4. SOIL MOISTURE STRESS AND INFECTION OF BLACKTHORN *(ACACIA MELLIFERA* SUBSP. *DETINENS)* BY FUNGI ASSOCIATED WITH BLACKTHORN DIEBACK

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ABSTRACT

The effect of defoliation and water stress on the aggressiveness of *Phoma glomerata, P. eupyrena, P. cava* and *Cytospora chrysosperma* was determined on potted blackthorn plants. All four fungi caused significantly more discolouration than wounding alone on plants subjected to water stress and defoliation prior to inoculation, followed by normal irrigation. However, only plants inoculated with *P. cava* were severely stunted and showed typical diagnostic symptoms of dieback (leaf chlorosis, defoliation, twig dieback and a wood discolouration of the base of the stem and upper taproot).

On plants subjected to controlled water stress for a 65-week period after inoculation, discolouration on plants inoculated with *P. eupyrena* and *C. chrysosperma* was significantly correlated with the soil water content. Data for *P. cava* showed no correlation with the soil water content and the pathogen was aggressive on plants growing in soil with a relatively high moisture content (21.8-42.5% of field water capacity). It is concluded that *P. cava* should be able to cause disease on blackthorn growing under normal field conditions and could play a decisive role in the disease complex.

INTRODUCTION

Previous studies (Part 1, 2, 3) have implicated *Phoma glomerata* (Cda) Wollenw. & Hochapf., *P. eupyrena* Sacc., *P. cava* Schulz. and *Cytospora chrysosperma* Pers. ex Fr. as causal agents of a destructive disease of blackthorn [*Acacia mellifera* (Vahl) Benth. subsp. *detinens* (Burch.) Brenan] in parts of northern South West Africa.

Although blackthorn is well adapted to the arid conditions of that region (Donaldson, 1969), the association of four different pathogens with dieback indicates that the disease could be similar in etiology to other stress.initiated diebacl-decline diseases. which are nearly always associated with a stress factor and organisms of "secondary action" (Houston, 1987). However, field inoculations showed that the organisms caused the most extensive discolouration in bushes growing in an area which had had normal precipitation during the previous 10 years (Part 2).

Studies reported in this paper were conducted to investigate the possible effect of defoliation and controlled water stress on the aggressiveness of *P. glomerata, P. eupyrena, P. cava* and *C. chrysosperma* on potted blackthorn plants.

MATERIALS AND METHODS

Inoculum

Isolates of *P. glomerata, P. eupyrena, P. cava* and *C. chrysosperma* from blackthorn bushes with severe dieback were grown on sterilized boiled wooden toothpicks on potato-dextrose agar (PDA) in petri dishes. The cultures were incubated at 25°C until toothpicks were covered with mycelium, then incubated for 5 d under intermittent light (black light, 12 h cycles) at 25°C to promote pycnidium formation.

Blackthorn seed and seedlings

Seedlings were raised from hot water-treated seed collected from apparently healthy bushes in an area in the Waterberg region where no dieback occurred. Seeds were planted in a 3-1 mixture of steam-disinfested sand and peat in 15cm plastic pots and held in a glasshouse at 18 ± 3-29 ± 3°C (nigh-day). Seedlings (one/pot) were watered regularly and fertilized once a month with Chemicult. Healthy, vigorously growing one-year-old seedlings were selected for further study.

Defoliation and soil moisture stress

The effect of defoliation and soil moisture stress prior to inoculation on infection was investigated on blackthorn plants subjected to 2-4 cycles of water stress and defoliation/refoliation during a 12-wk period in a glasshouse at 17 ± 3-25 ± 3°C (night-day). During this period plants were watered to field capacity (FC), left unirrigated, and the soil rewatered to FC when plants wilted and leaves started to drop. Pots were left to stabilize, the plants were then lightly irrigated and the cycle repeated as soon as the plants were covered with new leaves.

Plants were inoculated at a stage when they were partly defoliated. An oblique downward incision into the outer xylem was made with a sterile scalpel at the stem base approximately 1 cm above soil level. A split toothpick (1 cm long) was inserted into the wound and the inoculated area covered with Parafilm. Toothpicks from uninoculated plates were used for control inoculations.

Inoculated plants were kept dormant for 16 wks in a glasshouse at relatively low temperatures (13 ± 3-20 ± 3°C, nigh-day), after which temperatures were raised (18 ± 3-27 ±3°C, night-day), to promote active growth. Plants were regularly watered and fertilized once a month with Chemicult. Plants that died were removed and evaluated for disease development. Thirty-eight weeks after inoculation the remaining plants were removed and examined.

Soil moisture regimes

Since there is no information on the water relations of *Acacia mellifera* subsp. *detinens,* the lower limit of available water for the growth of young blackthorn plants potted in the sand-peat mixture had first to be estimated. The permanent wilting percentage (PWP) of the plants

was therefore determined by the method of Furr & Reeve (1945), and as recommended by Slatyer (1957). Nine one-year-old blackthorn seedlings were transferred to a growth chamber kept at 25 ± 2°C (15 h period of artifical light), watered to field capacity (FC) and each plant unit weighed. The plants were left unirrigated until the PWP for each plant was reached, the plant units weighed, seedlings removed and soil mass determined. The soil was then oven dried for 24 h at 105°C, cooled and the dry weight determined. The water content (SWC) of the soil mixture at the PWP of the blackthorn plants was determined as 4.4%.

Based on a PWP of 4.4% SWC, it was decided to investigate the effect of soil moisture on disease development by growing inoculated blackthorn plants in soil with a SWC of 7%, 15% and 30% (respectively 7.5, 16.2 and 32.4% FC). Since the weight of soil in the pots containing the selected plants was not known, a system had to be devised to predict the SWC of each pot on the basis of the total weight of a blackthorn plant unit (pot with plant and soil). The relationship (R_1) between FC (FC_{unit}) and the PWP (PWP_{unit}) of a plant unit at a SWC of 4.4% and that (R_2) between the weight of each plant unit (Q_{unit}) at a given SWC and FC (FC_{unit}) was therefore determined.

R_1 was calculated as 0.50 and, on the basis of the values of PWP_{unit}, FC_{unit}, Q_{unit} and R_1 obtained for the selected plant units, R_2 for soils at the chosen SWC's were calculated as 0.51, 0.56, and 0.66. The weight of a plant unit could therefore be predicted by the following equations:

$$Q_{unit} \text{ at } 7\% \text{ SWC} = 0.51 \times FC_{unit} \quad (1)$$

$$Q_{unit} \text{ at } 15\% \text{ SWC} = 0.56 \times FC_{unit} \quad (2)$$

$$Q_{unit} \text{ at } 30\% \text{ SWC} = 0.66 \times FC_{unit} \quad (3)$$

Plants selected for infection studies were transferred to a growth chamber kept at 25 ± 2°C (15 h period of artificial light), watered to FC, weighed and the weight of each plant unit kept at a given moisture regime predicted with the aid of either the equations 1, 2 or 3. The plants were left unirrigated until the predicted weight for each was reached. Water application to each pot was timed by daily weighing; when the weight of the pot declined, water was added to bring the moisture up to a figure corresponding with the desired value.

Plants were kept for 6-8 wks at their predicted value, inoculated as described previously and the SWC of each pot maintained for the duration of the experiment.

Disease assessment

Disease development was determined according to different indices. Plants were first examined for discolouration, stem girdling and the presence of pycnidium at the inoculation point, after which wound healing was assessed on a scale of 0-10 with 0 = no callus formation and 10 = wound completely covered by callus. Stems were then surface disinfested in 70% ethanol for 1 min, left to dry and cut with sterile secateurs at the inoculation point, first tangentially, then longitudinally. Tangential discolouration was measured and radial discolouration at the transverse cut determined on a scale of 0-10 with 0 = no discolouration and 10 = stem completely discoloured.

A discolouration index, based on the extent of longitudinal and radial discolouration at the inoculation point, was also determined (Fig. 1).

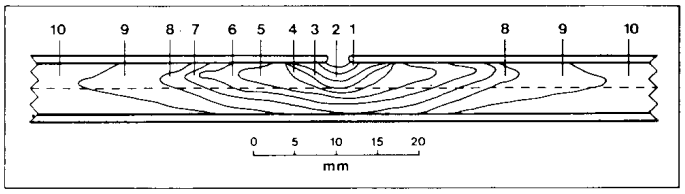

Fig. 1. Discolouration index of blackthorn seedlings, based on the extent of longitudinal and radial discolouration at the inoculation point.

Isolations were made from stems by plating small pieces (3-5mm) of tissue excised from the margins of discoloured wood on PDA. Plates were incubated at 25°C in the dark and organisms developing from the tissue identified after 10 d.

RESULTS

Induced moisture stress and defoliation

Plants were sparsely covered with leaves during the dormant period. Some of the leaves turned yellow and eventually dropped. However, no progressive defoliation or any dieback was observed. When transferred to the higher temperatures all plants showed active regrowth.

Typical dieback symptoms developed after approximately 23 wks on two plants inoculated with *P. cava* . Leaves turned yellow, dropped and twigs died back from the tips. Both plants died within 3-4 wks after the first symptoms were observed. No wound healing occurred at the inoculation point. The wood underneath was discoloured black-green. On one plant the discolouration extended 10mm upwards in the lower stem and 50mm in the taproot, with the entire stem discoloured at the inoculation point. On the other plant, discolouration, which extended 60mm upwards in the lower stem and 40mm in the taproot, was confined to the woody tissue and pith. In cross section the discolouration appeared as irregular radial streaks or patches interspersed with healthy tissue. *P. cava* was isolated repeatedly from discoloured wood from the stems and taproot.

No typical symptoms of dieback developed on any of the other plants during the 38 wks. However, those inoculated with *P. eupyrena* and *P. cava* appeared stunted.

Disease assessments made at the end of the experiment are shown in Table 1. *P. cava* and *P. eupyrena* inhibited plant growth drastically whereas all four fungi produced significantly more necrosis and discolouration than wounding alone. Tangential spread was most extensive in plants inoculated with *P. cava*, whereas *P. cava* and *C. chrysosperma* caused the most extensive radial discolouration. All the fungi, except *P. glomerata*, inhibited wound healing significantly. In the case of *C. chrysosperma*, virtually no callus was formed. Only *P. cava* was consistently recovered from the margin of discoloured wood.

Soil moisture regimes

Estimation of the real SWC at the termination of the experiment revealed that most plants were kept during the 65-wk period at values slightly above or below the predicted values (Tables 2-4). Thus some of the plants kept at a predicted SWC of 7% were in fact grown at a real value at or below PWP. These plants (No 24, 48, 71, 72, 95, 96, 120) died within the first 6 wks after inoculation and approximately 12 wks after some indication of moisture

stress. *C. chrysosperma* (No 71, 72) and *P. cava* (No 95, 96) were isolated from discoloured tissue of three plants, but not *P. eupyrena* (No 24) and *P. glomerata* (No 48). Except for plant No 48, no distinct wood discolouration was observed. The other plants that died were nearly all kept at a SWC of 5-8%, whereas two were grown at a SWC of 20 (No 27) and 34% (No 80) respectively. Except for plant No 23, all these plants died within 10-52 wks of inoculation. Fungi corresponding with the inoculum were repeatedly isolated from these plants.

Data (based on mean values) for plants kept at predicted SWC of 7, 15 and 30% are shown in Fig. 2. *P. cava* caused distinct disease symptoms irrespective of the SWC at which plants were kept, whereas the other pathogens caused disease only on plants kept at a predicted value of 7% SWC. Furthermore, *P. cava* was consistently re-isolated from nearly all the plants inoculated with this pathogen, whereas the other fungi were predominently recovered from plants kept at a low SWC.

No significant correlation was found between SWC and data for either the control or *P. glomerata*-inoculated plants. Regression analysis for data of the other organisms and SWC is given in Table 5. For *P. eupyrena* and *C. chrysosperma* a significant positive linear relationship exists between SWC and the extent of discolouration (longitundinal and radial discolouration and the discolouration index), whereas a negtive correlation exists between SWC and wound healing for *P. eupyrena* and *P. cava.*

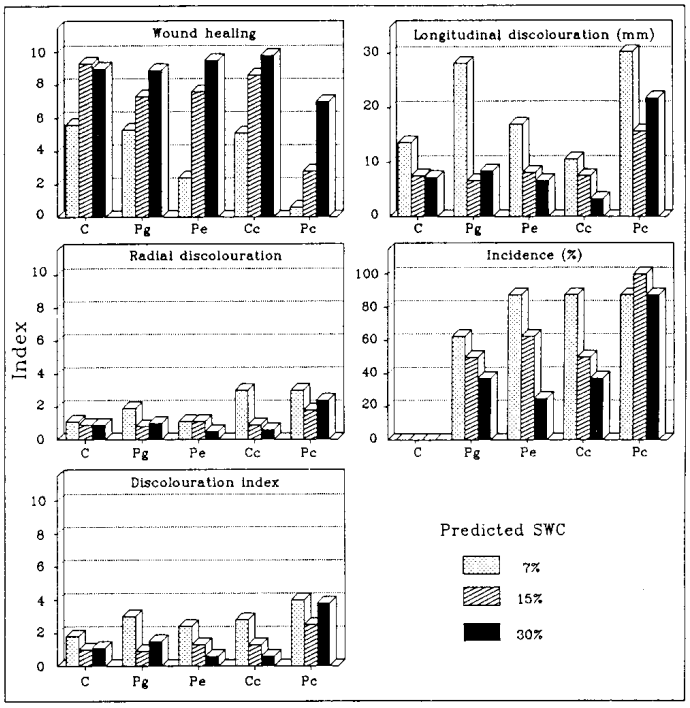

Fig. 2. Disease severity (mean values) of inoculated and uninoculated blackthorn seedlings kept for 65 wks at a predicted soil water content of approximately 7,15 and 30%. Pg = *Phoma glomerata;* Pe = *P. eupyrena;* Pc = *P. cava;* Cc = *Cytospora chrysosperma* and C = control.

Table 1 — Effect of water stress and defoliation prior to inoculation on desease severity of blackthorn seedlings 38 wks after inoculation with *Phoma glomerata, P. eupyrena, P. cava* and *Cytospora chrysosperma:*

Fungi	Wound healing[a]	Longitudinal Discolouration (mm)	Discolouration index[b]	Incidence (%)[c]	Mean weight (g)
P. eupyrena	4.6	9.7	2.7	91.7	8.5
P. glomerata	9.4	17.2	3.8	66.7	13.9
P. cava	4.6	24.1	3.8	100.0	6.7
C. chrysosperma	1.4	16.6	4.3	83.3	10.3
Control	10.0	5.1	0.6	0	13.1
LSD[d]	1.92	13.45	1.74		

[a]0 = no callus formed; 10 = 91-100% of wound covered with callus.

[b]See Fig. 1.

[c]Reisolation made after death or when experiment was terminated.

[d]Significant differences (P = 0.05) according to Student's *t* test.

Table 2 — Disease severity of blackthorn plants inoculated with *Phoma eupyrena, P. glomerata, P. cava* and *Cytospora chrysosperma* and kept for 65 wks at a predicted soil water content of approximately 30%:

Organisms	Plant No.	Soil Water content (%)	Wound healing[b]	Longitudinal discolouration (mm)	Radial discolouration[c]	Discolouration index[d]	Death (wks)[e]	Reisolated[f]
P. eupyrena	1	38.0	10	10.0	1	1		+
	2	37.0	7	13.0	1	1		-
	3	35.7	10	0	0	0		-
	4	32.5	10	15.0	1	2		-
	5	28.3	10	0	0	0		-
	6	28.0	10	0	0	0		-
	7	27.5	9	14.0	1	1		+
	8	24.9	10	0	0	0		-
P. glomerata	25	38.5	10	0	0	0		-
	26	36.6	10	2.0	0	1		-
	27	34.6	10	23.0	3	4	52	+
	28	33.9	5	13.0	1	2		-
	29	29.8	10	5.0	1	1		-
	30	27.9	10	4.0	1	1		+
	31	25.8	10	5.0	1	1		+
C. chrysosperma	49	32.0	10	9.0	1	1		+
	50	31.9	10	8.0	1	1		-
	51	28.4	10	3.0	1	1		+
	52	27.5	10	0	0	0		-
	53	25.1	10	0	0	0		-
	54	23.7	10	1.5	1	1		-
	55	23.5	8	5.0	1	1		+
	56	23.0	10	0	0	0		-
P. cava	73	39.0	6	14.0	2	2		+
	74	31.3	8	12.0	1	2		+
	75	29.8	10	6.0	1	1		-
	76	28.7	2	30.0	2	6		+
	77	28.5	5	14.0	1	2		+
	78	23.1	10	13.0	1	2		+
	79	22.0	7	24.0	1	6		+
	80	20.0	8	60.0	10	9	36	+
Control	97	34.6	10	8.0	1	1		-
	98	32.2	10	10.0	1	2		-
	99	31.3	8	7.0	1	1		-
	100	30.5	9	5.0	1	1		-
	101	30.4	10	8.0	1	1		-
	102	26.6	10	0	0	0		-
	103	24.3	5	8.0	1	1		-

Real SWC as determined at termination of the experiment.

[b]See Table 1.

[c]0-10 scale with 0 + no discolouration and 10 + stem completely discoloured.

[d]See Fig. 1.

[e]Number of weeks after inoculation.

[f]Reisolation made after death or when the experiment was terminated.

Table 3 — Disease severity of blackthorn plants inoculated with *Phoma eupyrena, P. glomerata, P. cava* and *Cytospora chrysosperma* and kept for 65 wks at a predicted soil water content of approximately 15%:

Organisms	Plant No.	Soil Water content (%)	Wound healing[b]	Longitudinal discolouration (mm)	Radial discolouration[c]	Discolouration index[d]	Death (wks)[e]	Reisolated[f]
P. eupyrena	9	18.9	10	6.0	1	1		+
	10	17.0	8	7.0	1	1		-
	11	16.9	10	10.0	1	2		+
	12	15.3	0	8.0	1	1		-
	13	14.9	4	11.0	2	2		+
	14	14.7	10	8.0	1	1		-
	15	14.0	9	9.0	1	1		+
	16	13.7	10	6.0	1	1		+
P. glomerata	33	20.9	0	8.5	1	1		+
	34	20.7	10	8.0	1	1		-
	35	19.4	10	11.0	1	1		+
	36	16.7	7	7.0	1	1		-
	37	14.3	6	8.0	1	1		+
	38	12.3	10	0	0	0		-
	39	11.9	10	0	0	0		-
	40	10.3	8	10.0	1	2		+
C. chrysosperma	57	19.1	10	0	0	0		-
	58	18.8	0	13.0	2	2		-
	59	17.6	10	0	0	0		-
	60	16.9	9	16.0	1	3		+
	61	16.1	10	7.5	1	1		+
	62	15.9	10	8.0	1	1		-
	63	15.7	10	9.0	1	2		+
	64	14.7	10	6.0	1	1		+
P. cava	81	16.7	5	13.5	2	3		+
	82	14.7	1	15.0	2	2		+
	83	14.1	0	15.0	2	2		+
	84	13.8	9	13.0	1	1		+
	85	13.3	3	13.0	1	2		+
	86	12.5	1	18.0	2	4		+
	87	12.5	1	22.0	2	3		+
	88	10.8	2	15.0	2	3		+
Control	105	20.7	9	10.0	1	1		-
	106	20.4	10	0	0	0		-
	107	19.9	9	7.0	1	1		-
	108	19.3	10	6.0	1	1		-
	109	17.0	10	14.0	1	1		-
	110	15.3	10	8.0	1	1		-
	111	14.9	10	3.0	1	1		-

[a-f]See Table 2.

DISCUSSION

Exposing young *A. mellifera* subsp. *detinens* plants to controlled water stress during a 65-wk period after inoculation increased susceptibility of stems to attack by the four pathogens. The extended period of growth at a soil water content at or even below the permanent wilting point, indicates the adaptability of blackthorn to drought stress.

Water stress usually results in increased susceptibility of woody plants to facultative parasites varying considerably in aggressiveness (Schoeneweiss, 1986). Research on woody plants subjected to controlled environmental stresses provides convincing evidence that threshold levels for water stress are required for predisposition to non-aggressive stem-canker fungi like *C. chrysosperma* (Bier 1964) and *Botryosphaeria dothidia* (Crist & Schoeneweiss, 1975). However, for more aggressive fungal pathogens, the influence of threshold levels of stress becomes less evident (Schoeneweiss, 1986). In this study no correlation was found between soil water content and the extent of discolouration caused by *P. cava*. Furthermore, this fungus caused plant death at 21.8% of field water capacity (20% SWC) and was aggressive on plants grown at a relative high soil moisture

content (21.8-42.5% of field capacity).

All four fungi caused significantly more discolouration than wounding alone on plants subjected to water stress and defoliation prior to inoculation and normal irrigation. however, only plants inoculated with *P. cava* were severely stunted and showed typical symptoms of die-back (i.e. leaf chlorosis, defoliation, twig dieback and discolouration of wood of the stem base and upper taproot). Therefore *P. cava* can be considered a more aggressive pathogen of blackthorn than *P. glomerata, P. eupyrena* and *C. chrysosperma* and should be able, in contrast with *P. eupyrena* and *C. chrysosperma*, to infect blackthorn under normal field conditions.

The role of the four organisms in the disease complex is still not clear. REcovery of the pathogens in culture from inoculated points on some nonstressed plants 65 wks after inoculation, shows that some of these organisms remain viable for many weeks in wounds on vigorous stems without extensive colonization, until plants are exposed to stress.

P. glomerata, although not as aggressive as *P. cava*, caused distinct disease symptoms on nonstressed potted plants. Furthermore *P. cava, P. eupyrena* and *C. chrysosperma* caused significant discolouration and decay of inoculated bushes growing in an area which had had no prolonged drought prior to inoculation, and

Table 4 — Disease severity of blackthorn plants inoculated with *Phoma eupyrena, P. glomerata, P. cava* and *Cytospora chrysosperma* and kept for 65 wks at a predicted soil water content of approximately 7%:

Organisms	Plant No.	Soil Water content (%)	Wound healing[b]	Longitudinal discolouration (mm)	Radial discolouration[c]	Discolouration index[d]	Death (wks)[e]	Reisolated[f]
P. eupyrena	17	10.1	3	13.0	1	2		+
	18	9.9	7	15.0	1	2		+
	19	18.4	8	9.0	1	1		+
	20	7.5	0	23.0	1	3		+
	21	6.6	1	40.0	2	6		+
	22	5.8	0	10.0	1	1	10	+
	23	5.0	0	17.0	1	3	17	+
	24	4.6	0	7.0	1	1	6	+
P. glomerata	41	9.4	10	4.0	1	1		-
	42	9.1	7	10.5	1	1		+
	43	8.3	10	4.0	1	1		+
	44	8.2	9	10.0	1	1		-
	45	8.2	4	6.0	1	1		+
	46	5.8	0	61.0	5	7	26	+
	47	5.7	0	18.5	3	5	17	+
	48	4.9	2	110.0	2	7	6	-
C. chrysosperma	65	10.3	10	7.0	1	1		+
	66	9.5	10	8.0	1	2		+
	67	9.5	10	9.0	1	1		+
	68	9.0	10	0	0	0		-
	69	7.8	1	30.0	10	8	12	+
	70	6.1	0	17.0	9	8	17	+
	71	3.9	0	8.0	1	1	6	+
	72	3.1	1	6.0	1	1	3	+
P. cava	89	7.3	0	42.0	6	7		+
	90	7.1	0	19.0	3	4		+
	91	6.6	0	12.5	3	3		+
	92	6.0	5	12.0	1	2		-
	93	5.5	0	120.0	7	10		+
	94	5.4	0	21.0	2	4	6	+
	95	4.9	0	6.0	1	1	3	+
	96	3.5	0	8.0	1	1	2	+
Control	113	10.1	10	7.0	1	1		-
	114	8.0	10	0	0	0		-
	115	8.0	10	5.0	1	1		-
	116	5.6	10	17.0	1	2		-
	117	5.3	0	6.0	1	1	10	-
	118	5.2	5	57.0	3	7		-
	119	5.1	0	7.0	1	1	6	-
	120	1.4	0	9.0	1	1	6	-

[a-f]See Table 2.

Table 5 — Correlations between soil water content and disease severity of blackthorn seedlings inoculated with *Phoma eupyrena, P. cava* and *Cytospora chrysosperma:*

	Independent variant (x) [Soil water content (g water/g oven dry soil)]		
Dependent variant(y)	*P. eupyrena*	*C. chrysosperma*	*P. cava*
Wound healing	y = 2.24 + 0.243x r = 0.6379*	y = 5.67 + 0.157x r = 0.3642	y = 0.22 + 0.238x r = 0.6404*
Longitudinal discolouration	y = 17.35 - 0.36x r = 0.4404**	y = 16.39 - 0.482x r = 0.5299**	y = 35.17 - 0.677x r = 0.2695
Radial discolouration	y = 1,35 - 0.024x r = 0.4841**	y = 4.44 - 0.158x r = 0.4697**	y = 3.52 - 0.061x r = 0.2604
Discolouration Index	y = 2.67 - 0.066x r = 0.5316**	y = 4.21 - 0.143x r = 0.505**	y = 4.70 - 0.064x r = 0.25

[a]See Table 2-4 for values at which plants inoculated with the different fungi were kept.

*Significant at P = 0.01.

normal precipitation after inoculation (Part 2). As both *P. glomerata* and *P. cava* were primary colonizers of discoloured wood on artificially-inoculated plants (Part 2), and are transmitted by seed (Part 2, 3), it is postulated that the four organisms act in concert, but that *P. glomerata* and *P. cava* play a primary and decisive role in the disease complex.

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