VARIATION AMONG EUCALYPT SPECIES IN EARLY SUSCEPTIBILITY TO THE LEAF SPOT FUNGI *PHAEOPHLEOSPORA EUCALYPTI* AND *MYCOSPHAERELLA* SPP.

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ABSTRACT

Premature defoliation is common in young plantations of *Eucalyptus nitens* (Deane & Maiden) Maiden in parts of New Zealand where stands are infected by the leaf spot fungus *Phaeophleospora eucalypti* (Cooke & Massee) F.A.Crous *et al.*, often accompanied by infection by species of *Mycosphaerella* Johanson. Four young eucalypt species and provenance trials aged between 1 and 3 years were evaluated for infection and juvenile leaf retention, to help identify alternative species or provenances that might be a suitable substitute for new plantings on disease-prone sites. Families and provenances of *E. nitens* from locations in New South Wales were less infected by both fungi, and had better foliage retention, than those originating from Victoria. Variation was not apparent between provenances within each State, but there were significant differences between families within provenances. Although common on *E. nitens*, infection by *P. eucalypti* was found only at a very low incidence, or not at all, on other species tested from Section *Maidenaria*. However, infection by *Mycosphaerella* species and premature defoliation were both heavy on subspecies of *E. globulus* Labill., particularly subspecies *globulus*, subspecies *pseudoglobulus* (Naudin ex Maiden) Kirkpatr., and subspecies *bicostata* (Maiden *et al.*) Kirkpatr. Infection and defoliation by *Mycosphaerella* species were moderate on *E. nitens*, comparatively low on *E. globulus* ssp. *maidenii* (F.Muell.) Kirkpatr., and very low on two seedlots of *E. benthamii* Maiden & Cambage. There was significant variation between provenances within several *E. globulus* subspecies in infection by *Mycosphaerella* species and in foliage retention. Infection by *Mycosphaerella* species was inversely correlated with foliage retention for most eucalypt species and subspecies, as was that of *P. eucalypti* on *E. nitens*. Tolerance to frost injury, as measured by percentage shoot survival, was greatest in *E. nitens* and *E. globulus* ssp. *maidenii*, and least in *E. globulus* ssp. *globulus*. Final selections will depend on further evaluation of health, wood production, and pulping quality, as trees mature and produce only adult foliage later in the rotation. However, initial results based on health alone confirm that there is alternative material available for reducing disease levels in young pulpwood plantations.

Keywords: susceptibility; disease; infection; defoliation; provenance; family; *Phaeophleospora eucalypti*; *Kirramyces eucalypti*; *Septoria pulcherrima*; *Mycosphaerella cryptica*; *Mycosphaerella nubilosa*; *Eucalyptus nitens*; *Eucalyptus globulus*.

INTRODUCTION

Young plantations of *Eucalyptus nitens* in warmer parts of New Zealand frequently suffer from a disorder known as Septoria leaf blight. Juvenile foliage, especially, becomes disfigured on diseased trees and is shed prematurely after becoming infected by the leaf spot fungus *Phaeophleospora eucalypti* (synonyms: *Septoria pulcherrima* Gadgil & M. Dick, *Kirramyces eucalypti* (Cooke & Massee) J. Walker *et al.*). Diseased leaves are also often infected by species of *Mycosphaerella* (Dick 1982; Gadgil & Dick 1983; Hood *et al.* 2002). One option for managing this problem may be to plant seedlings that are genetically more resistant or tolerant to infection, while still retaining desirable growth and fibre qualities. Given the short rotation period anticipated for these eucalypt plantations, this may be a realistic procedure in areas where the disease is prevalent, if there is sufficient variation in susceptibility to the condition to allow selection. To test this, foliage health and degree of infection by both fungi were measured on trees from different provenances of a number of eucalypt species, using four trials established in the coastal Bay of Plenty district where the disease is common. Genetic variation has been demonstrated for resistance to *Mycosphaerella* species in a number of eucalypt species (Wilcox 1982; Lundquist & Purnell 1987; Carnegie *et al.* 1994, 1998; Dungey *et al.* 1997), but information is not available concerning *P. eucalypti*.

MATERIAL

The first trial was designed specifically to investigate variation in susceptibility to Septoria leaf blight within and between provenances of *E. nitens* from three regions in south-eastern Australia (central Victoria, and southern and northern New South Wales). The New South Wales material consisted of open-pollinated families originating from known locations near Ebor (Ebor provenance, 20 families) in the north of the State, and from Tallaganda provenance (seven families), Glenbog provenance (seven families), and Badja provenance (six families) in the south. The Victorian region was represented by 18 open-pollinated families from seed collected in a New Zealand provenance-progeny trial, with the seed parent of each family traceable to three provenance locations within central Victoria (Toorongo, 13 families; MacAlister, three families; Rubicon, two families).

The trial was established at two locations near Te Teko, Hogg Road (longitude, 176°43´E; latitude, 38°03´S; altitude, 40 m) and Omataroa (longitude, 176°51´E; latitude, 38°04´S; altitude, 150–200 m). Trees were planted in November 1997, at a stocking of 1050 stems/ha (3.4 × 2.8 m spacing), using a modified split plot design with seven replicate blocks at Hogg Road and eight at Omataroa. Each block consisted of three rectangular plots measuring 35 × 18 m, to which the three regions were assigned at random. Each 64-tree plot contained three single-tree sub-plots from each of 18–20 families belonging to the different provenances within the specified region. Sub-plots were fully randomised within each plot.

The second trial was designed to compare seven commercial seedlots of *Eucalyptus nitens*. It was also planted in November 1997, in association with the *E. nitens* provenance trial described above, at a spacing of 3.4 × 2.8 m (1050 stems/ha). This trial used a randomised complete block design incorporating seven 64-tree, 35 × 18-m plots (one for each seedlot), with six block replications at Hogg Road and eight at Omataroa. All seedlots were derived solely from parents of central Victorian origin, except for one (Huntsman seed orchard) which also had New South Wales parentage.

The third trial was designed to determine the growth, form, health, and wood property performance of a number of provenances from native populations throughout the natural ranges of four subspecies of *Eucalyptus globulus*, *E. globulus* ssp. *globulus*, *E. globulus* ssp. *bicostata*, *E. globulus* ssp. *pseudoglobulus*, and *E. globulus* ssp. *maidenii*, henceforth denoted by their subspecies epithets (following Jordan *et al.* 1993). *Eucalyptus nitens* was also included for purposes of comparison. The trial was established at four locations in the North Island, but only one was evaluated in this study, at a site near Kawerau (longitude, 176°42´E; latitude, 38°04´S; altitude, 60 m). Trees were planted in July 1999, at a stocking of 1114 stems/ha.

This trial used a modified split-plot design, incorporating eight replicate blocks each consisting of five plots composed of 49 fully-randomised single-tree sub-plots. To each plot was randomly assigned one of seven subspecies or subspecies combination sets. Each standard set was composed of seven trees from each of seven seedlots (or six trees from eight seedlots, Set 5), comprising provenances, progenies, or bulked provenance mixtures of each subspecies or species. Sets were constituted as follows (details in Appendix 2):

Set 1 subspecies *globulus* (seven provenances/provenance mixtures);
Set 2 subspecies *globulus* (five provenances/provenance mixtures) and subspecies *pseudoglobulus* (two provenances);
Set 3 subspecies *maidenii* (seven provenances);
Set 4 subspecies *bicostata* (seven provenances);
Set 5 subspecies *globulus* (five progenies) and *E. nitens* (three seedlots, two from Victoria and one from New South Wales).

The same seedlot combinations were assigned to each set in all block replications. Overall, subspecies *globulus* was represented by 17 seedlots, subspecies *pseudoglobulus* by two provenance seedlots, and subspecies *bicostata* and *maidenii* each by seven provenance seedlots. Of the 17 seedlots of subspecies *globulus*, 12 were of single provenances or bulked mixtures of two to seven provenances, and five were of open-pollinated single-tree progenies collected in a seed orchard.

The fourth trial (Ngati Awa Species Trial), situated on the edge of Ohiwa Harbour near Ohope (longitude, 177°03´E; latitude, 37°59´S; altitude, 20 m), was designed to evaluate a number of eucalypt species and subspecies, particularly those in Section *Maidenaria*. The trial compared 14 provenance seedlots of the following taxa: *E. benthamii* (two seedlots), *E. globulus* ssp. *globulus* (four seedlots), *E. globulus* ssp. *maidenii* (four seedlots), *E. nitens*, *E. fastigata* Deane & Maiden, *E. regnans* F. Muell., and *E. saligna* Smith (one seedlot each). The trial was planted in 1998 using a randomised complete block design, assigning each seedlot to one of 14 plots (of 42 trees each), replicated in each of three blocks.

METHODS

Sampling

Leaf retention, and infection by *P. eucalypti* and *Mycosphaerella* species were determined on a sample of trees in each trial by two observers, each person evaluating all attributes on every tree sampled within the same blocks at all sites. Retention and infection were measured at approximately the same age on all trees, except for an earlier evaluation of infection on the trees in the faster-growing Kawerau *E. globulus* provenance trial. Trees in the two *E. nitens* trials and the Ohiwa species trial were evaluated at age 2–2¼ years, while still predominantly with juvenile foliage, and the *E. globulus* provenance trial was evaluated between ages 1½ and 2¼ years.

In the *E. nitens* provenance trial, one (Omataroa) or two (Hogg Road) single-tree sub-plots from each family were pre-selected at random within each plot, making eight trees per family at Omataroa and 14 trees per family in total at Hogg Road. Similarly, four (Omataroa) or eight (Hogg Road) trees were randomly pre-selected in each plot in the *E. nitens* commercial seedlot trial, making 32 trees per seedlot at Omataroa and 48 trees per seedlot at Hogg Road. In this trial selections were not made in the outermost row which was treated as a buffer zone around the boundary of each plot. In the *E. globulus* provenance trial, two trees of each seedlot were pre-selected at random in each of eight blocks, making 16 trees per seedlot. In the Ohiwa trial eight trees were pre-selected in each plot in all three blocks (also avoiding the outermost row surrounding each plot), making 24 trees per seedlot. However, four trees only were chosen in each plot of *E. saligna*, *E. regnans*, and *E. fastigata*. In all trials a substitute tree was randomly chosen if the selected one was missing or damaged.

Crowns were divided into quadrants (north, south, east, and west), and one quadrant was randomly pre-selected on each tree. A prominent primary branch with juvenile foliage was selected in this quadrant, at about breast height, approximately midway up the lower half of each tree. If a suitable branch was not available, one in another quadrant was chosen instead.

Evaluation

Five characteristics were measured on juvenile foliage only: leaf retention percentage, infection incidence percentage (by *P. eucalypti* and *Mycosphaerella* species, respectively), and spot incidence (by *P. eucalypti* and *Mycosphaerella* species, respectively). Leaf retention was evaluated on the full complement of foliage produced 1 year earlier than that on which infection was measured (except in the Kawerau *E. globulus* trial where the same 2000–2001 season's shoots were used). In each trial, leaf retention was measured as a percentage of leaves present, within a 1–2 week period between October and December (spring to early summer). A tally counter was used to count the number of leaves present as a proportion of those originally formed on each node along one side, only, of the full length of the previous season's complete shoot growth. This length was delimited by the distance between the short growth pause internodes of the two previous winters (Hood *et al.* 2002). A small amount of new, current season's growth was included only in the first two blocks evaluated in both the Hogg Road *E. nitens* trials.

Infection was determined in each trial within a 1–2 week period during late January or February (mid- to late-summer) on current season's foliage (that on both sides of the distal, younger 50% of nodes), using the same trees and quadrants as for leaf retention. The most recent two to three nodes with immature leaves not yet showing symptoms of infection were excluded. A count was made of the percentage of leaves with spots caused by *P. eucalypti* and *Mycosphaerella* species, respectively (infection percentage). In addition, the number of spots of each fungus on the leaf with the most spots (spot number) was recorded within the following categories: 1, 2, 3...10, 11–20, >20. In the Kawerau *E. globulus* trial, a subjective estimate was also made of the percentage of leaf area disfigured due to infection by *Mycosphaerella* species on the most discoloured leaf (leaf area percentage).

During field counts, infection by *P. eucalypti* was identified by characteristic yellow or crimson spots, with extruded spore tendrils visible through a hand lens. On *E. nitens*, *Mycosphaerella* species were characterised by a typical grey, or sometimes brownish, often angular and sometimes crinkled blotch, at times with pseudothecia visible along leaf veins, under a hand lens. On *E. globulus*, spots associated with *Mycosphaerella* species were recognised as regular or irregular rounded brownish blotches, also with pseudothecia on older leaves visible under a lens (distinct from black oil glands). Leaf samples were taken to confirm the identities of the microfungi associated with these different symptoms. *Mycosphaerella* species were identified from the distribution of pseudothecia (amphigenous or mainly hypophyllous) and by ascospore germ tube morphology (Crous 1998; Park *et al.* 2000). Minor atypical leaf spotting or disfiguration not fitting the above criteria was not counted, and shoots with foliage or buds chewed by insects were avoided as far as possible.

Severe frosting caused damage to trees at Kawerau during the winter after the evaluation of infection in the *E. globulus* trial. Use was made of this to evaluate susceptibility to frost damage by counting the percentage of residual sample branches remaining alive on study trees in the following spring (October 2001). Branch status was indicated by means of a brief examination of the tissues after nicking with a knife, and from the condition of branch tips and any remaining foliage.

Analysis

Data on leaf retention, infection, and spot incidence were subjected to analyses of variance (after arcsin transformation of the percentage variables for the *E. nitens* provenance and seedlot trials). The analysis of variance for the *E. nitens* provenance trial incorporated the following experimental factors: site, block (within site), region, provenance (within region), family (within region × provenance), aspect (N, S, E, W), and observer. To test the significance of each factor, a fixed effect, split-plot analysis of variance was used. Variance components were estimated using a mixed model in which aspect and observer were fitted as fixed effects, and all other factors were fitted as random effects. The other trials were analysed in the same way, testing an appropriate selection of experimental factors. Relationships between measures of infection and leaf retention were tested using Spearman rank correlation coefficients. Fungal spot numbers per leaf in the "11–20" and ">20" categories were treated as "15" and "25", respectively, during the analyses. Data for *E. saligna*, *E. regnans*, and *E. fastigata* were excluded from the analyses because of difficulties in precisely defining a year's growth complement for these species.

RESULTS

Eucalyptus nitens Provenance Trial

In the *Eucalyptus nitens* provenance trial, leaf retention was significantly greater in both New South Wales populations than in stock from Victoria at both Hogg Road and Omataroa (Table 1). At each site incidence and severity of infection by both fungi were also much lower on foliage of trees from the two regions in New South Wales. More foliage was retained on

TABLE 1–Least squares means for regions at each trial site, *E. nitens* provenance trial*

Site	Region	Leaf retention (%)	*Phaeo-phleospora* infection (%)†	*Phaeo-phleospora* spot number‡	*Myco-sphaerella* infection (%)†	*Myco-sphaerella* spot number‡
Hogg Road	North NSW	55 c	14 d	4 b	46 bc	13 b
	South NSW	44 d	19 d	5 b	48 b	13 b
	Victoria	32 e	60 b	18a	70a	19a
Omataroa	North NSW	86a	35 c	6 b	36 bc	7 cd
	South NSW	89a	32 c	7 b	34 c	6 d
	Victoria	76 b	74a	16a	61a	10 c

* Means linked by a common letter subscript are not significantly different (p>0.05, LSD test)
† Percentage leaves infected
‡ Number of spots on worst leaf

trees at Omataroa than at the Hogg Road site (Table 1). The variance components from the mixed model analysis are shown in Table 2, treating aspect and observer as fixed effects and the other factors as random effects. For most measures of leaf retention and infection, there were significant differences between the two trial locations, replications, regions of origin, and families within provenances. The interaction between region of origin and replication was also significant. However, variation between provenances within regions, and the interactions between provenance and replication, site and region, site and provenance, and site and family, were mostly not significant. The ranges of family means are shown by region and provenance in Fig. 1, and individual values are listed in Appendix 1. Inspection of means for separate replications indicated no association between block variation and evaluator.

TABLE 2–Variance components, *E. nitens* provenance trial

Component	Leaf retention	*Phaeo-phleospora* infection	*Phaeo-phleospora* spot number	*Myco-sphaerella* infection	*Myco-sphaerella* spot number
Site	756.6**	110.2**	0.00	32.8	27.03**
Replication (Site)	30.4**	68.4**	3.24	133.7**	4.44**
Region	58.0**	595.1**	47.16**	201.4**	5.10**
Provenance (Region)	0.0	3.6	0.12	0.0	0.00
Region × Site	30.3**	0.0	0.85	0.0	0.52
Provenance (Region) × Site	0.0	1.2	0.0	0.0	0.00
Region × Replication (Site)	9.9**	56.3**	9.44**	34.5**	1.51*
Provenance (Region) × Replication (Site)	0.0	0.0	0.0	0.0	0.0
Family (Provenance × Region)	4.7**	12.2**	2.27**	21.4**	3.03**
Site × Family (Provenance × Region)	4.3	9.4*	0.14	3.7	0.00
Residual	139.1	373.9	45.76	406.4	55.43

** significant at p = 0.01
* significant at p = 0.05

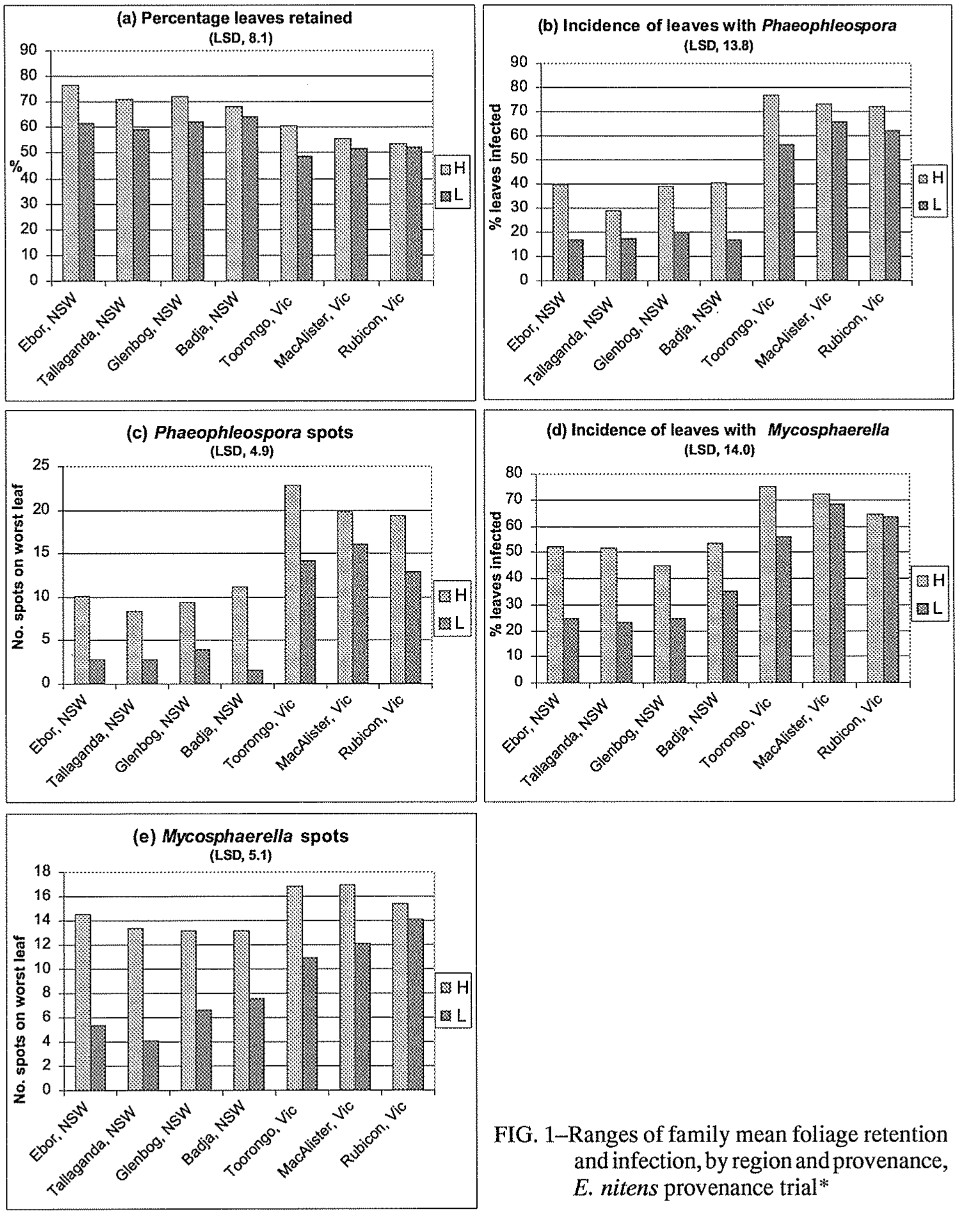


FIG. 1–Ranges of family mean foliage retention and infection, by region and provenance, *E. nitens* provenance trial*

* Highest (H) and lowest (L) least square family means (No. families per provenance: Ebor, northern NSW, 20; Tallaganda, southern NSW, 7; Glenbog, southern NSW, 7; Badja, southern NSW, 6; central Victoria region, one parent from each of 18 families, being 13 from Toorongo, 3 from MacAlister, and 2 from Rubicon). In each graph any two values separated by more than the given Least Significant Difference (LSD) differ significantly (p = 0.05).

Leaf retention was significantly and negatively associated with all measures of infection by both fungi at each site (Table 3). *Mycosphaerella* species spots on *E. nitens* leaf samples from Hogg Road were caused by *M. cryptica* (Cooke) Hansf.

TABLE 3–Significance of association between leaf retention and infection, *E. nitens* provenance trial†

Infection measure	Trial site	
	Hogg Road	Omataroa
Phaeophleospora infection	–0.42**	–0.39**
Phaeophleospora spot number	–0.37**	–0.28**
Mycosphaerella infection	–0.34**	–0.27**
Mycosphaerella spot number	–0.13**	–0.09*

** significant at p = 0.01
* significant at p = 0.05
† Spearman rank correlation coefficients;

Eucalyptus nitens Seedlot Trial

As with the *E. nitens* provenance trial, more foliage was retained in the seedlot trial at the Omataroa site (Table 4). Leaf retention and infection did not differ between six seedlots of *E. nitens* from Victoria, but the seedlot with a New South Wales component (Huntsman seed orchard) was better foliated and less infected than the others (Table 4). In this trial, there were again significant differences in leaf retention and in infection by both fungi between sites and replications (Table 5). There was also significant variation between plots, and seedlots, but not for the interaction between site and seedlot (Table 5). Foliage retention tended to be negatively associated with infection, but this trend was weaker than in the provenance trial (Tables 4, 6). Leaf retention was largely independent of crown aspect, but there was a tendency for slightly less infection by *P. eucalypti* in the southern quadrant of tree crowns. As with the *E. nitens* provenance trial, most parameters varied between blocks in a manner unrelated to evaluator.

TABLE 4–Least squares means for site and seedlot, *E. nitens* seedlot trial*

	Leaf retention (%)	*Phaeo-phleospora* infection (%)†	*Phaeo-phleospora* spot number‡	*Myco-sphaerella* infection (%)†	*Myco-sphaerella* spot number‡
Site					
Hogg Road	35.7a	57.3a	18.2a	63.6a	17.6a
Omataroa	79.1 b	74.5 b	17.0a	58.3a	8.4 b
Seedlot					
Waikuku clonal seed orchard	54.9ab	66.9a	18.0a	64.3a	13.2a
Waiouru provenance collection	58.1 b	65.8a	16.5a	64.4a	14.6a
VRD 36 AMCOR seed orchard	56.8ab	68.2a	20.1a	57.9ab	12.3a
VRD 26 AMCOR seed orchard	55.5ab	67.9a	18.7a	62.2a	13.4a
MacAlister State Forest native collection	57.2ab	69.0a	17.7a	59.3ab	11.2a
Sumner Spur seed orchard	53.8a	73.4a	19.0a	68.0a	14.5a
NFP Huntsman seed orchard	65.7 c	50.0 b	12.8 b	50.6 b	12.1a

* Means linked by a common letter subscript, for each experimental factor, are not significantly different (p>0.05, LSD test)
† Percentage leaves infected
‡ Number of spots on worst leaf

TABLE 5–Variance components, *E. nitens* seedlot trial

Component	Leaf retention	*Phaeo-phleospora* infection	*Phaeo-phleospora* spot number	*Myco-sphaerella* infection	*Myco-sphaerella* spot number
Site	928.8**	112.8**	0.46	0.0	41.75**
Replication (Site)	27.8**	71.7**	3.93*	101.4**	4.41**
Seedlot	13.4**	44.8**	4.11**	21.3**	0.63
Seedlot × Site	0.0	0.0	0.28	4.4	0.00
Plot (Replication)	10.0**	75.3**	12.56**	45.2**	3.53*
Residual	119.8	438.8	63.60	437.5	52.35

** significant at p = 0.01
* significant at p = 0.05

TABLE 6–Significance of association between leaf retention and infection, *E. nitens* seedlot trial†

Infection measure	Trial site	
	Hogg Road	Omataroa
Phaeophleospora infection	–0.19**	–0.12
Phaeophleospora spot number	–0.25**	–0.18**
Mycosphaerella infection	–0.15**	–0.02
Mycosphaerella spot number	–0.10	–0.04

** significant at p = 0.01
* significant at p = 0.05
† Spearman rank correlation coefficients;

Eucalyptus globulus Subspecies Provenance Trial

Only trace infection by *P. eucalypti* was present on occasional leaves of *E. globulus* subspp. *globulus* and *maidenii* during the evaluation of the Kawerau trial, and on no other species or subspecies. By contrast, leaf spotting caused by *Mycosphaerella* species was extensive. Incidence and severity of spotting by this fungus varied with species and subspecies (Tables 7, 8). There was substantially less damage on foliage of subspecies *maidenii* than on that of the other taxa tested (Table 7). Subspecies *globulus* was disfigured by *Mycosphaerella* species the most severely, but subspecies *pseudoglobulus*, and even subspecies *bicostata*, were only slightly less affected. The orchard-improved subspecies *globulus* was at least as diseased as the native material. *Eucalyptus nitens* was only moderately infected by *Mycosphaerella* species. Incidence and severity of *Mycosphaerella* species spotting did not vary with replication (Table 8), and was not influenced by crown aspect. Laboratory examination of pseudothecia and germinating ascospores indicated that the *Mycosphaerella* species spots on *E. globulus* were caused predominantly by *M. nubilosa* (Cooke) Hansf.

Trees in the Kawerau trial were severely damaged by frost in the winter after the evaluation for infection, and branches were not available on all trees for measurement of foliage retention during the subsequent spring. Frost damage was severest on subspecies *globulus*, while the least affected were subspecies *maidenii* and *E. nitens* (Table 7). These taxa also retained more foliage than the other subspecies on still-living branches (Table 7). Leaf retention tended to be lower where infection by *Mycosphaerella* species was greater,

TABLE 7–Least squares means for subspecies and species, *E. globulus* provenance trial*

Species/subpecies	Leaf retention (%)	*Myco-sphaerella* infection (%)†	*Myco-sphaerella* spot number‡	*Myco-sphaerella* leaf area (%)§	Branch survival (%)
subsp. *globulus* (orchard)	10a	89a	24a	57a	18a
subsp. *globulus* (native range)	16a	86a	23ab	48 b	14a
subsp. *pseudoglobulus*	19a	85a	25a	41 b	64 b
subsp. *bicostata*	17a	71 b	23ab	46 b	69 b
E. nitens	27 b	66 b	21 b	24 c	100 c
subsp. *maidenii*	30 b	43 c	17 c	11 d	88 c

* Means linked by a common letter subscript are not significantly different (p>0.05, LSD test)
† Percentage leaves infected
‡ Number of spots on worst leaf
§ Estimated percentage area spotted on worst leaf

TABLE 8–Variance components, *E. globulus* provenance trial

Component	Leaf retention	*Myco-sphaerella* infection	*Myco-sphaerella* spot number	*Myco-sphaerella* leaf area	Branch survival
Replication	11.6	11.7	0.00	2.6	13
Subspecies/Species	48.3**	295.4**	7.71**	292.4**	1243**
Subspecies/Species × Replication	12.3	4.1	1.26	6.7	9
Seedlot (Subspecies/Species)	36.9**	32.8**	0.00	28.4**	164**
Residual	143.7	379.0	37.09	355.3	1221

** significant at p = 0.01

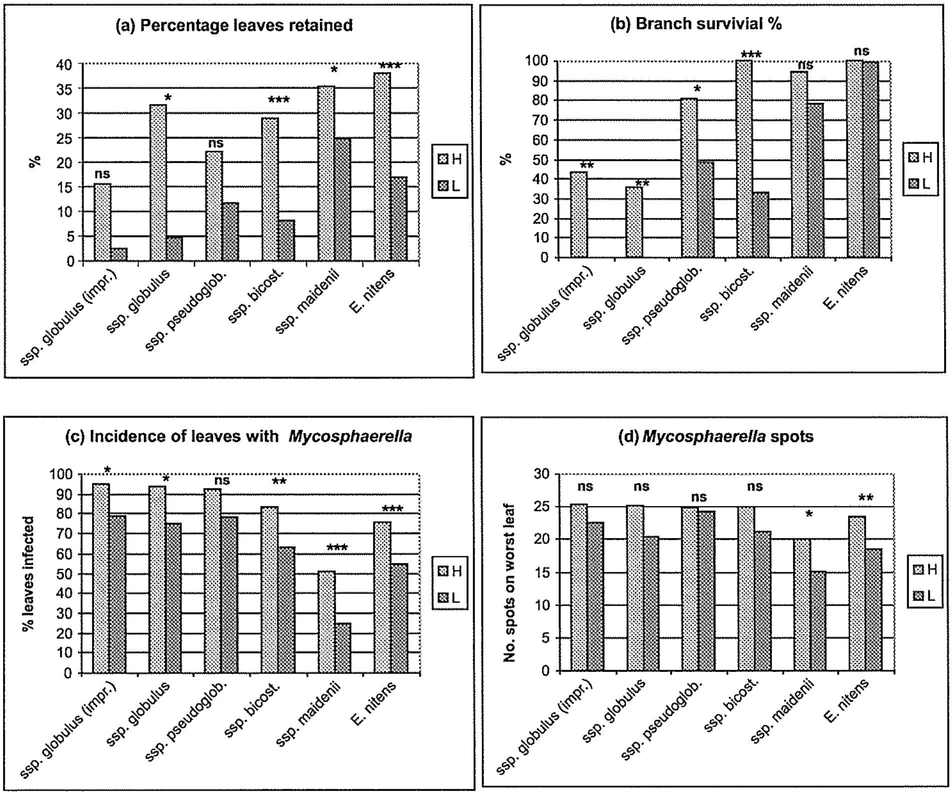
and this trend was significant for some measures of infection on *E. nitens*, subspecies *globulus*, and subspecies *bicostata* (Table 9).

Significant differences were also found in measures of infection by *Mycosphaerella* species, and in frost tolerance, between some provenance, provenance mixture, and progeny seedlots of all species and subspecies, except for subspecies *pseudoglobulus* with only two provenances (Table 8, Fig. 2). However, no clear provenance trends were apparent across the

TABLE 9–Significance of association between leaf retention and infection, *E. globulus* provenance trial†

Infection measure	*E. nitens*	*E. globulus* subspecies				
		subsp. *globulus* (native range)	subsp. *globulus* (orchard)	subsp. *pseudo-globulus*	subsp. *bicostata*	subsp. *maidenii*
Mycosphaerella infection	–0.28	0.04	0.30	–0.15	0.00	–0.13
Mycosphaerella spot number	–0.59**	–0.24	–	–0.07	0.13	–0.03
Mycosphaerella leaf area	–0.47**	–0.57**	–0.50	–0.35	–0.23*	–0.19

** significant at p = 0.01
* significant at p = 0.05
† Spearman rank correlation coefficients



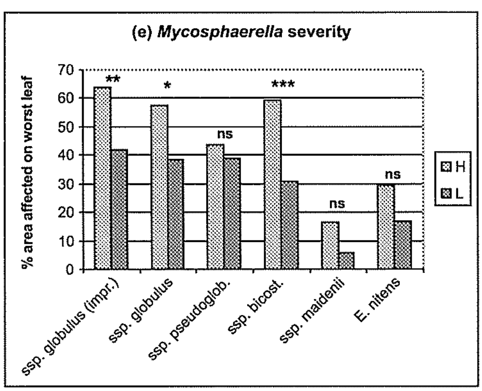


FIG. 2–Ranges of mean provenance foliage retention, infection by *Mycosphaerella*, and branch survival after frosting, by species and subspecies, *E. globulus* trial*

* Highest (H) and lowest (L) least square family means (No. provenance or provenance groups per species/subspecies: improved *E. globulus* subsp. *globulus*, 5; ssp. *pseudoglobulus*, 2; ssp. *bicostata*, 7; ssp. *maidenii*, 7; *E. nitens*, 3; fewer for retention). Significance between each pair of highest and lowest mean values is indicated (*** $p<0.001$; ** $p<0.01$; * $p<0.05$; ns not significant $p>0.05$).

natural subspecies ranges, except possibly for subspecies *globulus* (Appendix 2). The six provenance groups of this subspecies with the highest incidence of leaves infected by *Mycosphaerella* species (> 90%) all originated from Tasmania and Flinders and King Islands, while Jeeralang, east of Melbourne in Victoria, had the lowest levels (< 80%).

However, there was considerable overlap in means between mainland and island provenances. For *E. nitens*, lowest infection by *Mycosphaerella* species occurred on the seedlot from New South Wales, and highest on material from Victoria, as in the other trials. There were also provenance differences for foliage retention and branch survival after frost, within different species and subspecies (Fig. 2 a, b, Appendix 2). Again, there were no clear regional trends within each subspecies of *E. globulus*, except that for subspecies *bicostata* the highest values for both foliage retention (≥25%) and branch survival (≥94%) were recorded on two provenances from the northern portion of the natural distribution range, in New South Wales (Appendix 2). With *E. nitens*, highest leaf retention was again shown by the seedlot from New South Wales, and lowest by the two sources from Victoria. As previously, observer bias was not a factor in the Kawerau trial.

Eucalyptus Species Trial, Ohiwa

In contrast to the Kawerau trial, leaf spotting by both *P. eucalypti* and *Mycosphaerella* species was plentiful on trees in the Ohiwa species trial. There was significant variation between species or subspecies for all parameters of infection, and for leaf retention (Tables 10, 11). Infection by *P. eucalypti* was heavy on *E. nitens* (a seedlot from Victoria), light on subspecies *globulus*, and present only in trace amounts on subspecies *maidenii* (Table 10). As in the Kawerau *E. globulus* trial, there was less infection by *Mycosphaerella* species on seedlots of subspecies *maidenii* than on those of subspecies *globulus* and *E. nitens*

TABLE 10–Least squares means for species, Ohiwa eucalypt species trial*

Species/subspecies	Leaf retention (%)	*Phaeo-phleospora* infection (%)†	*Phaeo-phleospora* spot number‡	*Myco-sphaerella* infection (%)†	*Myco-sphaerella* spot number‡
E. nitens	18a	91a	15.1a	78ab	22.9a
E. globulus subsp. *globulus*	22a	8 b	1.0 b	85a	23.3a
E. globulus subsp. *maidenii*	49 b	0 c	0.1 b	55 b	12.0 b
E. benthamii	55 b	0 c	0.1 b	4 c	0.2 c

* Means linked by a common letter subscript are not significantly different (p>0.05, LSD test)
† Percentage leaves infected
‡ Number of spots on worst leaf

TABLE 11–Variance components, Ohiwa eucalypt species trial

Component	Leaf retention	*Phaeo-phleospora* infection	*Phaeo-phleospora* spot number	*Myco-sphaerella* infection	*Myco-sphaerella* spot number
Replication	38.0**	0	0	0	0
Species/Subspecies	339.6**	1909**	60.0**	1294**	115.9**
Seedlot (Species/Subspecies)	3.8	42**	0.0	118	5.8
Between Plots	26.6	9	1.7**	149**	6.4**
Residual within Plots	363.1	67**	5.4	603	42.9

** significant at p = 0.01

(Table 10). *Eucalyptus benthamii* was nearly free of infection by both leaf fungi. More foliage was retained on subspecies *maidenii* and *E. nitens* than on subspecies *globulus* and *E. nitens* (Table 10). Variation in infection and leaf retention was negligible with replication (Table 11) and crown aspect.

For subspecies with larger numbers of seedlots, there were significant differences between some seedlots in both leaf retention and susceptibility to infection (Tables 11, 12). The geographical distribution of values across the natural subspecies ranges generally concorded with those from the Kawerau trial. However, a slightly lower incidence of *Mycosphaerella* species infection was measured in a seedlot from Geeveston in south-eastern Tasmania (71%; but mean incidence of leaf infection by *P. eucalypti* on this provenance was 25%, compared with ≤4% on each of the others of this subspecies). As previously, there were negative correlations between leaf retention and infection by both fungi, but these were significant only for *Mycosphaerella* species on subspecies *maidenii* (Table 13). Laboratory examination indicated that *Mycosphaerella* species spots on foliage at Ohiwa were caused mainly by *M. nubilosa* on *E. globulus* subspecies, and by *M. cryptica* on *E. nitens*.

Data from *E. saligna*, *E. regnans*, and *E. fastigata* were not analysed. Foliage was healthy on all three species, apart from very minor leaf spotting on some trees of *E. regnans* and *E. fastigata* caused by species of *Mycosphaerella*, *Cercospora* Fresen. or *Pseudocercospora* Speg., and *Aulographina eucalypti* (Cooke & Massee) Arx & E. Müll. There was a significant incidence of *Ophelimus* Haliday sp. pimpling on many leaves of *E. saligna*. Other insect damage observed in different trials was caused by leaf mining sawfly (*Phylacteophaga frogatti* Rick), leaf rollers (e.g., *Strepsicrates macropetana* Meyrick), and gum emperor moth (*Antheraea eucalypti* Scott).

TABLE 12–Least squares means for provenances within species and subspecies, Ohiwa eucalypt species trial

Species/ subspecies	No. seed-lots†	Leaf retention (%)	*Phaeo-phleospora* infection (%)‡	*Phaeo-phleospora* spot number§	*Myco-sphaerella* infection (%)‡	*Myco-sphaerella* spot number§
E. nitens	1	18	91	15	78	23
E. globulus subsp. *globulus*	4	24,19,15,27 ns	2,2,25,5 **	0.3,0.2,2.3,1.0 ns	87,94,71,90 *	22,25,23,24 ns
E. globulus subsp. *maidenii*	4	53,43,46,55 *	0,0,0,0 ns	0,0,0,0 ns	32,78,50,61 ns	7,17,11,13 ns
E. benthamii	2	57,53 ns	0,0 ns	0,0 ns	0,8 ns	0.09,0.5 ns

Values ranked in same order as provenances listed below (significance of between-provenances difference: ** significant at p = 0.01; * significant at p = 0.05; ns, not significant, p > 0.05)

† Provenances:

E. nitens: Broadford S.O., Vic.
subsp. *globulus*: Jeeralang Nth, Vic.; King Is., Tas.; Geeveston, Tas.; APP S.O.
subsp. *maidenii*: Bolara Mtn., NSW; Bondi S.F., NSW; Belowra; Myrtle Mn., NSW
E. benthamii: Kedumba Valley, NSW; Bents Basin, NSW

‡ Percentage leaves infected

§ Number of spots on worst leaf

TABLE 13–Significance of association between leaf retention and infection, Ohiwa eucalypt species trial†

Infection measure	Species/subspecies			
	E. nitens	*E. globulus* subsp. *maidenii*	*E. globulus* subsp. *globulus*	*E. benthamii*
Phaeophleospora infection	–0.40	–	–	–
Phaeophleospora spot number	–0.35	–	–	–
Mycosphaerella infection	0.12	–0.27 **	–0.11	–0.23
Mycosphaerella spot number	–0.01	–0.27 **	–0.21	–0.22

** significant at p = 0.01
† Spearman rank correlation coefficients

DISCUSSION

The purpose of this study was to explore susceptibility to *Phaeophleospora eucalypti* within five eucalypt species and subspecies, in order to identify provenances or families that might replace the susceptible Victorian sources of *E. nitens* currently used in plantations on low-elevation, disease-prone sites in the North Island of New Zealand. Because of its prevalence it was impossible to ignore associated infection caused by species of *Mycosphaerella*. Infection by both fungi, and leaf retention, were evaluated using procedures that employed counting rather than estimation, to compare levels of precision between methods, and to promote objectivity. Any evaluator bias still present was controlled by incorporation within the block effect in the sampling design.

The evaluation methods were adapted to the field situation in a number of ways. Infection data were standardised by counting only foliage on the distal half of current internodes, in order to circumvent varying degrees of defoliation on the older, proximal portion. This accords with the sampling approach of Carnegie *et al.* (1994) who also selected a younger foliage complement. Shoots with tips damaged by insects were avoided as far as possible, to ensure equivalent comparisons along the respective portions of the full shoot length. Confining measurements to juvenile shoots avoided complications that arise in assessing whole crowns during the period when trees are in different stages of transition to mature foliage (Dungey *et al.* 1997).

Evaluations were made at the same times each year, for consistency. Infection was determined during the mid-to-late summer period, even though Carnegie *et al.* (1994) suggested that differences between provenances might be less distinct later in the season. There seemed little advantage in collecting data before trees had displayed their full susceptibility, even at the expense of some loss in discrimination between seedlots. All trials were evaluated before crown closure to avoid the confounding effects of light suppression on younger branches lower in the crown. *Eucalyptus saligna*, *E. regnans*, and *E. fastigata* do not have opposite juvenile leaves, and data from these species were not analysed because the correct season's shoot internode lengths could not be reliably identified and matched in the field.

With experience and laboratory verification of leaf samples, field identification of symptoms due to the respective fungi was undertaken with reasonable confidence. Symptoms of *Mycosphaerella* species were dissimilar on *E. nitens* and subspecies of *E. globulus*, and were caused by different species. Only *M. cryptica* was detected on *E. nitens*, while *M. nubilosa* apparently predominated on *E. globulus* subspecies. This agrees with Australian studies, except that both *M. cryptica* and *M. nubilosa* (sometimes reported as *M. molleriana* Crous & M.J. Wingf.) occur on juvenile foliage of subspecies of *E. globulus* (Dungey *et al.* 1997; Carnegie *et al.* 1998). Both pathogens have previously been recorded in the central North Island (Dick 1982). A nondescript discoloration on *E. nitens* believed to be a pre-dehiscence host response to infection by *P. eucalypti* was ignored (Hood *et al.* 2002), but extended browning on *E. globulus* subspecies associated with pseudothecia of *Mycosphaerella* species was considered to be genuine infection and counted.

A number of species in Section *Maidenaria* were evaluated on the assumption that there might be related eucalypts more suitable than *E. nitens* for planting on disease-prone sites. *Eucalyptus nitens* proved to be much the most susceptible species to *P. eucalypti*, at ages up to 3 years. Unfortunately, most subspecies of *E. globulus*, although resistant to *P. eucalypti*, were very susceptible to leaf damage by *Mycosphaerella* species. However, subspecies *maidenii* was consistently more resistant to *Mycosphaerella* species than the other subspecies, particularly subspecies *globulus*, and health and foliage retention by this taxon was acceptable in both trials in which it was present. This result agrees with previous work in Australia (Carnegie *et al.* 1994, 1998) and, on older material, in New Zealand (Low & Shelbourne 1999). The greater resistance shown by subspecies *maidenii* may have developed in response to higher inoculum pressures induced by warmer and wetter summer conditions than occur in the natural ranges of the other subspecies (Jordan *et al.* 1993). This idea was introduced to explain variation in susceptibility observed between provenances of subspecies *globulus* (Carnegie *et al.* 1994). *Eucalyptus nitens* was moderately susceptible to *Mycosphaerella* species spotting, whether or not accompanied by *P. eucalypti*. The least diseased species of all was *E. benthamii*.

There was also significant within-species and within-subspecies variation in disease resistance and leaf retention. Families and provenances of *E. nitens* from New South Wales were much less defoliated and more resistant to both fungi than those from Victoria (Fig. 1, 2; Appendix 2), a result that agrees with previous work, with respect to species of *Mycosphaerella* (e.g., Lundquist & Purnell 1987; cf. Low & Shelbourne 1999). Unfortunately, differences between provenances were not significant within each region, and families from provenances in Victoria were all less healthy than were those from New South Wales (Fig. 1). This might suggest that, based on juvenile health alone, it would be better to substitute Victorian *E. nitens* with other eucalypt material, rather than continue to search for a better provenance of *E. nitens* from within central Victoria. However, variation in susceptibility to *Mycosphaerella* species has previously been reported at the provenance level for *E. nitens* (Lundquist & Purnell 1987; Carnegie *et al.* 1998), and so more data may be needed. Dungey *et al.* (1997) noted the need to include sufficient numbers of families when making proper comparisons between provenances. There was also variation in leaf retention and susceptibility to *Mycosphaerella* species between provenances of *E. globulus* subspecies, as has also previously been reported (Carnegie *et al.* 1994, 1998), but again the caution of Dungey *et al.* (1997) applies regarding numbers of families per provenance. There were only slight indications of regional trends in susceptibility within the natural distribution ranges of each *E. globulus* subspecies, and there appeared to be no obvious relationships with rainfall distribution patterns, at least on the large scale (cf. Carnegie *et al.* 1994; Dungey *et al.* 1997). With both fungi, seedlots that were most infected tended to retain the least foliage, and significant inverse associations between these variables were confirmed on both *E. nitens* and also some subspecies of *E. globulus*. Such a result has previously been reported for species of *Mycosphaerella* (Lundquist & Purnell 1987; Carnegie *et al.* 1994), and supports the general presumption that both fungi contribute to the syndrome in *E. nitens.*

The occurrence of winter frost damage to trees in the Kawerau trial, after they had already been evaluated for infection, enabled within- and between-species comparisons to be made for this type of injury (Table 7). *Eucalyptus nitens* proved to be the species most tolerant of frost, and subspecies *maidenii* again fared well among subspecies of *E. globulus*. Both taxa occur naturally where frosts are common (Boland *et al.* 1994). Subspecies *globulus* was the most vulnerable subspecies, and numbers of young trees were killed as a result of frost injury. Because damage occurred before this trial had been measured for leaf retention, susceptibility to frost is a confounding factor in the inverse relationship between this variable and fungal infection in the Kawerau trial (Table 9).

The low level of infection of *E. nitens* foliage by *P. eucalypti* at the Kawerau trial was unexpected, as infection was heavy on epicormic shoots on trees in an older stand of *E. nitens* only 5 km distant. It appears that with *P. eucalypti*, an epidemic increase in infection (Hood *et al.* 2002) requires an adequate starting inoculum as well as favourable climatic conditions. At the Kawerau trial, still only $1^1/2$ years old when first evaluated, susceptible trees of *E. nitens* were scattered, mostly in small plots or as single individuals. Nevertheless, data from the trials at Ohiwa and Kawerau allowed comparisons between susceptibilities to *Mycosphaerella* species at sites where *P. eucalypti* was plentiful or negligible, respectively.

The results reported here are preliminary. For a complete picture of susceptibility it was necessary to determine infection and associated defoliation early, while trees were still in the juvenile foliage stage. However, ultimate selection will depend on further evaluation of tree health, as trees mature beyond the juvenile stage and produce only adult foliage. Final decisions will be based particularly on wood volume production and on other important attributes such as fibre and pulping qualities, and perhaps form, which will be evaluated later in the rotation. Some work has already indicated an early relationship between health and growth (T.Withers & E.Hay unpubl. data). It seems likely that despite its initial rapid growth, there may be better material available than the present Victorian *E. nitens* for short-rotation plantations on these sites. The use of fast-growing eucalypt hybrid clones has also been suggested as an option (Shelbourne *et al.* 1999), but hybrids must be tested well before operational deployment, since some have proved more susceptible to pathogens such as *Mycosphaerella* species than either parent (Dungey *et al.* 1997).

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APPENDIX 1

EUCALYPTUS NITENS INDIVIDUAL FAMILY PROVENANCE TRIAL, HOGG ROAD AND OMATAROA, WITH LEAST SQUARES FAMILY MEANS

Region	Provenance	Family (code)	Leaf retention (%)	*Phaeophleospora* infection (%)*	*Phaeophleospora* spot number†	*Mycosphaerella* infection (%)*	*Mycosphaerella* spot number†
Nth. NSW	Ebor	1	69	27	6	46	10
		2	72	33	6	40	12
		3	66	24	4	38	10
		4	73	22	4	49	10
		5	73	17	3	25	5
		6	74	20	3	30	9
		7	77	31	5	50	15
		8	69	29	7	42	8
		9	62	22	4	40	8
		10	70	24	4	31	8
		11	72	21	4	44	10
		12	71	19	5	52	12
		13	73	23	4	39	10
		14	65	22	5	36	7
		15	70	22	3	47	12
		16	73	22	5	36	7
		17	74	17	4	48	13
		18	75	26	5	38	10
		19	62	31	6	46	13
		20	71	40	10	43	11
Sth. NSW	Tallaganda	21	64	20	3	31	8
		22	59	18	3	41	10
		23	65	29	8	49	13
		24	70	20	5	52	9
		25	68	18	3	50	11
		26	64	22	4	23	4
		27	71	23	5	40	10
	Glenbog	28	62	31	7	41	10
		29	69	34	9	24	7

Region	Provenance	Family (code)	Leaf retention (%)	*Phaeophleospora* infection (%)*	*Phaeophleospora* spot number†	*Mycosphaerella* infection (%)*	*Mycosphaerella* spot number†
Sth. NSW (cont.)	Glenbog	30	72	20	4	44	13
		31	68	32	7	36	10
		32	67	24	6	42	8
		33	64	39	9	45	13
		34	67	29	5	38	12
	Badja	35	67	24	5	43	10
		36	68	17	3	38	9
		37	68	17	2	35	8
		38	64	41	9	53	13
		39	65	33	11	44	10
		40	66	23	5	41	6
Central Victoria	Toorongo	41	50	77	23	67	12
		42	55	69	18	75	16
		43	49	60	14	56	14
		44	49	73	21	61	13
		45	54	65	15	65	12
		46	50	71	17	72	17
		47	52	56	16	73	17
		48	53	69	17	66	11
		49	57	77	19	65	12
		50	58	58	15	60	14
		51	54	70	17	62	12
		52	61	57	17	59	12
		53	61	61	16	62	16
	MacAlister	54	56	66	16	70	17
		55	54	73	20	68	12
		56	52	71	17	72	17
	Rubicon	57	54	62	13	64	15
		58	52	72	19	65	14
Least significant difference‡			8	13	5	13	5

* Percentage of leaves infected; † Number of spots on worst leaf; ‡ Within each region and column, differences between family means exceeding this value are significant, $p<0.05$

APPENDIX 2

EUCALYPTUS GLOBULUS SUBSPECIES PROVENANCE TRIAL, KAWERAU, WITH LEAST SQUARES SEEDLOT MEANS

Set	Code	Subspecies/ species	Seedlot (provenance, prov. mix, or progeny)	Leaf retention (%)*	*Myco-sphaerella* infection (%)†	*Myco-sphaerella* spot number‡	*Myco-sphaerella* leaf area§	Branch survival (%)
1	2	*globulus*	Bruny Island		93	23	56	0
	6	(native range)	Clarke Is. (3 prov., 41 fam.)		85	25	58	18
	4		Geeveston		87	21	37	32
	9		Tasmania East Coast Nth. (3 prov., 30 fam.)		81	23	40	7
	10		Tasmania East Coast central (3 prov., 21 fam.)	14	90	25	46	18
	11		Tasm. East Coast Sth. Central (3 prov., 30 fam.)	10	91	23	51	18
	12		Tasmania West Coast central (3 prov., 21 fam.)	5	94	24	52	11
2	3	*globulus*	King Island (2 prov., 15 fam.)		90	24	50	36
	5	(native range)	Flinders Island (4 prov., 42 fam.)		91	22	55	11
	7		Otway Ranges (7 prov., 175 fam.)		82	23	48	0
	8		South Gippsland (5 prov., 25 fam.)		84	23	42	0
	1		Jeeralang North		77	21	51	20
	20	*pseudo-*	Wiebens	12	90	25	44	48
	21	*globulus*	Cann River	22	81	25	39	81
3	13	*maidenii*	Bolaro Mt.	25	45	19	6	79
	14		Bondi S.F.	26	47	18	15	89
	15		Belowra	27	28	16	6	92
	16		Myrtle Mt.	35	48	18	11	90
	17		Yambulla S.F.	35	55	18	14	94
	18		Tantawanglo	30	49	16	8	85
	19		Eden	33	35	14	15	90

Set	Code	Subspecies/ species	Seedlot (provenance, prov. mix, or progeny)	Leaf retention (%)*	*Myco-sphaerella* infection (%)†	*Myco-sphaerella* spot number‡	*Myco-sphaerella* leaf area§	Branch survival (%)
4	22	*bicostata*	Canberra	25	78	24	41	100
	23		Burrinjuck	10	66	24	51	75
	24		Tumbarumba	8	66	24	44	75
	25		Wollemi	29	69	22	32	94
	26		Benalla	13	84	25	61	38
	27		Kiewa	14	64	22	41	33
	28		Mansfield	11	79	23	57	71
5	29	*globulus*	Jeeralang (single mother tree)	12	77	23	42	43
	30	(orchard)	Jeeralang (single mother tree)	2	88	26	61	17
	31		Sth. Geeveston (single mother tree)		93	25	61	1
	32		W. Coast Tasm., Hently R. (single mother tree)	10	89	24	55	24
	33		Tasmania, Victoria (17 mothers, 8 provenances)	16	96	24	60	7
	34	*E. nitens*	Toorongo, central Victoria	25	76	23	28	100
	35		NSW	38	52	18	15	98
	36		Waikuku	17	67	24	27	99
Least significant difference¶				15	14	5	14	25

* Gaps in data due to severe frost damage to shoot or foliage (subsp. *globulus*)
† Percentage of leaves infected
‡ Number of spots on worst leaf
§ Estimated percentage area spotted on worst leaf
¶ Within each subspecies/species and column, differences between family means exceeding this value are significant, $p < 0.05$