Percentage infection was estimated visually by the method of Kershaw et al. (1982). This percentage score is the aggregate of the needles infected but remaining on the tree and those infected needles which had already been cast. Assessments were carried out at Riamukka at ages three years and eight years and at Nundle at age nine years after planting. Two observers scoring from opposite sides of each tree carried out the assessment of the Nundle trial and the age three assessment at Riamukka at ages and at Nundle trial and the age three assessment at Riamukka at ages and at Nundle trial and the age three assessment at Riamukka at ages and at Nundle trial and the age three assessment at Riamukka at ages and at Nundle at ages at a Nundle at ages at

Table 1. — Provenance collection details (information from ELDRIGE, 1978b).

Sub- population	Population	Altitude of stand (m)	Number of seed trees	Geomorphology	Soil Parent Material	Vegetation
01/1	Ano Nuevo	15-60	70	Rocky coast	Pliocene marine sediments: mud- stones, shales and sandstones	P. radiata
01/2	Ano Nuevo	120-330	40	First ridge inland from sea	As above	P. radiata with P. attenuata and Douglas fir
01/3	Ano Nuevo	60-245	40	Furthest inland and furthest south of Ano Nuevo stands	As above	P. radiata and P. attenuata
01/4	Ano Nuevo	60-215	29	Hillsides and marine terraces	As above	<i>P. radiata</i> on pasture
02/1	Monterey	5-60	54	Sand dunes close to sea	White Recent sand	P. radiata with Quercus
02/2	Monterey	25-60	38	Low sand dunes on north-eastern slopes of Monterey Peninsula	Recent sands and other sediments	As above
02/3	Monterey	60-215	36	Central Monterey	Leached shallow podsol on decomposed Santa Lucia granodiorite	As above but bordering small areas of Cupressu and P. muricata
02/4	Monterey	60-305	59	Ridges	As above	P. radiata
02/5	Monterey	15-60	22	Coastal rocky outcrops	Outcrops of Santa Lucia granodiorite Paleocene conglomerates and sandy shales	P. radiata with Cupressus adjacen
02/6	Monterey	85-580	31	Sides of steep ridges	Santa Lucia granodiorite	P. radiata with some redwood and Douglas fir.
03/1	Cambria	30-120	25	Gently sloping raised marine terraces.	Cretaceous sandstones	P. radiata
03/2	Cambria	30-120	50	As above plus some flat poorly drained areas	Highly podsolised soils on Cretaceous sandstones, cherts, slates and limestones	As above
03/3	Cambria	60-185	25	Well drained slopes and steep rocky outcrops	As above	P. radiata with Quercus

mukka. The age eight assessment at Riamukka was done by a single observer. Plot mean defoliation scores were calculated and then analysed by analysis of variance without transformation of data.

# Results

The provenance means are listed in *Table 2* and the analyses of variance and estimated population and subpopulation variance components for the three individual sites or assessment ages are shown in *Table 3*. All populations differed significantly. Cambria was always the most severely infected population and the seed orchard the least. The means of Monterey and Ano Nuevo were very similar and differed significantly from each other only at Riamukka where, at age eight, Monterey was the less

infected. Only at Nundle do subpopulations within populations vary significantly, with the greatest differentiation occurring within the Monterey population but significant differentiation is also present in the Cambria population.

Analyses of variance for the two possible comparisons between the sites on different soil parent materials are shown in *Table 4*. Neither population nor subpopulation by site interactions were significant in either analysis. The population term was significant in both analyses but subpopulation variation is significant only in the Nundle-Riamukka age three comparison. Each trial contained a sample of only 50 trees per subpopulation, which may have been insufficient for good estimation of the means. The differences between the pooled subpopulation means

Table 2. — Mean percentage infection at each of the three measurements.

Provenance		Defolia	tion (%)	
	Nundle 9 years	Riamukka 3 years	Riamukka 8 years	Mean
01/1	46.9	21.0	73.6	48.1
01/2	44.0	22.3	75.4	47.2
01/3	47.0	30.1	80.0	52.4
01/4	46.2	28.1	76.4	50.2
Ano Nuevo mean	46.0	25.4	76.4	49.3
02/1	49.1	24.1	65.5	46.2
02/2	51.5	32.9	77.5	54.0
02/3	41.6	22.7	70.9	45.1
02/4	52.7	28.1	71.7	50.8
02/5	42.8	24.8	73.5	47.0
02/6	42.5	24.7	73.4	46.9
Monterey mean	46.7	26.2	72.0	48.3
03/1	62.4	41.6	84.3	62.8
03/2	54.0	39.1	76.1	56.4
03/3	61.8	41.8	84.2	62.6
Cambria mean	59.4	40.8	81.7	60.6
Tallaganda seed				
orchard	32.2	15.8	59.7	35.9
LSD (P=0.05)				
Between sub- population means	7.9	7.5	9.0	
Site mean	48.2	28.4	74.4	

for Nundle and Riamukka age three were examined. The Least Significant Difference (Prob = 0.05), using the residual from the ANOVA in  $Table\ 4$  as error, is 5.1 %. There was significant variation between subpopulations in all three populations. In the Cambria population, subpopulation 03/2 was significantly less defoliated than both 03/1 and 03/3. In the Monterey population, 02/2 and 02/4 were the most severely infected, 02/3, 02/6 and 02/5 were were least infected and 02/1 was intermediate. Subpopulation 02/2 was significantly more infected than all the subpopulations except 02/4 which was significantly more infected than all the other subpopulations except 02/1. In the Ano Nuevo population 01/2 was significantly less infected than 01/3 and no other differences are significant.

An analysis of variance for the two assessment ages at Riamukka is shown in *Table 5*. The population by age interaction is statistically significant but small and does not obscure the differences between the populations.

## Discussion

The rankings of populations and subpopulations are very consistent for all ages and for both sites, despite there being large differences in overall disease severity, particularly between the two assessment ages at Riamukka. In *Figure 1* the subpopulation means at Nundle are plotted against the means at age three at Riamukka.

This is the comparison across the widest age differential but site and age are confounded. The close correspondence of the means suggest that there is really no interaction with age. The apparent population by age interaction at Riamukka may be an artifact of the two different assessment techniques and a scaling effect due to the higher disease severity at age eight. The age eight assessment was carried out by a single observer while the others were done by two observers scoring from opposite sides of each tree. Disease severity often differs considerably around the crowns of larger trees and they must be viewed from more than one aspect to obtain a reliable overall assessment of percentage infection. The much greater precision obtained by two observers is reflected by the smaller residual mean squares in Table 3 for the Nundle and Riamukka age three analyses. This is also shown by the values of the multiple correlation coefficients for the same analyses. The square of the multiple correlation coefficient (R2) is the proportion of the total variance accounted for by the analysis of variance model. In these analyses the  $R^2$  values are 0.57 and 0.55 for Nundle and Riamukka age three but only 0.44 for Riamukka age eight which was scored by a single observer.

Disease severity in the Riamukka trial increased from an average of 28% at three years to 74% at eight years while at Nundle there was insufficient infection at age three for an assessment to be carried out but at age nine the average severity was 48% (*Table 2*). This is typical

Table 3. — Analyses of variance for individual sites and ages of assessment.

Source of variation		Nur Age 5	Nundle Age 9 years			Ric	Riamukka Age 3 years			Riż Age 8	Riamukka Age 8 years	
	岩	Mean square	Eu,	Prob	岩	Mean square	re F	Prob	븀	Mean square	ie F	Prob
Replications	6	425.3	5.29	0.000	თ	250.7	3.49	0.001	6	409.1	4.01	0.00
Populations Subpopulations within populations	£ 01	2212.2 173.4	27.52 2.16	0.000	. 10	2290.8 132.3	31.90 1.84	0.000	10	1366.2 139.4	13.37	0.000
Interpopulation contrasts Ano Nuevo-Monterey	7	11.2	0.14	0.709	H	17.4	0.24	0.624	Ħ	439.1	4.30	0.040
Ano Nuevo-Cambria	П	3065.3	38.13	0.00	1	4105.7	57.13	0.00	-	444.9	4.36	0.039
Ano Nuevo-Seed Orchard	7	1524.2	18.96	0.00	-	727.9	10.13	0.002	-	2224.4	21.78	0.00
Monterey-Cambria	7	3219.5	40.05	0.00	7	4277.3	59.52	0.001	-	1727.0	16.91	0.00
Monterey-Seed Orchard	7	1799.0	22.38	0.00	-	925.4	12.88	0.001	-	1310.1	12.83	0.001
Cambria-Seed Orchard	-	5538.6	68.91	0.00	-	4692.9	65.3	0.000	₩	3538.0	34.64	0.00
Error	117	80.4			117	71.9			115	102.1		
Variance Components* (i) Populations (ii) Subpopulations		63.90	63.90 (42.63) 9.30 (8.73)			67.72 6.05	67.72 (59.23) 6.05 (5.71)			39.09	39.09 (18.24) 3.79 (3.79)	
24		0.57				0.55				0.44	=4	

\*) Values in brackets are the corresponding estimates from an identical analysis with the Tallaganda seed orchard population omitted.

†) Degrees of freedom reduced as one plot each of subpopulations 02/5 and 03/2 dead by age eight.

for *P. radiata* plantations in this area. Disease severity increases with age for at least the first four or five years then remains at high levels, although there are large fluctuations from year to year, due mainly to variation in the amount of rainfall during the infection period (J. A. Simpson and R. J. Bulley, unpubl. data). This is in contrast to the pattern of disease in *P. radiata* reported elsewhere, where the onset of mature resistance at about age 10

causes the disease severity to fall and may reduce it to insignificant levels by about age 16 (Gibson, 1972). The environment is so favorable for disease development that, in parts of the Nundle plantation, trees up to 66 years old are still heavily infected ( J. A. Simpson and P. K. Ades, unpubl. data).

The consistency of the provenance rankings over the study period during which disease greatly intensified,

	Nun	dle age 9 - Ri	amukka	age 3	Nun	dle age 9 - Ri	amukka a	ge 8
Source	đf	Mean square	F	Prob	đf	Mean square	F	Prob
Sites	1	27463.1	84.96	0.00	1	47858.1	84.90	0.00
Replication within sites	18	338.0	4.44	0.00	18	417.4	4.58	0.00
Population	3	4468.3	20.61	0.00	3	3412.0	11.10	0.01
Subpopulation	10	242.8	3.87	0.02	10	205.4	1.91	0.16
Population x site	3	36.8	0.59	0.64	3	198.1	1.91	0.19
Subpopulation x site	10	62.8	0.83	0.60	10	107.4	1.18	0.31
Residual	234	76.1			232	91.2		

and across the two sites on different soil types is a very desirable result for resistance breeding. This suggests that reliable selection for resistance could be carried out in plantations as young as three years. Furthermore, resistance seems likely to be stable on the various soil types in the high disease-risk areas although the average disease severity on those sites may vary.

The estimated population variances in Table 3 are about ten times the variances of subpopulations within populations. However, there still appear to be significant differences between subpopulations within populations, despite the very limited geographic areas over which they occur. There have been several studies of the genetic structure of the natural populations. Plessas and Strauss (1986) found that 3.5% of the diversity in allozymes was between the three mainland populations, 1.6% was between stands within populations and the remainder was within stands. Moran et al. (1988) similarly found that only 2% of allozyme diversity was between stands within populations. Their much higher estimate of 16.2% of the diversity being between populations is due mainly to the distinctive island varieties being included in the study. The study by Moran et al. (1988) is particularly relevant as the seed they used was from the same collections as the current study and their 'ecological stands' correspond to the current subpopulations. They concluded that Monterey was the most variable population, as measured by the proportion of polymorphic loci, but the greatest differentiation between stands, as measured by genetic distance, existed at Cambria. In the current study, the subpopulations in Monterey were the most variable in respect of susceptibility to Dothistroma needle blight. The range of subpopulation means for the Monterey population is 8.9% while the ranges for Ano Nuevo and Cambria are 5.2% and 6.4% respectively.

The relative resistance of the seed orchard progeny is is difficult to account for. This population originated from Monterey or Ano Nuevo, or as a mixture of both (Moran and Bell, 1987). It has undergone several generations of natural selection in southern Australia, where the rainfall occurs predominantly in the winter, and one generation of applied selection in the same region for growth rate, improved stem-form and for small diameter branching. All of this occurred before D. septospora became established. It is therefore most surprising that the seed orchard progeny are much less susceptible to Dothistroma needle blight than the Monterey and Ano Nuevo populations and are, in fact, completely out of the range of the subpopulations within these two populations. A similar

result was reported in New Zealand by Burdon and Bannister (1973). They found that the local population was less susceptible to *Dothistroma* needle blight than the populations from which it had been derived, predominantly Ano Nuevo in their case, even though there could have been no direct selection for resistance in New Zealand. Old et al. (1986) investigated the susceptibility to Western Gall Rust of the natural and the Australian and New Zealand populations of *P. radiata*. The pathogen, *Endocronartium harknessii* (Moore) Hiratsuka, is absent from Australia and New Zealand. The cultivated populations are intermediate in susceptibility between Monterey and Ano Nuevo, exactly as would have been expected, in contrast to the result for *D. septospora*.

The ranking of the natural populations in the current study does differ slightly from the results of Burdon and Bannister (1973) who concluded that Monterey was slightly more susceptible than Ano Nuevo. These two populations were almost equally infected at Nundle and at age three at Riamukka, but Ano Nuevo was more severely infected than Monterey at Riamukka at age eight when the overall disease severity was much greater. Monterey is the most variable population and the different and somewhat smaller sample of trees in the earlier provenance collections used by Burdon and Bannister may have caused the different results. Alternatively the pathogen itself may vary between Australia and New Zealand. Three varieties of D. septospora have been described (Ivory, 1967) two of which have an almost world-wide distribution, including Australia and New Zealand (Sutton, 1980). Most Australian isolates correspond to D. septospora var. septospora (EDWARDS and WALKER, 1978), but Evans (1984) after examining numerous collections from Central America and elsewhere has rejected the varietal concept in D. septospora. It would be most interesting to establish trials in Australia and New Zealand to compare the relative susceptibilities to Dothistroma needle blight of seedlots selected for resistance in each country. There may be differences in the pathogen due to different founder populations and, given the possible different origins of the P. radiata land-races in each country, there may also have been selection for different pathogenic races of D. septospora.

D. septospora is believed to be indigenous to Central America and western North America (Evans, 1984). Despite this, it has never been reported from natural stands of P. radiata (Old, 1979). P. radiata can, however, be severely infected by D. septospora when it is planted on other sites in California (Совв and Libby, 1968; Libby

Table 5. — Analysis of variance for two assessment ages at Riamukka 3 and 8 years.

Expected mean square

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Mean square

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Source of variation

Age         1 119652.1           Replicates         9 442.9           Populations         3 3361.9         7.74         0.02           Age x Replicates         9 188.0         188.0           Replicates x populations         27 102.2         42.9         0.03           Age x replicates x populations         3 274.9         6.42         0.03           Age x replicates x populations         10 219.2         2.17         0.05           Age x Subpopulations         10 38.9         0.68         0.74           Replicates x subpopulations         90 119.4         119.4           Residual         57.3         57.3	Age         1 119652.1           Replicates         9 442.9           Populations         3 361.9         7.74         0.02           Age x Peplicates x populations         27 102.2         102.2         Age x populations         3 274.9         6.42         0.03           Age x replicates x populations         10 219.2         2.17         0.05           Age x Subpopulations         10 38.9         0.68         0.74           Replicates x subpopulations         90 119.4         119.4           Residual         8         57.3	OL:						
Replicates         9         442.9           Populations         3         361.9         7.74         0.02           Age x Replicate         9         188.0         102.2         102.2         Age x populations         3         274.9         6.42         0.03           Age x replicates x populations         10         219.2         2.17         0.05           Age x Subpopulations         10         219.2         2.17         0.05           Age x Subpopulations         10         38.9         0.68         0.74           Replicates x subpopulations         90         119.4         119.4           Residual         57.3         57.3	Replicates         9         442.9           Populations         3         361.9         7.74         0.02           Age x Replicates x populations         27         102.2         6.42         0.03           Age x replicates x population         3         274.9         6.42         0.03           Age x replicates x populations         10         219.2         2.17         0.05           Age x Subpopulations         10         38.9         0.68         0.74           Replicates x subpopulations         90         119.4         Residual         57.3	n	Age	-	119652.1			02 + 2.9408ARP + 29.408AP + 11.408AR + 9.8208AS + 114.008A
Populations         3         361.9         7.74         0.02           Age x Replicates         9         188.0         188.0           Replicates x populations         27         102.2         6.42         0.03           Age x replicates x populations         10         219.2         2.17         0.05           Age x Subpopulations         10         219.2         2.17         0.05           Age x Subpopulations         10         38.9         0.68         0.74           Replicates x subpopulations         90         119.4         119.4           Residual         57.3         57.3         119.4	Populations         3         3461.9         7.74         0.02           Age x Replicates         9         188.0         188.0           Replicates x populations         27         102.2         6.42         0.03           Age x replicates x population         3         274.9         6.42         0.03           Age x replicates x populations         10         219.2         2.17         0.05           Age x Subpopulations         10         38.9         0.68         0.74           Replicates x subpopulations         90         119.4         Residual         57.3	19	Replicates	0	442.9			of + 2.810° ARP + 5.620° RP + 11.00° AR + 1.970° RS + 22.00° R
Age x Replicate         9         188.0           Replicates x populations         27         102.2           Age x populations         3         274.9         6.42         0.03           Age x replicates x populations         10         219.2         2.17         0.05           Age x Subpopulations         10         38.9         0.68         0.74           Replicates x subpopulations         90         119.4         Residual	Age x Replicate         9         188.0           Replicates x populations         27         102.2           Age x populations         3         274.9         6.42         0.03           Age x replicates x populations         10         219.2         2.17         0.05           Age x Subpopulations         10         219.2         2.17         0.05           Age x Subpopulations         90         119.4         Residual         8         57.3	79)	Populations	٣	3361.9	7.74	0.02	of + 3.120° ARP + 1.960° RS + 9.820° AS + 31.20° AP + 6.250° RP + 19.60° S + 0° P
Replicates x populations         27         102.2           Age x populations         3         274.9         6.42         0.03           Age x replicates x population         10         219.2         2.17         0.05           Age x Subcopulations         10         219.2         2.17         0.05           Age x Subcopulations         10         38.9         0.68         0.74           Replicates x subcopulations         90         119.4           Residual         57.3	Replicates x populations         27         102.2           Age x populations         3         274.9         6.42         0.03           Age x replicates x population         27         61.2         0.05           Subpopulations         10         219.2         2.17         0.05           Age x Subpopulations         10         38.9         0.68         0.74           Replicates x subpopulations         90         119.4           Residual         88         57.3	٠ +	Age x Replicate	6	188.0			or + 2.260° arp + 9.040° ap
Age x populations         3         274.9         6.42         0.03           Age x replicates x population         27         61.2         61.2           Subpopulations         10         219.2         2.17         0.05           Age x Subpopulations         10         38.9         0.68         0.74           Replicates x subpopulations         90         119.4           Residual         88         57.3	Age x populations         3         274.9         6.42         0.03           Age x replicates x population 27         61.2         61.2         0.05           Subpopulations         10         219.2         2.17         0.05           Age x Subpopulations         10         38.9         0.68         0.74           Replicates x subpopulations         90         119.4           Residual         88         57.3	his	Replicates x populations	23	102.2			OR + 3.140°ARP + 1.970°RS + 6.270°RP
Age x replicates x population 27       61.2         Subpopulations       10       219.2       2.17       0.05         Age x Subpopulations       10       38.9       0.68       0.74         Replicates x subpopulations       90       119.4         Residual       88       57.3	Age x replicates x population 27       61.2         Subpopulations       10       219.2       2.17       0.05         Age x Subpopulations       10       38.9       0.68       0.74         Replicates x subpopulations       90       119.4         Residual       88       57.3	. T	Age x populations	m	274.9	6.42	0.03	OR + 3.120°ARP + 9.820°AS + 31.20°AP
Subpopulations         10         219.2         2.17         0.05           Age x Subpopulations         10         38.9         0.68         0.74           Replicates x subpopulations         90         119.4           Residual         88         57.3	Subpopulations         10         219.2         2.17         0.05           Age x Subpopulations         10         38.9         0.68         0.74           Replicates x subpopulations         90         119.4           Residual         88         57.3	wit	Age x replicates x population	21	61.2			O2 + 3.14O2ARP
Age x Subpopulations 10 38.9 0.68 0.74 Replicates x subpopulations 90 119.4 Residual 88 57.3	Age x Subpopulations 10 38.9 0.68 0.74 Replicates x subpopulations 90 119.4 Residual 88 57.3	h	Subpopulations	ដ	219.2	2.17	0.05	of + 1.960° Rs + 9.800° As + 19.60° s
Replicates x subpopulations 90 119.4 Residual 88 57.3	Replicates x subpopulations 90 119.4 Residual 88 57.3	sus	Age x Subpopulations	9	38.9	0.68	0.74	of + 9.80c² As
Residual 88	Residual 88	sce		8	119.4			of + 1.980°Rs
	bî	pti <sup>°</sup>	Residual	88	57.3			<b>%</b>

\*) Pseudo F tests carried out by the method of Satterthwaite (1946)

et al., 1968; Old, 1979); this, with susceptibility to cold, may be one of the key factors limiting its natural distribution. In cooler, higher-rainfall sites on the coast of northern California, more favorable for the disease, *P. radiata* is replaced by varieties of *P. muricata* much more resistant to *D. septospora* (Ades and Simpson, unpubl. data). *P. attenuata*, the other species of subsection *Oocarpae* in California, is extremely susceptible to *D. septospora* (Kershaw et al., 1982) but is found mainly outside the coastal fog belt. The susceptibility of the three populations of *P. radiata* does not coincide with present-day

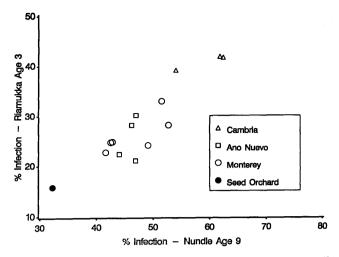


Figure 1. — Disease severity (i. e. percentage of needles currently infected by D. septospora or already cast as a consequence of earlier infection) at Riamukka at age three years plotted against disease severity at Nundle at age nine years.

annual rainfall; Ano Nuevo has the highest rainfall but is not the most resistant while Monterey and Cambria with similar annual rainfall are the most and least resistant populations. As *D. septospora* appears to be absent from the native stands there can currently be no natural selection for resistance, although this may have occurred during more mesic periods in the past (Axelrod, 1980).

The presence of statistically significant differences between subpopulations shows that genetic differentiation exists on a geographic or ecological basis within these populations. The precise ranking of the subpopulations is probably not important as the division of populations into subpopulations for seed collection was necessarily somewhat arbitrary. Although they were separated geographically and each constitutes a fairly continuous stand, not all of them coincide well with important ecological factors (Eldridge, 1978b).

The phylogenetic relationships of the three Californian populations are uncertain. Plessas and Strauss (1986) concluded that Monterey and Cambria were more closely related to each other than either was to Ano Nuevo. However, Moran et al. (1988), also using allozyme analysis concluded that Ano Nuevo and Monterey were closer. The most recent study (Millar et al., 1988) is equivocal as two different clustering procedures produced contradictory results. Studies of other characters have not clarified the situation. Murphy (1981) examined antigenic differences between seed proteins and found that he could not draw any conclusions on the relationships between the three mainland populations. The results of the current study support the conclusion of Moran et al. (1988). They do, however, contrast with the ranking of the populations for susceptibility to Western Gall Rust. Old et al. (1986) concluded that Ano Nuevo was the most susceptible population. Cambria the least and Monterey was intermediate but more similar to Cambria. Regardless of the phylogenetic relationship of the natural populations of P. radiata var. radiata our study has demonstrated that there are differences between them in susceptibility to Dothistroma needle blight and these differences are stable between contrasting sites and between three and nine years after planting. There also appears to be variation in susceptibility between subpopulations within these populations.

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# Spatial Genetic Structure Within Two Natural Stands of Black Spruce (Picea mariana (Mill.) B.S.P.)

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# Abstract

Needle tissue from approximately 500 adjacent trees in each of two lowland black spruce stands was electrophoretically analysed to resolve 5 and 8 loci respectively. All trees were mapped and clonal groups were identified on the basis on field evidence, identity of multilocus genotypes ,and map distances. Revised maps of all seed-origin trees were constructed to portray genotypes for

each locus and examined visually for evidence of spatial genetic patterning. Genotype data matrices were statistically analysed for spatial autocorrelation by calculating Moran's I. The visual and statistical approaches yielded similar results indicating an overall distribution of genotypes that is nearly random with a few loci indicating a patchy substructure. Evidence for low levels of inbreeding in black spruce may be related to this spatial