Seasonal development of septoria leaf blight in young Eucalyptus nitens plantations in New Zealand

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Summary

The leaf spotting fungus *Phaeophleospora eucalypti* (synonyms *Kirramyces eucalypti*, *Septoria pulcherrima*) occurs on eucalypt hosts throughout much of New Zealand. In parts of the country it is associated with a serious leaf-cast disease in young plantations of *Eucalyptus nitens*, often in association with infection by *Mycosphaerella cryptica*. Studies were undertaken over three seasons at one inland and three coastal sites in the Bay of Plenty–Taupo region to investigate disease epidemiology. Shoots on study trees were monitored monthly for production of new leaves, degree of fungal leaf spotting, and defoliation. Monthly records were also kept of fungal spore production, and glasshouse-raised potted seedlings were placed in the field at monthly intervals to determine the infection period of *P. eucalypti*.

Eucalyptus nitens produced leaves throughout most of the year, with least emergence during winter (when over a short period juvenile leaves were not produced at all), and greatest production during spring and summer. New leaves emerging in spring became infected by P. eucalypti, evidently from spores released from infected, residual, previous season's foliage. Most infection, in the seedling study, was restricted to the first few weeks after leaf appearance. Fertile pycnidia were present as soon as symptoms became visible, and infected leaves continued to produce conidia throughout the growth season, while still retained. Under suitable conditions an epidemic condition appeared to develop as successive sets of leaves emerged, became infected early, and in turn began producing new conidia, resulting in a sustained increase in the quantity of available inoculum. Seasonal infection decelerated in autumn, as the production of new leaves and spores declined. Infection by M. cryptica paralleled that by P. eucalypti, except that spotting was reduced on juvenile leaves and lacking on adult foliage, and infection of new season's foliage could also occur from ascospores produced in leaf litter. The disease progressed more vigorously at warmer, lower elevation coastal sites, where there was also more inoculum available at the start of the growth season

Keywords: defoliation; disease development; climate; Eucalyptus nitens; Phaeophleospora eucalypti; Kirramyces eucalypti; Septoria pulcherrima; Mycosphaerella cryptica

Introduction

Phaeophleospora eucalypti (Cooke & Massee) F.A. Crous et al. (synonyms, Septoria pulcherrima Gadgil & M. Dick, Kirramyces eucalypti (Cooke & Massee) J. Walker et al.) occurs naturally in south-eastern Australia where it has been known for over a century as a leaf parasite of indigenous species of Eucalyptus L'Herit. Infection normally causes minor leaf spotting on hosts in subgenus Symphyomyrtus, but occasionally symptoms are more severe (Heather 1961, 1962; Walker et al. 1992). Phaeophleospora eucalypti is also present in plantations of E. nitens (Deane & Maiden) Maiden in southern New South Wales, Victoria (Gippsland) and Tasmania, where it causes little or no damage (A. Carnegie, State Forests of New South Wales; T. Wardlaw, Forestry Tasmania, 2000, pers. comm.).

Beyond Australia, P. eucalypti has been recorded in New Zealand and possibly Italy (Walker et al. 1992). This fungus was first found in New Zealand in 1981 near Tokoroa in the central North Island (Gadgil and Dick 1983). It has gradually spread through much of the country over the past two decades on planted eucalypt hosts, mainly in subgenus Symphyomyrtus (all in section Maidenaria, except for one record on E. globoidea, subgenus Monocalyptus; App. 1). Although sometimes causing locally severe defoliation, P. eucalypti was not regarded as a serious pathogen in New Zealand (Dick 1982; Dick and Gadgil 1983). This was partly because of the limited commercial potential of the main host species, E. nitens, which was not widely planted, being particularly susceptible to attack by the eucalyptus tortoise beetle (Paropsis charybdis Stål). This situation changed when biological control of this pest (Bain and Kay 1989) coincided with a new demand for a hardwood fibre component in paper production. Short-rotation plantations of suitable eucalypt species were established in different parts of the country during the 1990s, particularly in the Bay of Plenty-Taupo district. Severe foliage blight subsequently became widespread in young stands of E. nitens, associated with leaf spotting by P. eucalypti and another leaf infecting fungus, Mycosphaerella cryptica (Cooke) Hansf. A research program was initiated as a consequence of serious concern; this paper reports the results of monitoring the seasonal development of the disease in response to fungal infection at sites with different environmental conditions. Data from climate

recording stations, together with longer-term meteorological information, were used to make comparisons between sites with different levels of disease severity.

Methods

Monitoring stands

Monthly monitoring of disease development was undertaken over three consecutive growing seasons at four sites within an area 85 km across in the Bay of Plenty–Taupo district (regions BP, TO, App.1). Sites were selected at different elevations and distances from the coast, in order to cover a range of climatic conditions. They were, in the period 1996–1998:

- Knights Block near Te Teko (lat. 38°02'S, long. 176°43'E; altitude about 20 m a.s.l.; distance from coast 16 km)
- Settlers Block near Matata (lat. 37°55'S, long. 176°39'E; about 100 m a.s.l.; 7 km);

and in the period 1998-1999:

- Douthetts Block near Matata (lat. 37°53.5'S, long. 176°41'E;
 120 m a.s.l.; 3 km)
- Coxs Block near Orakei Korako (lat. 38°31'S, long. 176°08'E; 480 m a.s.l.; 86 km).

Stands were about 2 y old when monitoring commenced in Knights, Douthetts, and Coxs Blocks, and 3 y old in Settlers Block (the Knights and Settlers monitoring stands also contained significant numbers of 8–9 mo younger infill trees that could no longer be distinguished from the initial crop). Seed for the stand at Douthetts Block (E 1406 Talbot) was collected from natural *E. nitens* 120–130 km east of Melbourne, and that for the stand at Coxs Block (E 1307 Whitelaw) came from a location nearby. The seed for the other blocks came from Victoria, but exact sources were not determined. The monitoring stands were established on hill country farmland sites and all were well infected by *P. eucalypti* when monitoring began, except for Coxs Block in which only a trace of infection by both fungi was present on some trees.

Foliage production and disease development

One primary branch with juvenile foliage in the lower crown, and one with adult foliage in the upper crown, were tagged in each of ten trees at each of Knights, Settlers, and Coxs Blocks. At Douthetts Block, three such branches were selected in each upper and lower crown on ten trees. Branches were selected in the open, to avoid shading by growth of adjacent trees during the observation period. Study trees were distributed over an area several hundred metres across at Knights and Settlers Blocks, but were clustered in one group at each of the other two sites. Production and age of current season's foliage were monitored monthly by recording the number of leaf nodes distal to a datum point marked near the tip on each stem at the start of the recording period. Each month an estimate was also made of the percentage surface area spotted by P. eucalypti and M. cryptica, to the nearest 10% (including zero values), on one leaf on every leaf node external to the datum mark (the same leaves each month). At Knights and Settlers Blocks assessments were made on both surfaces of adult and juvenile leaves, but at the other two blocks



Figure 1. Juvenile shoots of *Eucalyptus nitens* showing winter growth pause position, identified by the shortest length between two leaf nodes, and the smallest leaf pair (if present)

only one surface was assessed (the adaxial, on juvenile leaves). Recording began late in spring, 1996, at Knights and Settlers Blocks. At Douthetts and Coxs Blocks observations began earlier, in mid-winter 1998, and included residual, previous season's (1997–1998) leaves which were divided into 'earlier' (older 50% of nodes) and 'later' foliage (younger 50%). Assessments were made by two persons only, all estimates during each complete season being made by the same assessor. Tree means were determined for consecutive sets of emergent current juvenile and adult foliage of: number of leaf nodes produced; percentage of leaves infected (incidence) and leaf area spotted (extent) by each fungus; percentage undiseased green leaf surface; and percentage leaves retained. Means of tree means (and 95% confidence limits) were graphed for each site by month of observation. Graphs for infection were plotted cumulatively, to avoid the impression of an artificial decline in infection due to the shedding of infected leaves (i.e. monthly means were calculated to include the last recorded values for leaves after they had been cast, as if all were still present). Green leaf area was plotted non-cumulatively for foliage still retained each month, only. Tree means of 'earlier' and 'later' previous year's foliage were combined during graphing, where no differences were apparent.

Seasonal change in the frequency of leaf spots of P. eucalypti was also investigated. In May 1999, at the end of the third season, one primary branch with juvenile foliage was detached from each of eight additional, randomly selected trees in the study area at Douthetts Block, and from each of nine such trees at Coxs Block, and returned to the laboratory. The number of spots caused by P. eucalypti was counted on one leaf selected systematically at each leaf node on the current season's shoot growth (as delimited by the first winter growth pause position, Fig. 1). The spot density was determined by estimating leaf area using a transparent grid with squares of 1×1 cm. Leaf node positions were transformed proportionately to a hypothetical shoot length of 10 nodes, to enable comparisons to be standardized $(x/y \times 10)$, where x = leafnode position, and y = total number of nodes; e.g. the 7th node of a full season's complement of 15 leaf nodes converts to 4.6, or node position 5 on a standardised 10-node shoot length).

Spore production

Additional branches with juvenile foliage were tagged in the lower crown on trees adjacent to the disease monitoring trees, in order to follow the seasonal production of spores of P. eucalypti and M. cryptica. For instance, in the 1998-1999 season, branches were tagged on each of three trees at each of Douthetts and Coxs Blocks. Leaf age on current shoots was determined, as previously, by recording the number of new leaves produced each month. One branch was randomly selected from each tree each month, and stored at 4°C in a polythene bag. From May 1999, monitoring was continued by randomly selecting further equivalent branches from nearby trees. Within one or two days of sampling, spots on infected leaves were examined under the microscope for the presence of fruitbodies and for evidence of spores of each fungus. Graphs were plotted of the monthly proportion of infected leaves (those with leaf spots) with spores associated with at least one lesion per leaf, on successive sets of emergent foliage (or on later samples, as 'earlier' and 'later' foliage, as determined previously). In May 1999, a sample of leaf litter was collected from near the study trees at Douthetts and Coxs Blocks, and leaves were examined microscopically for the presence of spores of each fungus, before and after damp incubation at room temperature.

Infection period of Phaeophleospora eucalypti

At monthly intervals over an 18-mo period during 1998–2000, eight 3-mo-old, glasshouse-raised, potted seedlings of one seedlot of E. nitens were taken to the field monitoring area at Douthetts Block, eight were carried to the Coxs Block site, and eight were kept as controls under glasshouse cover. At each field site four plants were enclosed in each of two pens situated about 30 m apart, fenced and eventually also covered in wire netting to protect them from sheep and possums. During summer, seedlings were held in shallow, polythene-lined, waterfilled ditches dug within each pen, to prevent drying while in the field. After exposure for 1 mo, plants were sprayed with Orthene 75 insecticide (1 g L⁻¹) and returned to glasshouse cover. When in the glasshouse, all plants were kept slightly apart, avoiding foliage contact, and routinely watered from beneath. Uninfected control seedlings from the first two monthly batches were subsequently reused as older, field plants. This was to allow for the possibility that the very young seedlings might be more susceptible than older material, which is likely to be more typical of shoots on trees in the field. At monthly intervals from January 1999, two plants (now 7–9 mo old, about 1 m in height), were placed for 1 mo in each pen at Douthetts Block before being returned to the glasshouse for evaluation along with the younger seedlings.

The number of leaf nodes present along the stem of each seedling was recorded when taken from, and returned to, the glasshouse, in order to distinguish between foliage produced before, during, and after exposure to natural spore inoculum in the field. Foliage in the pre-exposure class was further subdivided into two equal sets of older and younger leaf nodes. All leaves in each foliage class were assessed for spotting by *P. eucalypti* three and six weeks after returning plants from the field. Combined results were graphed for three parameters of

this fungus each month: percentage leaves infected; mean percentage leaf area discoloured (estimated by the same observer, inclusive of zero values for uninfected leaves); mean leaf spot density (including zero leaf values). For the last variable, a transparent grid with squares of 1×1 cm was used to estimate leaf area (where spots merged, they were treated as being the same size as adjacent spots; for leaves with more than 100 spots, counting was simplified by placing three square quadrats, each 1×1 cm, over representative portions of the surface).

Comparison between sites

The health of trees was further compared between typical stands at coastal and inland sites in May 1997. Measurements were made on seven 3-y-old E. nitens trees in each of Knights Block, near the coast, and Poronui Block, inland. Data were also collected from ten 4-y-old trees in each of Poronui Block and Settlers Block, near the coast. Poronui Block is situated east of Taupo in the Kaimanawa Range foothills (lat. 39°02'S, long. 176°16'E; altitude about 600 m a.s.l.; distances from coast 133 km, Bay of Plenty, 67 km, Hawke Bay). Trees were selected at random in an area less than 50 m across at each site. For each tree, data were taken from one randomly selected lower-crown branch with juvenile foliage, and from a similar branch with adult foliage in the upper crown. On the lower branch a count was made of the percentage of leaves retained at all current and previous years' leaf nodes along the primary axis. Means were simultaneously determined for the percentage of green surface area uninfected by P. eucalypti and Mycosphaerella on one leaf still present on each of the same current and previous years' leaf nodes. Yearly foliage sets were determined from the position of the winter growth pause, as previously. Similar data were collected on the upper adult branch axis from the youngest 20 current year's leaf nodes, only. Results for current and previous year's juvenile, and current adult foliage, were compared graphically between sites.

Climate monitoring

Solar-powered automatic-recording meteorological stations were placed close to the field monitoring sites at Douthetts Block, near the coast, and Coxs Block, inland, between December 1998 and October 1999. This equipment electronically registered hourly measurements of ambient temperature, rainfall and relative humidity, and also the period of 'leaf wetness', using a sensor fastened within the crown of a nearby tree. Data were processed to facilitate comparisons between sites for each calendar month.

Results

Foliage production

New leaves were regularly produced on sample shoots throughout most of the year. Results for Douthetts and Coxs Blocks are shown in Figure 2. There was a brief lull in mean production of juvenile foliage over several months during winter (slightly longer at the inland site), but adult leaves were produced on some trees throughout the year, though at a low mean rate in winter. Greatest production occurred between September and February (maximum, six adult leaves per month, Coxs Block). Results at the other two sites were comparable.

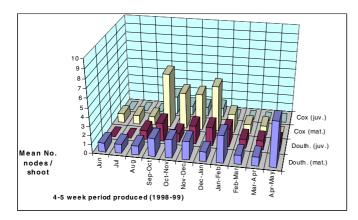


Figure 2. Monthly production of new adult (mature) and juvenile leaf nodes at Douthetts and Coxs Blocks, 1998–1999

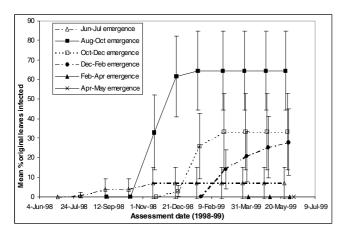


Figure 3. Mean incidence of leaves infected by *P. eucalypti* on different aged sets of current season's juvenile foliage at Douthetts Block, 1998–99 (with 95% confidence limits)

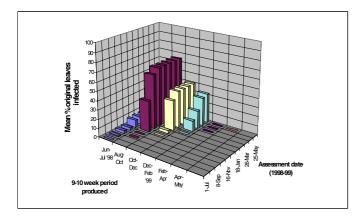


Figure 4. Mean incidence of leaves infected by *P. eucalypti* on different aged sets of current season's juvenile foliage at Douthetts Block, 1998–1999 (means of tree means)

Leaf spotting (incidence, extent, and frequency)

Representative examples of seasonal changes in the incidence of leaves infected by *P. eucalypti* are presented in Figures 3–6. Data from other sites, seasons and foliage types were similar, with minor differences. Confidence limits included in Figure 3 demonstrate the wide natural variation in values from different monitored branches, but for clarity other data are displayed as three-dimensional graphs, without confidence limits (e.g. Fig. 4;

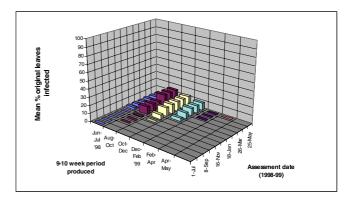


Figure 5. Mean incidence of leaves infected by *P. eucalypti* on different aged sets of current season's adult foliage at Douthetts Block, 1998–1999 (means of tree means)

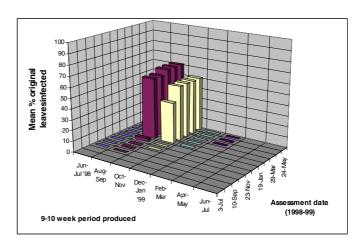


Figure 6. Mean incidence of leaves infected by *P. eucalypti* on different aged sets of current season's juvenile foliage at Coxs Block, during 1998–1999 (means of tree means)

the same data as in Fig. 3). Infection by *P. eucalypti* followed a characteristic developmental pattern. Each season, spots continued to appear on new juvenile leaves 1–3 mo after the emergence of successive complements of juvenile and adult foliage (Fig. 4). The incidence of infected leaves thereafter remained constant. Development on adult leaves was similar, but mean incidence was lower (Fig. 5). At Coxs Block a high incidence of infection was not observed until January (Fig. 6), whereas at Douthetts Block incidence was already substantial in November (Fig. 4; adult foliage behaved similarly at these sites).

The extent of infection (percentage leaf area discoloured) by *P. eucalypti* also varied greatly, with values on many leaves exceeding 50%. However, means were lower, ranging at most up to about 20% at Settlers Block. Graphs of mean leaf area spotted by *P. eucalypti* infection are not shown, but trends followed those of infection incidence. The degree of spotting was comparable on both leaf surfaces, and also appeared similar on opposite sides of the same juvenile leaf node. Spots were yellow when first formed, but gradually turned crimson, and finally in March–April many had become brown with a crimson margin. Unlike incidence, mean percentage current adult leaf area spotted by *P. eucalypti* was of a magnitude similar to that on equivalent sets of current juvenile foliage, at the same times during the monitoring period.

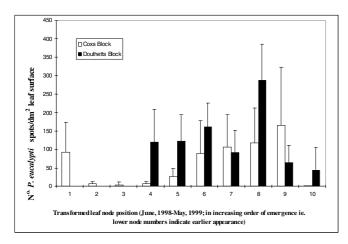


Figure 7. *P. eucalypti* spot frequency on leaves of one primary, current season's juvenile shoot axis, on each of 8 or 9 random trees at Douthetts and Coxs Blocks, respectively, May 1999 (number of spots dm⁻² leaf surface; means of tree means and 95% confidence limits)

Frequency of spots caused by *P. eucalypti* was low on older current season's foliage at Coxs Block in May 1999, but high on younger, more recently emerged leaves (Fig. 7). There appeared to be a similar trend at Douthetts Block (colonies were most numerous at the eighth equivalent node), but the oldest foliage had been shed prior to sampling. Spots were immature and still developing when assessed at the equivalent node positions 9 and 10.

On remaining previous year's (1997–1998) juvenile foliage, extent and incidence of spotting by *P. eucalypti* were both lower at Coxs than at Douthetts Block in June 1998, at the start the 1998–1999 monitoring season. Spotting was greater on the younger juvenile foliage set produced 'later' in the previous season. At Douthetts Block, mean incidence of 'later' leaves infected was about 50% in June 1998, and mean percentage leaf area of *P. eucalypti* spots was 10%. Mean values on equivalent foliage at Coxs Block did not exceed 5% incidence and 1% of leaf area. Incidence and extent of spotting remained constant while leaves remained during the monitoring period.

Spotting of the current (1998–1999) season's foliage by *M. cryptica* followed a pattern similar to that of *P. eucalypt*, except that virtually no spotting by this species was found on adult foliage at any site or season. Mean incidence of infected current juvenile leaves produced after August reached 40% in November–December at Douthetts Block, but the same foliage complement did not reach an equivalent high incidence at the inland Coxs Block until January. Despite its high incidence, mean percentage leaf area discoloured by this fungus did not normally exceed 5% on current juvenile foliage at most sites.

Mean extent of infection by *M. cryptica* was also less than 5% leaf area discoloured on the still-present previous year's (1997–1998) foliage at Coxs and Douthetts Blocks during the 1998–1999 monitoring season. Mean incidence of infection was lower at Coxs Block (up to 20% on 'later' foliage) than at Douthetts Block (up to 40% on equivalent foliage).

Besides *P. eucalypti* and *M. cryptica*, small amounts of the fungus *Phaeothyriolum microthyrioides* (G. Winter) H.J. Swart

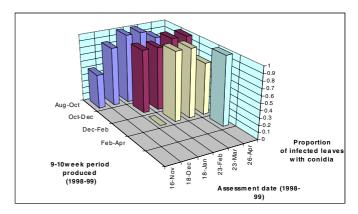


Figure 8(a). Incidence of *P. eucalypti* conidial production on different aged sets of current (1998–1999) season's juvenile foliage at Coxs Block, during 1998–1999 (means of tree means)

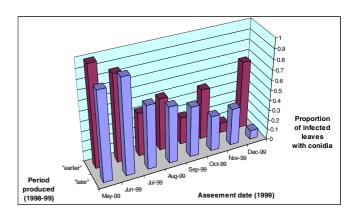
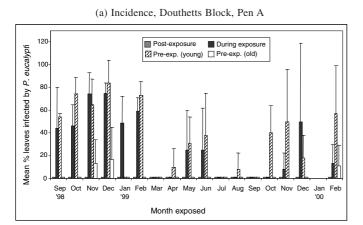


Figure 8(b). Incidence of *P. eucalypti* conidial production on two sets of 1998–1999 juvenile foliage at Coxs Block, later in 1999

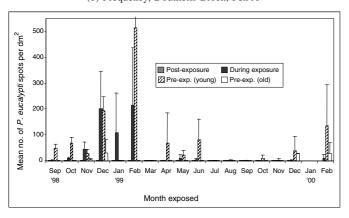
(synonym, *Microthyrium eucalypti* Henn.) were commonly observed on some still-retained previous season's and oldest current season's leaves at a number of blocks. This species was sometimes associated with minor local leaf tissue yellowing, but incidence was not recorded.

Spore production

Conidia of P. eucalypti were produced on the abaxial surface of infected juvenile leaves throughout the year right from the start of the season (Figs 8a,b; results were similar in other blocks). They were already present as soon as spots appeared on each complement of new foliage (initially within about eight weeks of leaf emergence). Conidia were observed on both yellow and crimson spots (including those on residual previous year's leaves), but were not detected once crimson spots had turned brown. From March 1999, onwards, conidia of P. eucalypti were found only within pycnidia and not also as extruded masses on the leaf surface, as in previous months. Incidence of *P. eucalypti* conidia declined later in the season. However, conidia were still found right through winter and on into early summer on residual leaves still present after more than 1 y, overlapping with the emergence of the next season's new foliage (Fig. 8b, October–December). Pycnidia and conidia of P. eucalypti were not recognised in the samples of leaf litter collected in May, even after damp incubation.



(b) Frequency, Douthetts Block, Pen A



(c) Extent, Douthetts Block, Pen A

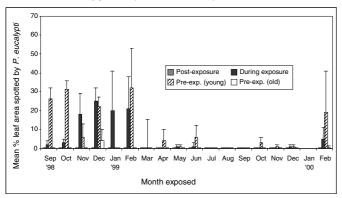


Figure 9. Infection by *P. eucalypti* on different sets of current juvenile foliage on potted 3-mo-old seedlings of *E. nitens* exposed to natural infection in different months, 1998–2000 (in each month, youngest leaves to left; means and 95% confidence limits)

Ascospores of *M. cryptica* were first observed in fruitbodies several months after the emergence of each set of new leaves, about the same time or slightly later than conidia of *P. eucalypti*. Fruitbodies were initially detected as tiny incipient pseudothecia, without ascospores, situated beneath stomata, often clustered along leaf veins (conidial and spermagonial fructifications were not recorded). Incidence of leaves with fertile fruitbodies was steady throughout summer, and also continued on into the new season, until leaves were shed. There was sometimes a slight reduction in the winter incidence of infected leaves with fertile ascocarps. Ascospores of *M. cryptica* were found on the sample of leaf litter collected in May, both before and after damp

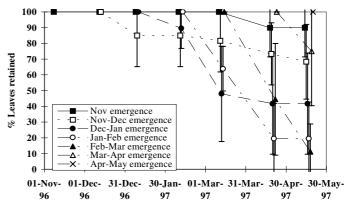


Figure 10. Retention of different aged sets of current season's juvenile foliage at Knights Block, assessed on different dates during 1996–1997 (means of tree means, with 95% confidence limits)

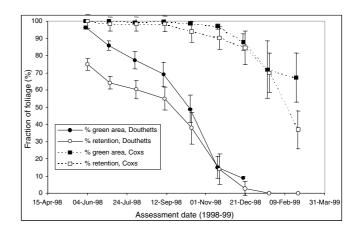


Figure 11. Mean percentage of green surface and retention of previous season's juvenile foliage at two blocks during 1998-99 (means of tree means, with 95% confidence limits; 'early' and 'later' sets combined)

incubation, as were conidia of *Microsphaeropsis conielloides* B. Sutton.

Infection period

Foliage on 3-mo-old potted seedlings became naturally infected in each pen at both sites throughout much of the 18-mo monitoring period between September 1998 and February 2000 (Fig. 9a,b,c). Results are shown for one pen at Douthetts Block, but results were similar in all pens at both blocks, except that values tended to be smaller at Coxs Block. Infection was distinctly lower between April and September 1999, being virtually absent in the coldest months, from July. Almost all infection occurred on the younger pre-exposure and during-exposure foliage classes (i.e. foliage less than 2.5 mo old when returned from the field. In fact, within the first of these classes, infection predominated on the younger leaves produced less than 8, and mostly 3–5 weeks, prior to exposure. Natural infection on the older seedlings, monitored after January at Douthetts Block, followed a similar pattern. On these plants only the last 2-3 pre-exposure leaf pairs became infected, with some exceptions. Apart from one leaf, no control plants became infected, and foliage produced after seedlings were returned from the field remained free of infection (with minor exceptions). No leaf spots were produced by Mycosphaerella

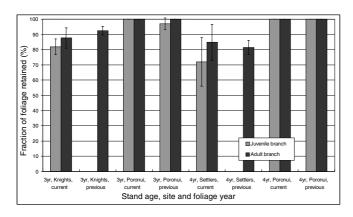


Figure 12. Percentage green leaf area on retained current and previous years' juvenile (grey bars) and adult (black bars) foliage at three sites in May, 1997 (means of tree means, with 95% confidence limits)

cryptica on any seedlings. Mild infection by the powdery mildew fungus Sphaerotheca alchemillae (Greville) Junell was observed on young plants in January 1999, became more extensive during April and May, and was thereafter present on a proportion of the younger seedlings throughout the remainder of the study period. Mildewed leaves were not evaluated, except in a few cases when infection by P. eucalypti was clearly visible. Because of this, data in later months are sometimes derived from only one seedling (indicated by an absence of error bars on non-zero values in Fig. 9). Powdery mildew did not occur on the foliage of the older seedlings.

Discoloration and defoliation

In coastal stands, percentage green leaf area on current juvenile foliage decreased appreciably, and many leaves were shed before they were a year old (Fig. 10). At these sites younger sets of current foliage were sometimes shed while older current leaves remained (Fig. 10). At the inland Coxs Block, discoloration and defoliation were less severe on all foliage types assessed (current and previous years' juvenile; adult current). At coastal locations, remaining previous season's foliage underwent a rapid decline in green leaf surface area during October–December, coincident with increased defoliation (Fig. 11). This was soon followed by the appearance of epicormic shoots. At Coxs Block shedding of the previous season's foliage was much less severe and did not occur until later in the season, following a period of vigorous spring-summer growth higher in the crown (Fig. 11).

Comparison between inland and coastal sites

Trees at Poronui Station Block appeared healthy in May 1997, and had lost few leaves. All foliage was green (Fig. 12), and there was only a trace of infection by the two fungi. On trees at Knights and Settlers Blocks near the coast, infection and foliage discoloration were significant, and were typical of the situation recorded in the same blocks during the field monitoring studies. Trees in the coastal stands retained only about half the current season's juvenile foliage still present on those of the same age at Poronui (Fig. 13). The coastal trees retained even less current adult foliage (not shown), and had lost virtually all the previous year's juvenile foliage (Fig. 13).

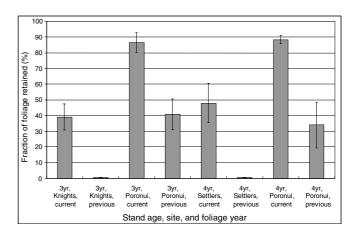


Figure 13. Percentage current and previous seasons' foliage retained on primary order juvenile branches at three sites in May 1997 (means of tree means, with 95% confidence limits)

Climate monitoring

Climate data recorded at the Douthetts and Coxs field monitoring sites during 1998–1999 are summarised in Tables 1 and 2. Temperatures at the inland Coxs Block were consistently lower than comparable values at the coastal site, but both were of similar order to longer-term data from nearby locations (Table 3). Much of New Zealand experienced very dry conditions during the 1998– 1999 summer; the five-monthly, January–May rainfall at Douthetts Block (367 mm) was lower than the regional averages (Table 3; rainfall was not monitored after June at this site), but adequate rainfall was recorded at Coxs Block (757 mm, January-May). Leaf wetness over this period, inclusive of condensation at night, appeared ample at both sites. Leaves were wet for 37% and 31% of the total available hours at Douthetts and Coxs Blocks respectively, during January-May (comparable values for the warmer daylight hours only were 29% and 26% respectively; Tables 1, 2).

Discussion

Phaeophleospora eucalypti is now widespread on eucalypt hosts throughout New Zealand, though not yet documented in the cooler southern half of the South Island. This fungus is believed to be the cause of septoria leaf blight in young stands of E. nitens in regions such as the coastal Bay of Plenty and parts of Northland. A consistent association of severe infection with discoloration and premature defoliation on many sites, regardless of the incidence of Mycosphaerella cryptica, gives strong support for the view that P. eucalypti is responsible for the disease. Heather (1961), in inoculation studies with E. dalrympleana Maiden and E. viminalis Labill., demonstrated that P. eucalypti is the cause of the characteristic yellow leaf spotting symptoms associated with this fungus, and in one experiment observed premature leaf necrosis and defoliation in inoculated but not control plants (though in the last study he was unable to confirm unequivocally that infection had occurred). In addition, leaves protected from infection by repeated fungicidal dipping were healthier and retained longer than heavily infected, untreated leaves on adjacent equivalent shoots on the same diseased trees at a coastal site in

 $\textbf{Table 1.} \ \textbf{Monthly climate data recorded at Douthetts Block, December 1998-October 1999} \\ ^{1}$

			Tem	perature ((°C)			Lea	f wetness p	eriod (h)		D 1 4
Month	Mean	Mean daily minim.	Extreme minim.	Mean daily maxim.	Extreme maxim.	Mean daily ²	Mean nightly ²	Tota	ıl Day ²	Night ²	Rainfall (mm)	Relative humidity (%)
Dec ³	19.4 (±5.7)	15.0 (±3.0)	6.1	28.0 (±2.2)	32.0			204	_		45	77 (±20)
Jan	20.7 (±5.0)	15.0 (±3.0)	8.1	28.3 (±2.7)	33.2	23.5 (±4.8)	17.9 (±3.4)	340	110	230	78	81 (±18)
Feb	18.8 (±5.4)	12.2 (±2.6)	5.7	27.5 (±1.9)	30.7	22.0 (±5.1)	15.5 (±3.4)	282	93	189	24	78 (±20)
Mar	18.9 (±4.9)	13.7 (±3.1)	7.1	26.6 (±2.7)	31.1	21.3 (±5.1)	16.4 (±2.9)	269	112	158	111	86 (±18)
Apr	14.7 (±5.0)	9.6 (±3.9)	0.1	22.3 (±2.6)	27.2	17.1 (±4.9)	12.3 (±3.7)	229	103	126	85	85 (±17)
May	12.8 (±5.1)	8.1 (±4.7)	2.7	20.2 (±2.1)	24.2	15.1 (±4.6)	10.4 (±4.4)	216	102	114	69	89 (±17)
Jun	9.7 (±4.9)	5.3 (±3.3)	-0.3	17.3 (±2.3)	12.4	12.0 (±1.9)	7.5 (±3.6)	190	953	96 ³	82 ³	90 (±15)
Jul	8.8 (±5.3)	3.6 (±4.0)	-2.3	17.2 (±2.2)	13.7	11.4 (±2.0)	6.2 (±4.1)		_	_	_	90 (±16)
Aug	9.3 (±5.0)	3.6 (±2.4)	-1.6	17.6 (±2.2)	22.7	12.2 (±1.5)	6.3 (±2.9)		_	_	_	86 (±18)
Sep	11.9 (±5.5)	5.9 (±3.3)	-0.9	20.7 (±2.7)	27.9	15.4 (±1.7)	8.3 (±3.0)		_	_	_	83 (±19)
Oct ³	14.4 (±5.2)	8.5 (±3.9)	1.2	22.0 (±3.0)	27.9	18.0 (±2.1)	10.8 (±2.8)		_	_	_	82 (±19)

Table 2. Monthly climate data recorded at Coxs Block, December, 1998–October, 1999¹

			Temp	perature ((°C)			Leaf w	etness pe	eriod (h)		Relative
Month	Mean	Mean daily minim.	Extreme minim.	Mean daily maxim.	Extreme maxim.	Mean daily ²	Mean nightly ²	Total	Day ²	Night ²	Rainfall (mm)	humidity (%)
Dec ³	17.5 (±5.2)	11.3 (±3.3)	5.4	24.0 (±3.8)	28.7	_	_	134	_	_	36	71 (±18)
Jan	18.9 (±5.4)	12.9 (±2.7)	7.1	26.5 (±4.0)	32.8	21.6 (±5.4)	16.2 (±3.9)	200	73	127	259	75 (±20)
Feb	16.8 (±5.3)	10.4 (±2.5)	4.0	24.8 (±3.3)	28.7	19.1 (±5.4)	14.5 (±3.9)	132	50	83	30	73 (±19)
Mar	16.4 (±3.8)	12.3 (±2.0)	7.0	22.5 (±2.7)	27.2	18.0 (±4.1)	14.9 (±2.6)	218	91	127	132	84 (±15)
Apr	12.1 (±4.4)	7.9 (±3.4)	1.6	18.0 (±2.8)	23.1	13.6 (±4.5)	10.6 (±3.6)	213	98	115	124	86 (±12)
May	10.3 (±4.2)	6.7 (±4.3)	0.6	15.0 (±2.0)	19.5	11.7 (±2.7)	8.8 (±3.7)	372	167	205	212	88 (±18)
Jun	7.5 (±4.0)	4.7 (±3.9)	-0.9	12.0 (±2.4)	16.8	8.7 (±2.7)	6.4 (±3.7)	334	132	202	164	93 (±8)
Jul	7.1 (±3.7)	3.8 (±3.5)	-2.3	11.9 (±1.7)	15.4	8.4 (±2.2)	5.7 (±3.1)	274	123	151	177	91 (±10)
Aug	6.7 (±3.8)	3.0 (±2.7)	-2.3	12.7 (±2.3)	17.5	8.5 (±1.5)	4.8 (±2.3)	288	140	148	172	88 (±12)
Sep	9.3 (±4.6)	4.6 (±3.5)	-2.7	16.2 (±2.4)	23.8	11.8 (±2.0)	6.8 (±2.7)	205	92	112	228	83 (±16)
Oct ³	11.5 (±4.6)	6.8 (±3.1)	0.22	18.3 (±2.8)	23.1	14.3 (±2.0)	8.6 (±2.9)	127	34	93	82	80 (±15)

¹With standard deviations in brackets

¹ With standard deviations in brackets 2 Day, 0700–1900 h; night, 1900–0700 h 3 Partial months only, December, June (leaf wetness, rainfall), October

²Day, 0700–1900 h; night, 1900–0700 h ³Partial months only, December, October

Table 3. Climate normals for locations in the study region

						Tei	remperature (°C)	G)		Mean rainfall	ıfall (mm)
Station	Latitude (S)	Longitude	Altitude (m)	Days of $\frac{2}{6\pi c^4}$	Mean daily	Mean daily	minimum	Mean daily m	naximum	Louise	Five-month
	(a)	(-)		11031	(y)	January	July	January	July	Amua	(Jan-May)
Tauranga Aerodrome	37°40'	$176^{\circ}12'$	4	8	14.2	14	5	24	14	1348	533
Whakatane	37°58'	$176^{\circ}57'$	2	1	14.3	14	4	24	14	1304	539
Edgecumbe	37°59'	$176^{\circ}50'$	5		13.7	13	4	23	14	1515	628
Te Teko Nursery	38°02′	$176^{\circ}49'$	8	1	14.0	12	ю	25	15	1533	627
Kawerau	$38^{\circ}05$	$176^{\circ}43'$	30	1	14.3	13	4	26	15	1819	742
Rotoehu Forest	37°54'	$176^{\circ}31'$	72		12.9	12	2	23	13	1680	675
Whakarewarewa	$38^{\circ}10'$	$176^{\circ}16'$	307	25	12.5	12	ю	23	12	1511	597
Atiamuri Power Station	38°24'	$176^{\circ}01'$	253	1	12.2	11	1	24	12	1370	492
$Taupo^3$	38°41'	$176^{\circ}04'$	376	39	11.8	11	2	23	11	1199	451
Waimihia Forest	38°50'	$176^{\circ}16'$	743		9.3	8	0	21	8	1704	642

Days with minimum air temperature below 0°C Values for 1998 (Taupo Airport): days of air frost, 38; mean daily minimum temperature, January 11.2°C, July 5.1°C; mean daily maximum temperature, January 23.3°C, July 12.4°C 1941–1970, New Zealand Meteorological Service and New Zealand Year Book (Department of Statistics, Wellington)

the Bay of Plenty district (Ray and Vanner 1997). The impact of the disease on growth has not been quantified.

This study sought to determine the progress of seasonal disease development, and to clarify the environmental conditions promoting it. The phenology of E. nitens is intricate, and the ability to produce juvenile, transitional, adult, and juvenile epicormic shoots enables the crown to respond quickly and efficiently to changing conditions. A difficulty throughout the study was the gradual loss of sample shoots during each monitoring season due to the destruction of terminal buds by tortricid caterpillars. In addition, leaf production eventually ceased on some juvenile shoots as a result of normal redeployment of resources higher in the crown, even though pains were taken to select monitoring branches that would not become shaded by encroaching crowns of adjacent trees during the study. Because of this, a number of bars graphed near the end of each monitoring period are derived from only one or two values (e.g. the tall April-May bar for mature foliage at Douthetts Block, Fig. 2), whereas means determined at the start are based on a greater quantity of data. Despite the complication of shoot attrition, the consistency between results from different sites indicates that real trends were detected (full data are available in the reports of Hood and Gardner 1997; Chapman et al. 1998; Hood et al. 1999). Three measures were used which revealed different aspects of infection. The first, extent of discoloured leaf area, was estimated by the same observer throughout each season to decrease the inherent subjectivity, while the other attributes of incidence of infected leaves and spot density have the advantage of being reasonably objective. The first two variables together depict the progress of the disease, while changes in spot incidence portray the development of the associated fungi.

In the Bay of Plenty–Taupo district, young E. nitens trees produce leaves throughout most of the year (Fig. 2). However, a periodicity is evident, with a brief, dormant or nearly quiescent phase during winter, and a steady increase in production during spring and summer. Conidia of *P. eucalypti* are present throughout the year, but incidence is lower during winter (Figs 8a,b), and availability possibly even less so. Despite some problems with powdery mildew, the results of the infection period study demonstrated that natural infection by P. eucalypti is low later in winter (when, in any case, normally fewer new leaves are available (Figs 9a-c). This is because either available conidia are few or even nonexistent, or the cold conditions are unfavourable for infection to occur (both factors may apply). It therefore appears that new leaves emerging at the start of the season in early spring are exposed to only a low level of spore inoculum from residual infected leaves of the previous season still present on diseased trees. No evidence was found that spores are produced from shed foliage in leaf litter, though this warrants further investigation. The potted seedling study further demonstrated that sets of new leaves are susceptible for only several weeks after emergence, thereafter showing little evidence of new infection. However, conidia, which are soon produced from pycnidia in the newly infected leaves, are released over a significantly longer period. A progressive rise in the level of available inoculum must therefore occur as sets of leaves sequentially emerge, become infected, and in turn continue releasing further conidia. This process may be enhanced by the warming conditions as the season advances. Under a favourable environment the fungus appears to build up





Figure 14. Current shoots with juvenile (upper) and adult foliage (lower), sampled in Coxs Block in February 1999, showing a higher infection frequency by *P. eucalypti* on leaves produced later in the 1998–1999 season

epidemically through spring and summer, as indicated when leaf spot density is used as the measure of successful infection events (Figs 7, 9b; cf. Fig. 14). Spores appear to be wind dispersed, perhaps in aerosols, since a low, widespread incidence of leaf spotting is observed in new plantations slightly less than one year after planting on open farmland coastal sites in the coastal Bay of Plenty district. However, the presence of dry, extruded conidial masses on the leaf surface also suggests that higher density, short distance dispersal may depend on rainfall. The infection rate declines only with the onset of cooler weather, and reduced numbers of available spores and susceptible leaves. Graphs of cumulative data (not shown) indicate that once formed, leaf spots did not increase in area, though spots of different size may occur on separate leaves. Heather (1961) explored the possibility that the host may produce a substance that prevents the fungus spreading further into healthy leaf tissue.

Infection by *Mycosphaerella cryptica* followed a seasonal progression broadly similar to that of *P. eucalypti*, except that virtually no infection occurred on adult leaves (even though a low-to-moderate incidence of *M. cryptica* is known on adult foliage of *E. nitens* in southeast Australia; Dungey *et al.* 1997). In addition, infection of new juvenile leaves in spring may occur as a result of the release of ascospores from leaf litter as well as from still-attached foliage. Observations on *M. cryptica* in this study agreed generally with detailed earlier work of Beresford (1978), Park and Keane (1982, 1987), Cheah and Hartill (1987), and Park (1988a,b). It is unclear why infection by *M. cryptica* was not detected on seedlings during the infection period study, unless possibly natural inoculum density was too low. Dick (1982) and

Dick and Gadgil (1983) have summarised information on *M. cryptica* on eucalypts in New Zealand.

Green leaf area decreased to a greater extent during the monitoring period than could be accounted for by the foliage area infected by these fungi. A general nondescript discoloration often developed prior to defoliation (Fig. 11), possibly a pre-dehiscence response to infection by trees stressed by disease. Both current and previous season's leaves were often shed prematurely with green zones still present. Younger current season's foliage was sometimes cast before leaves produced earlier in the same season (Fig. 10), perhaps reflecting the heavier incidence of infection that often developed later in the season. Disease stress may also have promoted the death of the tree terminal shoot on a number of individuals scattered through heavily infected, 3- to 4-y-old coastal stands, especially on exposed sites during dry summers. Trees so affected either eventually died, or recovered with the formation of a replacement leader. Heather (1961) found strong indication that plants infected by P. eucalypti transpire more rapidly at night than uninfected seedlings.

In the Bay of Plenty-Taupo region, the disease was most severe nearer the coast, whereas trees in Poronui Block, well inland, were comparatively healthy. Although there is evidence for variation in host susceptibility (Hood et al. 2002), the observed pattern suggests an environmental more than a genetic explanation (cf. also unpublished data of T.M. Withers and E. Hay, New Zealand Forest Research Institute, 2001, pers. comm.). Conditions are warmer at coastal sites (e.g. Douthetts, Settlers and Knights Blocks; cf. stations at Tauranga, Whakatane, Edgecumbe, Te Teko, Kawerau, Rotoehu; Table 3), and cooler inland (Poronui Block; cf. Waimihia). Coxs Block, inland but somewhat nearer the coast, falls between the two extremes with respect to both disease severity and temperature (cf. Atiamuri, Table 3). At in-between sites, disease development may vary in different years, with warmer seasons promoting greater disease development. Moisture is plentiful, and does not appear to be a controlling factor in the study region. Rate of increase of infection is also likely to depend on the level of the previous year's infection, which will dictate the amount of inoculum present at the start of the new season. Warmer conditions may promote infection, reduce host resistance, or do both. In its natural habitat, E. nitens grows at higher elevations in a cooler environment (Miller et al. 1992; Boland et al. 1994; Lindenmayer et al. 1996), and despite its rapid early growth, it may not be suited to the warmer coastal Bay of Plenty district. However, better knowledge is needed on how the disease progresses with tree age. Older stands tend to appear less affected, even though infection may be severe on adult foliage in younger stands on coastal sites where inoculum is plentiful. Present research is seeking to identify disease resistant or tolerant genetic material for planting on sites where conditions are more likely to foster the disease.

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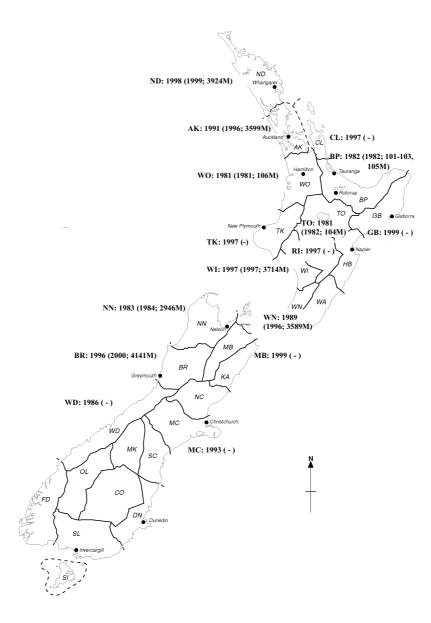
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Appendix

First year of record¹ of *Phaeophleospora eucalypti* in planted *Eucalyptus* in each bioregion of Crosby *et al.* (1976), with additional host records²



Earliest year recorded in the New Zealand Forest Research Institute Limited Forest Health Database or in Herbarium NZFRI-M (earliest year supported by a voucher collection noted in parentheses, with NZFRI-M collection number). Database records confirmed in the laboratory by M. Dick, K. Dobbie, M. Williams, J. F. Gardner, or documented reliably in the field by an experienced observer. Most collections or field records made by officers employed successively as Forest Biology Observers with Forest Biology Survey (New Zealand Forest Research Institute, New Zealand Forest Service); Forest Health Officers with Ministry of Forestry; Forest Health Advisors with Ministry of Agriculture and Fisheries Forest Health Services; and Forest Health Advisors with Vigil Forest Health Advisory Services (New Zealand Forest Research Institute Limited).

²Host records supported by voucher collections, additional to those recorded in Gadgil and Dick (1983), Dick (1982, 1990), comprise: *Eucalyptus aggregata* Deane & Maiden (Hochstetter Forest, B.H. Doherty, Mar 2000, NZFRI-M 4141); *E. aromaphloia* Pryor & Willis (Palmerston North, B. Rogan, Apr 1997, NZFRI-M 3714); *E. benthamii* Maiden & Cambage (Ohope, J.F. Gardner, Jan 2001, NZFRI-M 4419), *E. camaldulensis* Dehnh. (Whangarei, M.R. Twaddle, Feb 2001, NZFRI-M 4418), *E. cordata* Labill. (Whangarei, K. Dobbie, Jan 1999, NZFRI-M 3924); *E. globoidea* Blakely (Wellington, B. Rogan, Nov 1997, NZFRI-M 3768); *E. macarthurii* Deane & Maiden (Palmerston North, T.M. Withers, Apr 2000, NZFRI-M 4142); *E. nicholii* Maiden & Blakely (Auckland, L. Renney, Jun 2001, NZFRI-M 4466); *E. urnigera* J.D. Hook. (Palmerston North, B. Rogan, Feb 1999, NZFRI-M 3946); also *E. viminalis* Labill. (Rotoehu, M. Dick, Jul 1982, NZFRI-M 2527; cf. Dick, 1982). Additional records, confirmed by laboratory examination, without voucher collections, comprise *Eucalyptus grandis* Hill ex Maiden, *E. kitsoniana* Maiden (Section Maidenaria), *E. sideroxylon* Cunn (all Subgenus Symphomyrtus); *E. obliqua* L'Herit. (Subgenus Monocalyptus).