Dispersal of *Phytophthora cinnamomi* Through Lateritic Soil by Laterally Flowing Subsurface Water

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ABSTRACT

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Phytophthora cinnamomi was recovered from water flowing at the base of a lateritic soil about 1 m deep and overlying concreted duricrust on a hillslope supporting a severely diseased forest of *Eucalyptus marginata* (jarrah) in south-western Australia. The water was collected by 20-m-long throughflow interception trenches dug down to the duricrust. The fungus also was recovered at depths greater than 2 m from piezometers drawing water perched on clay beneath the duricrust. Most inoculum-bearing water was collected in winter and early spring when deeper soil was warmer than near-surface soil. Collections also were made in autumn and summer following unseasonably heavy rainfall. Subsurface water flowed through the soil at least 120 m down the hillslope following a moderately intense winter rain event. Propagule density averaged 60 propagules per liter on selected days in spring. At least half of the propagules were identified as zoospores.

Rapid, long-distance dispersal of *Phytophthora cinnamomi* Rands is known to occur by the action of flowing surface water (11,25). However, in most soils, the small dimensions and complexity of the pore structure hinder the passive dispersal of fungal spores by percolating water (5). Consequently, subsurface water movement has not often been considered a significant mechanism in the rapid, long-distance dispersal of spores (8).

Shea et al (20) demonstrated the lateral transmission of *P. cinnamomi* zoospores through lateritic soil in an area of severely diseased *Eucalyptus marginata* Sm. (jarrah) forest. They recovered inoculum in water flowing through soil overlying a concreted duricrust horizon 30 cm below the soil surface and 2 m downslope of a trench that had been filled with a water and zoospore suspension.

Disease caused by *P. cinnamomi* in the jarrah forest is most severe on the lateritic ridges and upper slopes where the flow of water over the gravelly surface soils is rare (22). However, perched water tables may develop on the interface between the gravels and the underlying duricrust or clays of duplex soils, resulting in subsurface throughflow of water downslope (3,18). Shea et al (20) postulated that the infrequent episodes of rapid mass decline and death of jarrah may have resulted from the infection and girdling of vertical roots at the surface of the duricrust layer where conditions suited the reproduction and dispersal of *P. cinnamomi.*

There is no information available on the natural dispersal of *P. cinnamomi* inoculum in soils by subsurface water. In this study, the occurrence of *P. cinnamomi* inoculum in subsurface laterally flowing perched water in a lateritic soil of the jarrah forest was determined and related to physical characteristics of the soil profile.

MATERIALS AND METHODS

Study area. The study site was located in an area of jarrah forest severely affected by *P. cinnamomi* near Dawn Creek (lat. 32°50′37″ S, long. 116°5′58″ E), 15 km SSE of Dwellingup in south-western Australia.

The climate of the region is Mediterranean with cool wet winters and warm-to-hot dry summers. The mean annual rainfall at Dwellingup is 1,300 mm, and 80% falls from May through September (7).

The soil profile is deeply weathered laterite comprising a superficial horizon of gravelly sand, typically 0–1 m thick, over duricrust 1–2.5 m, overlying mottled and pallid kaolinitic clay. The average profile depth in the region is more than 30 m (14). Duricrusts are hard, rocklike materials which, in the jarrah forest, commonly take the form of massive pavements, either extensive or as discrete slabs (22).

The area infested with *P. cinnamomi* extended for about 200 m down a hillside (12% slope), from 150 m below the ridgetop to the valley floor. Within this area, most of the jarrah overstory and many understory plants were dead. The remaining canopy cover ranged from 0 to 30% and ground cover from 20 to 40%.

The time course of disease development and spread was determined from black-and-white aerial photographs of the study area. No infection was evident in 1958, the year of the oldest aerial photograph. In 1969, the death of jarrah was evident in the opening of the canopy downslope of a road that angled from the valley bottom to the ridgetop at the southern edge of the site. By 1981, the area of dead jarrah had increased upslope of the road, and by 1984 it had covered the study area.

Soil characterization. The texture of surface soil and soil immediately above the duricrust were characterized by particle-size analysis. Soil samples of about 2 kg were taken from 0 to 10 cm from the surface and from immediately above the duricrust at five locations along 20-m-long trenches in the upper and lower slope positions and at four locations along the midslope trench (Fig. 1). The samples were dry-sieved through 13 mesh sizes ranging from 0.063 mm to 5.6 mm. The particle size limits for the various soil fractions were defined as follows (2): coarse silt, 0.02–0.06 mm; fine sand, 0.06–0.2 mm; medium sand, 0.2–0.6 mm; coarse sand, 0.6–2 mm; and fine gravel, 2–6 mm.

Measurement of subsurface flow. The lateral flow of subsurface water through the soil overlying the duricrust was collected and monitored by throughflow interception trenches. Trenches 20 m long were dug along the contour at upper-, mid-, and lower-slope positions of the study area (Fig. 1). Soil in the trenches was removed down to the duricrust, fissures in the trench floors were concreted, and the downslope trench faces were lined with waterproof plastic film (Fig. 2). The upslope face of the trenches was covered with a screened gravel filter, and the soil was replaced over a bed of gravel. The average depth of the trench floors was 40 cm for the upper slope, 35 cm for the midslope, and 70 cm for the lower slope. Water intercepted by the trenches was piped from drains along the downslope face to tipping bucket gauges. The volume of water collected by the buckets was recorded every 10 min with electronic data loggers.

Measurement of water table above clay. The height of water perched on the clay immediately beneath the duricrust was indicated by a 5-cm-diameter piezometer 20 m upslope from each trench

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(Fig. 1). The slotted end of the piezometer extended 25 cm on each side of the duricrust–clay boundary. The depth to clay was 2.5 m for the upper slope, 2.3 m for the midslope, and 1.6 m for the lower slope. Construction and installation of trenches and piezometers were described by Kinal (10).

Measurement of extent of lateral flow. A conservative estimate of the distance, D, that intercepted water flowed downslope following a discrete rain event was obtained from the relation: D (m) $\times$ 20 (m) $\times$ R (m) = throughflow volume (m^3). D defines the upper extent of the "effective" rectangular catchment area directly upslope from each 20-m-wide trench. R is the depth of rainfall.

D is derived by conceptually distributing the volume of throughflow collected by a trench over the catchment area immediately upslope from the trench, to the depth of rainfall. The actual boundaries of the catchment would be the ridgetop and an upslope extension of the ends of the trenches, assuming that throughflow occurred, on average, in a downslope direction.

Clearly, D is underestimated because some of the rain falling on the actual catchment is not intercepted by the trenches. Some water percolates down through the duricrust to groundwater, some may flow laterally beneath the trenches through fissures in the duricrust, and some may remain in soil storage.

Rainfall measurement. Rainfall was monitored by a tipping bucket rain gauge located on the upper hillslope (Fig. 1). Rainfall volume was recorded every 5 min by an electronic data logger.

Soil temperature measurement. Soil temperatures were monitored hourly throughout 1986 with a thermistor array located adjacent to, and midway between, the upper and mid-trenches with probes at 0.05, 0.25, 0.5, 1.0, 1.5, and 2.5 m depth, and recorded with an electronic data logger (Fig. 1). Daily means were calculated from the hourly readings.

Isolation and identification of *P. cinnamomi*. The presence of *P. cinnamomi* in subsurface water was determined from 500-ml water samples taken from the trenches and piezometers. Throughflow water was collected directly from outflow pipes leading from the trenches. Piezometer water was sampled by lowering a 30-cm-long open-ended PVC tube containing a ball valve at the lower end. This ensured that the water collected was closest to the surface of the water column. Sample bottles and equipment were surface-sterilized with ethanol and rinsed with distilled water prior to use. Samples were collected from November 1984 to October 1986 when perched water was present. Perching and throughflow of water occurred irregularly, depending on the occurrence, intensity, and pattern of rain events and on the position in the landscape.

The water samples were distributed among 10 lots of 50 ml each into styrofoam cups baited with six cotyledons of *Eucalyptus sieberi* L. Johnson floated on the surface (13) and incubated at 25 C. The underside of infected cotyledons showed a color change from a normal reddish hue to green. After 10 days, suspect cotyledons were plated onto modified selective agar (24). The presence of *P. cinnamomi* was determined by microscopic inspection of hyphal morphology and reproductive structures (13). Recovery of *P. cinnamomi* was recorded as the proportions of 10 subsamples that were positive.

The type (zoospores, chlamydospores, oospores, or mycelium) and density of propagules in subsurface water were determined from 250-ml water samples collected from the lowest trench on 17 and 21 October 1986. These samples were distributed among 10 lots of 25 ml, and each sample was plated directly onto 150-mm-diameter plates of selective agar. The plates were incubated in the dark at 25 C. Each distinct colony was assumed to arise from a single propagule.

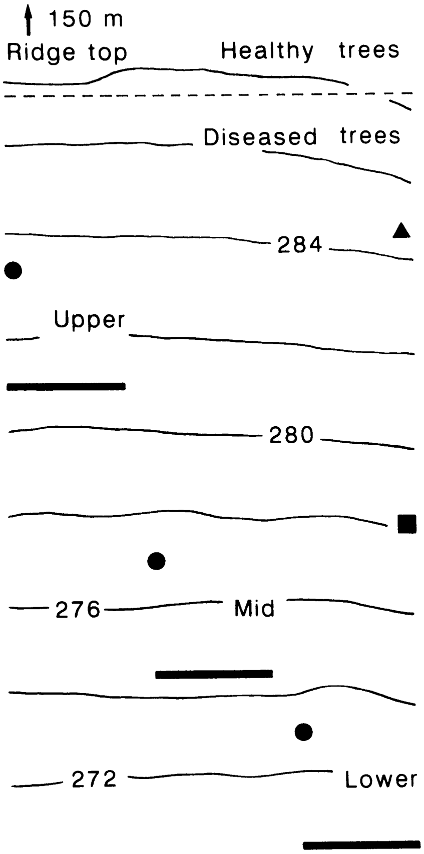

Fig. 1. Location of throughflow interception trenches (bar), piezometers (circle), thermistor array (square), and rain gauge (triangle) on hillslope at Dawn Creek. Contour lines at 2-m intervals show height above sea level.

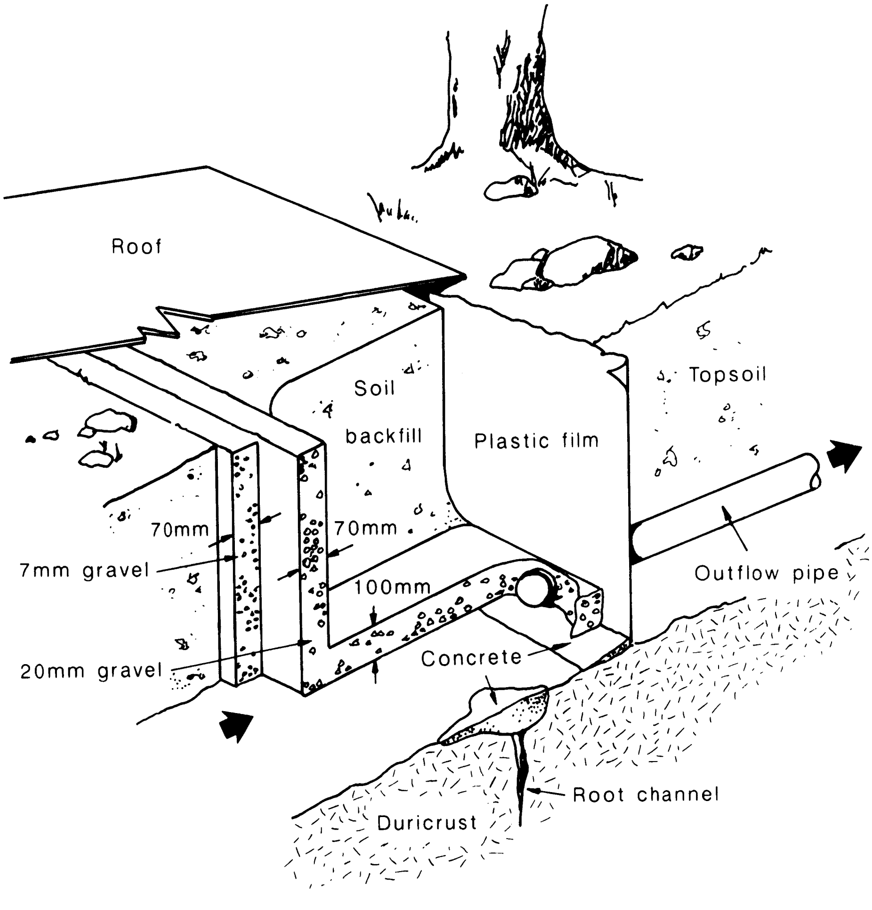

Fig. 2. Schematic cutaway view of throughflow interception trench. Broad arrows show direction of subsurface water flow.

The identity of the propagules was found by tracing the growth of the colonies back to their origin at 250× magnification.

RESULTS

Soil characterization. The soil immediately above the duricrust had a lower fine sand and coarse silt content than did the near-surface layers at all three slope positions (Fig. 3). Conversely, there was a higher coarse sand and fine gravel content in soil above the duricrust than in the near-surface soil.

Soil temperature profile. Daily mean soil temperatures followed a sinusoidal wave pattern through the year (Fig. 4). The amplitude of the annual temperature waves decreased with depth. Consequently, deeper soil was cooler in summer but warmer in winter than near-surface soil when the temperature waves inverted in autumn and spring.

The soil below 1.5 m remained above 15 C except for about 2 mo in late winter–early spring (Fig. 4). The soil below 1.0 m remained above 12 C throughout the year, and the soil below 0.5 m remained above a daily mean of 12 C except for about 1 mo in midwinter.

The range of daily soil temperature change decreased with depth, varying less than 1 C at 0.5 m and almost ceasing at 1 m. In late winter–early spring there were days when the soil down to 0.05 m reached temperatures above 15 C for several hours, although the daily mean for those depths was below 15 C.

Subsurface water flow. The behavior of water flowing across the exposed duricrust in the trenches was observed on several occasions following rain events and before the trench soil was replaced. Throughflow occurred from a zone of saturation in soil immediately above the duricrust. Flow was not uniform across the duricrust but was mostly channeled into streams in valleys, forming an anastomosing network in the microtopography of the duricrust surface. At times, localized seeps in the trench face flowed with a force sufficient to project a 1-cm-thick stream several centimeters from the trench face.

The rates, volumes, and duration of throughflow varied according to rainfall patterns and antecedent soil moisture conditions (10). The potential for subsurface dispersal of inoculum is demonstrated by the hydrological response of the hillslope following a typical, moderately intense winter rain event (Table 1). On 13 July 1985, 65 mm of rain fell over an 18-hr period following two rain-free days. Throughflow from the lower trench continued beyond 5 days, when more rain fell. Subsurface water flowed downslope at least 120 m (Table 1).

Inoculum recovery. Recovery of *P. cinnamomi* from subsurface water depended on the presence of water tables perched on the duricrust and clay hori-

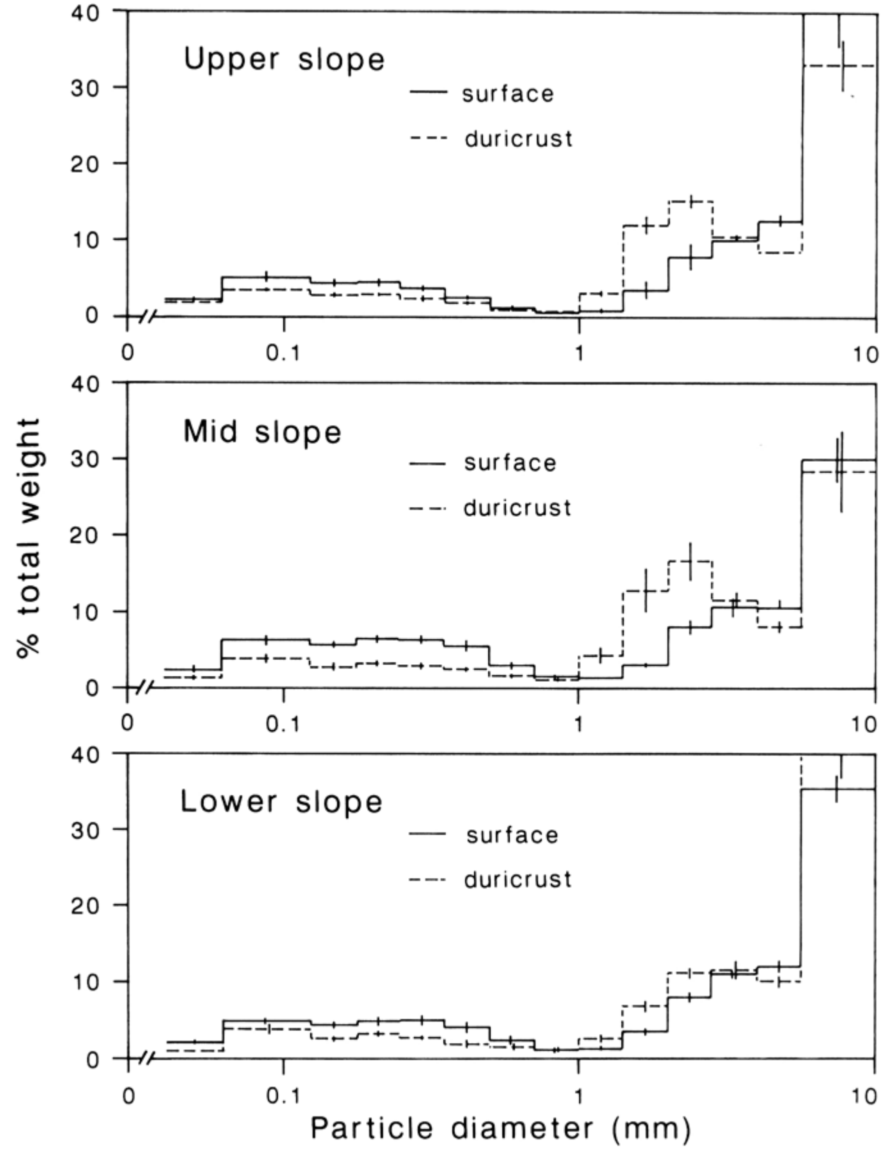

Fig. 3. Particle-size distribution of surface soil compared with soil immediately above duricrust at three elevations of hillslope. Vertical lines = standard error of mean.

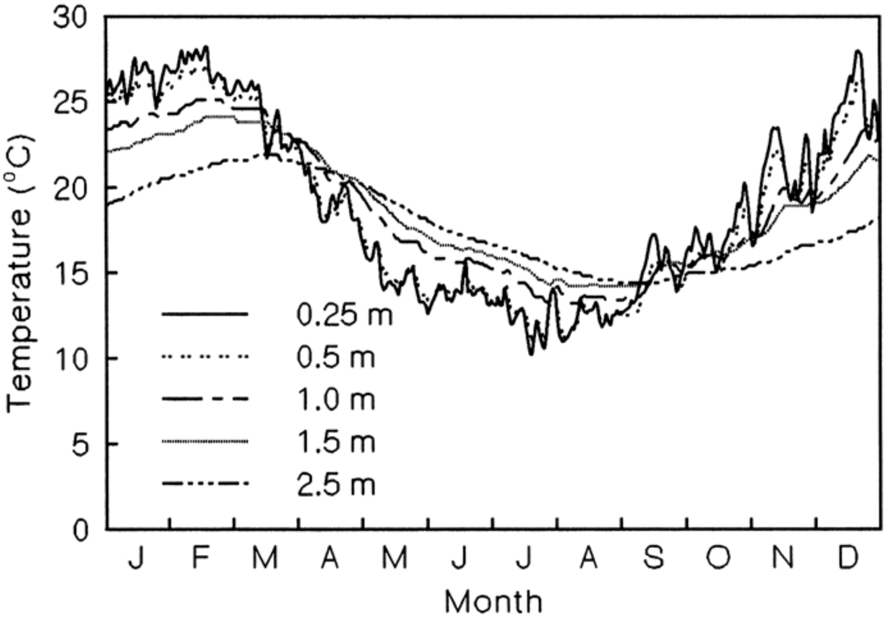

Fig. 4. Mean daily soil temperature at Dawn Creek at five depths for the year 1986.

zons. Most *P. cinnamomi* was recovered in winter and early spring, from June to September (Fig. 5). The fungus also was recovered during summer, spring, and autumn following either unseasonably heavy rain that initiated rapid perching or a succession of less intense rain events that resulted in a gradual buildup of a saturated zone.

Recovery of *P. cinnamomi* was more frequent and at a higher density from throughflow at the base of the soil above the duricrust than from piezometers drawing from below or within the duricrust in each of the upper-, mid-, and lower-slope positions (Fig. 5). Recovery from trenches and piezometers increased with the distance downslope.

An average of 60 propagules per liter was transported by throughflow in the soil above the duricrust in the lower slope position on two sample days in mid-spring. At least half of the propagules were zoospores (Fig. 6). The remainder could not be identified because of extensive mycelial growth.

The period of highest recovery of inoculum coincided with lowest seasonal soil temperature (Fig. 4). *P. cinnamomi* was present in piezometers in August–September when the soil temperature at 2 m was between 14 and 15 C (Fig. 4).

DISCUSSION

There are three basic requirements for the rapid long-distance lateral subsurface dispersal of propagules by water. First, the soil structure must be sufficiently porous to permit the passage of propagules (4). Second, subsurface water flow must have a predominantly lateral component. Third, the connections between the larger pores must be continuous over significant distances (16).

These criteria are satisfied at Dawn Creek. First, the consistent recovery of *P. cinnamomi* from water flowing at the base of the soil overlying the duricrust indicates that the soil is sufficiently coarse to transmit propagules at least the size of zoospores. Second, the lateral subsurface flow of water perched on rela-

Table 1. Hydrological parameters for throughflow interception trenches following rain on 13 July 1985

Slope position	Peak flow rate (L/min)	Total volume throughflow (kl)	Duration of flow (days)	Min. distance to catchment upper boundary D^a (m)
Upper	9	13	2.6	10
Mid	41	115	3.3	88
Lower	48	158	>5	122

^{a} $D\ (\mathrm{m}) \times 20\ (\mathrm{m}) \times \text{rain}\ (\mathrm{m}) = \text{throughflow volume}\ (\mathrm{m}^3)$.

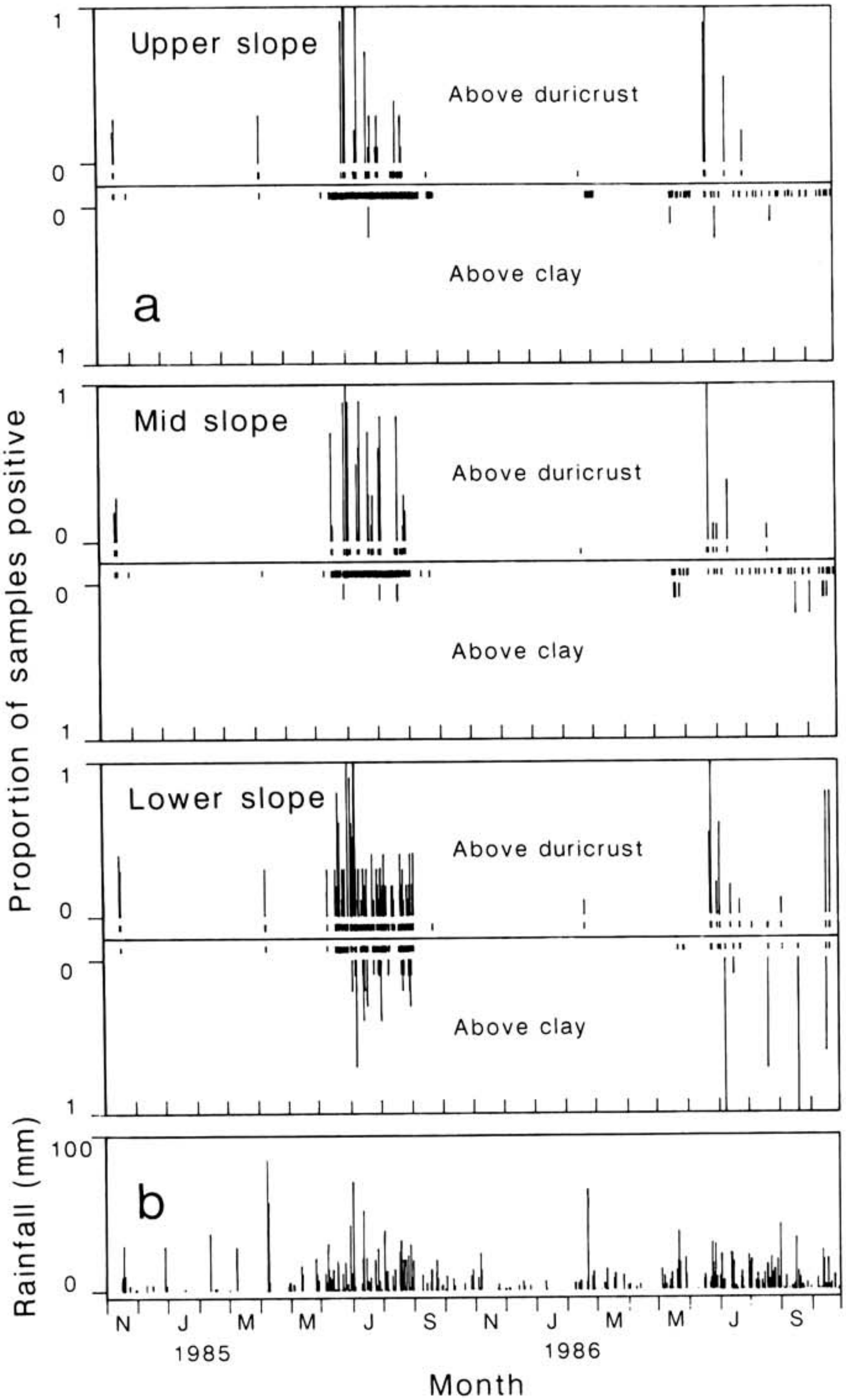

Fig. 5. (A) Recovery of inoculum of *Phytophthora cinnamomi* from subsurface water flowing through soil over duricrust and from water perched on clay beneath duricrust for the period November 1985 to October 1986. Days on which water samples were taken are indicated by bars immediately above and below abscissa. **(B)** Daily rainfall (bars) is shown for the sampling period.

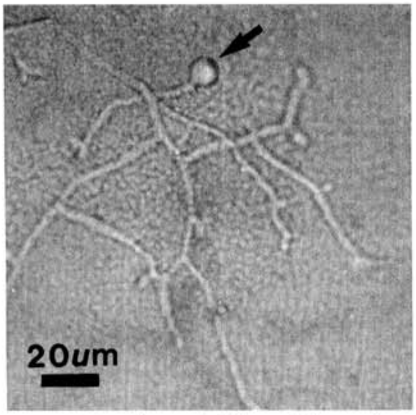

Fig. 6. Mycelium of *Phytophthora cinnamomi* originating from a zoospore cyst (arrow).

tively impermeable clay and duricrust horizons occurs frequently during a wet season. Third, the rapid rate and large volumes of water flowing from localized seeps at the interface of the soil and duricrust layers indicate a laterally continuous macropore network that forms preferred paths for water flow.

The hydrological behavior of the Dawn Creek site results from the peculiar morphology of the laterite profile (10). The limited capacity of the profile to conduct infiltrating water vertically down to groundwater is frequently exceeded during the course of a wet season. Consequently, perched water tables develop and increase in thickness both on the clay and on areas of relatively impermeable duricrust. The development of the saturated zone is accompanied by the downslope lateral flow of water over the clay through fissures in the duricrust and through the soil overlying the duricrust.

Apparently, long-term downslope flow and eluviation at the base of the soil profile at Dawn Creek has removed the fine soil fraction, thus opening continuous channels. Mosley (15,16) made a similar conclusion from his observations of rapid outflow at the base of a 1-m-deep soil profile overlying an impermeable horizon in New Zealand. At Dawn Creek, the porous soil immediately overlying the duricrust provides little impediment to zoospore movement and apparently predisposed the site to disease spread.

The drainage characteristics of jarrah forest soil profiles vary along a gradient between those favoring vertically percolating water and those which perch near-surface water (22). The extent of perched water table development and subsurface water flow on upper slopes in the jarrah forest are poorly understood (12) but have been observed on duricrust and clay horizons (10,19). Disease severity in the jarrah forest also varies along a gradient from no impact through low to high impact (22). However, the link between disease severity and the physical characteristics of jarrah forest soil profiles is poorly understood. This study at Dawn Creek, together with studies by Shea et al (20) and Kinal (10), helps to explain disease severity in terms of specific characteristics of the soil profile which affect the behavior of the fungus at depth in the soil.

The rate of water discharge from the throughflow trenches indicates a considerable force for propelling propagules through the soil. Inoculum may feasibly be dispersed over the distance that subsurface flow occurred. At Dawn Creek, following a single moderately intense rain event in winter, this may be the length of the hillslope, from infection front down to the valley floor.

The effect of successive episodes of dispersal may be cumulative. Whereas throughflow events are transient, lasting from hours to days after rain, perched water tables recur frequently during a wet season and occasionally at other times of the year. Consequently, inoculum may be dispersed in a general downslope direction through the soil in a saltatory manner.

The actual trajectory of a propagule is unlikely to be directly downslope but would probably meander along a path of preferred flow of water. Furthermore, the anastomosing network formed by the preferred flow paths would enhance the mixing of streams of inoculum-bearing water and hence of dispersal along the contours of the hillslope.

The action of water percolating downward through the soil following rain, upward as the perched aquifer grows thicker, and laterally as water flows downslope, enhances root infection by distributing zoospores through the soil profile. The probability of root infection also is increased by the coincidence of many roots with vertical flow paths through the duricrust (10,20) and the vertical distribution of tree roots across a range of soil temperatures. The root system of jarrah consists of distinctive lateral and vertical components (9). The lateral system extends up to 20 m from the stem, to a depth of 1 m (1). The lateral roots give rise to vertically descending sinker roots which extend down the soil profile to tap groundwater as deep as 40 m (1).

The percolating action of water increases the probability of coincidence of moisture and temperature conditions suitable for *P. cinnamomi* activity. Sporangium formation requires moist conditions, and zoospore release is greatest in soils with high matric potential (6). Infection by *P. cinnamomi* may occur at temperatures as low as 12 C (23), and establishment and growth in host tissues occurs at least as low as 10 C (21).

The soil profile deeper than 0.5 m was warmer than 12 C for most of the year at Dawn Creek, providing an environment suitable for root infection, establishment, and growth of *P. cinnamomi* in lesions. Soil temperatures also favored zoospore production, release, and survival since the year-round presence of zoospores in the soil was conditional only on rainfall.

The highest recovery of inoculum occurred when the soil was below 15 C. This suggests that a 15 C lower temperature limit for zoospore production and release by *P. cinnamomi* in jarrah forest soils reported by Nesbitt et al (17) may be too high.

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