Effects of Isolate and Time of Inoculation on Invasion of Secondary Phloem of *Eucalyptus* spp. and *Banksia grandis* by *Phytophthora* spp.

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ABSTRACT

Shearer, B. L., Michaelsen, B. J., and Somerford, P. J. 1988. Effects of isolate and time of inoculation on invasion of secondary phloem of *Eucalyptus* spp. and *Banksia grandis* by *Phytophthora* spp. Plant Disease 72:121-126.

Inoculated stems were used to compare the growth of isolates of *Phytophthora cactorum, P. cambivora, P. cinnamomi, P. citricola, P. cryptogea* A_1 and A_2, *P. megasperma* var. *sojae, P. nicotianae* var. *nicotianae, P. n.* var. *parasitica,* and *Phytophthora* species identified as unknown by the Commonwealth Mycological Institute in the secondary phloem of *Banksia grandis* and *Eucalyptus marginata.* Only isolates of *P. cinnamomi* grew faster in the phloem of *B. grandis* than *E. marginata.* In *E. marginata,* there were no significant differences in mean extension rates between *P. cactorum, P. cinnamomi, P. citricola, P. cryptogea* A_1 and A_2, *P. n.* var. *nicotianae,* and *P. n.* var. *parasitica.* In contrast, the mean lesion extension rate of 4.98 mm/day for *P. cinnamomi* in *B. grandis* was significantly ($P = 0.05$) greater than the mean rates of 0.11–2.44 mm/day for the other *Phytophthora* species. In *E. marginata,* variation in lesion extension was greatest between isolates of unknown *Phytophthora* species and *P. m.* var. *sojae* and least between isolates of *P. cinnamomi* and *P. cryptogea* A_2. Linear growth rate of the *Phytophthora* species in the two hosts was correlated with tangential growth. Stems of *B. grandis, E. marginata,* and *E. calophylla* were inoculated with *P. cinnamomi* and *P. citricola* in summer, autumn, and winter, and lesion size was assessed 6 wk and 6 and 12 mo after inoculation. Linear and tangential growth of *P. cinnamomi* and *P. citricola* in *E. marginata* was greatest in summer and least in winter. Except for the second assessment after summer inoculation, lesion extension of *P. citricola* in *E. marginata* and *E. calophylla* was consistently, though not always significantly, greater than that for *P. cinnamomi,* with greatest differences between the two *Phytophthora* species occurring in stems assessed in winter. In *B. grandis,* lesions of *P. cinnamomi* were consistently greater than those of *P. citricola.* Lesions of *P. citricola* in *B. grandis* were confined as were lesions of *P. cinnamomi* in the moderately resistant host *E. calophylla.* Infection of secondary tissue of *B. grandis* provides a mechanism for survival and spread of *P. cinnamomi* in the *E. marginata* forest. The *Phytophthora* species with slow rates of growth in *B. grandis* are likely to be confined, and infection of this host is unlikely to favor their survival and spread as much as it does that of *P. cinnamomi.*

Phytophthora cinnamomi Rands is a widespread and destructive root-infecting pathogen in heathlands and the *Eucalyptus marginata* Donn. ex Smith forest of southwestern Australia (8), but it is not the only *Phytophthora* species occurring in this area. *P. citricola* Sawada, *P. cryptogea* Pethybr. & Laff., *P. megasperma* Drechs. var. *sojae* Hildebrand (*P. m.* var. *sojae*), *P. nicotianae* Breda de Haan, and *Phytophthora* species classified as unknown by the Commonwealth Mycological Institute also have been recovered from *E. marginata*-forested areas (11).

Little is known of the susceptibility of native vegetation to *Phytophthora* species other than *P. cinnamomi.* Shearer et al (11) compared the pathogenicity of seven *Phytophthora* species in stems and excised roots of *Banksia grandis* Willd. and *E. marginata. P. cactorum* (Lebert & Cohn) Schroet., *P. cambivora* (Petri) Buism., *P. cinnamomi* (A_2), *P. citricola, P. cryptogea* (A_1 and A_2), *P. m.* var. *sojae,* and *P. nicotianae* var. *parasitica* (Dast.) Waterhouse (*P. n.* var. *parasitica*) grew at a similar rate in secondary tissue of *E. marginata; P. cinnamomi* was the only one that grew faster in *B. grandis* than *E. marginata* (11). *B. grandis* is a dominant understory component of the *E. marginata* forest, occurring as scattered individuals or in localized thickets (10). The rate of growth of a *Phytophthora* species in tissue of this widespread understory species can have an important influence on the epidemiology of the pathogen in the *E. marginata* forest environment (11).

Shearer et al (11) examined one isolate for each *Phytophthora* species tested and inoculated stems on one date. In this study we compared a range of isolates of *Phytophthora* species for their ability to invade phloem of *B. grandis* and *E. marginata.* Because the interaction between a pathogen and host may change with time, we also inoculated *B. grandis, E. calophylla* Lindley, and *E. marginata* with *P. cinnamomi* and *P. citricola* in summer, autumn, and winter and assessed lesion size at different times after inoculation.

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MATERIALS AND METHODS

Experimental design. There were two experiments in which each host-isolate combination was replicated five times.

In experiment 1, hosts (*B. grandis* and *E. marginata*) and isolates were the independent variables with longitudinal and tangential lesion development 6 wk after inoculation as the dependent variables. Isolates of each *Phytophthora* species maintained at 25 C on Difco cornmeal agar are described in Table 1. Where only one isolate could be obtained, the *Phytophthora* species were included for comparison with the previous study (11).

In experiment 2, hosts (*B. grandis, E. calophylla,* and *E. marginata*), *Phytophthora* species (isolate SC72 of *P. cinnamomi* and isolate HI1 of *P. citricola*), inoculation time (summer, autumn, and winter, Fig. 1) and sampling time (6 wk and 6 and 12 mo after inoculation) were the independent variables with longitudinal and tangential lesion development at each sampling time as the dependent variables. *E. calophylla* was included because this host is moderately resistant to *P. cinnamomi* (12); it was not included in experiment 1, because it was difficult to find an area where enough stems of the three hosts suitable for inoculation occur together. *P. cinnamomi* and *P. citricola* were chosen for comparison because they were the most frequently recovered *Phytophthora* species from *E. marginata*-forested areas (11).

Inoculation. The site at which stems were inoculated was a gently sloping convex upland area of an ancient lateritic peneplain 320 m above sea level. The Havel vegetation type (5) was mainly S with a T component. The S vegetation type is a broad group occurring on slopes, ridges, and plateaus with gravel in a sandy loam matrix. The T type is characterized by dense stands of *E. marginata* in free-draining soils of higher fertility than S. The area was covered with an open forest of *E. marginata* and *E. calophylla* with *B. grandis* in the understory. The soils were a loamy to clayey sand with pisolitic gravel 0.5 m thick over a duricrust.

Stems of *B. grandis* (diameter over bark 19–51 mm, mean 30 ± 0.4 mm at point of inoculation) and *E. calophylla* and *E. marginata* (diameter over bark 30–80 mm, mean 55 ± 1 mm at point of inoculation) were wound-inoculated.

Table 1. Isolates of *Phytophthora* species used in pathogenicity studies

Isolate no.[a]	Name	Isolated from[b]	IMI[c] no.	Source[d]	Culture no.
1	*Phytophthora cactorum*	*Diplolaena angustifolia*, WA	129908	DAWA	C1084
2		*Lupinus angustifolius*, WA	129909	DAWA	C1085
1	*P. cambivora*	*Malus sylvestris*, WA	131092	DAWA	C2503
1	*P. cinnamomi* A_2	*Hovea elliptica*, WA		CSIRO	SC57
2		*Hibbertia subvaginata*, WA	264384	CSIRO	SC72
3		*Persoonia longifolia*, WA		CSIRO	SC179
4		*Hypocalymma cordifolium*, WA		CSIRO	SC191
5		*Pultenaea* sp., WA		CSIRO	SC317
1	*P. citricola*	*Eucalyptus marginata*, WA		DCE	DCE236
2		Nursery soil, WA		FDWA	HI1
3		*Pinus radiata* plantation soil, WA		FDWA	327S
4		*P. radiata*, WA		FDWA	15 B-2-6C
5		*Santalum spicatum*, WA		FDWA	GRI3
1	*P. cryptogea* A_1	Pine forest, Qld		DCE	DCE33
1	*P. cryptogea* A_2	Pine forest, SA		DCE	DCE34
2		*P. radiata*, WA		FDWA	227a-R
3		*P. radiata*, WA		FDWA	R21W-3
4		*P. radiata*, WA		FDWA	272-R
5		*S. spicatum*, WA		FDWA	DCE232
1	*P. megasperma* var. *sojae*	*Malus sylvestris* fruit rot, WA	133317	DAWA	C1113
2		*P. radiata*, WA		FDWA	48C3-R
3		*P. radiata*, WA		FDWA	282R8
4		*P. radiata*, WA		FDWA	283R1-2
5		*E. caesia*, WA		FDWA	AHP-1
1	*P. nicotianae* var. *nicotianae*	*E. marginata*, WA		DCE	DCE242
1	*P. nicotianae* var. *parasitica*	*Clianthus speciosus*, WA	147252	DAWA	C2508
2		*E. gomphocephala*, WA	148503	DAWA	C2509
3		*Carthamus*, WA	144150	DAWA	C1755
1	*Phytophthora* spp. Group II[e]	*Melaleuca coccinea*, WA		DCE	DCE165
2	VI	*M. hypericifolia*, WA		DCE	DCE166
3	VI	*P. radiata*, WA	260776	FDWA	359C
4	V or VI	*E. marginata* forest soil, WA	260777	DCE	DCE214
5	VI	Landing soil, WA		DCE	DCE238

[a] Indicates isolate position in Figures 2 and 3.
[b] SA = South Australia, WA = Western Australia, and Qld = Queensland.
[c] Imperial Mycological Institute.
[d] CSIRO = Commonwealth Scientific Industrial and Research Organisation, Forest Research Institute, Kelmscott, Western Australia; DAWA = Department of Agriculture, Western Australia; DCE = Department of Conservation and Environment; and FDWA = Forests Department, Western Australia (now Department of Conservation and Land Management).
[e] Waterhouse (14) group with which the species has greatest affinity.

The inoculation procedure was as described previously (11) with an agar disk containing mycelium of the test fungus being placed in a fresh cut into the phloem and bound. Controls were inoculated with sterile agar disks.

Assessment. Stems were removed from the field, and transverse and longitudinal cuts were made through the point of inoculation with a band saw. The cut surface was trimmed, lesion length above and below the inoculation point was measured, and tangential spread at the inoculation point was estimated. The presence of the test fungus was verified by plating tissue at lesion margins onto selective medium (11). Inadvertently, margins of 12-mo-old lesions of *P. cinnamomi* and *P. citricola* in *E. marginata*, *E. calophylla*, and *B. grandis* were not plated.

The lesion linear extension rate was calculated by averaging the lesion lengths above and below the inoculation point and dividing by the number of days. Correlation coefficients and analysis of variance were determined (9).

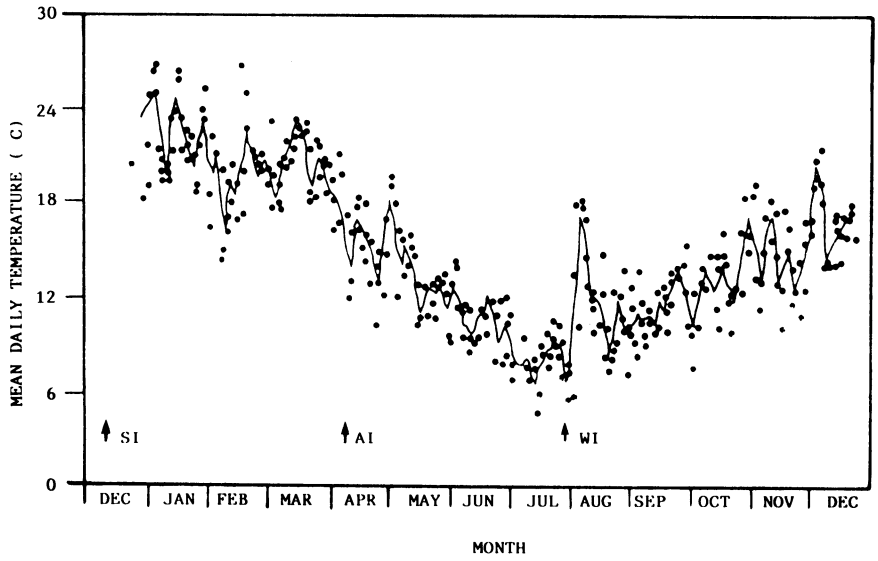

Fig. 1. Seasonal changes in the temperature of stems of *Eucalyptus marginata* and times when the stems were inoculated with *Phytophthora* species. Dots indicate mean daily temperature; the continuous line, a running mean of five. The time of inoculation in summer, autumn, and winter is indicated by SI, AI, and WI, respectively.

Temperature of stem phloem (Fig. 1) was measured by sealing thermistor probes attached to a recorder in holes 5 mm in diameter and 50 mm long drilled at an angle into the phloem of control stems.

RESULTS

Comparison between isolates. According to their linear growth rate in *E. marginata* phloem, the *Phytophthora* species could be divided into two broad groups within which differences among *Phytophthora* species were not significant ($P = 0.05$). Mean extension rates per *Phytophthora* species for *P. cactorum, P. n.* var. *nicotianae, P. citricola, P. n.* var. *parasitica, P. cinnamomi,* and *P. cryptogea* A_1 were between 2.28–4.02 mm/day and significantly ($P = 0.05$) greater than 0.65–1.80 mm/day for the second group of *P. cambivora, P. m.* var. *sojae, P. cryptogea* A_2, and unknown *Phytophthora* species (Fig. 2). Lesions in stems inoculated with *Phytophthora* species were significantly greater than those in stems receiving control inoculations.

Variation in lesion extension was greatest between isolates of unknown *Phytophthora* species and *P. m.* var. *sojae* and least between isolates of *P. cinnamomi* and *P. cryptogea* A_2 (Fig. 2). For the unknown *Phytophthora* species and *P. m.* var. *sojae*, the extension rates of two isolates were similar to those of *P. cinnamomi* although the extension rates of three of the isolates were less than those of *P. cinnamomi.* The two isolates of unknown *Phytophthora* species with extension rates similar to those of *P. cinnamomi* in *E. marginata* were both isolated from *Melaleuca* species, but they were not from the same Waterhouse (14) group (Table 1, Fig. 2). The two isolates of *P. m.* var. *sojae* with similar extension rates to *P. cinnamomi* were isolated from different hosts (Table 1, Fig. 2).

Growth of isolates of the *Phytophthora* species in the secondary phloem of *B. grandis* was different from that in *E. marginata* (Fig. 2 and 3). *P. cinnamomi* grew faster while the other *Phytophthora* species grew slower in *B. grandis* than in *E. marginata.* The mean lesion extension rate of 4.98 mm/day for *P. cinnamomi* in *B. grandis* was significantly ($P = 0.05$) greater than mean rates of 0.11–2.44 mm/day for the other species (Fig. 3). Variation in lesion extension in *B. grandis* between isolates was greatest for *P. cinnamomi, P. n.* var. *parasitica,* and unknown *Phytophthora* species and least for *P. citricola, P. cryptogea* A_2, *P. m.* var. *sojae*, and *P. cactorum.* For *P. cinnamomi* and unknown *Phytophthora* species, growth of isolates in *B. grandis* was correlated with growth in *E. marginata* ($R^2 = 0.92$ and 0.91, respectively, $P = 0.01$). For isolates of *Phytophthora* species other than *P. cinnamomi* and unknowns, lesion extension in *B. grandis* was not correlated with lesion extension in *E. marginata.*

Plotting growth rate in *B. grandis* against growth rate in *E. marginata* best illustrates the differences in behavior of the *Phytophthora* species in secondary phloem of the two hosts (Fig. 4). If growth rates in *B. grandis* were greater than in *E. marginata*, the points would fall below the 45° bisector and above for the converse. *P. cinnamomi* was the only species tested that grew faster in the phloem of *B. grandis* than in that of *E. marginata* (Fig. 4).

Differences among isolates of the *Phytophthora* species were similar for both tangential and longitudinal growth. In both hosts, tangential growth was correlated with linear growth rate ($R^2 = 0.82$ and 0.71 for *B. grandis* and *E. marginata*, respectively, $P = 0.01$).

P. cinnamomi, P. cryptogea A_1, and *P. n.* var. *parasitica* were readily recovered from both hosts while the

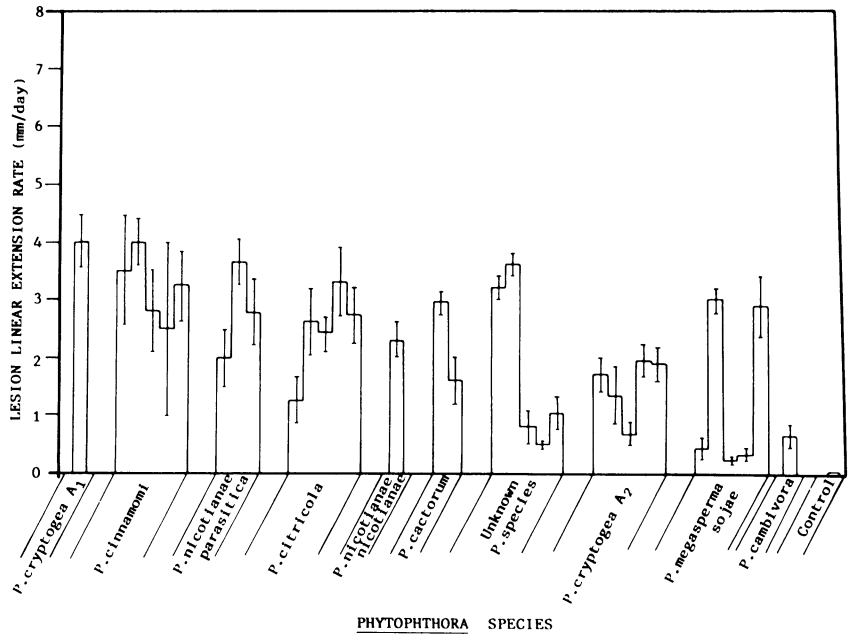

Fig. 2. Lesion linear extension rate 6 wk after summer inoculation of stems of *Eucalyptus marginata* with isolates of *Phytophthora* species. Values are the mean of five replicates, with bars indicating the standard errors of the means.

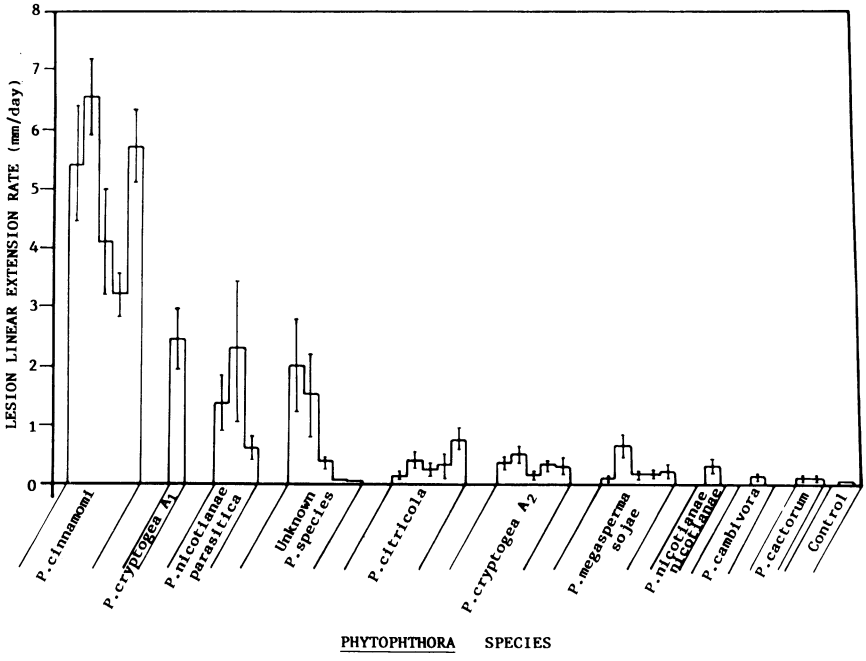

Fig. 3. Lesion linear extension rate 6 wk after summer inoculation of stems of *Banksia grandis* with isolates of *Phytophthora* species. Values are the mean of five replicates, with bars indicating the standard errors of the means.

other species were recovered more frequently from *E. marginata* than *B. grandis*. There was a low frequency of recovery of *P. cambivora* from both hosts. *Phytophthora* species that grew the fastest in *E. marginata* and *B. grandis* were more frequently recovered from *B. grandis* than species with slow rates of growth; recovery from *B. grandis* was positively correlated ($P = 0.01$) with rate of lesion extension in *E. marginata* and *B. grandis* ($R = 0.67$ and 0.58, respectively, $P = 0.01$). No *Phytophthora* species were isolated from controls.

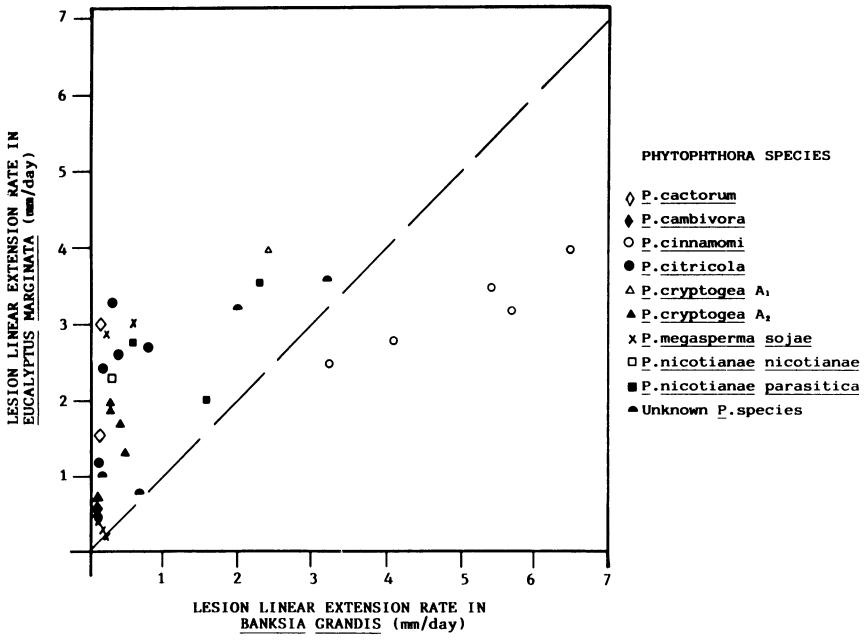

Fig. 4. Relationship between lesion linear extension rate of *Phytophthora* species in secondary phloem of stems of *Banksia grandis* and *Eucalyptus marginata* determined 6 wk after summer inoculation. Broken line indicates the 45° bisector.

Table 2. Tangential spread of *Phytophthora cinnamomi* and *P. citricola* after inoculation of stems of *Eucalyptus marginata, E. calophylla*, and *Banksia grandis* in summer, autumn, and winter and assessment three times after inoculation

Host	Inoculation	Assessment (months)	Tangential spread (degrees)	
			P. cinnamomi	*P. citricola*
Eucalyptus marginata	Summer	1.5	210 ± 65[a]	252 ± 31
		6	254 ± 60	360
		12	256 ± 41	359 ± 1
	Autumn	1.5	169 ± 51	298 ± 35
		6	204 ± 44	325 ± 20
		12	156 ± 20	254 ± 38
	Winter	1.5	48 ± 20	165 ± 22
		6	46 ± 6	212 ± 54
		12	143 ± 42	199 ± 33
E. calophylla	Summer	1.5	106 ± 65	271 ± 38
		6	162 ± 25	122 ± 18
		12	99 ± 28	169 ± 35
	Autumn	1.5	109 ± 17	164 ± 58
		6	133 ± 34	223 ± 62
		12	101 ± 22	252 ± 39
	Winter	1.5	29 ± 6	57 ± 12
		6	48 ± 7	138 ± 56
		12	48 ± 10	165 ± 40
Banksia grandis	Summer	1.5	360	206 ± 44
		6	360	...[b]
		12	360	181 ± 33
	Autumn	1.5	316 ± 27	178 ± 40
		6	360	198 ± 45
		12	360	240 ± 36
	Winter	1.5	95 ± 27	95 ± 29
		6	360	102 ± 26
		12	360	132 ± 34

[a]Standard error of the mean.
[b]No assessment.

Effects of time of inoculation and assessment. Longitudinal and tangential lesion extension of *P. cinnamomi* and *P. citricola* in *E. marginata* was greatest in summer and least in winter (Fig. 5, Table 2). Except for the second assessment after summer inoculation, lesion extension of *P. citricola* was consistently, though not always significantly, greater than that of *P. cinnamomi*, with greatest differences occurring in winter.

P. cinnamomi established in stem phloem of *E. calophylla* at all three inoculation times, but lesions were confined and did not increase with time after inoculation (Fig. 5, Table 2). In summer, *P. citricola* established and grew in *E. calophylla* similar to *P. cinnamomi*, but in autumn and winter, lesions of *P. citricola* increased with time after inoculation. Although *P. cinnamomi* rapidly invaded stems of *B. grandis*, *P. citricola* did not (Fig. 5, Table 2); not all estimates of lesion size are shown in Figure 5 because *P. cinnamomi* rapidly girdled stems of *B. grandis* (Table 2) and lesion length could not always be accurately determined in dead tissue. Lesions of *P. citricola* in *B. grandis* were confined (Fig. 6) and did not increase with time after inoculation. The pattern of lesion development of *P. citricola* in *B. grandis* was similar to *P. cinnamomi* in *E. calophylla* (Fig. 5). The two *Phytophthora* species could be recovered from 6-wk- and 6-mo-old lesions in the three hosts.

DISCUSSION

Stems instead of roots were inoculated with the different *Phytophthora* species because stem inoculations enhance differences in susceptibility among hosts (12). Furthermore, inoculation of stems overcomes the problems of large variation in root size and the large amount of labor needed to excavate enough roots for adequate replication. In previous work (11), growth of *Phytophthora* species in excised roots under controlled conditions was correlated with growth in intact stems in the field.

Most of the *Phytophthora* species grew at a similar rate in secondary tissue of *E. marginata*, but in *B. grandis*, lesions caused by *P. cinnamomi* expanded at a faster rate than those caused by other *Phytophthora* species. This confirms previous work (11), with a wider range of isolates and environmental conditions. Brown (1) found similar pathogenicity of *Phytophthora* species in *Eucalyptus* after assessing inoculated seedlings for root damage and determining reisolation frequency.

Pathogenicity of *Phytophthora* species in stems of *B. grandis* and *E. marginata* in summer may reflect the suitability of host tissue for growth and the effect of active host resistance. In stems assessed 6 wk after inoculation, *P. cinnamomi* probably utilized secondary tissue of *B. grandis*

better than the other species. Within this period, *P. cinnamomi* rapidly invaded and girdled stems of *B. grandis* and there was no evidence of host resistance before death. In contrast, *P. citricola* grew much slower in *B. grandis* than *P. cinnamomi*, and with time, active host resistance confined lesions. In *B. grandis*, lesions of *Phytophthora* species that grew slower or at the same rate as *P. citricola* would probably be confined with time.

In summer, confinement of lesions of *P. cinnamomi* and *P. citricola* in *E. calophylla* was similar to that described by Tippett et al (12). For *Phytophthora* species with the same rate of growth as *P. cinnamomi* in *E. marginata,* the outcome of the interaction may be comparable to that described by Tippett et al (13) for *P. cinnamomi.*

That *P. citricola* formed longer lesions than *P. cinnamomi* in stems of *E. calophylla* and *E. marginata* inoculated in autumn and winter may in part be the result of different growth responses of the two *Phytophthora* species to temperature. In *E. marginata*, the growth rate of *P. citricola* was greater than that of *P. cinnamomi* at temperatures lower than 15 C (11). Low temperatures in winter and autumn may have inhibited growth of *P. cinnamomi* more than growth of *P. citricola.*

Alternately, *E. calophylla* may be less resistant to invasion by *P. citricola* than by *P. cinnamomi*, especially under conditions unfavorable for rapid host response such as cool temperatures in autumn and winter. That *P. citricola* killed water-logged seedlings of *E. calophylla* in summer in a nursery (B. L. Shearer, *unpublished*) lends support to this conclusion. More information is needed on the effects of environment on the relative susceptibility of *E. calophylla* to a range of *Phytophthora* species.

For all *Phytophthora* species where more than one isolate was tested, variation in virulence to *E. marginata* was observed. However, there was no significant difference in extension rates between isolates of *P. cinnamomi* and four of the five isolates of *P. citricola* and *P. cryptogea* A_2 in secondary phloem of *E. marginata* after wound inoculation. Our results differ from tests by Marks and Kassaby (6) where isolates of *P. cinnamomi* caused greater root damage than those of *P. citricola* and *P. cryptogea* when a small amount of inoculum was buried in soil at the edges of pots containing seedlings of *E. oblique* L'Herit. and *E. sieberi* L. Johnston. Direct comparison between the two studies is difficult because of different techniques and hosts.

In *E. marginata*, greatest variation in extension rate occurred between isolates of the unknown *Phytophthora* species and *P. megasperma* var. *sojae.* Large variation in virulence between unknown *Phytophthora* species is not unexpected because the isolates may be different species. That the growth of two of the unknown *Phytophthora* species in *E. marginata* was not significantly different from that of *P. cinnamomi* is of concern, especially when their identity remains unknown. Though the isolates of *P. m.* var. *sojae* tested in *E. marginata* showed considerable variation in virulence, there was no evidence of the host specificity observed in other host-*P. m.* var. *sojae* isolate combinations (4). One isolate that showed greatest lesion extension in *E. marginata* was isolated from a *Eucalyptus* species; the other was from *Pinus radiata.* Although two of the isolates of *P. m.* var. *sojae* in *E. marginata* had extension rates not statistically different from those of *P. cinnamomi*, three of the five isolates had the lowest extension rates of all isolates tested. Slow growth of isolates of *P. m.* var. *sojae* in *E. marginata* agrees with the observation of Newhook and Podger (8) that an isolate of this *Phytophthora* species from an area of dying native vegetation was not pathogenic to *E. marginata*. Because of the large variation in pathogenicity between the isolates of *P. m.* var. *sojae,* occurrence alone cannot be used to assess the threat that this pathogen may pose to native communities without additional information from pathogenicity tests.

The host range of *P. cinnamomi* in southwestern Australia is well known (15), and interspecific variation in the

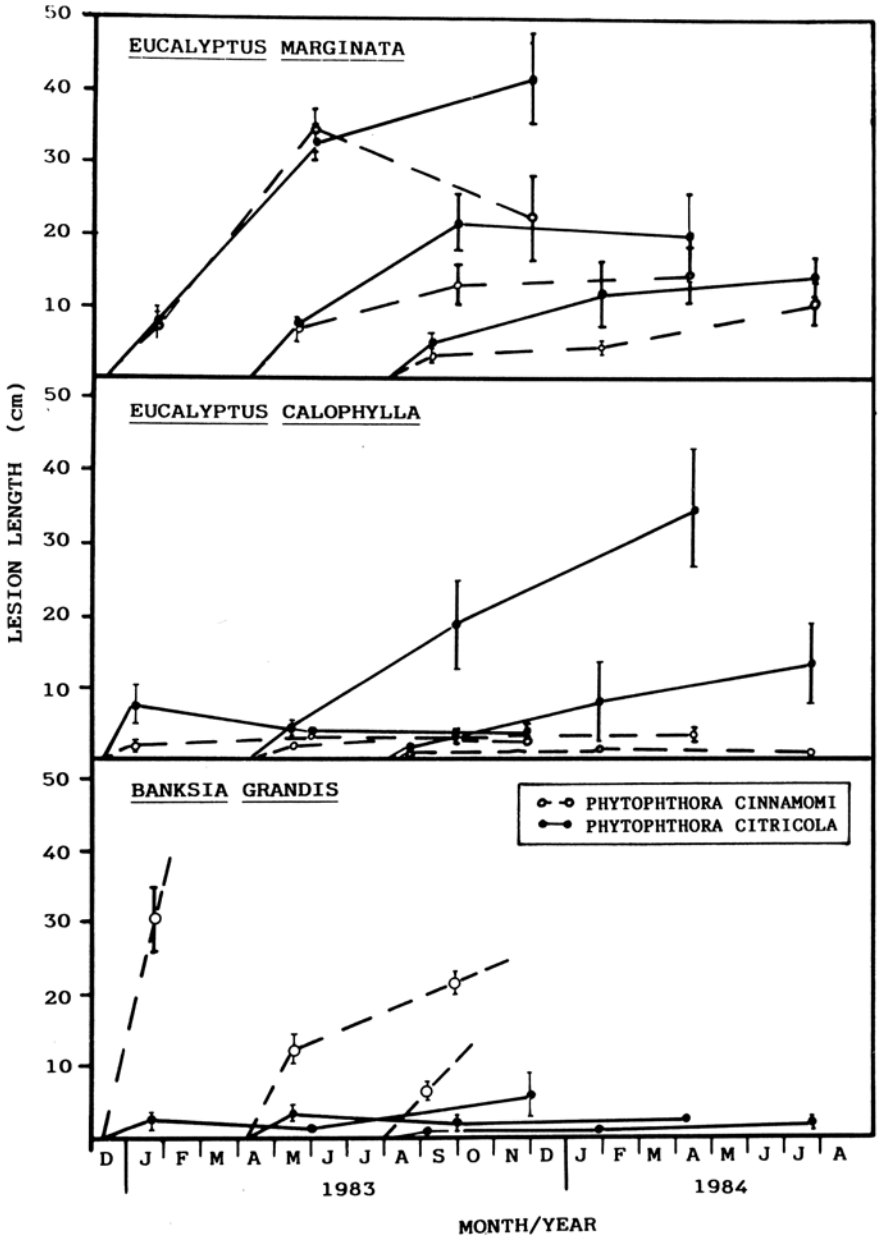

Fig. 5. Lesion lengths determined 6 wk and 6 and 12 mo after inoculation of stems of *Eucalyptus marginata, E. calophylla,* and *Banksia grandis* with *Phytophthora cinnamomi* and *P. citricola* in summer, autumn, and winter (Fig. 1). Values are means of five replicates, with bars indicating standard errors of the means. Lesion assessments at the three times are represented by points on the one line; inoculation times, by the three sets of lines for each host.

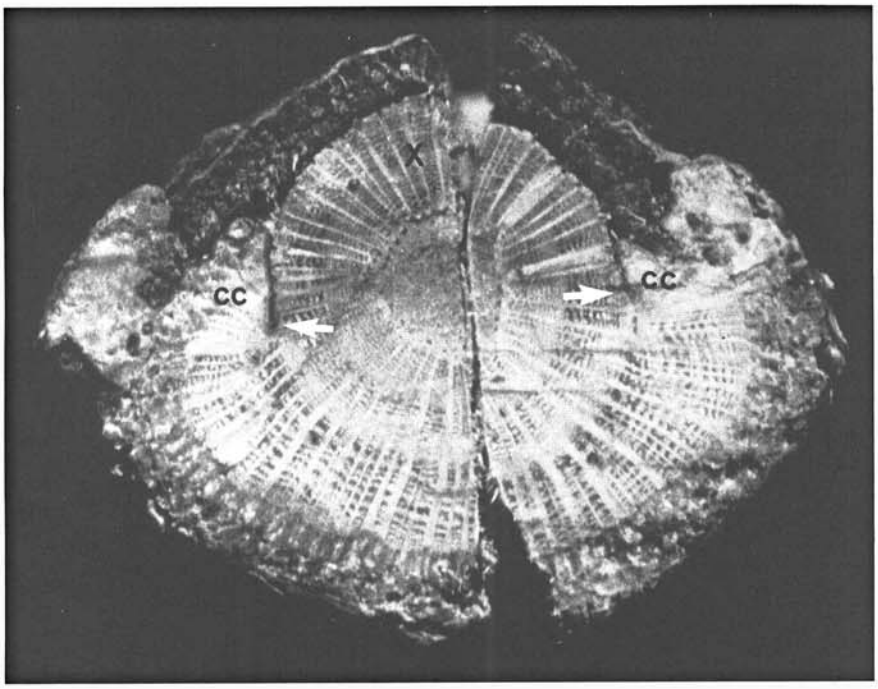

Fig. 6. Confined lesion of *Phytophthora citricola* in a stem of *Banksia grandis* inoculated in autumn and harvested 12 mo after inoculation. Xylem callus curls (cc) had not closed gap where cambium was killed (arrows). The xylem adjacent to killed cambium was discolored (X). Stem diameter over bark was 39 cm.

susceptibility of *Banksia* and *Eucalyptus* species has been determined (1–3,7,12). However, little is known of the susceptibility of native vegetation to infection by *Phytophthora* species other than *P. cinnamomi*. A number of *Phytophthora* species have been recovered from *Banksia* species other than *B. grandis* (3,11). Not all *Banksia* species will have the same differences in susceptibility to a range of *Phytophthora* species as we observed for *B. grandis*.

B. grandis is a widespread understory species throughout the *E. marginata* forest, and the ability of *P. cinnamomi* to rapidly invade the secondary tissue of this host has important implications for the epidemiology of the pathogen in the mediterranean climate experienced in southwestern Australia (10,11). Infection of secondary tissue of *B. grandis* provides a mechanism for survival when surface soil is dry and a reservoir for the production of inoculum when the soil is moist (10). *B. grandis* has an extensive root system that can provide a mechanism for spread through the soil profile when temperatures are favorable for growth but when surface soil is too dry for pathogen development. As lesions of *Phytophthora* species with slow rates of growth in *B. grandis* are likely to be confined, infection of the secondary tissue of this host is unlikely to be as favorable for their survival and dispersal as it is for *P. cinnamomi*. However, the rate of growth of several *Phytophthora* species from different hosts was not significantly different from that of *P. cinnamomi* in secondary tissue of *E. marginata*. The susceptibility of endemic species other than *B. grandis* to these *Phytophthora* species needs to be determined before an accurate evaluation of the relative significance of *Phytophthora* species to the health of native communities in southwestern Australia can be made.

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