

## 2. PATHOGENICITY OF *PHOMA GLOMERATA*, *P. CAVA*, *P. EUPYRENA* AND *CYTOSPORA* *CHRYSOSPERMA* ON BLACKTHORN (*ACACIA MELLIFERA* SUBSP. *DETINENS*)

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### ABSTRACT

Blackthorn (*Acacia mellifera* subsp. *detinens*) in parts of South West Africa showed increasing dieback and mortality during 1985-1988. A previous study suggested that blackthorn dieback might be a stress-related disease with the fungi *Phoma glomerata*, *P. cava*, *P. eupyrena* and *Cytospora chrysosperma* acting as primary causal organisms. In this study *P. glomerata* caused leaf chlorosis and restricted defoliation on glasshouse inoculated seedlings, *P. cava* induced wilting and chlorosis on seedlings and toothpick-inoculated potted plants, and *P. cava*, *P. Eupyrena* and *C. chrysosperma* caused significant wood discolouration in field inoculated blackthorn bushes. Wood discolouration was most extensive on bushes in an area with normal precipitation. We postulate that drought stress might have a differential effect on the organisms involved.

### INTRODUCTION

A previous paper (Part 1) reported a dieback disease of blackthorn [*Acacia mellifera* (Vahl) Benth. subsp. *detinens* (Burch.) Brenan] and suggested a causal role of the four fungi *Phoma glomerata* (Cda) Wollenw. & Hochpf., *P. eupyrena* Sacc., *P. cava* Schulz. and *Cytospora chrysosperma* Pers. ex Fr.

These fungi also cause severe diseases on other hosts. *P. eupyrena* has been associated with needle cast and blight of red fir and Douglas-fir (Kliejunas *et al.*, 1985), *P. aposphaeriodes* (+ *cava*) with canker of oak (Carter, 1941), *P. glomerata* with canker and twig blight of pears (Chohan & Chand, 1980) and decline and death of grapevines (Granata & Refatti, 1981) and *C. chrysosperma* with canker and collar rot of *Populus* (Schreiner, 1931; Domanski, 1983). The present study was established to determine which of the fungi are pathogenic on blackthorn and what influence rainfall has on disease development.

### MATERIALS AND METHODS

#### Field inoculations

Isolates of *P. glomerata*, *P. eupyrena*, *P. cava*, *C. chrysosperma* and other fungi occasionally recovered from bushes with dieback (*Melanophoma*, *karoo*, *Diplodia mutila*, *Sphaeropsis*, sp., *Haplosporella* sp., *Stagonospora* sp. and *Phomopsis* sp.) were used in field inoculations. Freshly-recovered isolates were grown on boiled sterile wooden toothpicks on potato-dextrose agar (PDA) (200g potato, 20 g glucose, 15 g agar/l) plates in the dark at 25°C. When the toothpicks were covered by mycelium, the plates were incubated for 5 d under intermittent light (black light, 12 h cycles) at 25°C to promote pycnidium formation. Toothpicks from uninoculated plates were used for control inoculations.

Two trials were conducted, one at Uitkomst Experimental Farm near Grootfontein, the other at Neudamm Experimental Farm near Windhoek.

Uitkomst is situated in the Mountainous Savanna and Kartsveld with mean daily temperatures of 15°C (June-July) to 30°C (October-March). Median annual precipitation based on a standard period of 30 years (1956-1985) is 517,3mm (Katsiambirtus, 1988). The soils are a shallow melanic topsoil (dark coloured clay structure) on hardpan calcrete. Vegetation was a mixed stand of blackthorn, *Combretum apiculatum* (kudubush), *Tarchonanthus camphoratus* ("vaalbush") and *Schmidtia pappaphroides* (kalahari sand quick).

Neudamm is situated in the Highland Savanna with mean daily temperatures of 10°C (June-July) to 25°C (October-March). Median annual precipitation is 377,6mm (Katsiambirtas, 1988). The soils are a shallow structureless orthic topsoil on a lithocutanic B grading tongue-like to solid rock. Vegetation was predominantly blackthorn and *Aristida* spp. (bristle grass).

Sites chosen were part of the natural bush vegetation and had no history of dieback prior to 1985 (F.V. Bester, *personal communication*). Vigorous, healthy bushes or trees (six/isolate) were selected at random for inoculation. On each plant six shoots differing in diameter (6-20mm) were selected. Holes (2mm in diameter) were drilled with a sterile hand drill into shoots, and each plant was inoculated by forcing half toothpicks into the holes. Inoculated zones were marked with wire ties and the bushes numbered.

After 6, 21 and 30 months, inoculated shoots and branches were collected and examined for lesions or cankers. Segments were cut from shoots or branches and parts showing wood discolouration were debarked, surface disinfested for 1 min in 70% ethanol and dried. They were then split open and the extent of wood discolouration measured. Small 3-5mm long chips, adjacent to the wound (1-2cm from toothpicks), from the centre of discoloured wood, and from the extremity of the discolouration were excised and incubated on PDA (Part 1).

#### Glasshouse inoculations

*With spore suspensions:* Isolates of fungi used for field inoculations were grown on PDA at 25°C under intermittent light (black light, 12 h cycles) to promote pycnidium formation. After 3 wks spore suspensions were prepared by adding 5ml sterile distilled water to plates, dislodging mycelium and pycnidia with a glass rod and homogenizing the fungal structures in a Waring blender. Homogenized suspensions were filtered through layers of sterile muslin. Spores were counted with a haemocytometer and the suspensions diluted to approximately 4.5 x 10<sup>5</sup> spores/ml.

Blackthorn seeds collected from the Waterberg region were disinfested (30 min in a hot water bath at 50°C) and sown in seed trays in a steam-infested peat-sand (3:1) potting mixture. The seedlings were watered regularly, fertilized once a month with Chemicult and sprayed to control red spider mites. Seedlings (48/organisms/tray), 8-10 wks old, were sprayed with a spore suspension. Half the seedlings of each treatment were wounded by removing a few petioles and cutting off parts of some leaves. Control seedlings were similarly treated and sprayed with sterile distilled water. After treatment, trays with seedlings were immediately covered with plastic bags to maintain a high humidity and kept for 48 h at 25°C. Bags were then removed and the seedlings kept at 18-27°C (night-day).

After 16 wks seedlings were removed and examined for lesion formation. Ten seedlings from each treatment were selected at random, the stem base and upper taproot of each examined for fruiting structures, surface-disinfested for 1 min in 70% ethanol and kept for 48 h in a moist chamber at 25°C. Fungal growth developing from the seedlings was identified microscopically, or transferred to PDA for further identification. The remaining seedlings were split open and examined at the stem base and upper taproot for internal discoloration.

*With toothpicks:* Blackthorn seedlings were raised in plastic pots (15 cm in diameter, one seedling/pot) and inoculum *P. eupyrena*, *P. cava* and isolates N3, N7 and N26 of *P. glomerata* prepared as previously described. Seven-month-old seedlings, raised from undisinfested seeds, were inoculated (12 seedlings/fungal isolate) by inserting split, half toothpicks into a hole made with a sterile dissecting needle approximately 5 cm above the soil line. Toothpicks from uninoculated plates were used for control inoculations. After 8 wks the seedlings were removed and examined for lesion formation and the presence of fruiting structures. They were then surface disinfested for 1 min in 70% ethanol, dried, cut longitudinally with sterile secateurs and examined for wood discoloration. Isolations from discoloured wood were made on PDA.

## RESULTS

### *Glasshouse inoculations*

*With spore suspensions:* After 3 wks leaves of some seedlings sprayed with *P. cava* spores wilted, whereas those of some *P. glomerata* N26-inoculated seedlings became chlorotic. The petioles eventually turned necrotic and dropped. Leaves and petioles were extremely fragile; therefore no isolations were made from them. Later on, new leaves formed but no further disease symptoms developed on them or on any of the other seedlings.

After 16 wks, pycnidia of *P. glomerata* were observed on the stem base and upper taproot of all the *P. glomerata*-inoculated seedlings and on one each of those inoculated with *C. chrysosperma*, *P. cava* and *M. karoo*. No other pycnidia were observed, nor were any lesions noted on the stems. After surface disinfestation and incubation in moist chambers, *P. glomerata* developed from the stem base and upper taproot of all, and from the petioles and leaves of five *P. glomerata* N26-inoculated seedlings. *P. cava* was also recovered from the stem base and upper taproot of (3 of 10) seedlings inoculated with this fungus, but not from leaves. The other fungi were not recovered from any plant part.

All the seedlings showed distinct fissures at the stem base, and the cortex had a blistered appearance. However internal tissue at the stem base and upper taproot of all the seedlings appeared healthy.

*With toothpicks:* About 2 wks after inoculation, leaves and petioles on plants inoculated with *P. cava* became chlorotic. Later on, those leaves and petioles near the inoculation site wilted, shrivelled and dropped. Leaves and petioles on the other plants were not affected.

No external lesions or cankers formed within 8 wks on inoculated stems. However, there was a green-yellow to black-green internal discoloration of the wood. Tangential discoloration in the different plants were essentially similar (15-20mm), but *P. cava* caused a more pronounced radial discoloration which extended virtually through the stem at the inoculation site. The target fungi were consistently isolated from the margin of discoloured wood from inoculated plants. However, *P. cava* was isolated from two seedlings; one uninoculated and the other inoculated with *P. glomerata* N26. In both these seedlings discoloration extended approximately 35mm into the taproot. Furthermore, when seeds were sown for inoculation studies, a distinct lesion was observed on the hypocotyl of one seedling approximately 3 months after germination. The seedling eventually died. Closer inspection revealed distinct necrosis of the upper taproot. Pycnidia of *P. glomerata* occurred on the hypocotyl and upper taproot and the organism was consistently isolated from lesions.

### *Field inoculations*

*Natural disease development.* Although care was taken to choose disease-free sites for inoculation studies, natural dieback was observed at Neudamm during April 1986 and at Uitkomst during November 1987. As most of the bushes at Neudamm, and some at Uitkomst showed natural dieback during the last sampling in April 1988, inoculated bushes were evaluated for natural twig and branch dieback and decline.

Bushes were then excavated, rated for basal rot and the percentage trees showing no, light and severe symptoms of disease determined. Disease severity of the bushes due to natural dieback is given in Table 1.

At Uitkomst some of the bushes selected for inoculation with *P. glomerata* N7, *P. cava*, *C. chrysosperma* and the control had natural dieback and showed a light degree of basal rot, whereas at Neudamm bushes of all the treatments were affected. Furthermore, on most bushes (77%) treated at Uitkomst no basal rot was found, whereas most (91,2%) bushes at Neudamm showed light to severe basal rot (Table 2).

*Pathogenicity.* Inoculated shoots or branches were removed at intervals, examined for external lesion or canker formation and the extent of internal wood discoloration determined. Due to the natural occurrence of blackthorn dieback, bushes were not evaluated for any other diagnostic symptoms of the disease.

The fungi did not cause any external lesions or distinct cankers, and in most cases toothpicks were completely sealed off. However, *P. cava*, *P. eupyrena*, *P. glomerata* and *C. chrysosperma* caused a distinct internal green-yellow to black-green discoloration of the wood. The discoloration advanced up and down from the original infection site and was primarily confined to the old wood.

Only in a few cases was radial extension to new wood seen. The other fungi caused no significant discoloration (results not shown) and are not discussed further. No spreading discoloration or decay was observed on the control treatments whereas mean and maximum values of these treatments at the two sites were essentially similar.

**Table 1 — Disease severity, due to natural dieback, of bushes selected for infection studies at Uitkomst and Neudamm:**

Inoculum Inoculum	Disease indices of bushes at					
	Uitkomst			Neudamm		
	Branch dieback <sup>a</sup>	Decline <sup>b</sup>	Basal rot <sup>c</sup>	Branch Dieback <sup>a</sup>	Decline <sup>b</sup>	Basal rot <sup>c</sup>
<i>P. glomerata</i> N3	0.50	0.33	0	2.16	3.16	3.03
<i>P. glomerata</i> N7	2.16	2.16	1.00	2.83	4.33	6.18
<i>P. glomerata</i> N26	0.16	0	0	1.50	1.80	2.80
<i>P. eupyrena</i>	0.16	0.33	0	1.50	2.66	2.00
<i>P. cava</i>	1.66	0	1.66	1.50	4.66	3.30
<i>C. chrysosperma</i> N2	0	1.00	0.33	1.33	3.00	2.00
<i>C. chrysosperma</i> N20	2.16	0	1.16	2.80	5.80	6.10
Control	0.16	0	0.33	2.30	3.00	4.50
Mean	0.87	0.89	0.60	2.04	3.62	3.85

<sup>a</sup>Branch dieback: 0 = no twig or branch dieback evident; 10 = 91-100% of twigs and branches dead.

<sup>b</sup>Decline: 0 = no twig or branch dieback or defoliation evident; 10 = 91-100% of twigs and branches dead and defoliated.

<sup>c</sup>Basal rot: 0 = no internal discolouration or decay at the base of the trunk or upper taproot; 10 = virtually all the sapwood and heartwood discoloured or decayed.

**Table 2 — Natural dieback of blackthorn bushes after infection studies at two localities in South West Africa:**

Site	Bushes (%) with								
	Dieback <sup>a</sup>			Decline <sup>b</sup>			Basal rot <sup>c</sup>		
	None	Light	Severe	None	Light	Severe	None	Light	Severe
Uitkomst	79.2	14.6	6.2	83.3	10.4	6.3	77.0	18.8	4.2
Neudamm	2.1	87.5	10.4	2.1	75.0	22.9	8.3	62.5	29.2

<sup>a</sup>Dieback: none = no dieback; light = index 1-5; severe = index 6-10. For index see Table 1.

<sup>b</sup>Decline: none = no decline; light = index 1-5; severe = index 6-10. For index see Table 1.

<sup>c</sup>Basal rot: none = no basal rot; light = index 1-5; severe = index 6-10. For index see Table 1.

**Table 3 — Wood discolouration in blackthorn shoots at Uitkomst at three periods after inoculation with isolates of *Phoma glomerata*, *P. eupyrena*, *P. cava* and *Cytospora chrysosperma*:**

Fungus	Discolouration <sup>a</sup> (mm) after					
	6 months		21 months		30 months	
	mean	max	mean	max	mean	max
<i>P. glomerata</i> N3	36	65	31	50	43	60
<i>P. glomerata</i> N7	19	35	43	130	67	115
<i>P. glomerata</i> N26	43	85	34	75	44	66
<i>P. eupyrena</i>	46	80	38	58	82	120
<i>P. cava</i>	48	80	86	105	81	194
<i>C. chrysosperma</i> N2	49	80	63	130	65	120
<i>C. chrysosperma</i> N20	64	95	95	160	110	195
Control	17	20	27	30	28	50
LSD <sup>b</sup>	36.1		53.3		52.4	

<sup>a</sup>Values are the mean of 12 shoots (six replicates) or the maximum observed at each period.

<sup>b</sup>Significant differences ( $p = 0.05$ ) according to Student's *t* test.

**Table 4 — Wood discolouration in blackthorn shoots at Neudamm at three periods after inoculation with isolates of *Phoma glomerata*, *P. eupyrena*, *P. cava* and *Cytospora chrysosperma*:**

Fungus	Discolouration <sup>a</sup> (mm) after					
	6 months		21 months		30 months	
	mean	max	mean	max	mean	max
<i>P. glomerata</i> N3	11	15	36	80	27	45
<i>P. glomerata</i> N7	14	22	13	17	19	23
<i>P. glomerata</i> N26	10	12	10	12	16	25
<i>P. eupyrena</i>	14	25	15	29	15	25
<i>P. cava</i>	14	20	21	39	44	83
<i>C. chrysosperma</i> N2	24	57	23	44	43	90
<i>C. chrysosperma</i> N20	21	35	27	34	34	70
Control	16	25	23	45	31	58
LSD <sup>b</sup>	13.3		23.8		32.0	

<sup>a</sup>See Table 3.

<sup>b</sup>Significant differences ( $p = 0.05$ ) according to Student's *t* test.

Wood discolouration was more pronounced at Uitkomst than at Neudamm (Table 3-4). At 6 months only *C. chrysosperma* N20 caused significantly more discolouration, whereas both *C. chrysosperma* N20 and *P. cava* caused significantly more discolouration at 21 months than the control. At 30 months, significantly more discolouration than wounding alone was caused by *C. chrysosperma* N20, *P. cava* and *P. eupyrena*. However, individual shoots or branches with extended discolouration, from which the target fungus was consistently isolated, were obtained from some bushes at each sampling.

extended discolouration, no significant difference were detected between inoculated and uninoculated shoots.

*Colonization of discoloured wood.* Occurrence of the target fungi in discoloured wood of the different treatments is shown in Fig. 1. When used as inoculum *P. glomerata* was consistently isolated at 6 months as the predominant wood discolouring organism. Thereafter its incidence declined. It was also regularly isolated from discoloured wood in all the other treatments. It was isolated more frequently from these shoots after 6 months than after 21 and 30 months.

At both the 21- and 30-months samplings, *P. cava*, *C. chrysosperma* and *P. eupyrena* were frequently recovered from inoculated shoots, whereas *P. cava* and *P. eupyrena* were occasionally isolated as secondary fungi at the 30-month sampling.

Other fungi isolated infrequently included species of *Camarosporium*, *Phomopsis*, *Diarimella*, *Coniothyrium*, *Melanophoma*, *Haplosporella*, *Diplodia*, *Stagonospora* and *Pleurophomopsis*.

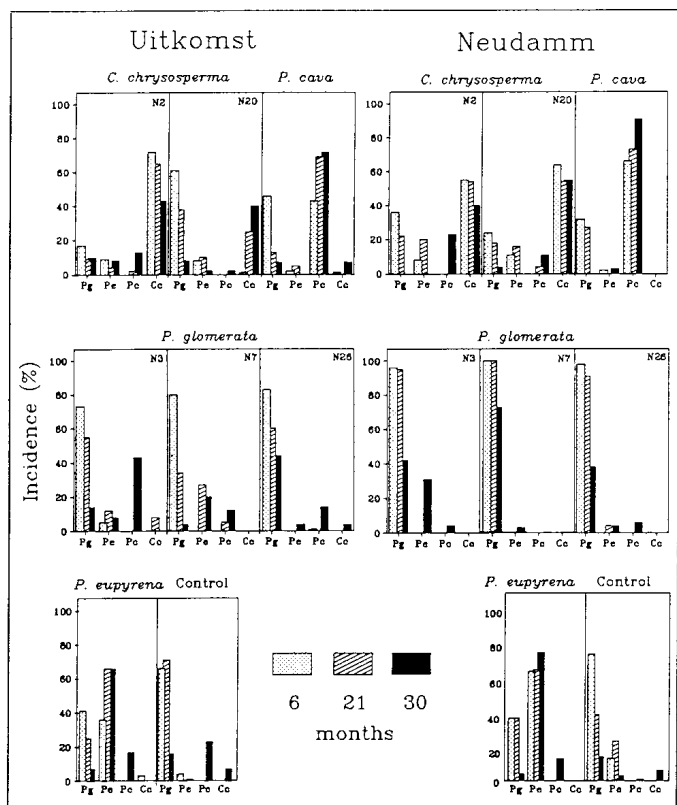
#### Distribution of target fungi in discoloured wood

Frequency of isolation of the target fungi from different positions in discoloured wood is shown in Fig. 2. At Neudamm, discolouration was restricted and although the fungi were frequently isolated, they were primarily confined to the area adjacent to toothpicks. At the 21- and 30-months sampling only *P. cava* and *C. chrysosperma* were consistently recovered from the marginal position, but at low frequencies.

At Uitkomst *C. chrysosperma*, *P. cava* and *P. eupyrena* were consistently recovered from all the positions at each sampling. Of these fungi *P. cava* was more or less evenly distributed in the different positions. At the 30-months sampling *C. chrysosperma* (shoots inoculated with isolate N2/), *P. cava* and *P. glomerata* (shoots inoculated with isolate N26) were recovered at relatively high frequencies from the marginal position.

#### Rainfall

Precipitation at each site during a 10-year period preceding the 1987/88 season is shown in Fig. 3. Both sites had normal precipitation during the period 1984/85-1987/88. However, at Neudamm precipitation during the four seasons preceding 1984/85 was slightly to very much below normal.



**Fig. 1.** Recovery of *Phoma glomerata* (Pg), *P. eupyrena* (Pe), *P. cava* (Pc) and *Cytospora chrysosperma* (Cc) from discoloured wood of blackthorn shoots at three periods after inoculation with isolates of these fungi.

At Neudamm, discolouration by these organisms was restricted, and although some shoots or branches inoculated by *P. cava* and *C. chrysosperma* N2 showed

## DISCUSSION

Previously dieback was ascribed to an internal decay at the base of the trunk or upper taproot which could in most cases be traced to an incoming dead shoot or branch. Predominantly *P. eupyrena*, *P. cava* and *C. chrysosperma* were isolated from these parts (Part 1). In this study, these fungi caused significant wood discolouration and decay in shoots under normal field conditions. In most dieback/decline diseases studied, infection frequently occurs many months or even years prior to tree mortality (Houston, 1987). At the extension rate exhibited in blackthorn shoots, the fungi should be able, upon entry of the trunk base or upper taproot, to grow into these tissues to initiate discolouration and decay.

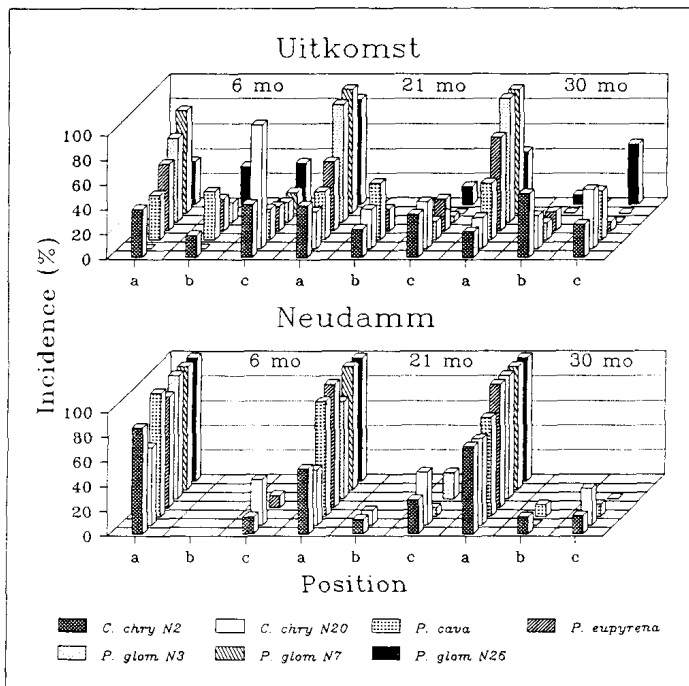
Blackthorn is usually a many-stemmed shrub (1-6 m high) with a short, compact main trunk branching prolifically at or above soil level. Occasionally a tree or a single stem occurs. To overcome the problem of a large variation in trunk size and the excavation of bushes to expose trunk bases at each sampling, shoots, instead of trunk bases were inoculated.

The route by which these organisms reach the woody tissue at the stem base or upper taproot and their relative role in this complex disease remain unclear. It is apparent that whereas *P. glomerata* and *P. cava* can colonize and cause disease on young seedlings, *P. eupyrena* and *C. chrysosperma* are unable to infect young or unwounded tissue. The ubiquity of *P. glomerata* in discoloured wood (Part 1) and in wounds made during this study indicate a primary role for this fungus in the disease. The fact that this fungus can be isolated from apparently healthy petioles, causes chlorosis and defoliation of artificially-inoculated seedlings causes visible lesions on petioles (Part 1) and that restricted discolouration of wood (colonized predominantly by this pathogen) usually occurs near the leaf axis on some defoliated bushes (Part 1), suggest that wood discolouration of twigs and shoots might be initiated internally from mycelium which has spread systematically down the petiole from a leaf infection. At least three other closely-related species *P. tracheiphila* (Perrotta, Magnano Di San Lio & Bassi, 1980), *P. tracheiphila* f. sp. *chrysanthemii* (Baker *et al.*, 1985) and *Leptosphaeria maculans* (Nathaniels & Tayler, 1983; Hammond, Lewis & Musa, 1985) also have a systemic phase.

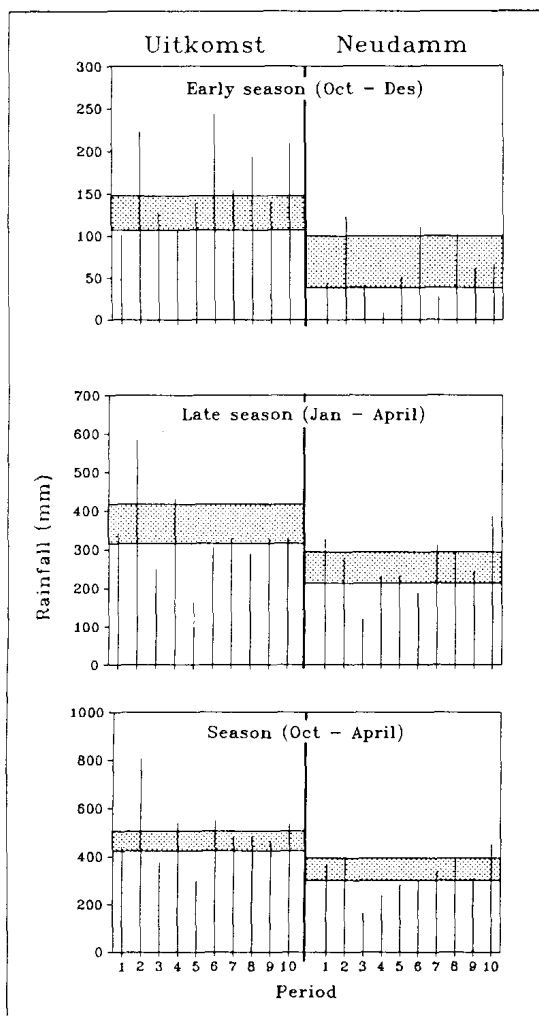
The abundance of viable inoculum on branches and stems (Part 1) might also provide inoculum for infection whenever moisture and temperature are favourable. This is confirmed by the fact that on artificially-inoculated bushes the four fungi in question were frequently obtained from the stem base and upper taproot of young healthy-looking artificially-inoculated blackthorn plants, even after rigorous surface disinfestation. Furthermore *P. glomerata* and *P. cava* were also recovered from naturally-infected seedlings originating from untreated seed. These fungi might therefore inhabit blackthorn plants from an early stage.

The induction by *P. cava* of wilting, chlorosis and defoliation, especially on toothpick-inoculated plants, suggests that this fungus could produce a toxin in infected tissue. This fungus is part of a toxigenic genus (Nachmias *et al.*, 1977; Suguwara & Strobel 1986), and a wilt-inducing toxin, cavoxin, has been isolated from the culture filtrates of an isolate of *P. cava* from *Castanea* spp. (Evidente *et al.*, 1985).

Many pathogens of woody hosts are typical slow-acting pathogens (Schoeneweis, 1978) and several workers, e.g. Bier (1959a, b, c), Bloomberg (1962), Bertrand *et al.*,



**Fig. 2.** Incidence of *Phoma glomerata*, *P. eupyrena*, *P. cava* and *Cytospora chrysosperma* in parts of discoloured wood at three periods after inoculation with isolates of these fungi. Positions are: a = adjacent to the wound (1-2 cm from toothpicks); b = centre of discoloured wood; c = margin of discolouration.



**Fig. 3.** Rainfall data during the period 1978/79-1987/88 for the experimental farms Uitkomst and Neudamm. Averages (shaded) for each locality are based on the 4th to 7th decile number values calculated for a standard period of 30 years (1956-1985) by Katsiambirtas (1987, 1988).

(1976) have shown that such pathogens may enter their hosts, remain latent and become aggressive parasites only when the host has been weakened by water stress. However, this increase in susceptibility to facultative parasites is often reversible and if the stress is relieved by ample rain before girdling or death of plant parts then host defence reactions may arrest disease development (Schoeneweiss, 1978, 1986).

Whether such an association is applicable to blackthorn dieback is uncertain. In field inoculations extension rates of *P. eupyrena*, *P. cava* and *C. chrysosperma* were most rapid in bushes inoculated at Uitkomst, an area which had no prolonged period of drought during the past 10 years and normal precipitation during the four seasons following inoculation. Blackthorn usually has an extensive lateral and vertical root system and with the aid of a deep taproot is able to utilise deep-seated moisture (Donaldson, 1969). Due to the shallow soil bushes at the Uitkomst site were shallow-rooted and periodic drought stress might have occurred. On the other hand, the Neudamm site had a prolonged drought during the 4 years preceding inoculation. Although normal precipitation was recorded during the period after inoculation, most of the bushes were already subjected to natural infection at the base of the trunk when inoculated. These data indicate that blackthorn dieback might either not be a typical stress-initiated disease or that drought stress might have a differential and subtle influence on the organisms involved.

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