EFFECTS OF WATER ON THE DEVELOPMENT OF POWDERY MILDEWS

By

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ABSTRACT

This investigation examined the effects of water, as films and impacting drops, on powdery mildew development, especially of Erysiphe graminis on barley, Erysiphe pisi on pea and Sphaerotheca pannosa on rose. Conidia were most affected. They either failed to germinate in water films or were washed from leaves by impacting drops. Mycelial growth and conidiophore production were reduced by water films but were then enhanced when the leaves were air dried. Also, mycelial growth to conidiophore initiation could take place on leaves immersed in water. Impacting water drops damaged both mycelium and conidiophores in ways related to colony development and size.

Washing leaves before inoculation with these fungi also affected their development.

The germination of conidia of a wide range of mildew species on or in water was also examined. Species could be divided into four groups based mainly on the length and branching of germ-tube.

The results are discussed in relation to the epidemiology of powdery mildews.

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CONTENTS

INTRODUCTION

There are many statements in the literature which suggest that powdery mildews are more severe in dry weather or that rain adversely affects mildews. In the latter connexion much emphasis has been placed on the failure of mildew conidia to germinate well in water films and most experimental work relating to water and powdery mildews has concentrated on this aspect. The effect of water films on other stages in the asexual cycle such as mycelial growth, conidiophore initiation and production of conidia have not been examined in a quantitative way. Similarly, while mention is made of the deleterious effect of rain impacting on the vertically oriented conidiophores there is little experimental data on this and virtually none on the effects of rain on other growth stages. This lack of precise data prompted the present investigation.

LITERATURE REVIEW

Powdery mildew fungi are obligate parasites that develop predominantly on the surface of their host. They are thus exposed for much of their life cycle to the direct effects of the environment. However, opinions differ widely regarding the kind of environment that favours their development. For example, the weather conditions that are said to be conducive for various species are: wet (Johnston et al.,1937); cool (Deslandes,1954); high humidity (Tapio,1972); humid conditions accompanied by mists at night (Fernando,1971); dews (Eastham & Ruhmann,1924); heavy dews and abundant sunshine (Ubrizsy, 1946); rain (Blodgett,1913); frequent rain and humid weather (Reid & Josephson,1947); short showers with excess dew (Peries,1973); rain and fog (Jacob, 1929); warm weather and wet fog (Carter, 1915); a dry spell followed by rain (Kheswalla,1936); warm (Nour,1958); warm and dry with dew at night (Butt,1975); dry (Woodward,1927; Cherewick,1944; Weltzien,1965; Odintsova,1978); hot and dry (Corner,1935; Drozdovskaya,1978); extremely hot and dry (Jensen,1967; Drandarevski,1969; Palti,1971).

Despite these indications that powdery mildews can develop well in a wide range of environmental conditions, most emphasis has been placed on their ability to grow under dry conditions (eg. Boughey,1949; Palti,1972). In a recent review, Butt (1978) concluded that powdery mildews are adapted to dry environments but that species differ in their degree of xerophytism. Indeed, most investigators agree on two points - that powdery mildews are adversely affected by rain and the presence of free water on the leaf surface is detrimental to their growth. This review

examines the water relationships of the powdery mildew fungi in its broadest sense.

a. Moisture requirements of mildew conidia

Most fungal spores require free water for their germination but powdery mildew conidia seem to be an exception. Several workers have attempted to explain this unique feature. Some (Graf-Marin,1934; Brodie,1945) have suggested that a high osmotic pressure enables the conidia to absorb the water necessary for germination from the atmosphere. Others (Corner, 1935; Yarwood,1950b; Jhooty & McKeen,1965; Somers & Horsfall, 1966) showed that powdery mildew conidia have a high water content and this led to the suggestion that much of the water necessary for germination is therefore provided internally (Yarwood,1952,1957). A variation on this theme is that mildew conidia have a high lipid content (McKeen et al.,1967) and that the water needs of the conidium could be partly provided by the oxidation of fats (McKeen,1970).

Whatever the explanation, powdery mildew conidia are considered as self sufficient propagules with regards to their moisture requirement for germination. Indeed, an external source of water is harmful to mildew conidia.

b. Free water and conidial germination

Most studies on the effect of water on conidial germination have been made on glass surfaces and this review is concerned mainly with these. Many workers have claimed that germination of mildew conidia is inhibited or reduced in the presence of water or conidia do not germinate at all in water (table 1).

Table 1. Germination of conidia of different powdery mildew fungi

Pathogen	Host	% Germination Glass	Water	Leaf	Temp.°C.	Author
Erysiphe cichoracearum	Helianthus	52	30	-	18	Morrison, 1964
	lettuce	90	20	-	25	Schnathorst, 1960
	sun flower	9	on water 24 in water 13	-	22	Yarwood, 1936
E.graminis	barley	-	low	-	?	Sawada, 1927
	barley	71.5	10	-	15	Graf-Marin, 1934
	barley	-	on water low in water 0	-	20	Corner, 1935
	barley	5	on water 15 in water 0	-	20	Clayton, 1942
	barley	60	on water 50 in water 10	-	20	Hossain & Manners, 1964
	oat	39	on water 59 in water 41	-	22	Yarwood, 1936
	oat	47	8	-	22	Grainger, 1947
	wheat	-	low	-	25	Arya & Ghemawat, 1954
	wheat	-	low	-	11-17	Jiafeng et al., 1976

Table 1. contd.

E.horridula	Myosotis	-	low	-	21	Zaracovitis, 1964
E.polygoni	Delphinium	29	15	15	22	Brodie & Neufeld, 1942
	red clover	35	on water 6 in water 0	-	20	Clayton, 1942
	red clover	86	on water 65 in water 57	-	22	Yarwood, 1936
Leveillula taurica	Cynara	49	on water 26 in water 10	-	27.5	Nour, 1958
Oidium begoniae	Begonia	-	low	-	21	Zaracovitis, 1964
O.euonymi	Euonymus	-	on water low in water 0	-	20	Corner, 1935
Phyllactinia corylea	papaw	50.2-56.9	42.8	-	25	Clerk & Ankora, 1971
Podosphaera leucotricha	apple	-	2-3	-	19-25	Woodward, 1927
	apple	5	on water 1 in water 0	-	22	Berwith, 1936
	apple	-	0	-	20	Suvorova, 1974

Table 1. contd.

Sphaerotheca fuliginea	cucumber	30	on water low in water 0	-	28	Hashioka, 1937
S.macularis	strawberry	28	on water 8 in water 4	82	20	Peries, 1962
S.pannosa	rose	-	low	-	?	Neger, 1902
	rose	-	low	-	?	Foex, 1924
	rose	-	low	-	18	Hammarlund, 1925
	rose	-	on water low in water 0	-	20	Corner, 1935
	rose	20.3	on water 13.8 in water 5.3	76.8	21	Longrée, 1939
	rose	62.4	0	-	20-24	Leu & Kao, 1975
Uncinula necator	vine	95	81	-	25	Delp, 1954
	vine	37.8	low	-	21	Weltzien-Stenzel, 1959

Unfortunately some reports only state that germination is poor in water and make no quantitative comparison with germination on other surfaces. Also, some workers fail to indicate the position of conidia in water, though this is important. For example, it has been reported that conidia floating on the surface of water germinate better than conidia submerged under water (Corner,1935; Schnathorst,1959b,1965; Zaracovitis,1964 and see also table 1). Immersion of conidia in water for 1-3 hours (Corner,1935), 2 hours (Yarwood,1950a) or as brief as 5 min (Zaracovitis,1966) and 3 min (Peries,1961) has been reported to kill most spores.

Many investigators have also observed that condensation of water onto conidia (at high relative humidities) not only resulted in poor germination (Hashioka,1937; Longree,1939; Delp, 1954; Schnathorst,1960; Manners & Hossain,1963; Zaracovitis,1964; Hewitt,1974; Uchiyama et al.,1978) but in abnormal germ-tube development (Delp,1954; Coyier,1961; Populer,1972), though there are relatively few details. In water conidia have variously been reported to produce a single germ-tube (Graf-Marin,1934; Hashioka,1937; Nour,1958), 2-6 germ-tubes (Hossain,1959; Hossain & Manners,1964) or many small protruberances which never develop into germ-tubes (Corner,1935; Longree,1939). The germ-tubes may be long (Hashioka,1937), short (Kunkel,1936), straight (Graf-Marin,1934), distorted (Longree,1939) or sometimes branched (Nour,1958) and they may be septate (Corner, 1935) or aseptate (Graf-Marin,1934; Hashioka,1937).

Immersion under water appears to alter the internal structure of conidia, most notably there are changes in the vacuoles

(Zaracovitis,1966), these sometimes disappearing completely (Mitchell & McKeen,1970) and the cytoplasm becomes granular or disintegrated (Corner,1935; Longree,1939; Clayton,1942; Sakurai & Hirata,1959; Peries,1962; Zaracovitis,1964,1966; Uchiyama et al.,1978). Often the conidia burst after a short period in water (Sawada,1927; Delp,1954; Sakurai & Hirata,1959; Manners & Hossain,1963) or the cytoplasm otherwise exudes through pores or ruptures in the conidial wall (Clayton,1942; Yarwood, 1952) or by the detachment of a peg like structure at the ends of conidia (Sakurai & Hirata,1959). The active Brownian movement within the conidium vacuoles generally ceases shortly before these events (Zaracovitis,1966). These changes are accelarated by adding small amounts of detergents or wetting agents (Zaracovitis,1964; Mitchell & McKeen,1970), once these changes occur the conidia will not germinate (Mitchell & McKeen,1970). Several suggestions have been made to explain the collapse of mildew conidia in water including plasmoptysis (Hashioka,1937; Delp,1954; Sakurai & Hirata,1959), excessive intake of water which disrupts the protoplasmic colloids and/or interferes with normal germination (Zaracovitis,1964), lack of oxygen (Corner,1935; Longree,1939) or the combined effect of lack of oxygen, carbon dioxide accumulation and a self inhibitor of germination (Hossain & Manners,1964).

Conidia on the surface of water drops are less affected but the germ-tubes tend to grow vertically, away from the water surface (Corner,1935; Longree,1939; Dickinson,1949; Arya & Ghemawat,1954; Nour,1958, Hossain & Manners,1964).

There is little information to indicate whether a conidium in water produces an appressorium. In the experiments of Hashioka (1937), Delp (1954) and Zaracovitis (1964) they did not. However, Nour (1958) reported that although appressoria were rarely formed by conidia floating on water drops, they were produced abundantly by conidia submerged in a shallow film of water. Also, Hossain (1959) and Hossain & Manners (1964) found that conidia floating on water occasionally produced appressoria when they come into contact with another conidium or germ-tube.

Similarly, few workers have examined the effects of water on hyphal growth and conidiophore production but Sakurai & Hirata (1959) reported that when detached conidial chains and conidiophores were immersed the cells became disorganised and burst and hyphal pieces at the margin of pustules broke at the tips.

Because of these effects, suspending conidia in water has not been considered a satisfactory method for inoculations (Corner, 1935; Yarwood, 1951; Zaracovitis, 1964), but a few workers have obtained infections by this method. For example, Reuveni & Rotem (1973) successfully inoculated tomato and eggplant (but not pepper) with aquous suspensions of Leveillula taurica conidia. Also Yarwood (1978b) claimed that aquous conidial suspensions of Erysiphe polygoni and E.cichoracearum were satisfactory as inocula if used soon after preparation, though infectivity was lost after one hour (Yarwood, 1952).

c. Leaf wetness and mildew development

Several workers have reported that mildew intensity was reduced when leaves were covered with water films either in experiments (Woodward,1927; Clayton,1942; Cherewick,1944; Morrison,1964) or under field conditions involving sprinkler irrigation (Rotem & Cohen,1966) or covers that induced condensation of water (Garibaldi et al.,1976). On the other hand, Reuveni & Rotem (1974) have shown that periods of leaf wetness up to 12h progressively increased the number of infections produced by Sphaerotheca fuliginea on squash and Yarwood (1978b) reported that immersing cucumber leaves, inoculated with this fungus, under water for 2 days increased mildew severity.

A few of the early workers also suggested that there was an association between mildew and periods of heavy dew (Carter,1915; Eastham & Ruhmann,1924; Jacob,1929; Ubrizsy, 1946), an idea which finds some support in more recent papers by Peries (1973) and Royle (1975). However, Duvdevani et al. (1946) prevented dew formation at nights and found that this practice did not reduce disease incidence. Also, Rogers (1959), Perera (1972) and Perera & Wheeler (1975) have shown that small water droplets in the form of mist on leaves retarded mildew development to an extent related to the length of wet period.

There is some published information on the effect of leaf wetness on various stages of mildew growth, though sometimes it is contradictory. Thus some authors have reported a significant reduction in conidium germination on wetted leaves

(Woodward,1927; Burchill,1958; Rogers,1959; Schnathorst,1960; Morrison,1964; Ward,1973) whereas Gaumann (1946) claimed that mildew conidia need water films or heavy dews for germination and Weinhold (1961) reported that conidia of Sphaerotheca pannosa on peach germinated better in the presence of water droplets on leaves.

Whether conidia that germinate on wet leaves can infect them is another matter. Perera & Wheeler (1975) postulated that water prevents contact of the germ-tube with the leaf surface and so delays infection atleast until the drop evaporates (Schnathorst,1958).

Water also adversely affects the growth of mycelium on leaves (Rogers,1959; Perera,1972; Perera & Wheeler,1975) and the development of mildew pustules (Ward,1973) though there are less data than for conidium germination. The effect is persistent and more marked if wet periods immediately follow inoculation (Perera & Wheeler,1975; Wheeler,1973,1978) and in some instances the hyphae swell and branch abnormally (Schnathorst, 1959a).

Conidiophores are often not produced when leaves are moist (Woodward,1927; Hashioka,1937; Boughey,1949) and existing conidial chains collapse (Rogers,1959) and adhere to one another, possibly because on wetting the conidia burst and release cytoplasm which then sticks the ruptured conidia together (Sakurai & Hirata,1959). Small water droplets do not damage the conidiophores extensively (Hammett,1966) but flatten them and temporarily prevent spore release (Ward & Manners,1974;

Ayres,1977). However, the conidial chains continue to grow (Hammett & Manners,1973) and sporulation returns to normal within 2 days after wetting (Ward & Manners,1974). However, Yarwood (1978a) reported that submerging mildew colonies in water prior to the formation of conidiophores prevented their production.

d. Rain and mildew development

Several early accounts claimed that rain favoured the development of powdery mildew fungi (Bioletti, 1907; Blodgett, 1913; Brisley,1926; Jacob,1929; Bremer,1940) but generally there have been more reports to the contrary (Yarwood,1936,1950a; Boughey,1949; Burchill,1958; Fernando,1971; Peries,1973; Leu & Kao,1975; Jiafeng et al.,1976). Possibly differences in the intensity and duration of rain account for the conflicting reports. Indeed there are some indications that light showers of short duration (Beeley,1932; Wastie,1972) or intermittent rain (Peries,1966) favour mildew whilst frequent, prolonged or heavy rain is inimical to mildew development (Beeley,1932; Fernando,1971; Dixon,1978). Thus a 1-2 day rainy spell favours the initiation of an epidemic of Oidium heveae on rubber but if, subsequently, there is a prolonged rain, heavy infections are unlikely (Wastie,1969).

The adverse effect of rain on mildew has been experimentally demonstrated both by Yarwood (1936) and Wellman (1972). They found that when mildewed plants were protected from rain, they became severely infected while the unprotected plants were relatively free of mildews. This led Wellman to suggest that in some tropical areas mildews might disappear once the rains

commenced. However, this does not seem altogether likely since the mildew growth might be protected on the lower surface (Hashioka,1937) and even on the upper surface by shading of other leaves (Kranz & Aust,1979).

The adverse effect of rain on mildew development may result from several factors. Conidia may be washed off leaves by rain (Fernando,1971; Built & Lafon,1978), though probably not easily once they have germinated (Nour,1958; Smiljakovic,1966). There may be physical damage to the mycelium (Yarwood,1936,1950a, Butt,1970; Built & Lafon,1978) or developing conidiophores due to the impaction of the raindrops (Yarwood,1936,1957). Additionally, rain affects both the release of conidia and their distribution in air (Hirst & Stedman,1963; Leu & Kao,1975 ; Jiafeng et al.,1976). Often there is a significant increase in airborne conidia at the onset of rain as the leaves are shaken by impacting drops (Hirst,1953; Hirst & Stedman,1963; Fernando, 1971; Hammett & Manners,1971). Then, if the rain continues, most conidia are washed out of the air and spore release, if it occurs at all, is variable (Sreeramulu,1964; Hammett & Manners, 1971; Eversmeyer et al.,1973; Jenkyn,1974; Royle,1978; Sutton & Jones,1979). After heavy rain it may take some 2-5 days before concentrations of conidia in the air reach their pre-rain levels (Hirst,1953; Peries,1962; Sreeramulu,1964).

Indirectly, rain may affect mildew in other ways, some beneficial, for example by increasing atmospheric humidity (Yarwood,1978c), by washing off protective layers of fungicide used to control mildew (Wastie,1969; Yarwood,1978c) and by favouring the growth of susceptible host tissue (Yarwood,1978c). Rain washing of leaves before inoculation with powdery mildew

may also influence subsequent disease development. For example, Purnell & Preece (1971) found that Erysiphe cruciferarum initially grew less well on washed swede leaves but subsequently grew better if inoculations were delayed 5 days or longer. Podosphaera clandestina also grew better on washed hawthorn leaves (Khairi & Preece,1979).

e. Mildew control by water sprays

The detrimental effect of water on the development of mildew colonies suggests that powdery mildews might be controlled by water sprays. Evidence in support of this has been given by many workers (Yarwood,1936,1939; McClellan,1942; Cherewick,1944; Delp,1954; Rogers,1959; Sakurai & Hirata,1959; Jarvis & Slingsby, 1977) though there are some reports to the contrary (Crawford, 1927; Spraque,1953). Opinions vary slightly concerning the most effective type of spray. McClellan (1942), Kohl (1956) and Rogers (1959) found that intermittent mist was effective in controlling rose mildew. Kohl (1956) reported that this helped to raise disease free rose plants for flower production. However, Yarwood (1978a)reported that water sprays at low impact pressure increased mildew severity but at high impaction it prevented infection and cured established infections. He maintained that control was largely achieved through the mechanical effect of impacting water drops.

Control by water sprays has the added advantage of controlling red spiders (Yarwood,1939) but it has the greater risk of favouring the development of black spot fungus, Diplocarpon rosae on roses (McClellan,1942) and apparent

parasitism of Ampelomyces quisqualis on flowers and fruits of host plants (Jarvis & Slingsby,1977).

Although spraying with water can control mildew, it is not commercially practicable as the syringing necessary must be vigorous and frequent (McClellan,1942). However, Sitterly (1978) suggests that home gardeners and small growers could control mildews by spraying them with a garden hose in the afternoon.

f. Mildew incidence in relation to mode of irrigation

In tropical countries crops are often supplied with water through furrow or overhead irrigation. Several investigators have noticed that with sprinkler irrigation the onset of mildew is delayed and its development is slight (Curl & Weaver,1958; Bennett,1962; Rotem & Cohen,1966; Rotem & Palti,1969; Ruppel et al.,1975). Rotem & Cohen (1966) suggest that overhead irrigation, especially in the evenings, plus dew formation at night keep plants wet for long periods and this suppresses mildew growth. The extent to which mildew growth is restricted appears to depend on the crop and the atmospheric conditions. Palti (1971) found that Leveillula taurica was less markedly inhibited on very susceptible cultivars than on others and that sprinkling was less effective when the atmospheric humidity was low. Not all the evidence supports the idea that sprinkling adversely affects mildew development. For example, Spraque (1953) claimed that Podosphaera leucotricha on apple was increased. Butt (1978) suggests that this might be related to the high moisture requirement of this species. Furthur evidence that sprinkler

irrigation increases mildew is to be found in reports by Reeves & Blodgett (1949) and Khlebarodau & Zabara (1978).

g. Water relations of host plant and mildew development

There are statements in the literature that powdery mildews develop better on wilted plants (Cherewick, 1944) or that low soil moisture favours the development of mildews (Yarwood, 1949; Drandarevski, 1969). Yarwood (1978c) believes that the effect of soil moisture must be a predisposition effect as the fungus is on tissues well removed from soil. However, Cole (1966) reported that plants grown under conditions of water stress developed less disease while plants grown under liberal watering became very susceptible. Tapke (1951) has given evidence that exposing plants to drought toughens them and develop resistance to disease. Recently, Ayres (1977) demonstrated that mycelial growth and sporulation of Erysiphe pisi were significantly reduced by imposing water stress on pea plants. Later Ayres & Zadoks (1979) and Ayres & Woolacott (1980) showed that infection, conidial germination and appressorium formation of E.graminis were less on barley plants grown in dry soil and the mildew colonies grew more slowly. This reduction in mildew development was more marked on adult plants than on seedlings suggesting the development of an adult plant resistance by plants grown under water stress.

I. MILDEW GROWTH IN RELATION TO LEAF SURFACE WETNESS

Perera & Wheeler (1975) have shown that minute water droplets retard the overall development of Sphaerotheca pannosa on rose especially if the leaves are wetted immediately after inoculation. The present investigation extends their work and examines in detail the effects of leaf wetness on the different stages of mildew development.

Materials and methods

a. Host plants and mildew

Three mildews were studied in this investigation, Erysiphe graminis DC.f.sp.hordei on barley (cv. Zephyr), E.pisi DC. on pea (cv. Kelvedon wonder) and Sphaerotheca pannosa (Wallr.) Lev. on rose (cv. Frensham). Barley seeds were sown in John Innes compost (J.I.) no.1 in 12 cm pots and thinned to 10-15 seedlings per pot. These were used in experiments after 7-9 days, when the first leaves were well expanded. Pea seedlings were also raised in J.I. no.1, 3-4 seedlings per 12 cm pot and were used after c.2 weeks. Roses were pruned and then planted singly in 30 cm pots containing J.I. no.3 and kept well watered to encourage a new flush of young leaves. All plants were maintained on a moist sand bench within a filtered air cabinet in a glass house at 20±3°C. with a 16h photoperiod. In most experiments leaf pieces, c.2 cm long, cut centrally from the first leaf of barley and leaf discs (1 cm diam.) cut with a punch (no.224, Maun Industries, England) from the last fully expanded

leaves of pea and leaflets of rose were used.

The mildew fungi were maintained on their respective hosts in a separate filtered air cabinet. They were transferred periodically to fresh plants by shaking the infected plants over them. The mildews were also maintained on leaf segments or discs floating on distilled water in clear polystyrene boxes with tightly fitted lids (5.5x3.5x2.0 cm, Stewarts Plastics Ltd, England) in an illuminated cabinet at 20±1°C. Conidia were removed daily from colonies by blowing air over them. This ensured a ready supply of young (24h) conidia.

b. Standardisation of leaf-surface wetness

Inoculated leaf segments and discs were floated on the surface of glass distilled water in small polystyrene boxes. This material was sprayed for 1-2 min with a fine mist of glass distilled water discharged from a hand-held Shandon Laboratory Spray Gun, 1-1.5 m away. The boxes were then closed with lids and placed in an illuminated cabinet at 20±1°C. At the end of required wet period the boxes were removed from the incubator, their lids opened and the leaf tissues were dried by means of a fan held at 1.5-2 m away for 5-10 min. After drying the leaves were re-incubated as required.

The distribution of water droplets obtained with this technique was examined by spraying sample leaves with 0.1% aq. $CuSO_4$, drying them and pressing them on duplicating paper impregnated with rubeanic acid as described by

Large & Taylor (1953). Figure 1.1 shows the typical distributions obtained.

c. Inoculation of leaf tissues

Leaf segments or discs, usually 10-20 per treatment were inoculated on the adaxial surface by allowing 24h conidia to deposit on them via a cardboard cylinder (60 cm high 12 cm diam.) from an infected leaf (Perera,1972). Seedlings (or large quantities of leaves) were inoculated with 24h conidia using a settling tower described by Round & Wheeler (1978) (Fig 1.2).

d. Assessment of mildew growth

Mildew development was assessed as follows:

Germination: After the required incubation (usually 24h) either celloidin peels (1% Gurr's celloidin in 1:1 absolute alcohol and diethyl ether) or sellotape impressions of the inoculated surface were taken. These were gently warmed in a drop of cotton-blue lactophenol on a slide before examining under the microscope (x100). For immediate assessment of germination sellotape impressions were preferred as they could be prepared quickly. However, they did not store well so where counting had to be delayed or for detailed studies of germ-tube growth, celloidin peels were preferred. Usually 100-200 conidia were assessed at random on each of 5-10 leaf samples. A conidium was considered to have germinated

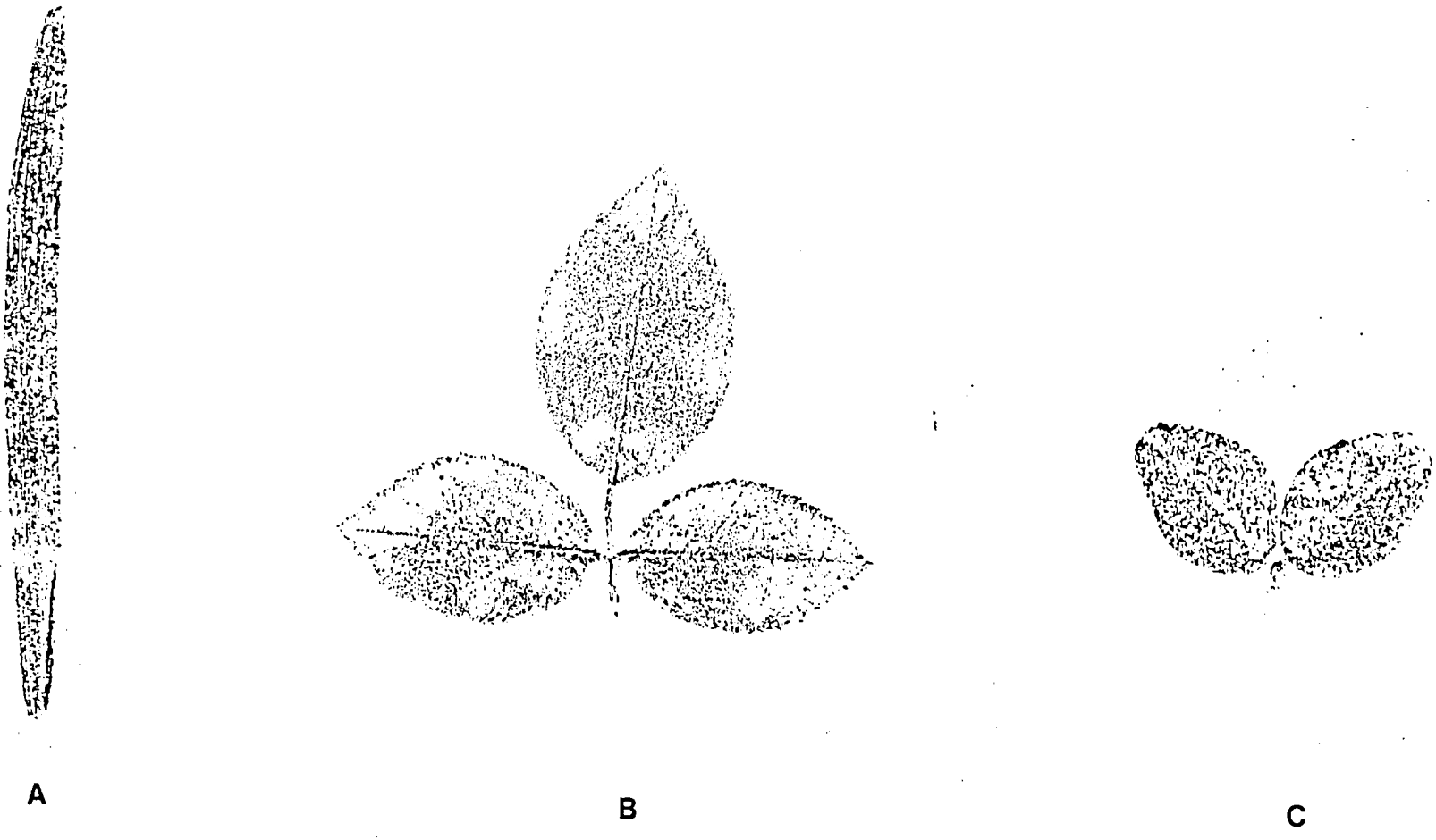


Fig. 1.1 Distribution of water droplets on mist sprayed leaves. A - barley, B - rose and C - pea.

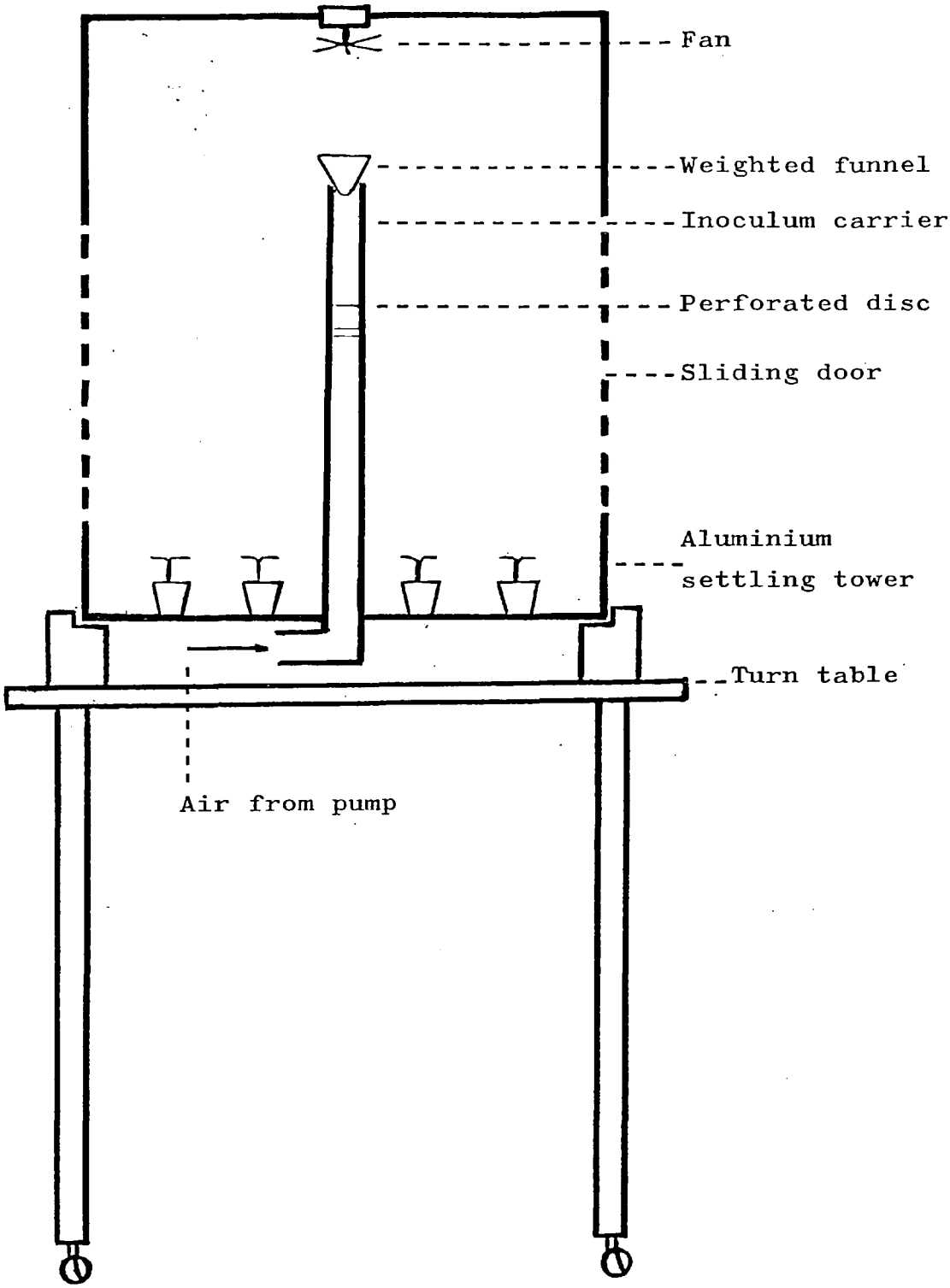


Fig.1.2 Settling tower

if its germ-tube exceeded the breadth of the conidium (Manners & Hossain, 1963).

Infectivity of conidia: Conidia that germinated successfully usually produced elongating secondary hyphae (ESH) 48h after inoculation. These subsequently formed colonies. The number of conidia forming ESH was thus used as a measure of infectivity and was assessed on a sample of conidia similar to that used for germination.

Mycelial growth: The total mycelial growth of 25-50 colonies was assessed from celloidin peels of inoculated leaf material or leaf tissues cleared overnight in absolute methanol within each experimental treatment. Lines corresponding to hyphae were drawn using a camera lucida and these were related to a known length from a similar tracing of a stage micrometer scale using a map measure (opisometer).

Colony size: Colonies of E.graminis were assumed elliptical, their smaller and larger diameters measured and area determined. In the case of E.pisi and S.pannosa the colonies were considered circular and area determined by measuring the diameter along the long axis.

Production of conidiophores: Assessments of the number of conidiophores were based on counts within 10 microscope fields (x100) taken at random from each leaf sample. The values are usually expressed as the number per mm^2 of colony. Occasionally (for E.graminis in particular), the

total number of conidiophores per colony was determined and expressed as the number per colony or per unit area of the colony.

Production of conidia: The numbers of conidia were determined from haemocytometer counts of suspensions prepared from colonies of known size. In preliminary experiments with barley, leaf pieces with mildew colonies were shaken with 10 ml water plus a drop of Tween 80 in a specimen tube. This method tended to remove immature conidia in conidial chains so, subsequently, leaf tissues with colonies were tapped gently over a tube of water plus Tween 80. Productivity is expressed as the number of conidia per unit area of colony.

Experimental

A. Effects of leaf wetness on barley mildew

The initial experiments investigated the overall effects of a 6h period of leaf wetness applied at different stages in the establishment of E.graminis on barley.

In the first of these experiments, 80 leaf segments were inoculated with 24h conidia, half of these were sprayed with water and kept wet for 6h and half were left unsprayed. Samples of 10 segments from both regimes were taken at intervals for assessments of growth as indicated in Table 1.1.

Table 1.1 Effect of a 6h wet period immediately after inoculation on the development of E.graminis.

Growth stage	Hours after inoculation	Mean values* Treated	Control
% germination (10)	24	32.4	69.3
Mycelial growth (mm) (50)	48	1.31	2.14
Conidiophores/mm^2 colony (50)	72	20	90
Conidiophore initials (i) and mature conidiophores (m) /colony (50)	96	i. 285 m. 83	189 256

*Detailed results are given in Appendix Table 1.1.
Figures in brackets are number of replicates.

A second experiment, essentially similar to the first, examined the effects of 6h leaf wetness applied 24h after inoculation when the conidia had already germinated and some infections had been established. Mycelial growth and conidiophore production were measured as before. Additionally, production of conidia at 120h was determined on 5 leaf samples from each treatment and expressed as conidia per cm^2 leaf (Table 1.2). In three subsequent experiments this last method was used to assess the effects on conidia production of wetting leaves 48, 72 and 96h after inoculation (Table 1.3).

The results of these experiments indicate that wetting leaves either immediately or 24h after inoculation had considerable effects on mildew development which could still be discerned after 5 days. Comparatively, wetting leaves immediately after inoculation had the greater effect (Table 1.4). A curious feature of both experiments was the apparent stimulation by wet periods of the initiation of conidiophores, 96h after inoculation. Applying wet periods at 48, 72 or 96h decreased sporulation. The effect was more serious as conidiophore production became progressively well advanced but there was some recovery (Table 1.5).

The effects of wetting noted in these experiments were partly to delay mildew development. So, in a further experiment, in which leaf segments were kept wet for 6h immediately after inoculation with conidia, assessments of the various stages were compared on unwetted and wetted

Table 1.2 Effect of a 6h wet period applied 24h after inoculation on the development of E.graminis.

Growth stage	Hours after inoculation	Mean values* Treated	Control
Mycelial growth (mm) (50)	48	0.83	1.16
Conidiophores/ mm^2 colony (50)	72	10	21
Conidiophore initials (i) and mature conidiophores (m) /colony (50)	96	i. 172 m. 85	119 148
Conidia/cm^2 leaf (10^{-3}) (5)	120	5.3	10.9

*Detailed results are given in Appendix Table 1.2.

Figures in brackets are no. of replicates

Table 1.3 Effects of a 6h wet period applied 48, 72 and 96h after inoculation on the conidia production of *E.graminis*.

Time of assessment (h after inoculation)	Conidia x 10^{-3}/ cm^2 leaf*					
	48h		72h		96h	
	T	C	T	C	T	C
96	1.8	2.4	2.2	3.6	-	-
120	9.3	12.4	7.5	12.0	12.2	17.6
144	16.5	20.9	13.4	18.0	21.8	31.5
168	-	-	20.1	25.4	28.9	52.6
192	-	-	-	-	43.6	57.5

*Mean of 5 leaf segments for wetted (T) and control (C).

Detailed results are given in Appendix Table 1.3.

Table 1.4 Effects of 6h wet period (as % of control) applied immediately (0) and 24h after inoculation of barley with E.graminis.

Growth stage	Hours after inoculation	Wet period applied at 0	Wet period applied at 24h
% germination	24	46.8	-
Mycelial growth(mm)	48	61.2	71.6
Conidiophores/ mm^2 colony	72	22.2	37.0
Conidiophores/ colony (initials-i, mature-m)	96	i. 150.7	144.5
		m. 32.4	57.4
Conidia/ cm^2 leaf	120	-	48.6

Table 1.5 Effects of a 6h wet period (as % of control) applied 48h, 72h and 96h after inoculation on the conidia production of E.graminis.

Time of assessment(h)	Wet period applied at 48h	72h	96h
96	75.0	61.1	-
120	75.0	62.5	69.3
144	78.9	74.4	69.2
168	-	79.1	54.9
192	-	-	75.8

leaf segments at 24h and 30h, 48h and 54h and at 72h and 78h respectively to determine the effects on mildew growth if the wet period was not taken into account (Table 1.6).

There was only a slight increase in germination when the wetted leaves were given a further 6h incubation but total mycelial growth and conidiophore production increased considerably and the values obtained were higher than those for unwetted leaves 6h earlier. Leaf wetness does not thus appear to have a permanent effect on mycelial growth and conidiophore production but it does on germination.

In the light of these results, the effects of leaf wetness on the various stages of mildew growth were examined in detail.

B. Leaf wetness and germination of conidia

Germination of mildew conidia was not much improved on water-sprayed leaves when they were given a further incubation period of 6h (Table 1.6). However, this did not exclude the possibility that germination might improve if leaves, once dried, were incubated for longer periods. This was tested in an experiment in which 90 barley leaf pieces were inoculated with E.graminis and 60 of these were given a 6h wet period immediately after inoculation. Percentage germination was assessed on the control and treated leaves at 24, 48 and 72h and additionally on the treated leaves at 30, 54 and 78h after inoculation.

Table 1.6 Effect of 6h wet period applied immediately after inoculation on the development of E.graminis after different incubation periods.

Growth stage	Hours after incubation	Mean values* Treated	Control
% germination (10)	24	41.2	71.9
	30	46.6	-
Mycelial growth (mm) (50)	48	1.14	1.67
	54	1.87	-
Conidiophores/ mm^2 colony (50)	72	2	8
	78	12	-

- = no test

*Detailed results are given in Appendix Table 1.4.
Figures in brackets are no. of replicates

The results (Table 1.7) demonstrate that although germination was slightly higher with extended incubation it was not much improved suggesting that some conidia lost their ability to germinate on wet leaves.

It seemed likely that these conidia were those trapped in water droplets, so the relative distribution of water droplets and mildew conidia on sprayed leaves were examined. Thirty leaf segments of barley were inoculated with E.graminis and then divided at random into three groups of 10 segments. One group was sprayed with water and kept wet for 6h as in previous experiments and another group was left unsprayed as a control. Both groups were incubated at 20° in an illuminated cabinet for 24h when germination was assessed. The third group of leaf segments was not incubated, but immediately after inoculation was sprayed with 0.1% aq. neutral red, using the standard technique for applying water to leaves (p.23). The segments were then dried for 5 min under a fan. Sellotape impressions taken from these segments were mounted in liquid paraffin. In this, the neutral red droplets remained intact whereas in other substances such as water, glycerol and lactophenol the stain diffused out. The number of conidia stained with neutral red and the unstained spores were determined on these leaf segments.

The results (Table 1.8) suggest that the reduction in germination on water sprayed-leaf segments is indeed caused by the incorporation of conidia in water droplets. The residual germination is that of conidia between water droplets.

Table 1.7 Effect of 6h wet period applied immediately after inoculation on germination of conidia of E.graminis after different incubation periods.

Hours after inoculation	* Mean % germination	
	Treated	Control
24	31.1	71.6
30	37.6	-
48	38.8	72.7
54	39.9	-
72	41.8	75.1
78	42.3	-

- = no test

*Mean of 10 replicates (detailed results are given in appendix Table 1.5).

Table 1.8 Distribution of water droplets and conidia when leaves inoculated with E.graminis were mist sprayed.

Leaves wetted with	Assessment	*Mean % values
Water(6h)	Germination	49.7
Unwetted	Germination	80.8
Aq. neutral red	No. conidia stained	45.9

*Mean of 10 replicates (detailed results are given in Appendix Table 1.6)

The next two experiments examined the effects of different periods of leaf wetness. In the first, inoculated leaf segments of barley were kept wet for periods ranging from 1h to 10h; in the second experiment the effects of wet periods less than 1h were examined. The results are presented in Fig.1.3 and Fig.1.4 respectively. Percentage germination declined progressively with length of wet period; even short periods of no more than 5 or 10 min caused a marked reduction. The relationship was not linear and provided some further circumstantial evidence that only conidia trapped in water droplets are affected. However, the data also suggested that the population of conidia was somewhat variable in its response to water. This is reflected in the gradient obtained from the regression of % inhibition of germination (as probits) on time (as logarithms) (Fig.1.5 and Fig.1.6).

The final experiment in this series examined the effect of a 6h wet period, applied immediately after inoculation, on germination of E.pisi conidia on pea and S.pannosa conidia on rose. Germination, assessed after 24h, was reduced on wetted leaves from 94% to 77% with E.pisi and from 83% to 56% with S.pannosa (detailed results are given in Appendix Table 1.9). The reduction with S.pannosa is of the same order as that obtained with E.graminis on barley but E.pisi appears much less affected. However, a microscopic examination of sprayed leaves indicated that many conidia of E.pisi had germinated abnormally and had thin, attenuated germ-tubes. Some abnormal germination was also

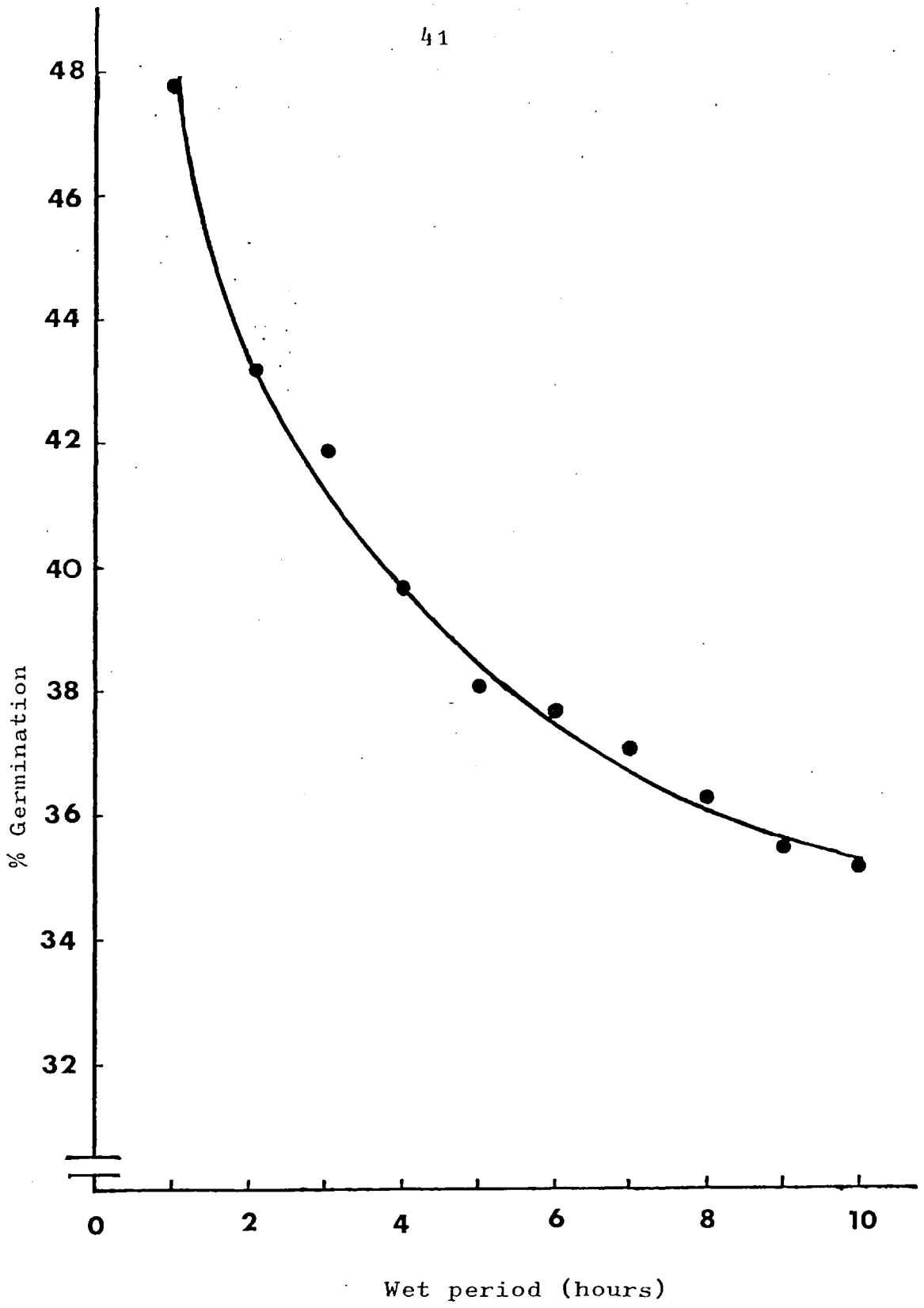


Fig.1.3 Effect of different periods of wetness applied immediately after inoculation on germination of conidia of E.graminis.

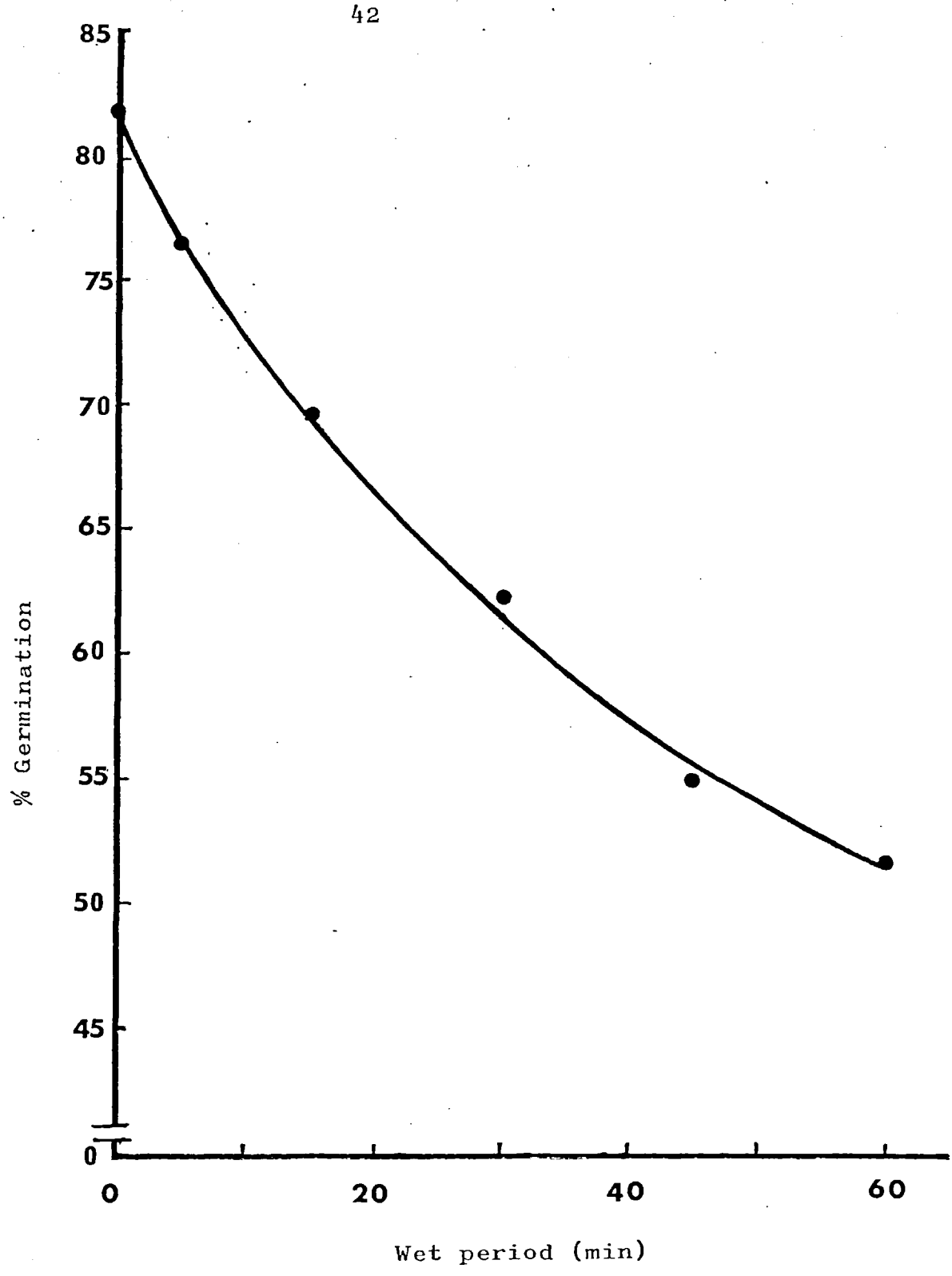


Fig. 1.4 Effect of different periods of wetness applied immediately after inoculation on germination of conidia of E.graminis.

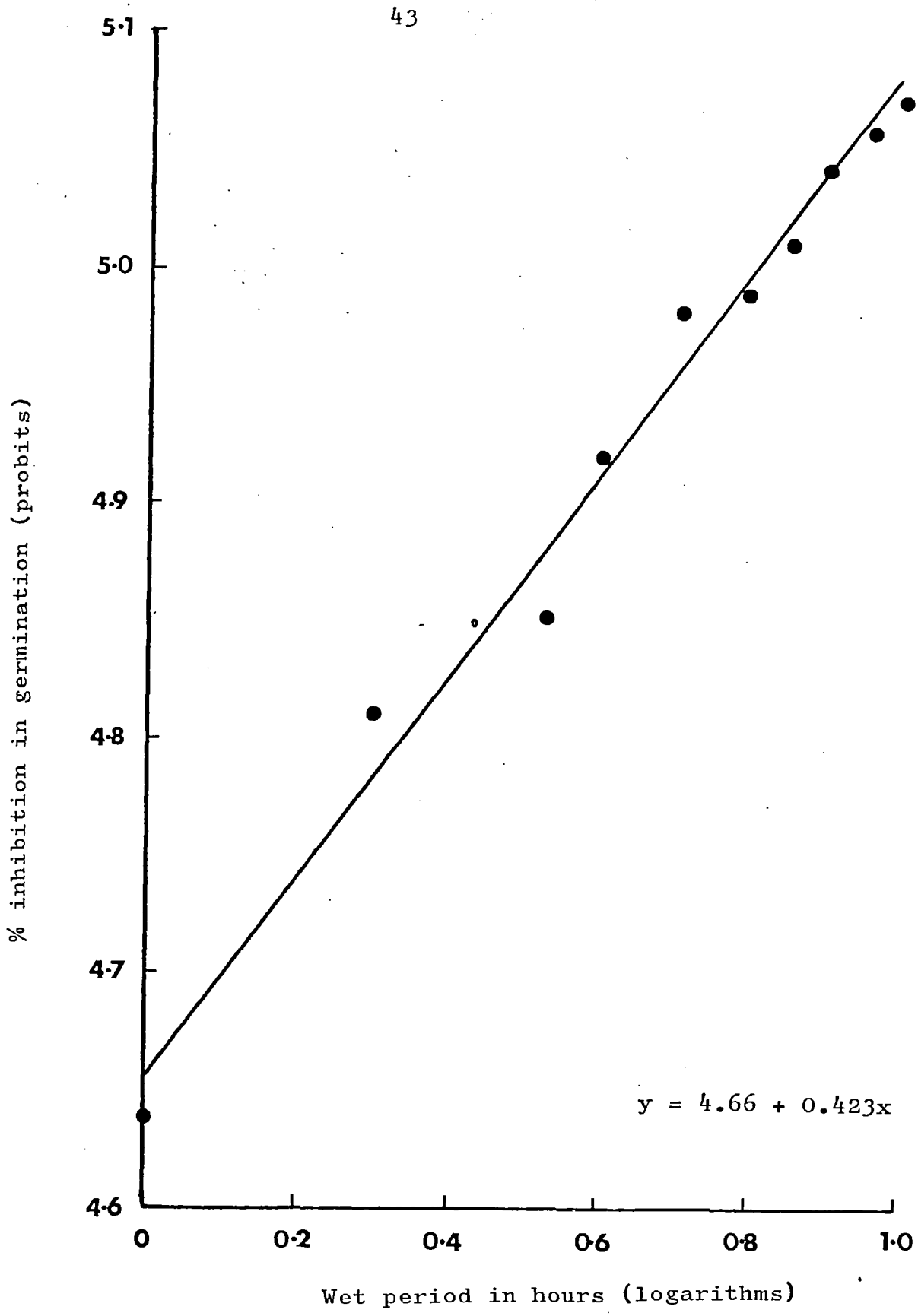


Fig. 1.5 Regression of % inhibition in conidial germination on periods of leaf wetness.

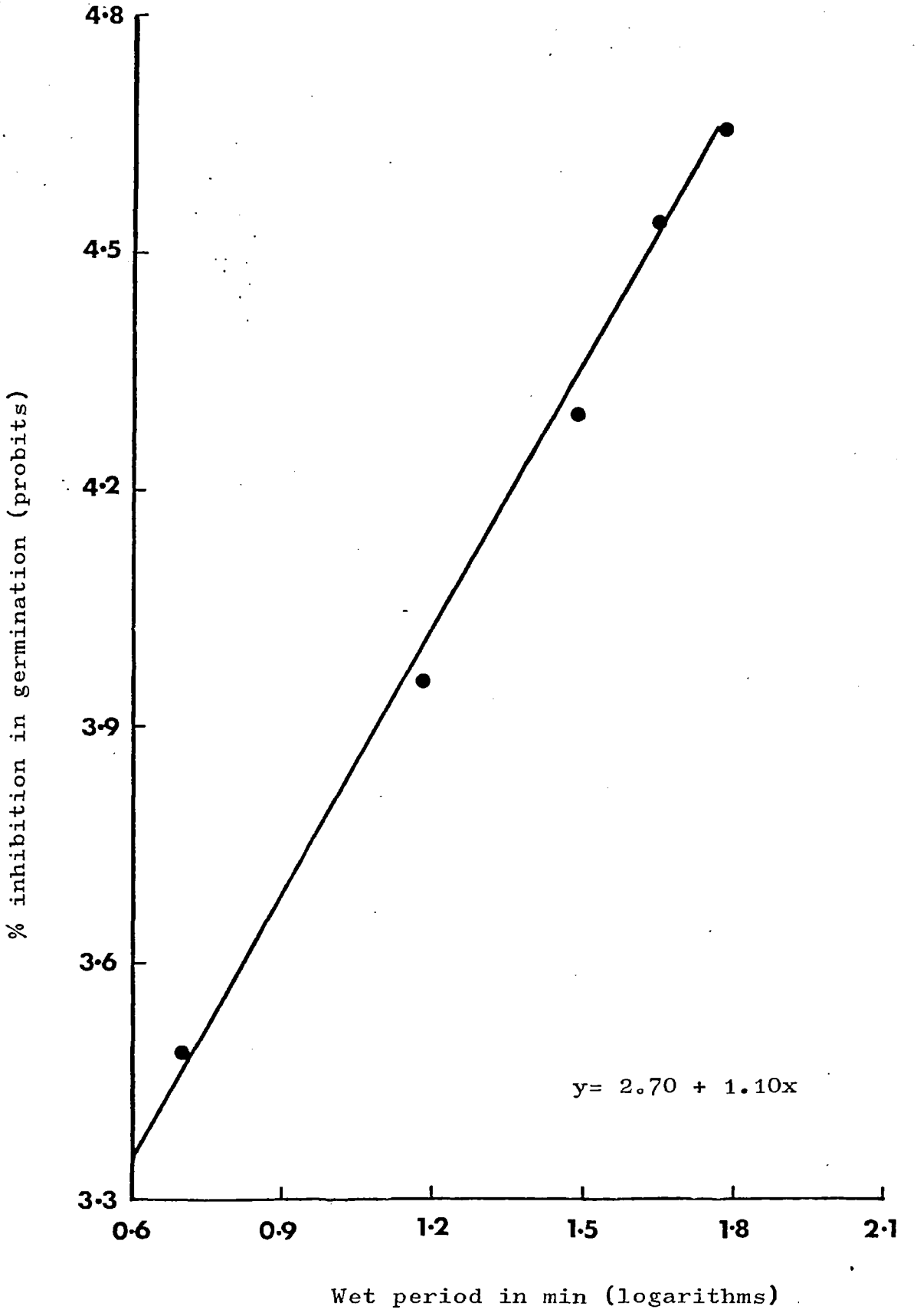


Fig. 1.6 Regression of % inhibition in conidial germination on periods of leaf wetness.

observed with S.pannosa and E.graminis in comparable experiments. It seemed likely that such germinated conidia would not be able to infect leaves and this was explored further in experiments described next.

C. Infectivity of mildew conidia

Some leaf tissue of barley, pea and rose inoculated with respective powdery mildew fungi was given a 6h wet period immediately after inoculation; other samples were not wetted and served as controls. After 24h at 20° germination was assessed on 10 leaf segments or discs from each treatment. Similar samples were taken at 48h and on these the number of conidia producing ESH was determined. The results are given in full in Appendix Table 1.10 and are summarised in Table 1.9. These show that with E.graminis and S.pannosa water mainly suppresses conidial germination whereas with E.pisi it is the establishment of ESH that is most affected. In terms of number of conidia applied to leaves the overall effect is similar, 50% of the conidia on wetted leaves eventually forming ESH.

The effect of wetting leaves on the overall infection was next examined using barley seedlings. Fifteen pots were selected, each with 10 uniformly-spaced seedlings, and these were inoculated with E.graminis in a settling tower. Then the seedlings in 5 pots were sprayed with distilled water using an atomiser held 1 m above the pots for 5 min. Another set of 5 pots was treated similarly 24h later and the remaining pots were not sprayed. Seedlings sprayed with water were kept wet

Table 1.9 Effect of 6h wet period applied immediately after inoculation on the establishment of infection.

	E.graminis		E.pisi		S.pannosa	
	T	C	T	C	T	C
% Germination*	63.3	88.6	76.5	94.0	55.9	84.1
% ESH*						
(i)of total conidia	54.6	74.1	52.8	89.9	47.2	73.6
(ii)of germinated conidia	86.3	83.6	69.0	95.6	84.4	87.5

*Means of 10 replicates for both treated (T) and controls (C).

Detailed results are given in Appendix Table 1.10.

for 6h by enclosing them in a humid chamber and then dried under a fan. Otherwise, plants were kept in an illuminated filtered air cabinet in the glass house at 20±3°. All seedlings were examined after 5-6 days when mildew colonies were just visible to the naked eye. These colonies were counted on both leaf surfaces, then the leaves were detached and their areas measured by a leaf planimeter (Paton electronic planimeter, Paton Industries Pty. Ltd., Australia). The results (Table 1.10) indicate that water applied immediately after inoculation reduced infection markedly but that wetting 24h after inoculation had little effect. Generally, throughout the treatments there was considerable variation in the number of mildew colonies that developed even between the two surfaces of one leaf. This probably reflects the difficulty of obtaining an even distribution of conidia within the settling tower on leaves borne vertically.

A further experiment with seedling barley examined the overall effect on infection of applying a 6h wet period immediately before and after inoculation with E.graminis. This contrasted, therefore, the behaviour of conidia landing on water drops and conidia covered with water. The treatments were: (i) leaves were sprayed, inoculated, kept wet for 6h and then air dried; (ii) leaves were inoculated kept wet for 6h and then air dried and, (iii) leaves were inoculated only. There were 5 pots each with 10 seedlings within each of the 3 treatments. The number of mildew

Table 1.10 Effect of 6h wet period applied immediately (0) and 24h after inoculation on the development of E.graminis.

Wet period applied at	Colonies/ cm^2 leaf*
0	4.3
24h	20.6
Control	19.5

*Mean of 50 replicates

Detailed results are given in Appendix Table 1.11.

colonies was assessed after 5-6 days as in the previous experiment. The results (Table 1.11) establish that conidia on water drops are less damaged than those covered by water.

D. Leaf wetness and mycelial growth

The results of Table 1.10 showed that applying a 6h wet period 24h after inoculation had relatively little effect on colony establishment. The effect of this treatment on mycelial growth was examined in more detail in the following experiment.

Leaf tissues of barley, pea and rose were inoculated with conidia of respective mildews and were incubated in an illuminated cabinet at 20° for 24h. Then half of the leaf segments and discs of each host were sprayed with water, kept wet for 6h, air dried and returned to the cabinet. Subsequently at intervals of 6h, starting 30h after inoculation, 5 leaf samples were removed from each treatment/host combination. These samples were decolourised overnight in absolute methanol, stained in cotton blue lactophenol and the total length of mycelium in 5-10 colonies with ESH was measured using a camera lucida (p.27).

With all three mildews mycelial growth was depressed following wetting (Figs. 1.7-1.9) but later recovered, particularly with E.graminis and S.pannosa to a level not significantly different to that of the control. These results

Table 1.11 Effect of wetting leaves for 6h before or after inoculation on the development of *E.graminis*.

Wet period applied	Colonies/ cm^2 leaf*
before inoculation	10.4
after inoculation	4.2
control	16.8

*Mean of 50 replicates

Detailed results are given in Appendix Table 1.12.

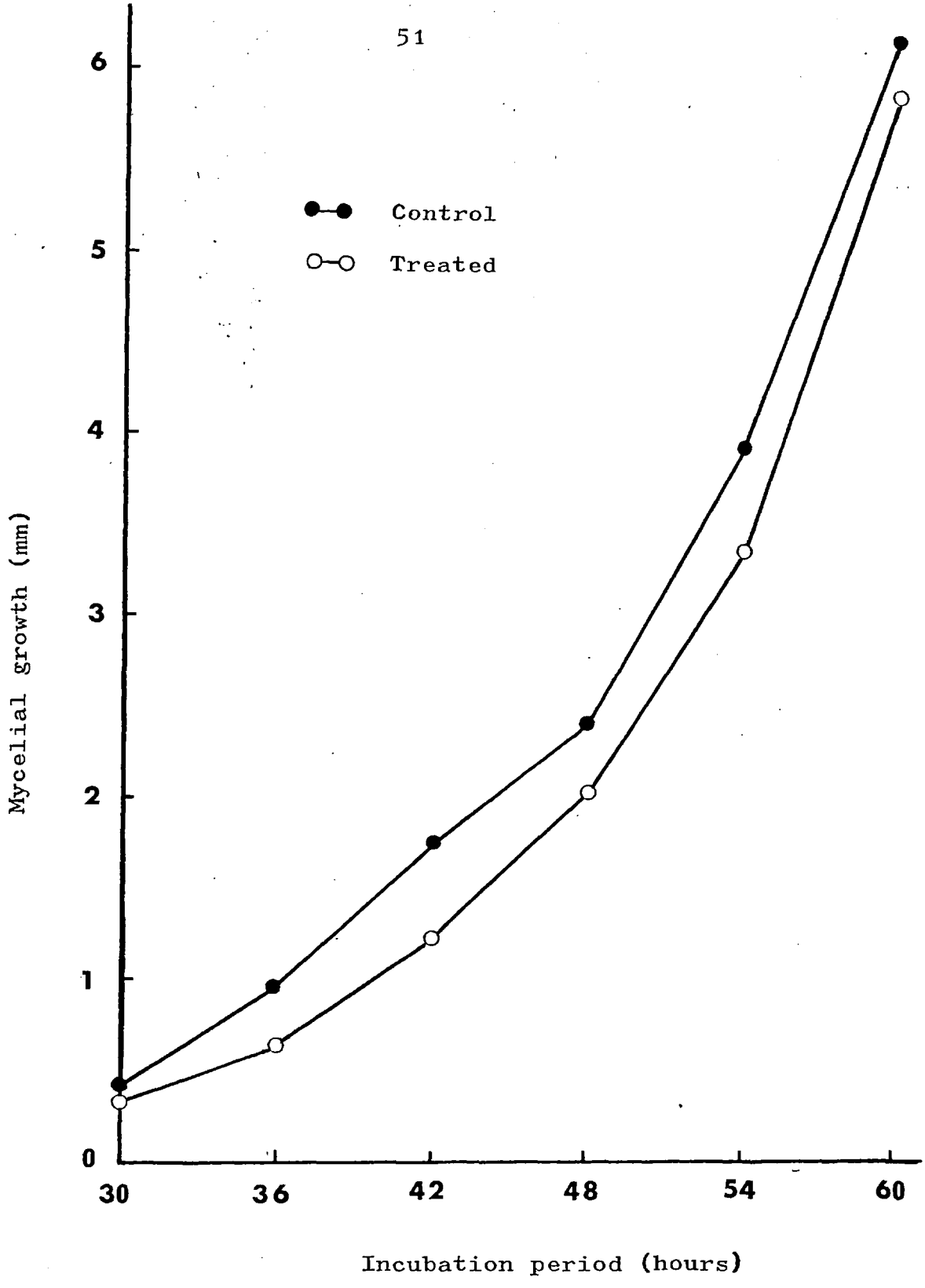


Fig. 1.7 Effect of 6h wet period applied 24h after inoculation on the mycelial growth of E.graminis.

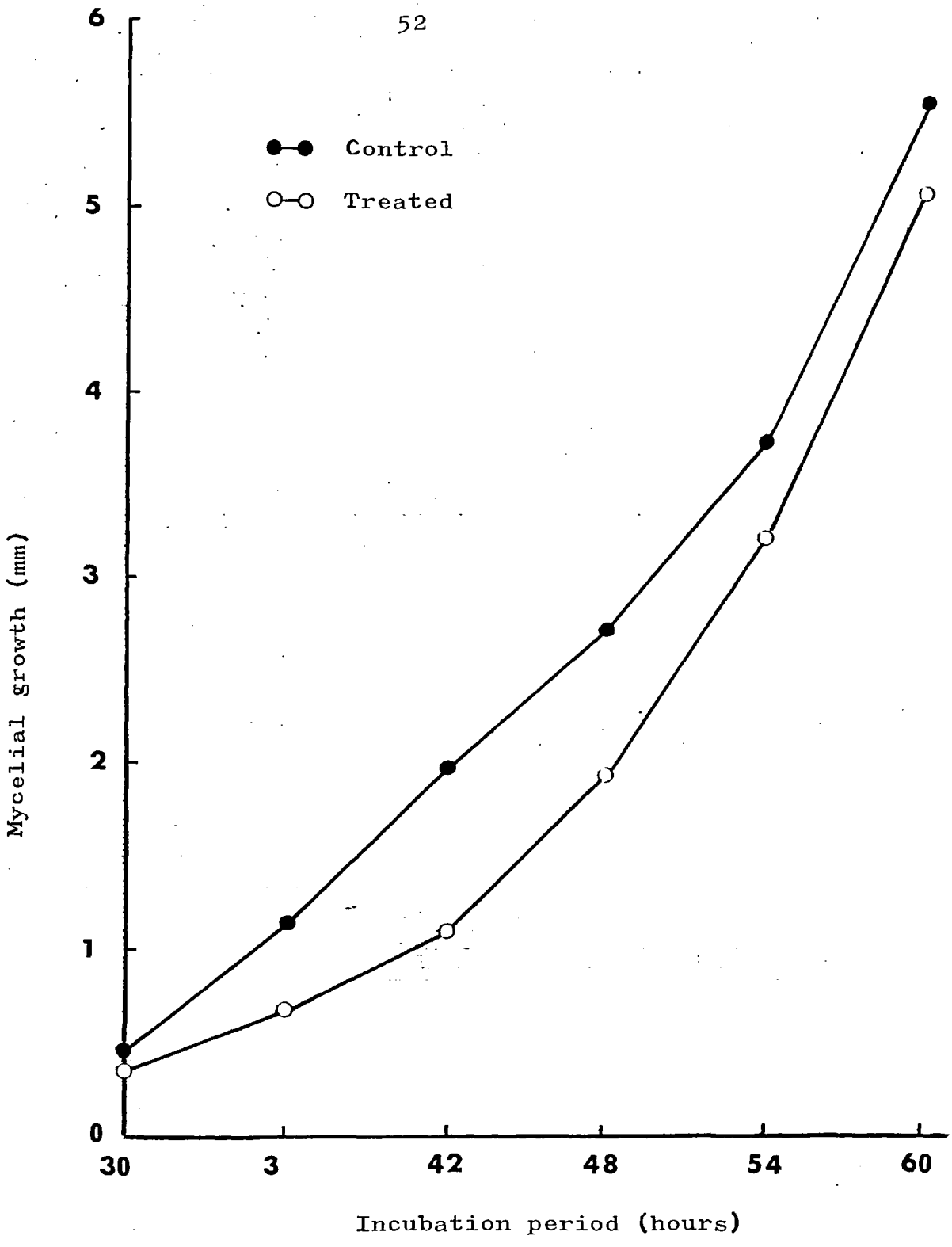


Fig. 1.8 Effect of 6h wet period applied 24h after inoculation on the mycelial growth of E.pisi.

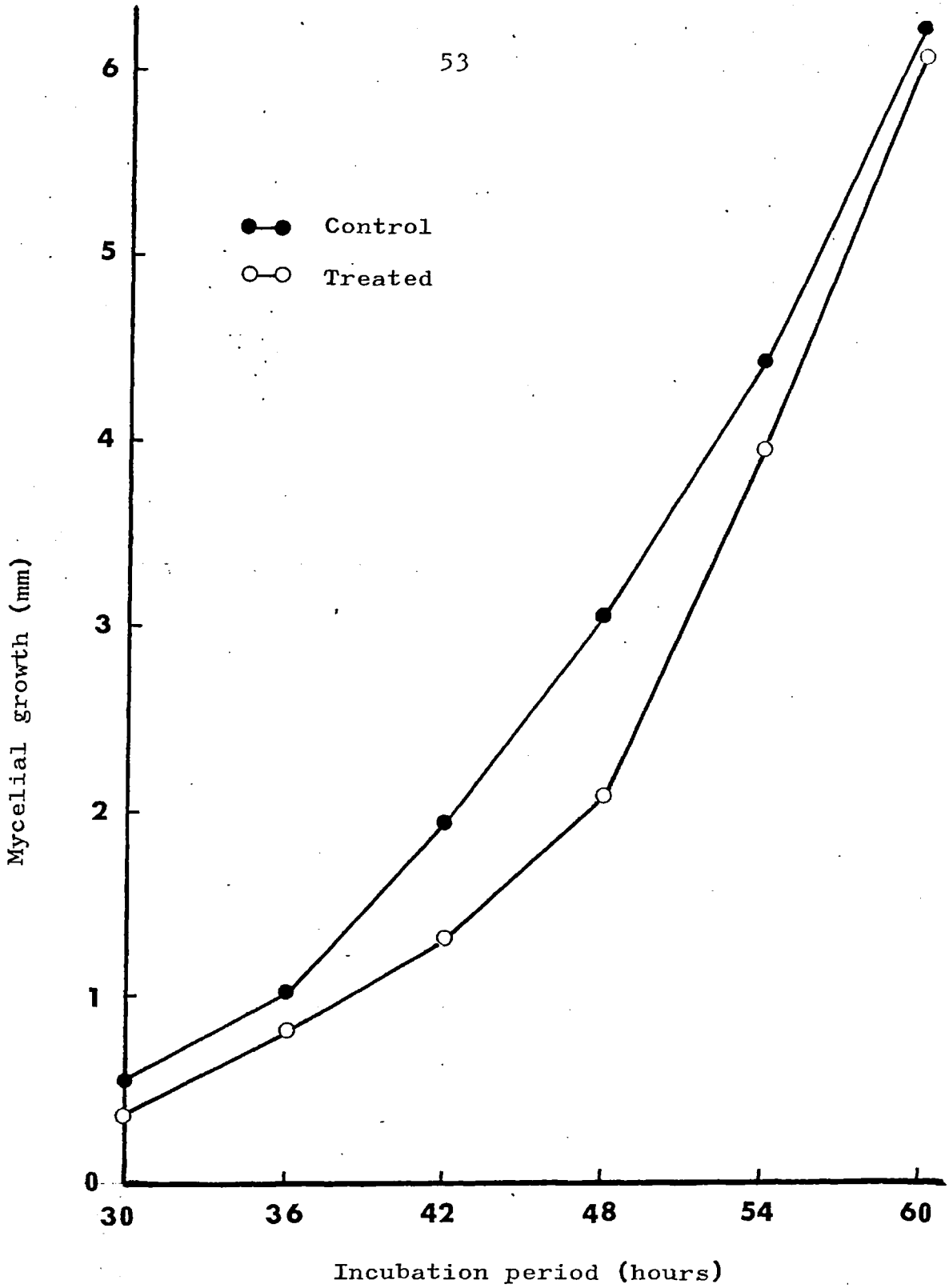


Fig. 1.9 Effect of 6h wet period applied 24h after inoculation on the mycelial growth of S.pannosa.

suggest that eventually mycelial growth was more rapid following wetting.

E. Conidiophore initiation

The time taken for E.graminis, E.pisi and S.pannosa to initiate conidiophores on their respective hosts at 20° was examined in several preliminary trials and was established as 72h, 80h and 54h respectively. This information was used in an experiment in which each mildew was grown on its host for the period necessary for conidiophore initiation, some leaf segments and discs were given a 6h wet period and conidiophores were assessed (on these and controls) 18h later, i.e. 24h after applying water. With all three mildews the formation of conidiophores was delayed by the wet period (Table 1.12).

F. Production of conidia

The effects of a 6h wet period on production of conidia were examined in an experiment involving the mildews on barley, pea and rose. Preliminary trials using the settling tower (p.26) were first carried out to determine the inoculum level giving on average one colony per leaf piece. Many leaf segments and discs were then inoculated and incubated at 20° for 72h when they were checked under a binocular microscope. Only leaf tissues with a single colony were retained and these were re-incubated. After a further 48h, a sample of each inoculated host was taken.

Table 1.12 Effect of 6h wet period on the initiation of conidiophores.

Mildew	Hours after inoculation	*Conidiophores/mm^2 colony	
		Treated	Control
E.graminis	96	24	42
E.pisi	104	34	51
S.pannosa	78	15	25

*Mean of 50 replicates (detailed results are given in Appendix Table 1.14)

The old conidia were removed from each colony by blowing air over it and the leaf piece was sprayed with water, kept wet for 6h and then allowed to air dry. Commencing from the 6th day after inoculation, 5 leaf pieces were removed daily from both the wetted and control regimes. The conidia were removed from each leaf piece by tapping it gently over a specimen tube containing 1 ml distilled water plus Tween 80. The numbers of conidia collected were assessed using a haemocytometer and the area of the colony calculated.

The results (Figs. 1.10-1.12), expressed as conidia per mm^2 colony, show that conidia production was reduced initially by leaf wetness but recovered 3 days after wetting. With E.graminis and S.pannosa the numbers of conidia collected 5 days after wetting were not different from those of the controls. A microscopic examination of mildew colonies immediately after wetting showed that many conidiophores and conidial chains had adhered to one another and on drying had formed white 'crusts' above the colonies. These could be seen quite clearly with the naked eye on treated leaves (Plate 1), and also in the field, on rose infected with S.pannosa, following rain. The recovery in sporulation is therefore likely, as with the mycelial growth (Figs. 1.7-1.9), to represent enhanced growth in other parts of the colony following a wet period.

The recovery of sporulation following a wet period was demonstrated further by using treated barley seedlings as sources of inoculum. Ten pots of barley, each with fifteen

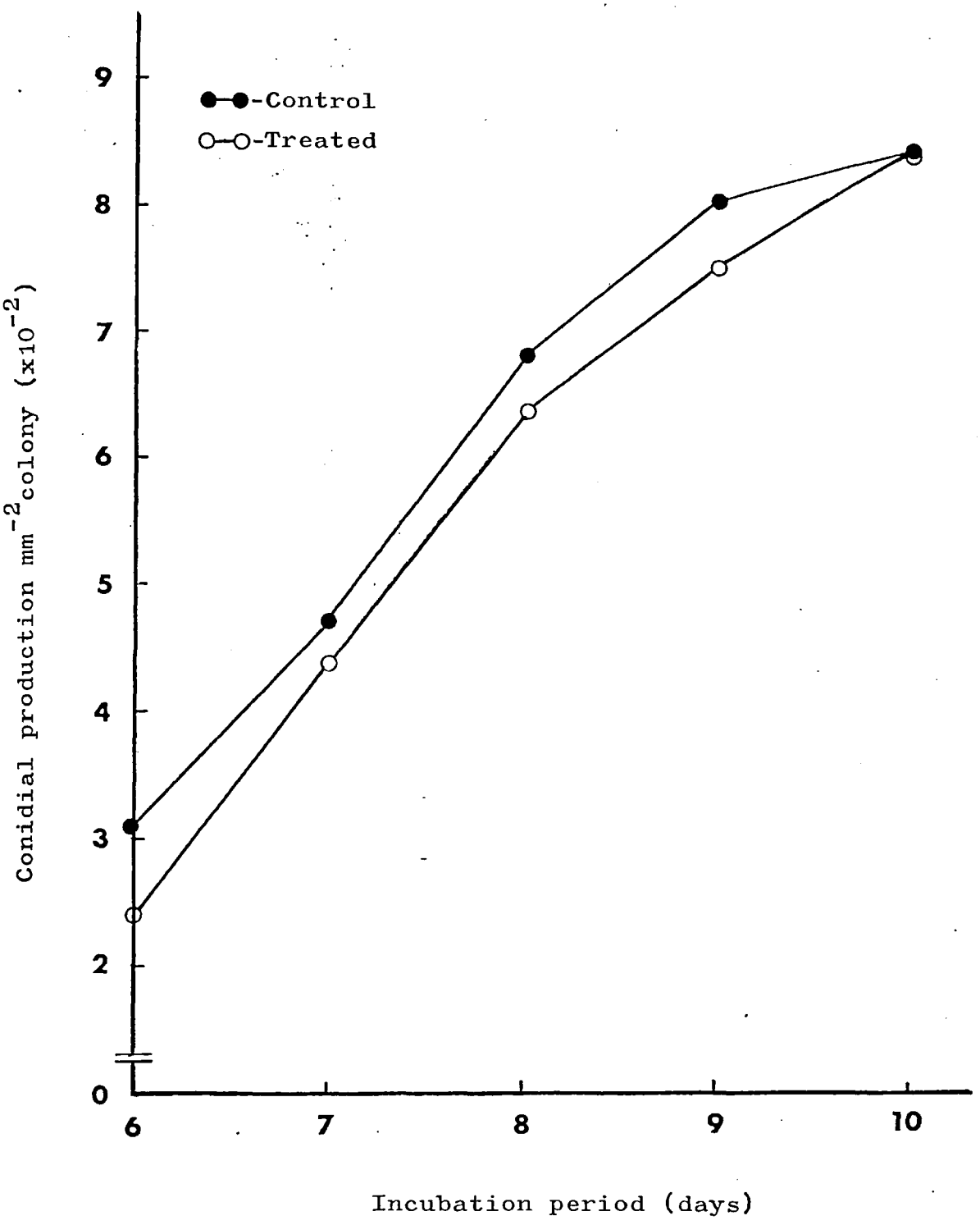


Fig.1.10 Effect of 6h wet period on the production of conidia by E.graminis (water applied on 5th day after inoculation).

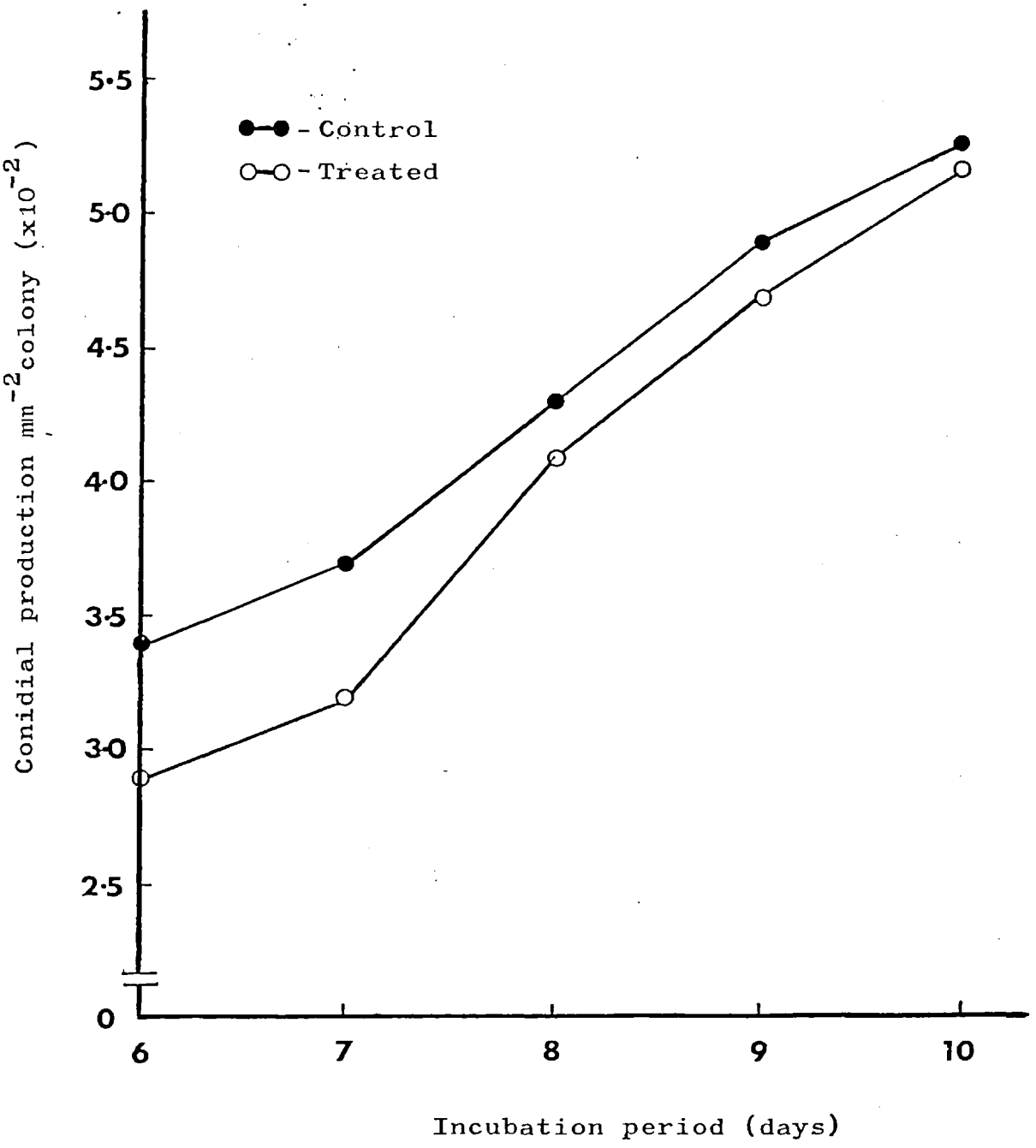


Fig.I.11 Effect of 6h wet period on the production of conidia by E.pisi (water applied on 5th day after inoculation).

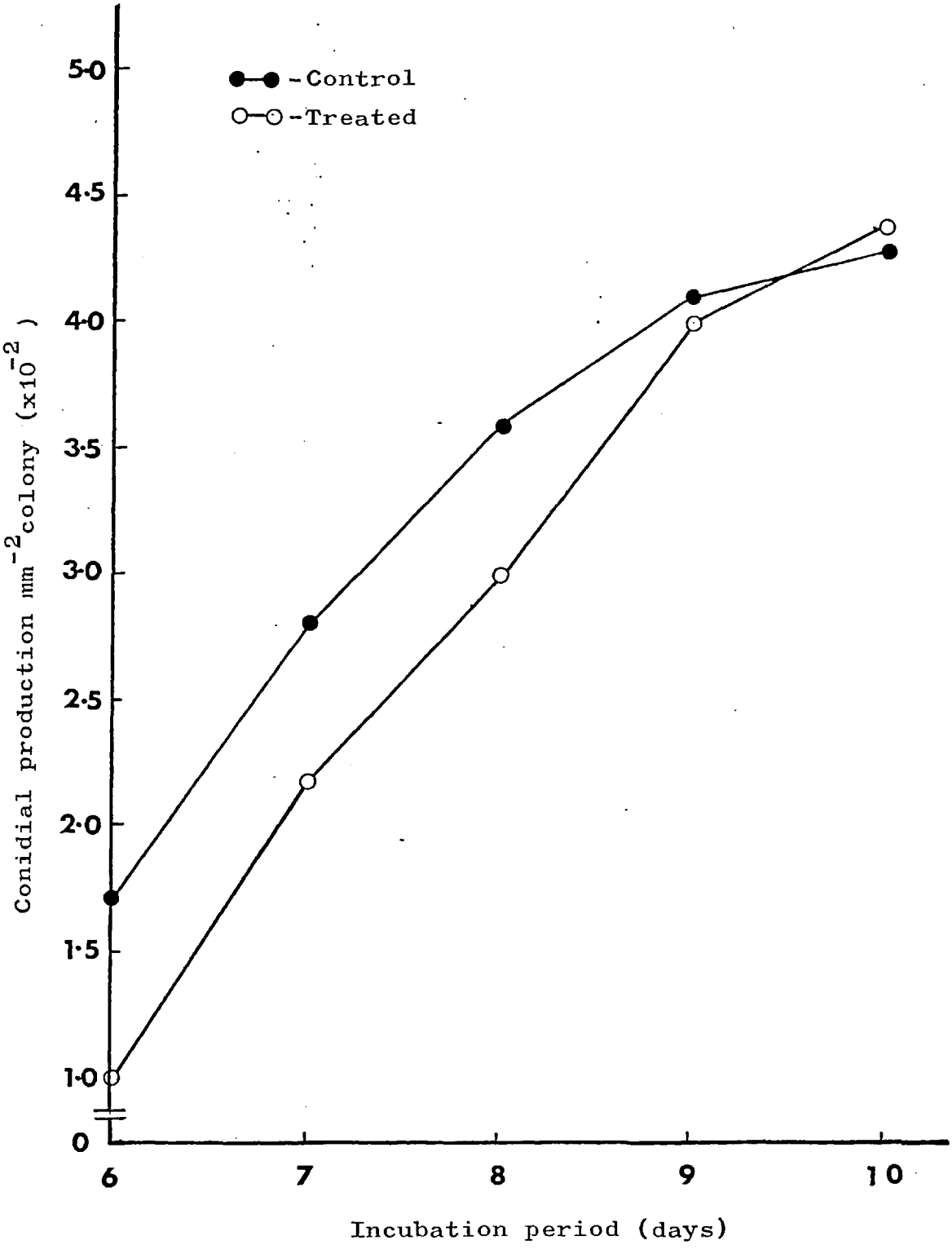


Fig. 1.12 Effect of 6h wet period on the production of conidia by S.pannosa (water applied on 5th day after inoculation).

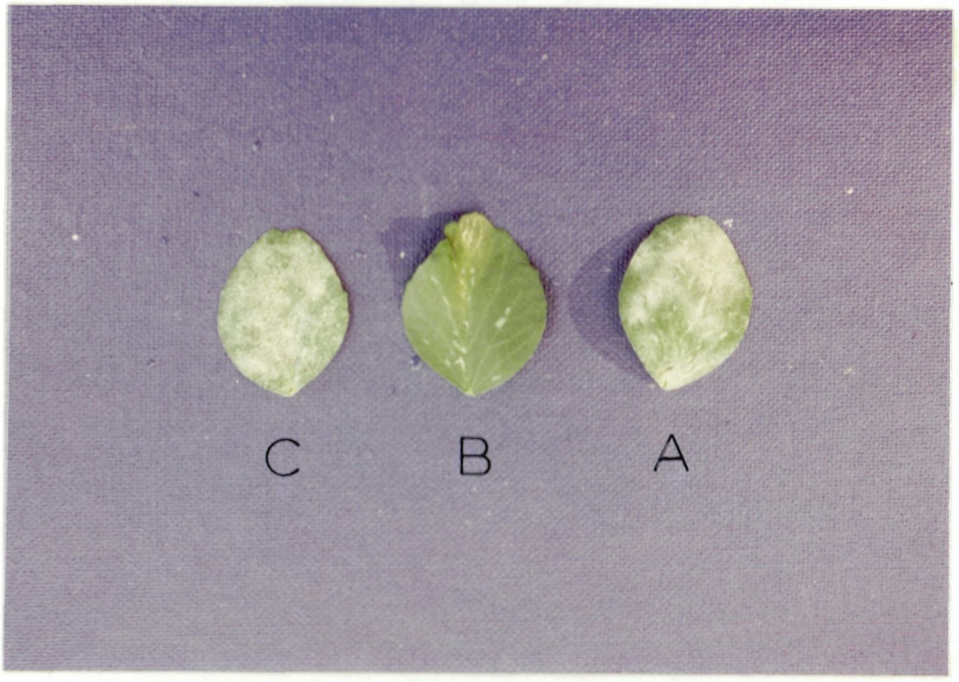


Plate 1 Formation of 'crusts' of conidiophores and conidia when wetted colonies of E.pisi were dried. Leaves inoculated not wetted (A), wetted (C) and uninoculated (B).

7 day old seedlings were inoculated together, in a settling tower, with E.graminis. The plants were kept for a further 7 days to allow colonies to develop. The pots were then divided into five pairs. The seedlings in one pot of each pair were sprayed with water for 30 secs. As the seedlings were almost covered with sporulating colonies they became wet quickly. The seedlings in the other pot were left untreated as the control. The water-treated seedlings were kept wet for 6h and then allowed to dry. At intervals, the seedlings in each in pair of pots were used separately as sources of conidia for the inoculation of 5 pots of 7 day old barley seedlings. These seedlings were placed at the base of a cardboard bin (70 cm high, 35 cm wide), the infected pot of seedlings was held at the top of this bin and the conidia dislodged by air from a fan operated for 5 secs. The conidia were then allowed to settle on the test plants. A pair of pots was used in this way at 0, 6, 24, 48 and 72h after wetting. Each set of 10 inoculated pots was kept in the glass house for 5-6 days when mildew colonies were counted on both leaf surfaces. The results (Appendix Table 1.16) are summarised in Table 1.13. They indicate a progressive recovery in the production of viable and infective conidia by wetted colonies.

Table 1.13 Effect of 6h wet period on the production of viable conidia by E.graminis.

Period(h) between wetting and use as inoculum	*Colonies/cm^2 leaf		Reduction in mildew (as % of control)
	Treated	Control	
0	2.1	11.7	82.1
6	6.6	14.9	55.7
24	14.7	19.8	25.8
48	12.6	16.1	21.7
72	13.0	14.3	9.1

*Mean of 50 replicates

Detailed results are given in Appendix Table 1.16.

II EFFECTS OF FREE WATER ON MILDEW DEVELOPMENT

An experiment with E.graminis and barley (p.50) inferred that conidia landing on the surface of water drops were less affected than those which were immersed. The experiments in this section investigated in detail the germination of conidia from a wide range of mildews on and in water.

Materials and methods

a. Source of inoculum

Young leaves,heavily infected with powdery mildew were collected from their hosts at Silwood Park during June to October 1979 whenever the opportunity arose. These were transferred to the laboratory in polythene bags. Old conidia were removed from both leaf surfaces by blowing air over them vigorously with a Pasteur pipette. The leaves were incubated in an illuminated cabinet at 20±1° in closed polystyrene seed germination trays (Stewarts Plastics Ltd.) with their lamina resting on perspex plates and the petioles immersed in water. Some mildews were transferred to young host plants in pots and kept in filtered air cabinet at 20±3° in the glass house. Conidia were removed from mildewed leaves or plants every 24h to encourage the production of new conidia.

b. Source of host tissue

Young fully expanded leaves of host plants were obtained from vigorously growing plants at Silwood Park. They were brought to the laboratory and examined under a binocular microscope and any with mildew infection were discarded. The healthy leaves were washed gently in tap water for a few minutes, blotted dry and transferred to separate seed germination trays in an illuminated cabinet until required. In some instances, healthy leaf tissues were also obtained from appropriate host plants grown in filtered air cabinets in the glass house. Depending on the nature of the host species , the experimental unit was a leaf disc (1 cm diam.) or a leaf piece (c.1x2 cm), cut from the middle of a leaf and excluding the midrib and major veins or, when the leaves were compound, whole leaflets.

c. Method of inoculation

Germination studies with water were made in clear polystyrene boxes (5.5 x 3.5 x 2.0 cm) with tightly fitted lids. Conidia were deposited on the surface of glass distilled water in these boxes. As they were not easily wetted, the conidia floated on the surface and their behaviour could be observed in this situation.

Immersing conidia in water proved more difficult. Two methods were used. In the first, conidia deposited in the

base of a dry polystyrene box were covered by pouring glass distilled water gently into the box. This method was sometimes less than satisfactory as often conidia were found associated with air bubbles especially when they landed in groups. In the second method, conidia were deposited on water in a polystyrene box and the contents were transferred to a specimen tube which was then shaken. The suspension was then transferred to another polystyrene box and the conidia were allowed to settle. With both these methods, a small proportion of conidia floated again and these were removed with a wire loop.

The leaf tissues whether leaf discs, pieces or leaflets were usually inoculated on the adaxial surface by the method described on p. 24.

d. Assessment of germination

Germination on host tissue was assessed by counting 100-200 conidia on each of 10 leaf samples. Conidia floating on water were either assessed directly under the microscope, which was difficult because they tended to move, or they were transferred to a coverslip. This was achieved by gently touching the water surface with a clean coverslip to which the conidia then adhered by surface tension. They were fixed to the coverslip by warming it gently and stained in cotton blue lactophenol. Germination was assessed on 100-200 conidia on each of 10 coverslips.

Table 2.1 Mildews and host plants studied.

Mildew species	Host species (and family)
1. E.aquilegiae DC. ex Merat	Aquilegia coerulea L. (Ranunculaceae)
2. E.artemisiae Grev.	Artemisia vulgaris L. (Artemisiae)
3. E.asperifolium Grev.	Myosotis alpestris Schmidt. (Boraginaceae)
4. E.asperifolium Grev.	Pulmonaria officinalis L. (Boraginaceae)
5. E.asperifolium Grev.	Symphytum officinale L. (Boraginaceae)
6. E.betae (Vanha) Weltzien	Beta vulgaris L. (Chenopodiaceae)
7. E.cichoracearum DC. ex Merat	Aster novae-belgii L. (Compositae)
8. E.cichoracearum DC. ex Merat	Centaurea macrocephala Puschk. (Compositae)
9. E.cichoracearum DC. ex Merat	Cirsium arvense L. (Compositae)
10. E.cichoracearum DC. ex Merat	Echinops ritro L. (Compositae)
11. E.cichoracearum DC. ex Merat	Hieracium alpinum L. (Compositae)
12. E.cichoracearum DC. ex Merat	Solidago canadensis L. (Compositae)
13. E.cichoracearum DC. ex Merat	Sonchus oleraceus L. (Compositae)
14. E.cichoracearum DC. ex Merat	Taraxacum officinale L. (Compositae)

Table 2.1 contd.

15. E.communis (Wallr.) Link.	Dipsacus fullonum L. (Dipsacaceae)
16. E.cruciferarum Opiz. ex L.Junell	Brassica napus L. (rape) (Cruciferae)
17. E.cruciferarum Opiz. ex L.Junell	Brassica napus L. (swede) (Cruciferae)
18. E.depressa (Wallr.) Schlecht.	Arctium lapa L. (Compositae)
19. E.fischeri Blumer	Senecio vulgaris L. (Compositae)
20. E.galeopsidis DC. ex Merat	Lamium album L. (Labitae)
21. E.graminis DC. ex Merat	Hordeum vulgare L. (Graminae)
22. E.heraclei DC. ex St.-Am.	Chaerophyllum temulum L. (Umbelliferae)
23. E.heraclei DC. ex St.-Am.	Heracleum spondylium L. (Umbelliferae)
24. E.martii Lev.	Lathyrus odoratus L. (Leguminosae)
25. E.martii Lev.	Lupinus polyphyllus Lindl. (Leguminosae)
26. E.martii Lev.	Trifolium compestre Schreb. (Leguminosae)
27. E.pisi DC. ex St.-Am.	Pisum sativum L. (Leguminosae)
28. E.polygoni DC. ex St.-Am.	Polygonum aviculare L. (Polygonaceae)
29. E.ranunculi Grev.	Delphinium elatum L. (Ranunculaceae)
30. E.ranunculi Grev.	Ranunculus repens L. (Ranunculaceae)

Table 2.1 contd.

31. E.salviae (Jacz.) Blumer	Salvia nemarosa L. (Labitae)
32. E.sordida L.Junell	Plantago major L. (Plantaginaceae)
33. E.verbasci (Jacz.) Blumer	Verbascum thapsus L. (Scrophulariaceae)
34. M.alphitoides Griff. & Maubl.	Quercus rober L. (Fagaceae)
35. M.berberidis (DC. ex Merat) Lev. (Berberidaceae)	Mahonia aquifolium (Nutt.) Pursh.
36. M.euonymi (DC. ex Merat) Sacc.	Euonymus europaeus L. (Celestaceae)
37. Oidium sp.	Clianthus puneceus Banks & (Leguminosae) Soland
38. O.begoniae Putt.	Begonia hybrida-multiflora (Begoniaceae)
39. O.oxalidis McAlp.	Oxalis corniculata L. (Oxalidaceae)
40. P.clandestina (Wallr. ex Fr.) Lev.	Crategus monogyna Jacz. (Rosaceae)
41. P.leucotricha (Ell. & Everh.) Salm.	Malus sylvestris (L.) Mill. (Rosaceae)
42. S.epilobii (Wallr.& Link) Sacc.	Epilobium angustifolium L. (Onagraceae)
43. S.fugax Penz. & Sacc.	Geranium molle L. (Geraniaceae)
44. S.fuliginea (Schlecht. ex Fr.) Poll.	Cucumis sativus L. (Cucurbitaceae)
45. S.fuliginea (Schlecht. ex Fr.) Poll.	Cucurbita pepo L. (Cucurbitaceae)
46. S.fuliginea (Schlecht. ex Fr.) Poll.	Veronica arvensis L. (Scrophulariaceae)

Table 2.1 contd.

47. S.macularis (Wallr. ex Fr.) Lind.	Potentilla sterilis (L.) Garcke (Rosaceae)
48. S.pannosa (Wallr. ex Fr.) Lev.	Rosa sp. (Rosaceae)
49. U.bicornis (Wallr. ex Fr.) Lev.	Acer pseudoplatanus L. (Aceraceae)
50. U.necator (Schw.) Burr.	Vitis vinifera L. (Vitaceae)

E - Erysiphe, M - Microsphaera, O - Oidium, P - Podosphaera, S - Sphaerotheca and U - Uncinula.

The germination of conidia under water was measured from direct observations. This was possible because they tended to stick to the bottom and remain stationary. Occasionally, the water was drained off carefully and a celloidin peel prepared on which 100-200 conidia were assessed for germination.

Germ-tube lengths were measured on 50 conidia selected at random from each substrate.

Experimental

A. Germination of conidia on and in water

The behaviour of conidia from 50 different collections of powdery mildew, listed in Table 2.1, were studied. The identity of these collections was checked by the host plant-pathogen lists in Blumer (1967) and Junell (1967). For each mildew, 15-20 host leaf units and 4 polystyrene boxes for each of the treatments, floating and submerged conidia, were inoculated simultaneously with 24h conidia in the settling tower. The inoculated leaf tissues were floated on water in small polystyrene boxes and these, together with the water treatments were incubated in an illuminated cabinet at 20±1°. Germination and germ-tube growth were measured after 24h on all samples and on some 48h after inoculation.

The results of this experiment reveal several features

of interest. First, the conidia of some mildews can apparently germinate equally well on host leaf tissue and on or in water whereas the conidia of other types germinate poorly in the presence of water. These two groups are distinguished in Table 2.2.

It is clear from this classification that the conidia of all species tested of Podosphaera, Sphaerotheca and Uncinula germinated poorly in the presence of water whereas conidia of Microsphaera and Oidium germinated well. Within the genus Erysiphe, of which there were most samples, the response to water varied with the species though even here some divisions could be made. Thus conidia of Erysiphe spp. from Leguminosae, Cruciferae, Umbelliferae and Ranunculaceae germinated well in the presence of water but Erysiphe spp. on Boraginaceae did not. The Erysiphe spp. on Compositae, especially E.cichoracearum varied in their ability to germinate on or in water depending on the source of conidia. Generally, fewer conidia germinated when immersed in water than floating on water.

A second feature was that conidia germinated in different ways in the three situations and the germ-tubes grew to different extents. On leaves, 24h after inoculation, conidia usually produced 1-3 germ-tubes, sometimes well branched, with well developed appressoria. The germ-tubes of conidia on or in water varied in size and shape and the germination was atypical. These different patterns of germination are shown in Plate 2 and Figs. 2.1-2.4.

Table 2.2 Percentage germination of conidia on leaf tissue, on water and in water after 24h at 20°.

A. Germination similar on leaf and on/in water

No.*	Mildew	Host genus	on leaf	on water	in water
1.	E.aquilegiae	Aquilegia	97.7	95.8	94.9
6.	E.betae	Beta	77.1	75.0	73.5
8.	E.cichoracearum	Centaurea	87.3	82.8	82.3
9.	E.cichoracearum	Cirsium	95.1	86.4	82.3
10.	E.cichoracearum	Echinops	88.4	83.5	82.5
16.	E.cruciferarum	Brassica	92.2	91.2	89.4
17.	E.cruciferarum	Brassica	96.3	94.9	89.1
18.	E.depressa	Arctium	93.3	92.4	93.6
22.	E.heraclei	Chaerophyllum	96.7	94.1	93.8
23.	E.heraclei	Heracleum	94.8	93.6	93.6
24.	E.martii	Lathyrus	95.1	90.1	87.2
25.	E.martii	Lupinus	93.4	88.7	85.3
26.	E.martii	Trifolium	90.4	85.0	75.9
27.	E.pisi	Pisum	96.7	85.5	80.1
28.	E.polygoni	Polygonum	96.2	90.1	81.2
29.	E.ranunculi	Delphinium	84.8	79.6	84.1
30.	E.ranunculi	Ranunculus	87.9	87.3	84.9
31.	E.salviae	Salvia	95.3	87.0	81.6

Table 2.2 contd.

32. E.sordida	Plantago	90.9	82.0	75.7
33. E.verbasci	Verbascum	86.8	77.5	74.2
34. M.alphitoides	Quercus	97.5	96.4	95.7
35. M.berberidis	Mahonia	96.3	93.3	91.3
36. M.euonymi	Euonymus	83.8	77.5	70.4
37. Oidium sp.	Clianthus	90.4	88.9	88.9
38. O.begoniae	Begonia	94.2	88.7	86.5
39. O.oxalidis	Oxalis	92.8	88.4	82.3

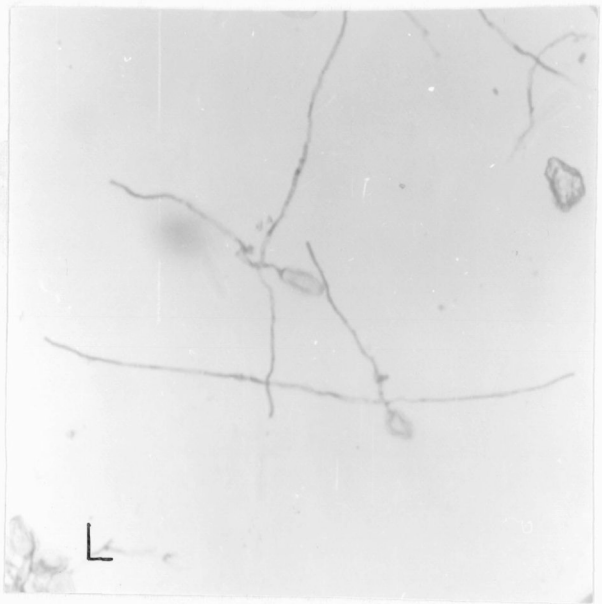
B. Germination poor on/in water

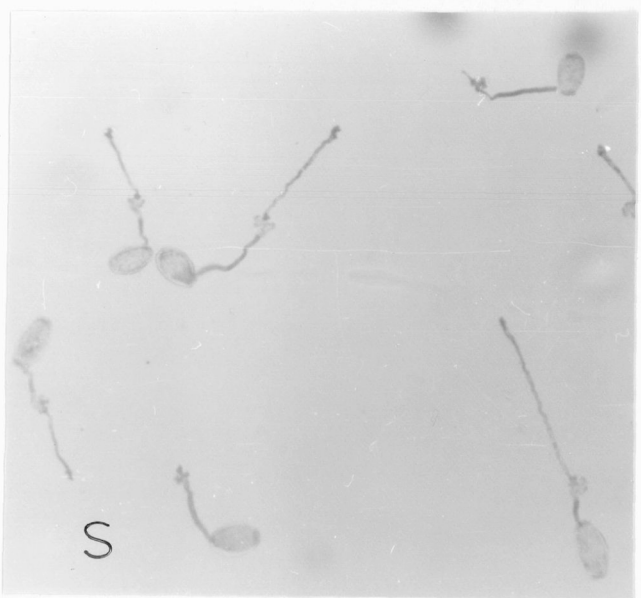
2. E.artemisiae	Artemisia	73.4	23.3	14.0
3. E.asperifolium	Myosotis	69.4	22.5	14.6
4. E.asperifolium	Pulmonaria	84.4	29.0	15.0
5. E.asperifolium	Symphytum	93.8	25.3	12.9
7. E.cichoracearum	Aster	72.0	44.0	34.1
11. E.cichoracearum	Hieracium	63.1	17.4	10.3
12. E.cichoracearum	Solidago	75.0	51.2	32.7
13. E.cichoracearum	Sonchus	95.3	42.6	21.4
14. E.cichoracearum	Taraxacum	69.7	2.7	2.6
15. E.communis	Dipsacus	71.9	25.7	15.9
19. E.fischeri	Senecio	77.9	52.6	41.5
20. E.galeopsidis	Lamium	80.5	36.1	22.6

Table 2.2 contd.

21. E.graminis	Hordeum	86.7	50.1	40.2
40. P.clandestina	Crategus	82.5	27.9	17.2
41. P.leucotricha	Malus	91.4	44.3	35.7
42. S.epilobii	Epilobium	85.1	17.5	14.2
43. S. fugax	Geranium	84.8	34.9	14.7
44. S.fuliginea	Cucumis	79.5	45.4	36.5
45. S.fuliginea	Cucurbita	91.0	55.9	36.5
46. S.fuliginea	Veronica	83.6	35.6	31.9
47. S.macularis	Potentilla	72.1	27.7	19.0
48. S.pannosa	Rosa	85.9	49.1	41.6
49. U.bicornis	Acer	86.0	44.9	26.9
50. U.necator	Vitis	89.2	56.4	46.7

* See Table 2.1





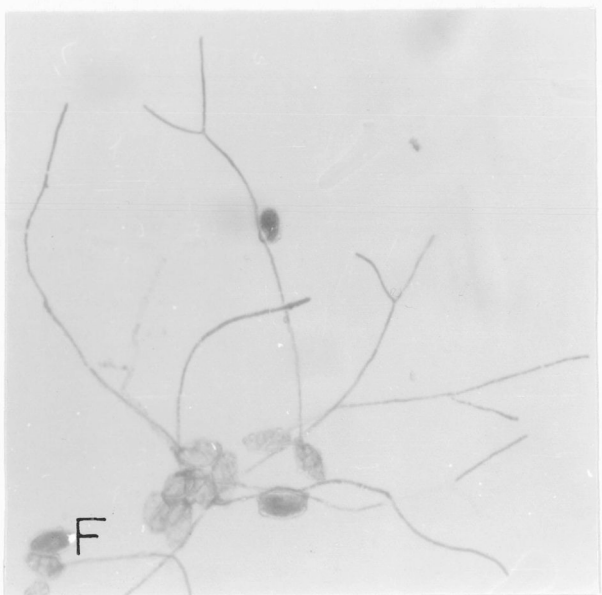


Plate 2 Germination of conidia of M. alphitoides from Quercus rober after 24h at 20°.
L - on leaf, F - on water, S - in water.
(x 150)

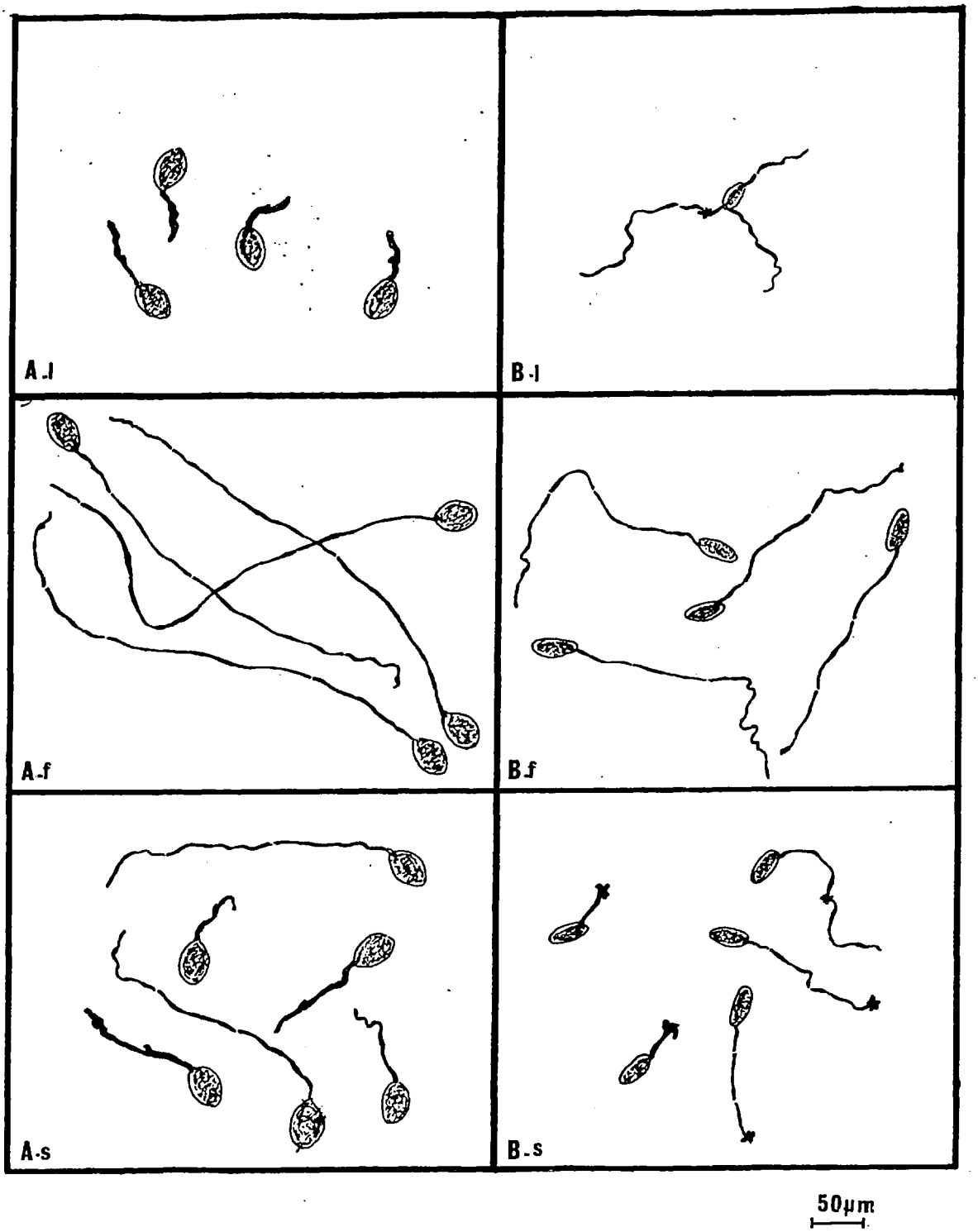


Fig. 2.1 Germination of conidia after 24h at 20°.
A - E.verbasci from Verbascum thapsus,
B - O.oxalidis from Oxalis corniculata,
l - on leaf, f - on water and s - in water.

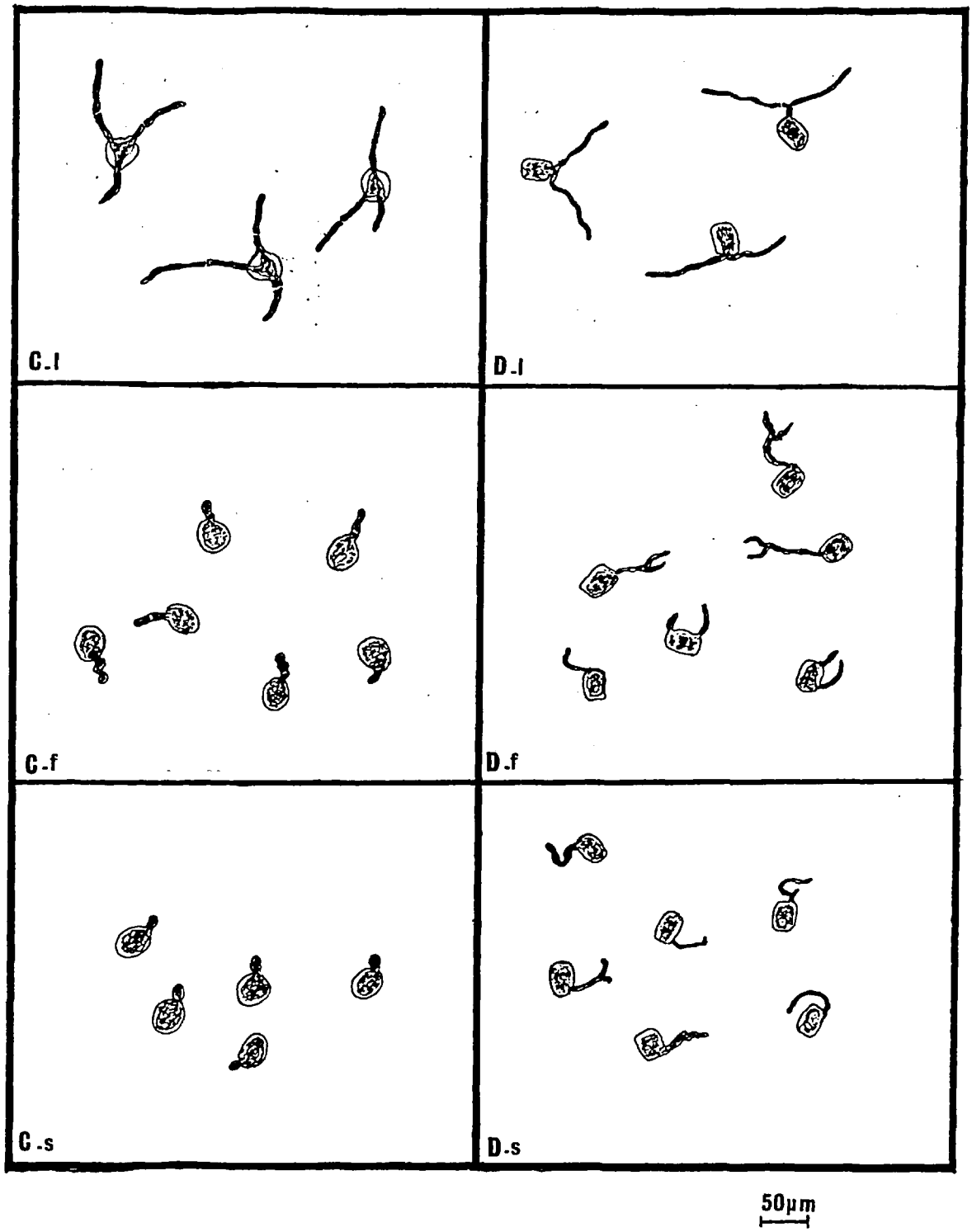


Fig. 2.2 Germination of conidia after 24h at 20°.
C - E.cichoracearum from Taraxacum officinale,
D - S.fuliginea from Cucurbita pepo,
l - on leaf, f - on water and s - in water.

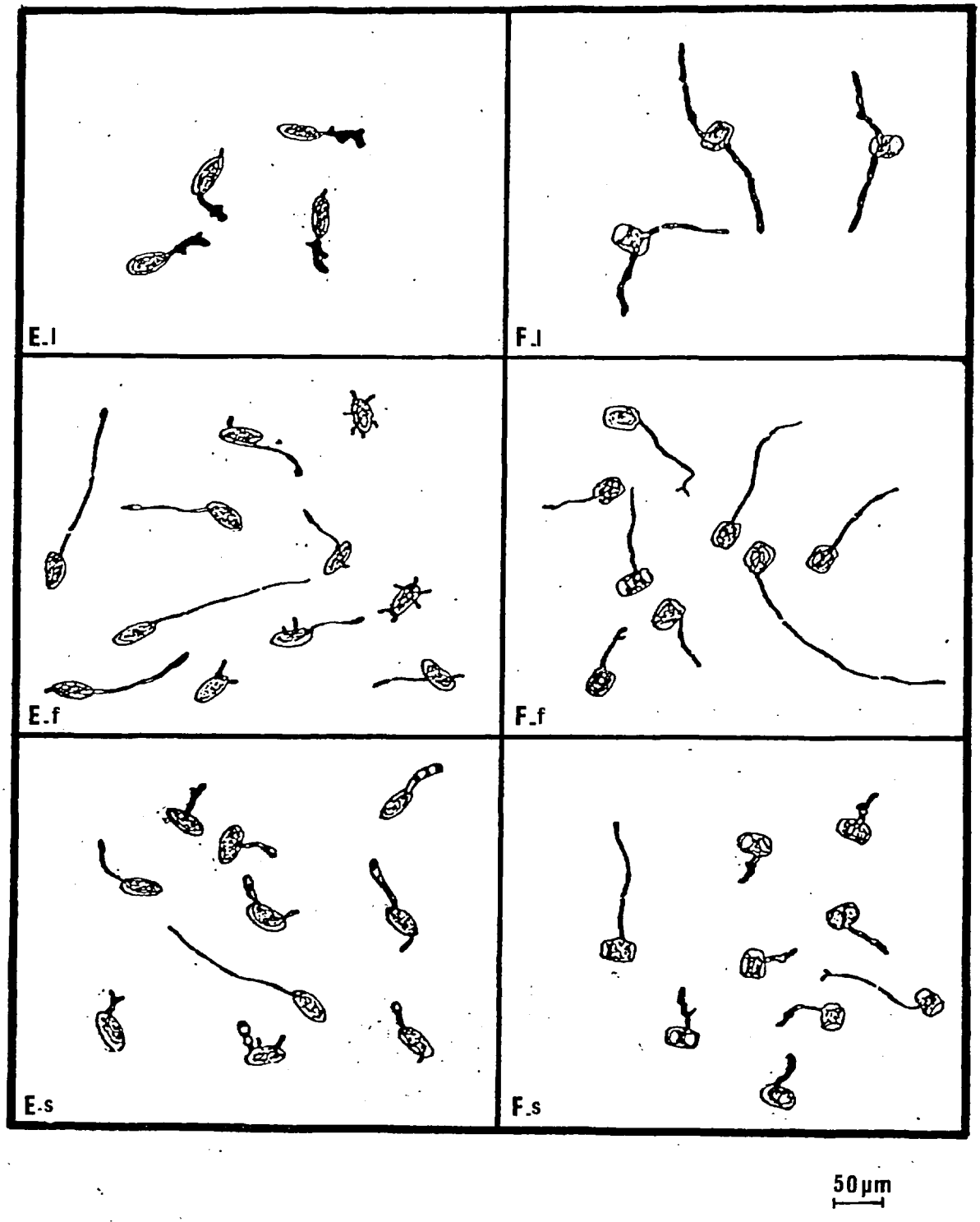


Fig. 2.3 Germination of conidia after 24h at 20°.
E - E.graminis from Hordeum vulgare,
F - S.pannosa from Rosa sp. 1 - on leaf,
f - on water and s - in water.

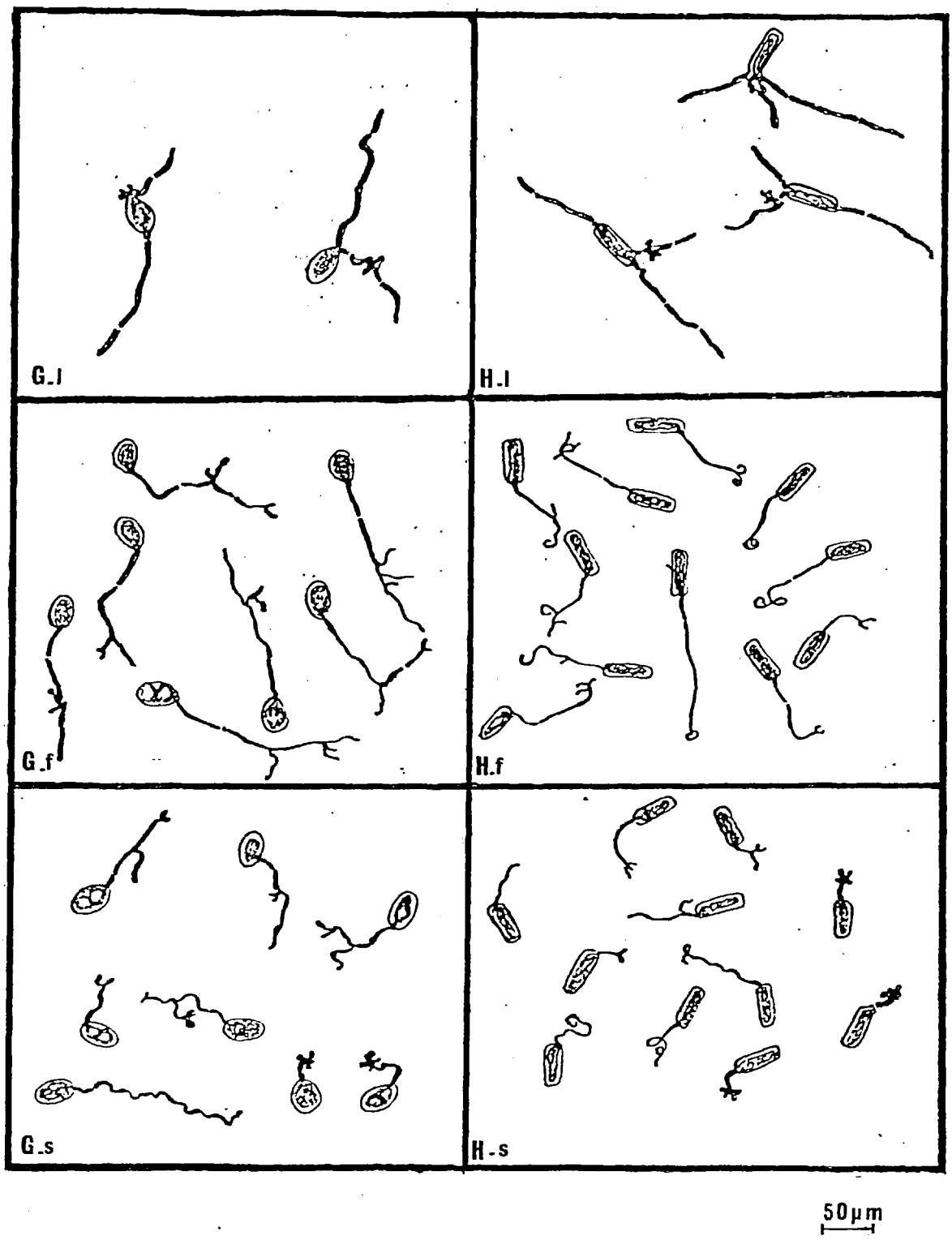


Fig. 2.4 Germination of conidia after 24h at 20°.
G - E.heraclei from Heracleum spondylium,
H - E.martii from Lathyrus odoratus,
l - on leaf, f - on water and s - in water.

Often the germ-tubes of conidia on or in water were thin and septate and their length was highly variable compared to those on leaves. Usually conidia on or in water produced a single germ-tube but some appeared to produce more. These were often little more than projections or buds and were particularly evident with E.graminis. Plates 3-6 show some examples of conidial germination on water including E.depressa which produced the longest germ-tube. With some mildews, germ-tube growth initially was faster on water than on leaves but after 48h germ-tubes usually ceased to extend on water.

Typical appressoria were never observed with conidia on water of any mildew but the apex of some germ-tubes became swollen. In contrast, germinated conidia in water of almost all mildews produced appressoria though less frequently than on leaves and their position along the length of the germ-tube varied.

These features of germ-tube growth particularly on water enabled the mildews that were studied to be divided into four groups. The classification and diagnostic characters of the groups are given in Table 2.3. The type of appressorium produced by submerged conidia helped further to distinguish mildews within groups. For example, appressoria were either lobate, characteristic of E.polygoni or club shaped, characteristic of E.cichoracearum. Some of the features on which these groups are distinguished

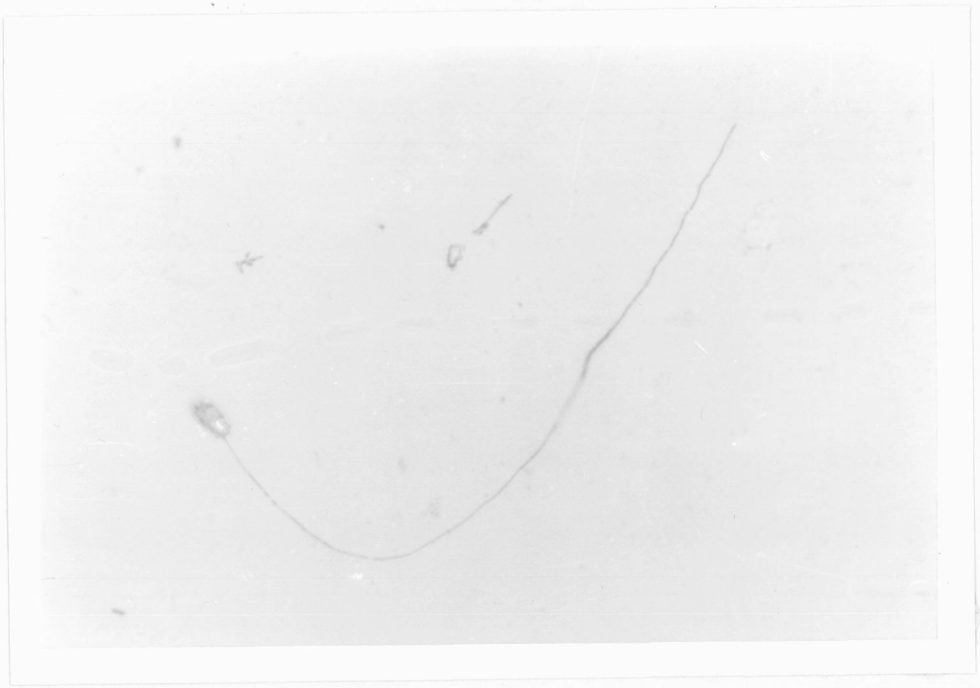


Plate 3 Germination on water of conidia of E.depressa (from Arctium lapa) after 24h at 20°. (x 150)

Plate 4 Germination on water of conidia of O.begoniae (from Begonia multiflora) after 24h at 20°. (x 150)

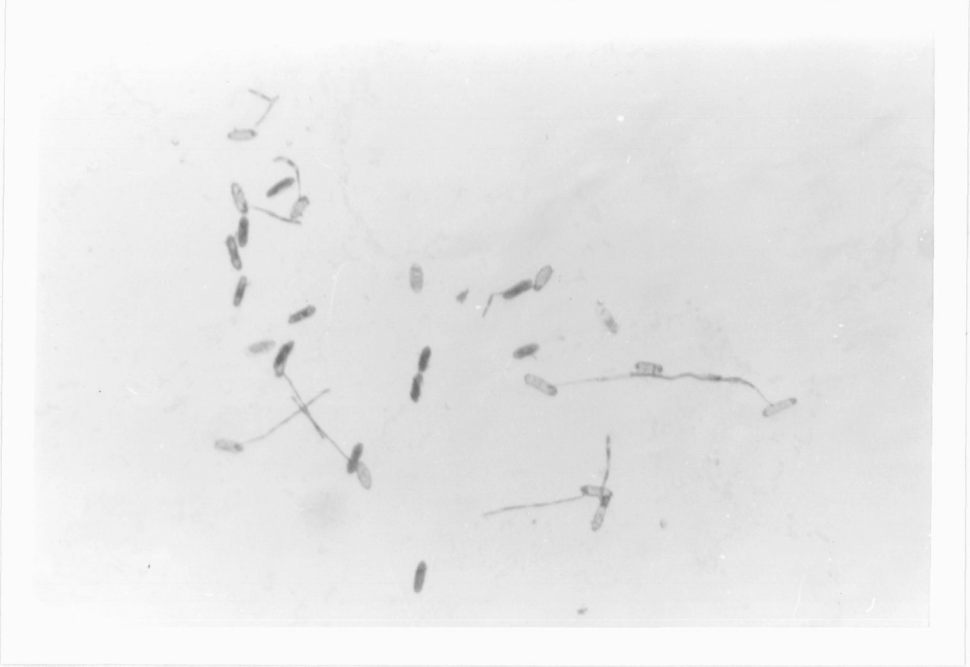


Plate 5 Germination on water of conidia of E.graminis (from Hordeum vulgare) after 24h at 20°. (x 150)

Plate 6 Germination on water of conidia of E.pisi (from Pisum sativum) after 24h at 20°.

(x 150)

Table 2.3 Germ tube growth (µm)** from conidia on leaf tissue, on water and in water after 24h at 20°.

No.*	Mildew	Host genus	on leaf	on water	in water
Group A. Single, unbranched, long germ tubes					
8.	E. cichoracearum	Centaurea	228	257	176
9.	E. cichoracearum	Cirsium	232	289	106
10.	E. cichoracearum	Echinops	265	383	265
18.	E. depressa	Arctium	181	572	353
33.	E. verbasci	Verbascum	171	254	185
34.	M. alphitoides	Quercus	305	433	277
39.	O. oxalidis	Oxalis	458	279	216
Group B. Single, unbranched, short germ tubes					
3.	E. asperifolium	Myosotis	205	40	27
4.	E. asperifolium	Pulmonaria	240	45	18
11.	E. cichoracearum	Hieracium	144	19	18
14.	E. cichoracearum	Taraxacum	246	19	14
20.	E. galeopsidis	Lamium	162	36	11
38.	O. begoniae	Begonia	246	43	19
40.	P. clandestina	Crategus	163	31	14
42.	S. epilobii	Epilobium	156	31	16
44.	S. fuliginea	Cucumis	224	33	22

Table 2.3 contd.

45. S.fuliginea	Cucurbita	215	42	29
46. S.fuliginea	Veronica	219	60	47

Group C. Single/multiple germ tubes of intermediate length with infrequent branching

2. E.artemisiae	Artemisia	189	122	120
5. E.asperifolium	Symphytum	239	147	36
7. E.cichoracearum	Aster	184	104	57
12. E.cichoracearum	Solidago	269	94	39
13. E.cichoracearum	Sonchus	229	117	46
15. E.communis	Dipsacus	260	106	24
19. E.fischeri	Senecio	236	92	53
21. E.graminis	Hordeum	190	121	95
31. E.salviae	Salvia	237	102	60
32. E.sordida	Plantago	249	159	42
41. P.leucotricha	Malus	194	130	79
43. S.fugax	Geranium	179	137	93
47. S.macularis	Potentilla	115	155	47
48. S.pannosa	Rosa	337	138	54
49. U.bicornis	Acer	101	129	73

Table 2.3 contd.

Group D. Single/multiple germ tubes of intermediate length with frequent branching

1.	E.aquilegiae	Aquilegia	261	176	148
6.	E.betae	Beta	119	122	65
16.	E.cruciferarum	Brassica	260	116	57
17.	E.cruciferarum	Brassica	192	85	56
22.	E.heraclei	Chaerophyllum	263	115	83
23.	E.heraclei	Heracleum	258	136	87
24.	E.martii	Lathyrus	174	210	108
25.	E.martii	Lupinus	309	171	63
26.	E.martii	Trifolium	317	154	108
27.	E.pisi	Pisum	216	176	118
28.	E.polygoni	Polygonum	233	122	100
29.	E.ranunculi	Delphinium	249	92	79
30.	E.ranunculi	Ranunculus	240	141	72
35.	M.berberidis	Mahonia	237	162	80
36.	M.euonymi	Euonymus	149	159	42
37.	Oidium sp.	Clianthus	234	169	116
50.	U.necator	Vitis	212	90	62

** Mean germ tube length of 50 conidia

* See Table 2.1

are illustrated in Figs. 2.1-2.4 and Plates 2-6. Within group A, M.alphitoides and O.oxalidis produce appressoria of E.polygoni type and the rest E.cichoracearum type. M.alphitoides was the only mildew species that showed branching in this group and the forked type of branching is characteristic of this species (Plate 2F). In group B except O.begoniae and S.fuliginea from Cucurbita pepo all others produce single unbranched germ-tubes. The production of 1-5 germ-tubes and E.polygoni type of appressoria separate O.begoniae from the rest. Within group C, the production of a number of tiny abortive germ-tubes is characteristic of E.graminis. Coiling of tips of germ-tubes is characteristic of mildew species on Leguminosae in group D.

B. Water and viability of conidia

The previous experiments showed that when conidia were placed on or in water some of them germinated and produced atypical germ-tubes while others failed to germinate. The experiments in this section were designed specifically to determine whether these conidia had the ability to develop further if transferred to leaves. Basically,conidia that were sown on or in water were transferred at intervals after inoculation to leaf tissues of their appropriate hosts. Two mildews, E.graminis on barley and E.pisi on pea were used.

The first experiment was concerned with conidial germination. Conidia were transferred at 2h intervals from

0-10h and also once at 24h and 48h after inoculation. Transfers of floating conidia were made by touching the surface of water with the adaxial leaf surface and of submerged conidia by first draining off the water and similarly touching the bottom surface of the polystyrene box. Five leaf units were used in each transfer. These were dried under a fan and floated on water in polystyrene boxes. Germination of conidia was assessed 24h after their transfer to leaves. This was compared with germination after 24h on leaf tissue, on water and in water. All initial inoculations were carried out at the same time in a settling tower.The results are presented in Table 2.4.

Generally when conidia had been kept for 24h on or in water there was no improvement in their germination when they were transferred to leaf tissue even after a further 24h or 48h incubation. Only with E.pisi conidia floated on water was there any change in germination that might be considered an improvement. Transferring conidia from water after periods ranging from 2h-10h did result in an improvement in germination compared to 24h period on or in water. The viability of some conidia, therefore, was not impaired by these water treatments - a result consistent with some of those in previous section. This was further supported by the observation that some conidia, germinating atypically in water, produced new germ-tubes of normal appearance and with appressoria

Table 2.4 Mean* percentage conidia germinated when transferred from water to host leaf.

A. E.graminis

After 24h on leaf only: 88.2

on water only: 55.4

in water only: 44.2

After 24h following period of contact with water of:

	0**	2	4	6	8	10	24	48h
on water	86.7	83.6	74.5	71.5	66.7	62.9	57.1	55.7
in water	87.9	81.3	74.1	63.9	57.8	53.7	45.2	45.3

B. E.pisi

After 24h on leaf only: 91.4

on water only: 73.9

in water only: 68.0

After 24h following period of contact with water of:

	0**	2	4	6	8	10	24	48h
on water	90.8	90.7	88.7	86.0	84.0	82.7	80.1	77.2
in water	90.5	87.0	83.3	81.0	78.3	74.3	69.2	67.2

*Mean of 5 replicates (Appendix Table 2.1)

**Conidia removed immediately after contact with water.

when transferred to leaves. The atypical germ-tubes aborted. New germ-tubes were also seen to emerge from conidia of E.graminis with many minute projections as shown in Fig. 2.3E. This tendency to form new germ-tubes declined with duration of conidia on or in water.

The second experiment examined the potential for further growth of germ-tubes produced by conidia on or in water. It was essentially similar in design but production of ESH was measured 48h after the germinated conidia were transferred to leaf tissue and this was compared with the numbers of conidia forming ESH after 48h on leaf tissue only.

The results(Table 2.5) showed that for E.graminis very few of the conidia which had germinated on or in water retained the ability to infect leaves when transferred after 24h and rather less than a third of the germinated conidia had this ability after 10h in the presence of water. However, about 20-25% germinated conidia of E.pisi did produce ESH on pea leaves after 24h on or in water. Further observations on samples of germinated conidia transferred to leaf tissue showed that some continued to grow normally but the colonies were rather small (Table 2.6) and sporulation was much delayed (Table 2.7).

Table 2.5 Mean* percentage conidia producing ESH when transferred from water to host leaf.

A. E.graminis

After 48h on leaf only: 78.9

After 48h following period of contact with water of:

	0**	2	4	6	8	10	24	48h
on water	79.5	71.3	61.0	52.9	44.2	31.6	3.0	0
in water	74.5	67.2	57.4	44.7	35.3	25.6	1.6	0

B. E.pisi

After 48h on leaf only: 81.8

After 48h following period of contact with water of:

	0**	2	4	6	8	10	24	48h
on water	80.3	73.9	66.0	60.3	51.7	39.7	26.0	2.8
in water	81.1	67.6	58.3	50.2	42.5	34.4	21.7	1.2

*Mean of 5 replicates (Appendix Table 2.2)
Conidia removed immediately after contact with water.

Table 2.6 Mycelial growth* (mm) of conidia when transferred from water to host leaf.

A. E.graminis

After 48h on leaf only: 2.70

After 48h following period of contact with water of:

	0**	2	4	6	8	10	24	48h
on water	2.72	2.45	2.22	1.82	1.61	1.40	0.75	0
in water	2.68	2.37	2.16	1.75	1.53	1.38	0.59	0

B. E.pisi

After 48h on leaf only: 2.74

After 48h following period of contact with water of:

	0**	2	4	6	8	10	24	48h
on water	2.74	2.63	2.43	2.16	1.93	1.71	1.18	0.64
in water	2.75	2.60	2.40	2.14	1.82	1.52	1.08	0.52

*Mean of 25 colonies (Appendix Table 2.3)

**Conidia removed immediately after contact with water.

Table 2.7 Conidiophore* production/mm^2 colony when conidia were transferred from water to host leaf.

A. E. graminis

After 96h on leaf only: 65

After 96h following period of contact with water of:

	0**	2	4	6	8	10	24	48h
on water	69	41	28	19	4	0	0	0
in water	65	43	19	13	0	0	0	0

B. E. pisi

After 96h on leaf only: 86

After 96h following period of contact with water of:

	0**	2	4	6	8	10	24	48h
on water	84	53	42	26	19	12	0	0
in water	82	50	36	24	10	9	0	0

*Mean of 10 colonies (Appendix Table 2.4)

**Conidia removed immediately after contact with water.

C. Inoculation of barley with aquous suspension of conidia

In view of the results of the previous experiments, the possibility was examined of using aquous suspension of conidia for the inoculation of barley with E.graminis.

Conidia from severely infected barley seedlings were allowed to deposit on a watch glass within a settling tower. These were then washed into a beaker of glass distilled water and the volume made upto 800 ml. The contents were agitated gently and divided into two 400 ml portions, to one of which 0.04 ml Tween 80 (0.01%) was added to wet the conidia. Immediately after preparation and at intervals of 0.5, 1, 2, 4, 6, 8 and 10h, each suspension was atomised separately onto 40 barley seedlings (10 per pot). After spraying, the plants were dried under a fan and kept in a glass house at 20±3°. The number of mildew colonies on both leaf surfaces was counted 5 days later.

The results (Fig. 2.5) showed that infections decreased with the time that conidia were immersed in water. The effect was more drastic with conidia wetted with Tween 80. When the inoculated leaves were examined microscopically it was found that some conidia had germinated abnormally and these failed to infect (Fig. 2.6).

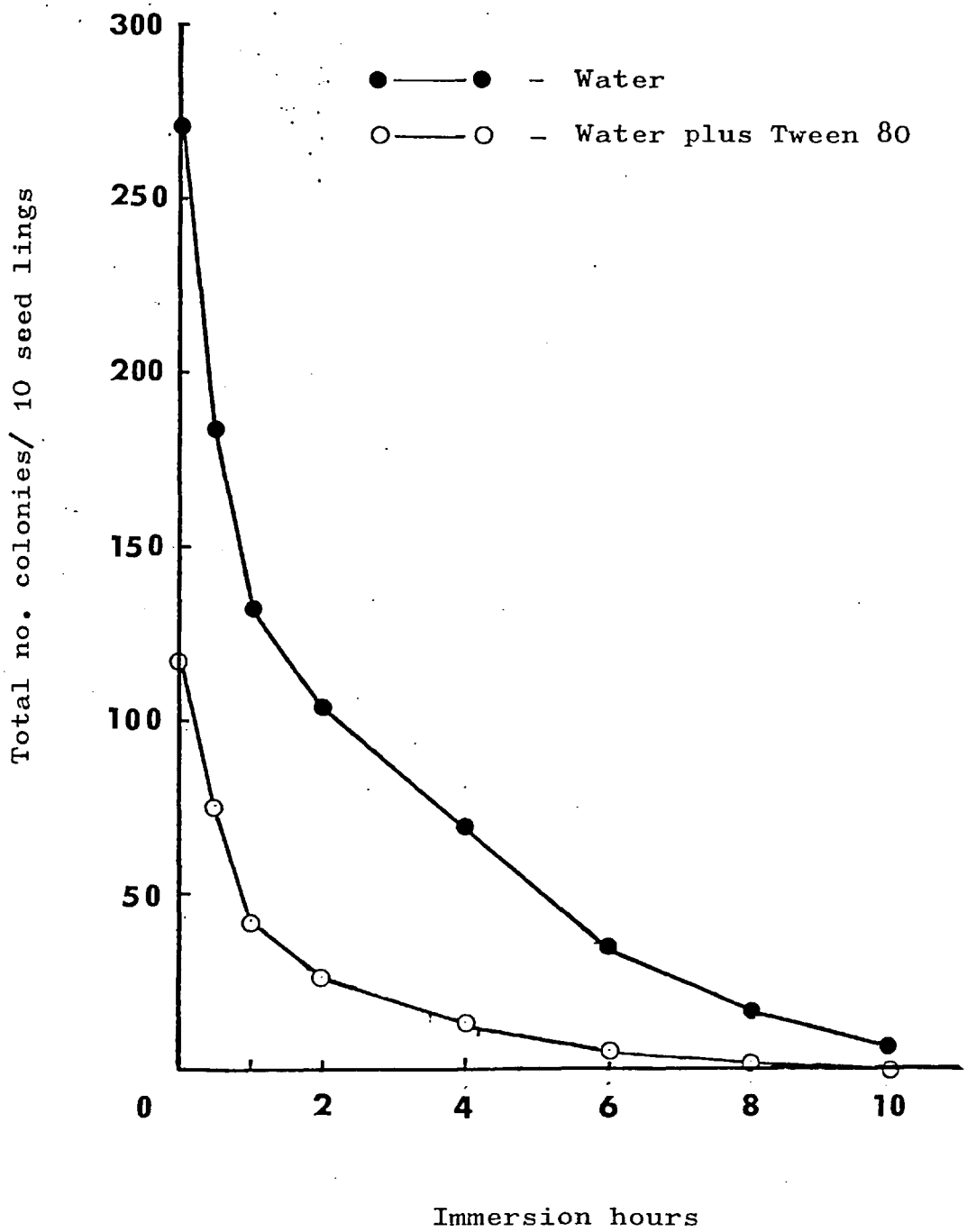


Fig. 2.5 Development of E.graminis on barley when conidia were applied as aquous suspension.

Fig. 2.6 Abnormal germination of E.graminis conidia when applied to barley leaves as aquous suspension (water only).

D. Development of mildews on leaves immersed in water

(i)

The next series of experiments studied the germination of conidia and mildew development on leaf tissue immersed in water. Leaf segments and discs of barley, pea and rose were used. Young leaf tissue of these plants are difficult to wet and three methods were adopted to submerge them in water.

(a) Inoculated leaf units were held in the base of small polystyrene boxes by placing rectangular strips of glass over their edges. Glass distilled water was then poured into the boxes.

(b) Distilled water was poured first into polystyrene boxes and inoculated leaf tissues were then submerged and held in place by glass strips.

(c) Uninoculated leaf tissue, held in empty polystyrene box by glass strips was covered with aquous suspension of conidia.

In all three methods some conidia floated to the surface and was thus lost from the experimental system. This loss was greatest with method (b) which involved most handling of inoculated tissue (Table 2.8).

In the first experiment of the series a set of leaf tissues were immersed immediately after inoculation and kept at 20±1° in an illuminated cabinet. After 24h some leaf tissues were removed carefully and air dried. Germination

Table 2.8 Effect of submerging leaves immediately after inoculation on the number of conidia retained.

	*Conidia/ mm^2 leaf		
	E.graminis	E.pisi	S.pannosa
Submerged leaf	33	32	23
Control leaf	45	53	32

*Mean no. conidia assessed on microscope field (x100) on each of 15 leaves (Appendix Table 2.6)

was assessed by taking celloidin peels of these and appropriate unimmersed controls. Germination was reduced on leaf tissue under water but not as much as might be expected from previous experiments (Table 2.9). This probably resulted from the uneven wetting of immersed leaves. Some air was found trapped on the leaf surface and when leaves were removed after 24h some areas still appeared relatively dry. This was more pronounced with barley and pea than with rose.

Further leaf samples were taken after 48h to determine the number of conidia with ESH (Table 2.9). Although there was again a reduction on submerged leaf tissue, the number of successful infections was relatively high. The experimental results thus suggest that the wettability of the leaves plays an important role in determining the effects of water on germination and also that water may have relatively little effect on established colonies.

These aspects were explored in a second experiment using plants whose leaves showed marked differences in relation to wetting. The mildews and hosts were:

E.aquilegiae on Aquilegia (leaves very difficult to wet)
E.depressa on Arctium (upper leaf surface easily wetted)
E.verbasci on Verbascum (leaves apparently wetted easily but covered with stellate hairs)
M.alphitoides on Quercus (leaves easily wetted)

Leaf discs of these plants were inoculated with conidia of their respective mildews and were then divided into three

Table 2.9 Effect of submerging leaves immediately after inoculation on germination and production of ESH by conidia.

	*Mean values		
	E.graminis	E.pisi	S.pannosa
(i) % germination			
submerged	56.2	76.8	61.3
control	87.3	90.0	83.5
(ii) % ESH**			
submerged	41.5	44.5	45.2
control	73.2	85.6	72.4

*Results are based on means of 5 replicates assessed 24h (germination) and 48h (ESH) after inoculation (Appendix Table 2.7).

**ESH represented as % of total conidia.

sets. The discs in one set were floated on water, with the inoculated surface upper, in polystyrene boxes at 20±1°. Samples were removed at 24 and 48h to assess germination and production of ESH respectively. The discs in the second set were immersed immediately after inoculation; germination and ESH were similarly assessed at 24 and 48h. Discs in the third set were incubated normally on water for 24h and then immersed for a further 24h after which the production of ESH was determined.

The results (Table 2.10) show that while conidial germination on all four hosts submerged in water immediately after inoculation was apparently not much different to the control, development of ESH was related to the ease with which the leaves were wetted. Thus no conidia of E.depressa formed ESH and few of M.alphitoides did so. However, when established conidia were wetted 24h after inoculation there was little effect on the development of ESH irrespective of the 'wettability' of the leaf tissue. A microscopic examination of submerged burdock (Arctium) and oak (Quercus) leaf discs 24h after inoculation showed many conidia with abnormal germination.

(ii)

In further experiments with barley, pea and rose the effects of submerging leaves on total mycelial growth were studied first. Inoculated leaf units were divided into three sets. The tissues in one set were immersed in water immediately

Table 2.10 Effects of submerging leaves immediately after inoculation on germination and production of ESH (expressed as % relative to controls*).

Mildew species	Submerged immediately after inoculation		Submerged 24h after inoculation
	Germination	ESH	ESH
E.aquilegiae	95.8	85.2	96.5
E.depressa	98.4	0	96.2
E.verbasci	89.7	82.6	100.0
M.alphitoides	97.0	11.0	100.0

*Results are based on means of 5 replicates assessed 24h (germination) and 48h (ESH) after inoculation (Appendix Table 2.8

after inoculation, those in another set were immersed 24h after inoculation and those in the remaining set were kept as controls. Total mycelial length of 25 colonies from each set was measured 48h after inoculation.

Mycelial growth was reduced by both water treatments, but less so when leaves were immersed 24h after inoculation (Table 2.11). The effects were most marked with E.graminis on barley and least with S.pannosa on rose, again possibly a reflection of the ease with which the young host leaves are wetted.

A second experiment with these hosts investigated the effect of immersing leaves on the production of conidiophores. Some inoculated leaf tissues were submerged under water immediately after inoculation and others 24h, 48h and 72h later. The number of conidiophores (per mm^2 colony) was determined at 96h after inoculation. The results (Table 2.12) showed that the production of conidiophores was reduced on immersed leaves to an extent dependent on the period of immersion.

These experiments indicated that mildews can develop on leaves under water though the growth rate is slower. Some pustules even produced chains of conidia under water. An examination of colonies grown under water for long periods showed that the hyphae were slightly thicker than normal and highly vacuolated. The hyphal tips of E.pisi and S.pannosa became coiled or re-curved and sometimes swollen

Table 2.11 Effects of submerging inoculated leaves on mycelial growth* (mm).

Leaves submerged at	Hours under water	E.graminis	E.pisi	S.pannosa
inoculation	48	1.33 (52.2)**	1.59 (58.0)**	2.43 (76.2)**
24h later	24	1.88 (73.7)**	2.27 (82.8)**	2.65 (83.0)**
control	0	2.55	2.74	3.19

*Mean of 25 colonies (Appendix Table 2.9)

**Figures in brackets as % of control.

Table 2.12 Effect of submerging inoculated leaves on the production of conidiophores.

Leaves submerged at (h after inoculation)	Hours in water	*Conidiophores/mm^{2}colony		
		E.graminis	E.pisi	S.pannosa
0**	96	11	3	3
24	72	30	8	10
48	48	48	19	16
72	24	61	24	23
Control	0	77	36	31

*Mean of 15 replicates (Appendix Table 2.10)

**Leaves submerged immediately after inoculation.

and the entire colony appeared wrinkled. There was no coiling or curving of the hyphae with E.graminis but the hyphal tips became thick and swollen. Colonies of all mildew species began to disintegrate after 96h immersion but so did the leaf tissue, especially of barley.

(iii)

Another series of experiments was designed to investigate mildew development on leaves following periods of immersion, again using barley, pea and rose.

Germination was studied first. Inoculated leaf units were divided into four sets. One set was kept as control, the rest were immersed under water immediately after inoculation. The immersed set was then removed from water 6h, 12h and 24h after inoculation. It was difficult to float the leaf pieces on water once they had been immersed so after drying their surface in air they were placed on moist filter paper in tightly closed polystyrene boxes. Sample leaf pieces from the control set were thus similarly treated at these times. Germination of conidia within all treatments was assessed 24h after inoculation. The amount of germination increased on leaf tissue once it was removed from water compared with that on tissue immersed for 24h but it did not reach the level attained on unwetted tissue (Table 2.13).

A similar experiment investigated effects on mycelial growth. Some leaf tissues were kept immersed for 6h, 12h,

Table 2.13 Effects of submerging leaves immediately after inoculation on germination* of conidia when leaves were subsequently removed.

Hours in water (h after inoculation)	Mean % germination**		
	E.graminis	E.pisi	S.pannosa
0(control)	75.7	92.3	82.2
6	65.5	82.3	71.9
12	61.8	77.3	63.0
24	56.5	74.0	54.9

*Germination assessed 24h after inoculation

**Mean of 10 replicates (Appendix Table 2.11).

24h and 48h after inoculation; others were not wetted (controls). The total mycelial growth of 10 colonies was measured 48h after inoculation. The detail results are given in Appendix Table 2.12 and are summarized in Fig. 2.7. However, it is more useful to examine mean mycelial growth rate per hour on the assumption that extension of growth during the first 24h after inoculation is negligible but occurs mainly between 24 and 48h after inoculation. The growth rates shown in Table 2.14 are derived on this basis. These show that in most instances growth rates are improved relative to those on leaf pieces immersed for 48h ; an exception is E.pisi on discs immersed for 24h. However, the rates do not attain those on unwetted leaves.

The production of conidiophores was examined in a subsequent experiment. Leaf samples were immersed immediately after inoculation and some were removed 6h, 12h, 24h, 48h and 72h later. The number of conidiophores per mm^2 colony was assessed on these samples 96h after inoculation and also on leaf tissue not immersed (control) and immersed for 96h.Overall, the results (Appendix Table 2.13, summarized in Fig. 2.8) indicate a marked delay in the initiation of conidiophores with length of immersion in water. Table 2.15 shows the rate of conidiophore production per mm^2 colony per hour on the basis that this process occurs mainly between 48h and 96h. The rates are apparently much depressed on leaf tissues

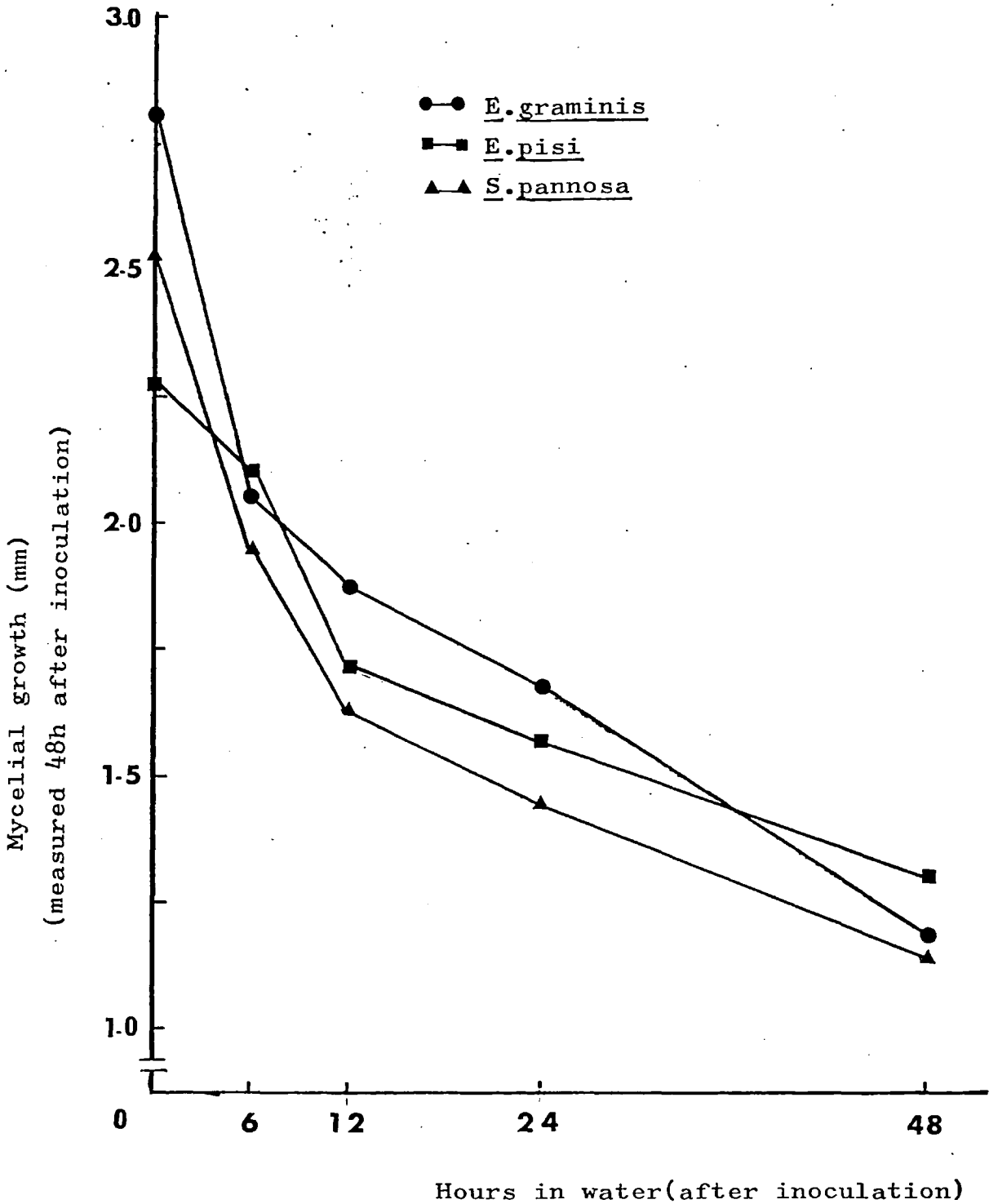


Fig. 2.7 Effect of submerging leaves immediately after inoculation on mycelial growth when leaves were removed.

Table 2.14 Mycelial growth rates (μm/h) on immersed and non-immersed leaves.

	E.graminis	*E.pisi*	*S.pannosa*
Non-immersed leaves (control)	116	94	105
Leaves immersed for:			
6h	84	88	80
12h	78	70	68
24h	70	56	61
48h	51	56	48

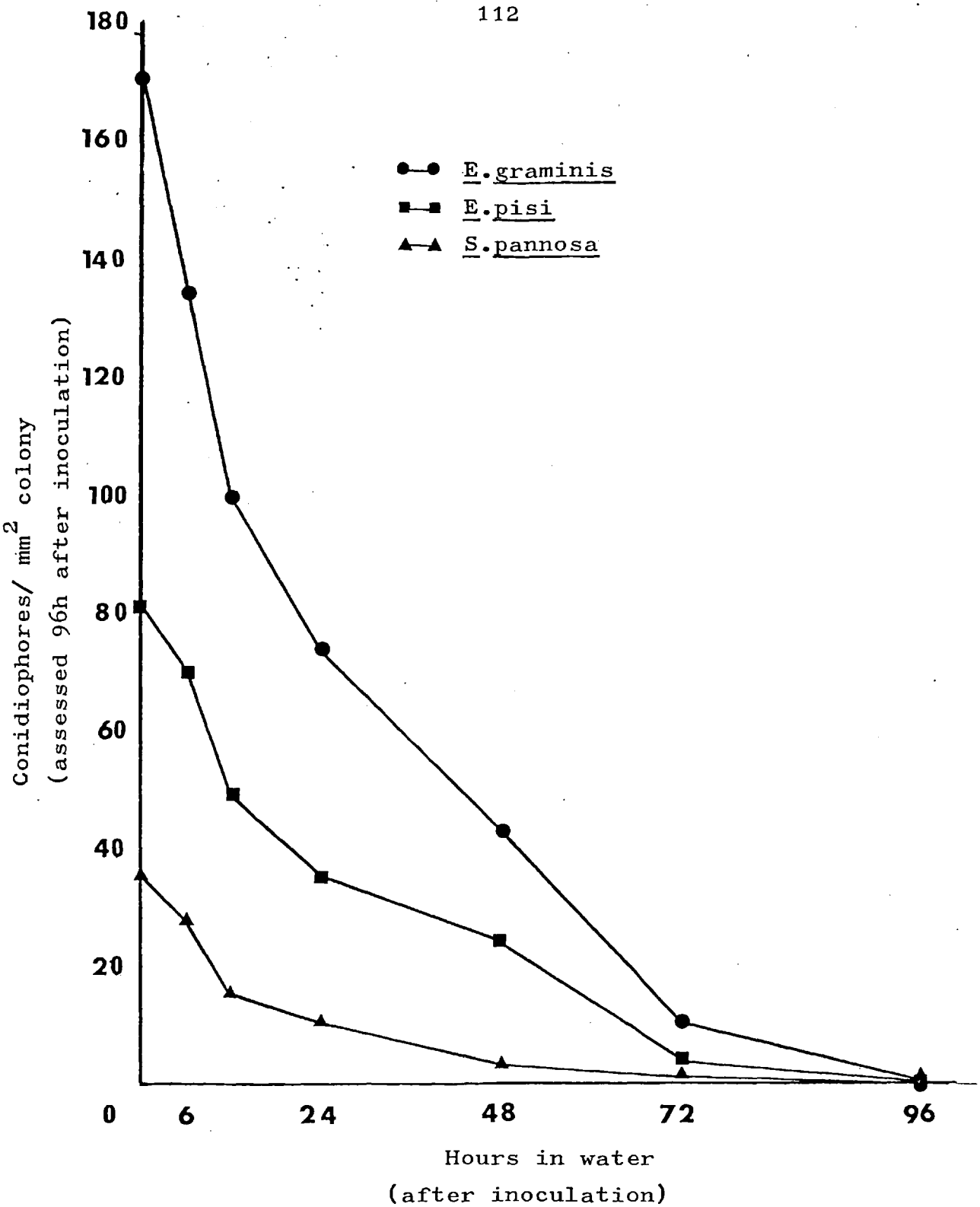


Fig. 2.8 Effect of submerging leaves immediately after inoculation on conidiophore production when leaves were removed.

Table 2.15 Rates of conidiophore initiation (no./mm^2/h) on immersed and non-immersed leaves.

	E.graminis	E.pisi	S.pannosa
Non-immersed leaves (control)	3.54	1.69	0.75
Leaves immersed for:			
6h	2.79	1.46	0.58
12h	2.06	1.02	0.31
24h	1.52	0.73	0.21
48h	0.90	0.50	0.06
72h	0.21	0.08	0.02
96h	0	0	0

immersed in water and there is no indication that once removed from water they improve substantially.

(iv)

The results of the previous section indicate that removal from water does not have any stimulatory effect on mildew growth. These relate to immersion immediately after inoculation. The next experiment examined the possibility that established colonies might eventually be stimulated by immersion in water.

Inoculated leaf samples were floated on water in polystyrene boxes and incubated at 20° for 24h when half of the leaf tissues were submerged under water. Leaf samples from both treatments were taken at 6h intervals commencing from 30h until 60h after inoculation and cleared in methanol overnight. Total mycelial lengths of 10 colonies from each sample were measured. The results (Fig. 2.9, Appendix Table 2.14) indicate that with E.graminis and S.pannosa there was a recovery after wetting so that mycelial growth at 60h was not different from that in the controls. This suggests that for some period following wetting mycelial growth on the wetted leaf pieces was faster than in the controls. An analysis of mycelial growth rates for each 6h period between 30h and 60h lends weight to this view (Table 2.16). For both these mildews 48h to 54h after inoculation, growth rates were somewhat higher on wetted leaf pieces than on the controls. With E.pisi, growth rates were similar throughout so that by 60h total mycelial growth on wetted

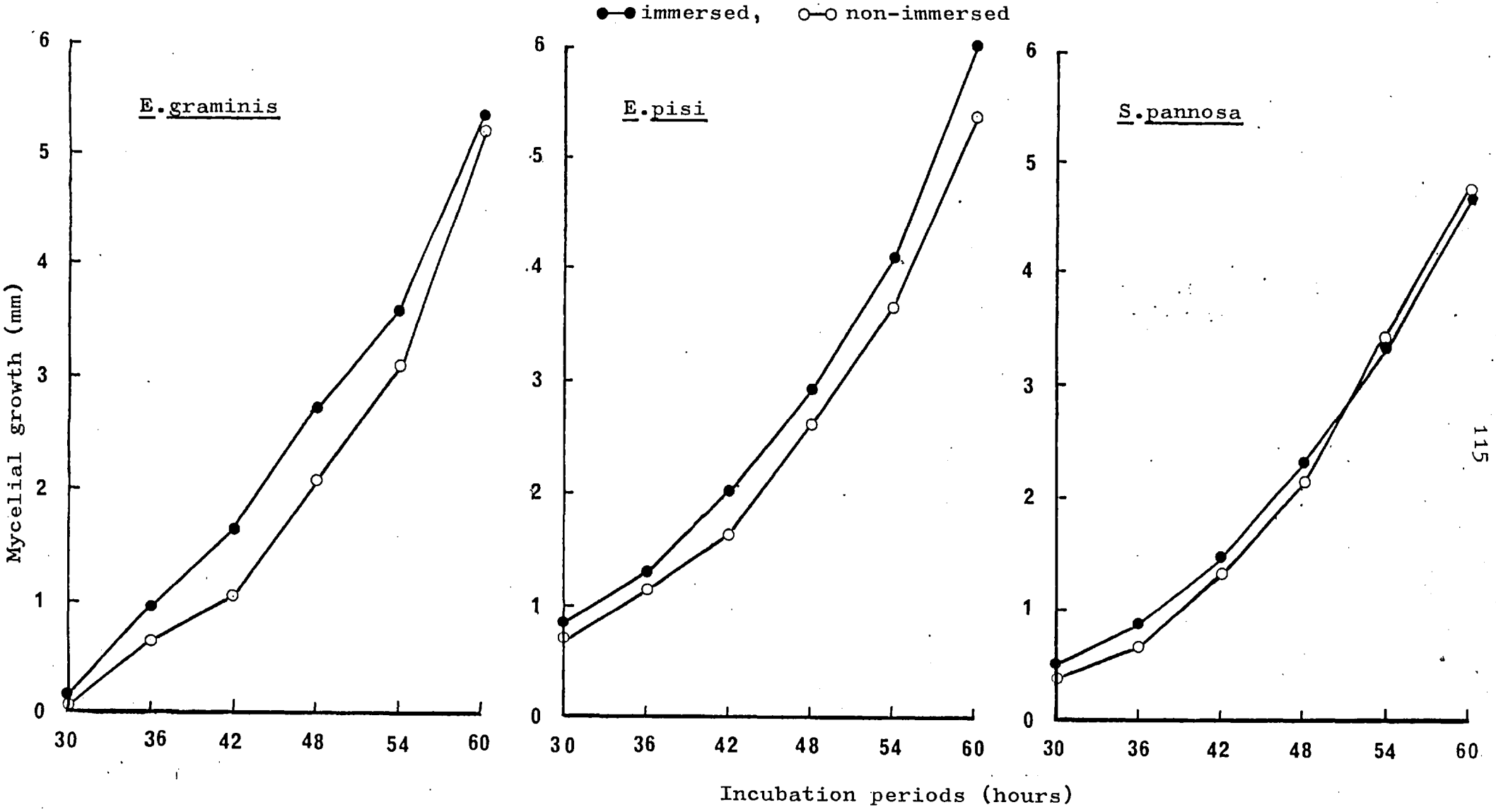


Fig. 2.9 Effect of submerging leaves for 6h, 24h after inoculation on mycelial growth.

Table 2.16 Mycelial growth rates (μm/h) on leaf tissue immersed 24h after inoculation and on non-immersed leaves.

Period (h after inoculation)	E.graminis		E.pisi		S.pannosa	
	T	C	T	C	T	C
30-36	98	138	75	75	45	65
36-42	70	115	83	118	113	102
42-48	173	182	167	156	133	142
48-54	168	145	167	200	225	172
54-60	350	295	283	317	223	225

T - treated, C - control

(Appendix Table 2.14)

leaf pieces remained below that of the control.

A similar experiment examined the effect of 6h period of immersion on the production of conidiophores. Inoculated leaf pieces were floated on water and incubated at 20° for 84h. One half of the leaf samples were then immersed in water for 6h. Samples were removed from both treatments every 6h commencing 90h after inoculation. Conidiophore production was determined and is presented in Fig. 2.10 (Appendix Table 2.15) as number of conidiophores per mm^2 colony. Some stimulation is again apparent, especially with S.pannosa and this is confirmed by an analysis of the rates of conidiophore production for the various periods studied (Table 2.17), there being a marked increase in the rates for wetted leaves in the period 108h to 114h after inoculation.

(v)

The final experiment in this series examined the infectivity of conidia produced on water treated colonies. Some inoculated leaf pieces were immersed under water 72h after inoculation and kept there for 48h; other similar leaf pieces were not wetted. At 120h (after inoculation) the immersed leaf pieces were removed, air dried and kept on moist filter paper. Conidia were removed by blowing air overthe control leaf piece and these too were kept on a moist filter paper. Both sets of leaf pieces were used separately to inoculate fresh host leaf segments and discs 24h later. Since sporulation was relatively sparse on the

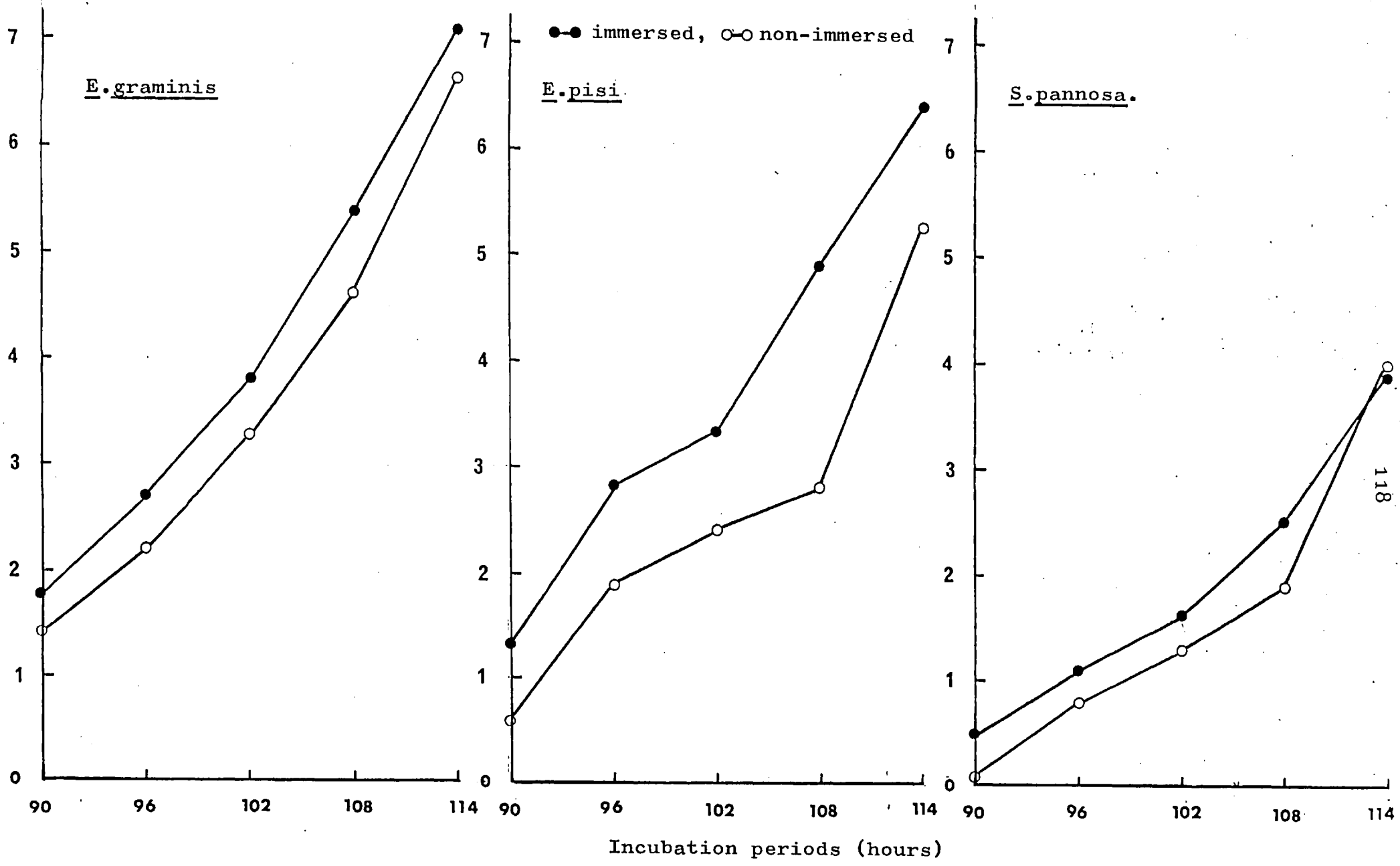


Fig. 2.10 Effect of submerging leaves for 6h, 84h after inoculation on conidiophore production.

Table 2.17 Rates of conidiophore production (no./mm^2/h) on leaf tissue immersed for 6h, at 84h after inoculation and on non-immersed leaves.

Period (h after inoculation)	E.graminis		E.pisi		S.pannosa	
	T	C	T	C	T	C
90-96	1.3	1.5	2.2	2.5	1.2	1.0
96-102	1.8	1.8	0.8	0.8	0.8	0.8
102-108	2.2	2.7	0.7	2.7	1.0	1.5
108-114	3.5	2.8	4.2	2.5	3.5	2.3

T - treated, C - control

(Appendix Table 2.15)

previously-immersed leaf pieces, inoculation was achieved by pressing these gently against healthy tissue. The number of conidia producing ESH was determined on the inoculated leaf pieces after 48h. The results (Table 2.18) indicated no loss of infectivity with conidia from water-treated colonies.

E. Biological activity in water drops on leaves

It has been assumed so far that water on leaves has a direct effect on mildew development. It could be argued that water films or drops allow other micro-organisms, already present on leaf surfaces, to develop to levels that might be inimical to mildew growth. This was examined in the following experiment. Drops (0.05 µl) of water were placed with an Agla microsyringe on uninoculated leaf pieces of barley and pea, on pieces just inoculated with conidia of E.graminis and E.pisi and over colonies of these fungi on their respective hosts.

After 6h incubation at 20°, the drops were collected with a microsyringe and bulked within each of the treatments. The number of bacteria was then estimated by plating known volumes onto nutrient agar plates and counting colonies after 3 days at 20°.

Although the method only gives an overall estimate of bacteria on leaf tissue that will grow on nutrient agar,

Table 2.18 Effect of submerging sporulating colonies on the production of viable conidia.

Mildew	% ESH production*	
	immersed	non-immersed
E.graminis	57.2	62.9
E.pisi	70.9	73.6
S.pannosa	63.9	69.5

*Mean of 5 replicates (Appendix Table 2.16)

the results (Table 2.19) suggest that during 6h only minor increases in bacteria occur where mildew conidia or colonies are present.

The results thus give little support to the hypothesis that the effects of water on mildew development are mediated through other micro-organisms, atleast for wet periods of 6h.

Table 2.19 Bacterial population in water droplets kept on leaves for 6h.

Water collected from leaves	Bacteria/ml(10^{-3}) A	B
(i) inoculated with conidia	1.90	3.91
(ii) covered with colonies	1.79	3.73
(iii) not inoculated	1.56	3.63

A and B - water droplets collected from E.graminis/barley and E.pisi/pea respectively.

III. EFFECTS OF IMPACTING WATER DROPS ON MILDEW GROWTH

In the previous studies on leaf wetness and mildew growth, water was applied gently to leaves either by immersing leaf tissue in water or by allowing a fine mist of water droplets to deposit on leaves. No account was taken of the fact that in the field leaves become wetted by rain and that this involves the impaction of water drops which itself might physically damage mildew growth. The effects of impacting water drops on mildew development were elucidated in the experiments described here.

Materials and Methods

a. Host plants and mildews

Experiments involved either E.graminis on barley (cv. Zephyr) only or this fungus plus E.pisi on pea (cv. Kelvedon Wonder) and S.pannosa on rose (cv. Perle d' Alcanada). The rose cutivar was chosen because it is a miniature type (susceptible to mildew) and some experiments involved the use of potted plants. Roses were usually pruned lightly some 2-3 weeks before they were required so that for experiments they had young, susceptible shoots. Barley seedlings were used when 7 days old and peas when 2 weeks old. Barley and peas were grown in J.I. no.1 in 7.5 cm pots containing 5 seedling and one plant respectively. Roses were also grown in J.I. no.1 but singly in 15.5 cm pots. Unless

stated otherwise, plants were inoculated with conidia of their respective mildews using the settling tower described on p. 26.

b. Rain simulator.

An apparatus was devised to simulate rain and is illustrated in Fig. 3.1. Basically, water passing through a watering-can rose impinged on a drum (20cm long and 12cm diam.) held directly below. This drum was a plastic container from which strips along the horizontal axis were removed at regular intervals. It was made to rotate by a variable speed motor causing the water which was directed onto it to be thrown off as small droplets, like a light rain. The intensity and size of droplets were controlled by varying the water flow and the speed with which the drum rotated. The simulated rain fell within an area adjucent to the tower and the distribution within this area was monitored by a rain gauge in several preliminary trials. The rain simulator was operated for atleast 30 min before the start of an experiment to attain a steady fall of rain and the apparatus was adjusted generally to 1 mm rain/h. However, the amount was always checked with a rain gauge for each experiment. The entire apparatus was built within a pre-cast building and this avoided drift of rain.

The size of rain drops was measured by allowing them to fall onto a 1:1 mixture of vaseline and paraffin liquid, in which they are retained with negligible change in shape

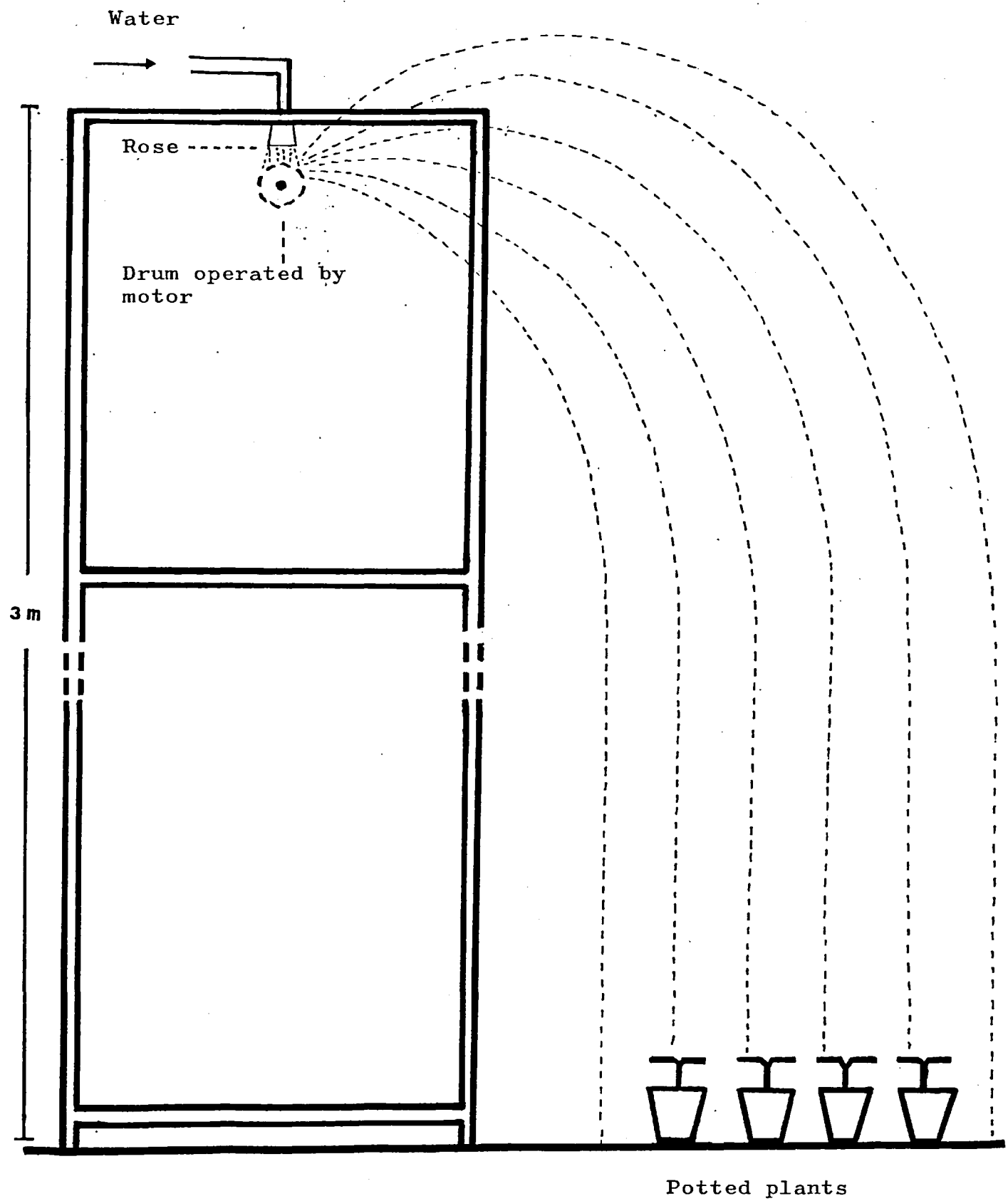


Fig. 3.1 Rain simulator

(Mabett & Phelps,1976) and assessing under a microscope with an ocular grid. Droplet size varied between 2 and 4mm.

Experimental

A. Simulated rain and mildew development

Experiment 1: Initially the washing effect of rain on conidia deposited on leaves was examined. Potted plants of barley, pea and rose were inoculated with conidia of their respective mildews. Some of each were kept as controls; others were subjected to 1h simulated rain (1.2 mm) immediately after inoculation. The washed leaves were allowed to dry and then celloidin peels were taken of the adaxial and abaxial leaf surfaces of 10 barley seedlings and the adaxial surfaces of 10 pea leaves and 5 rose leaves, using in both instances the last fully expanded leaves on shoots. The number of conidia per mm^2 leaf was estimated from counts of 5 microscopic fields (x 100) per leaf.

The results (Table 3.1) show that most conidia were removed by the washing especially from pea and rose, both of which have smooth leaves. Fewer conidia were removed from barley leaves, probably because of their vertical orientation in relation to the water drops.

Experiment 2: The next experiment investigated the effect of rain washing at intervals after inoculation using E.graminis and barley. This was preferred because the discrete colonies

Table 3.1 Effect of rain on mildew conidia immediately after inoculation.

Mildew	*Mean conidia/mm^2 leaf		Reduction in no. (as % of control)
	T	C	
E.graminis	10	63	84.1
E.pisi	<1	159	99.5
S.pannosa	1	102	99.0

T - treated, C - control

*Detailed results are given in Appendix Table 3.1.

readily provide a measure of infection. Thirty pots, each with 10 seedlings, were inoculated with conidia and then divided into 6 sets of 5 pots. One set was kept as control, the remainig sets were each subjected to rain (1 mm/h) at one of the following times after inoculation: 0, 2, 4, 6 and 8h after inoculation. After these treatments the leaves were allowed to dry and the pots were transferred to a filtered air cabinet at 20±3°. The number of mildew colonies was counted on both leaf surfaces after 5 days and the leaf areas were then measured.

There was a gradual increase in the amount of infection as the time between inoculation and rain lengthened (Table 3.2). This suggests that as conidia germinate they are less easily removed by rain. Under the conditions of this experiment, germination appeared to start between 2h and 4h.

Experiment 3: A similar experiment studied the effect of rain at either 24h or 48h after inoculation. Potted plants of barley, pea and rose were inoculated with their respective mildews. These were divided equally amongst the four treatments: none (control), rain immediately (1 mm) after inoculation and rain after 24h (1.1 mm) and 48h (1 mm) respectively. Mildew was assessed 6 days after inoculation, by counting colonies on both leaf surfaces of barley, on the adaxial surface of pea leaves and by scoring mildew on the adaxial surface of rose leaves on a

Table 3.2 Effect of rain on E.graminis during its initial development on barley.

		Period (h) between inoculation and rain				
	Control leaves	0	2	4	6	8
*Colonies/cm^2 leaf	15.5	2.0	2.2	3.6	6.8	8.1
% reduction (as control)	-	86.9	85.9	76.7	56.0	47.4

*Each figure is the mean of 50 leaves (Appendix Table 3.2)

scale 0-10 (where 0 = no mildew and 10 = leaf completely covered with mildew). The results (Table 3.3) suggest that rain is most inhibitory to the development of E.graminis during the first 24h after inoculation but is more damaging to E.pisi 24-48h after inoculation. S.pannosa is fairly severely affected during both periods.

Experiment 4: The next experiment examined the effects of several periods of rain on the development of E.graminis on barley. There were three rain treatments: at (i) 0, 24 and 48h, (ii) 24, 48 and 72h and (iii) 48, 72 and 96h after inoculation. The amount of rain at 0, 24, 48, 72 and 96h were 1.0, 1.1, 1.2, 1.0 and 1.0 mm/h respectively. One set of inoculated seedlings were used for each of these treatments and one set with no rain served as a control. Mildew colonies were counted at 6 days. The results (Table 3.4), taken in conjunction with those of the previous experiment (Table 3.3) indicate that while further periods of rain may cause some additional damage, the major effect is due to the first period of rain.

Experiment 5: The fifth experiment in this series studied the effect of rain on sporulating colonies. Inoculated plants of barley, pea and rose were kept in a glass house at 20±3° for 7 days, by which time they were covered with sporulating colonies. At this stage, old conidia were removed and the plants were re-incubated for a further 24h. Then half of the plants were subjected to 1h rain (1.2 mm),

Table 3.3 Effect of rain applied immediately (0), 24h and 48h after inoculation on mildew development.

Period (h) between inoculation and rain	Reduction in mildew (as % of control)		
	E.graminis	*E.pisi*	*S.pannosa*
0	93.8	100.0	100.0
24	46.4	83.1	54.0
48	32.4	14.7	18.4

Detailed results are given in Appendix Table 3.3.

Table 3.4 Effect of several periods of rain on the development of E.graminis.

Rain (1h) periods at	*Colonies/cm^2 leaf	Reduction in mildew (as % of control)
(i) 0,24,48h	0.7	94.5
(ii) 24,48,72h	5.9	54.7
(iii) 48,72,96h	8.4	35.0
(iv) None(control)	12.9	-

*Mean of 50 leaves (Appendix Table 3.4).

the other plants were not (controls). Extra care was taken to avoid shaking the plants during this operation. Rain treated plants were allowed to dry and then these and the controls were divided into 4 equal sets (each comprising barley, pea and rose). These plants were used as sources of conidia for the inoculation of healthy plants of the appropriate hosts immediately or at 24h, 48h or 72h later by the method described on p.61. Mildew intensity on the recipient plants was assessed 6-8 days after inoculation. The results (Table 3.5) indicate that sporulation was greatly reduced by rain and suggest that even 72h after wetting it was not fully restored to that of the controls.

A preliminary examination of mildew development on leaves subjected to rain revealed various types of damage from loss of conidia to removal of mycelium and conidiophores. This led to a more detailed study of the damage caused by a water drop impacting on mildews at different stages in their development.

B. Effects of impacting drops on mildews

For these series of experiments young, single leaves or leaflets of barley, pea and rose were used. These were held individually within the mouth of small McCartney bottles with cotton wool plugs through which the leaf base (barley) or petiole (pea and rose) was inserted into

Table 3.5 Effect of rain on the production of viable conidia.

Period (h) between rain and use as inoculum	Reduction in mildew (as % of control)		
	E.graminis	E.pisi	S.pannosa
0	91.0	100.0	100.0
24	64.2	92.5	70.2
48	52.3	71.3	58.6
72	30.5	53.0	36.8

Detailed results are given in Appendix Table 3.5.

water below. A circular area (1 cm diam.) was marked centrally on the upper surface of each leaf and formed the target area for impacting drops.

Water drops were generated in the apparatus shown in Fig. 3.2. Basically, drops were formed at the tip of a pipette or capillary tube (Gregory et al., 1959) through which water flowed from an aspirator. Rate of flow was controlled by a tap on the aspirator and a Hoffman clip on the tubing from this to the pipette. The pipette was held by a clamp on a retort stand and its height could thus be varied. A vertical tube through which the drops passed to the target area prevented horizontal drift. Once the rate of drop release had been obtained for a particular experiment unwanted drops were caught on a blotting paper held at the base of the tube.

(i)

The first series of experiments examined the ability of drops to remove conidia deposited on barley leaves and was thus comparable to the initial experiment with the rain similator.

In the first experiment two drop sizes were used: 4 mm diameter, generated by a pipette and 2 mm diameter generated by a capillary tube. These sizes were selected to cover the range obtained with the rain simulator. These drops were released 0.5 m above the target at the rate of one drop per

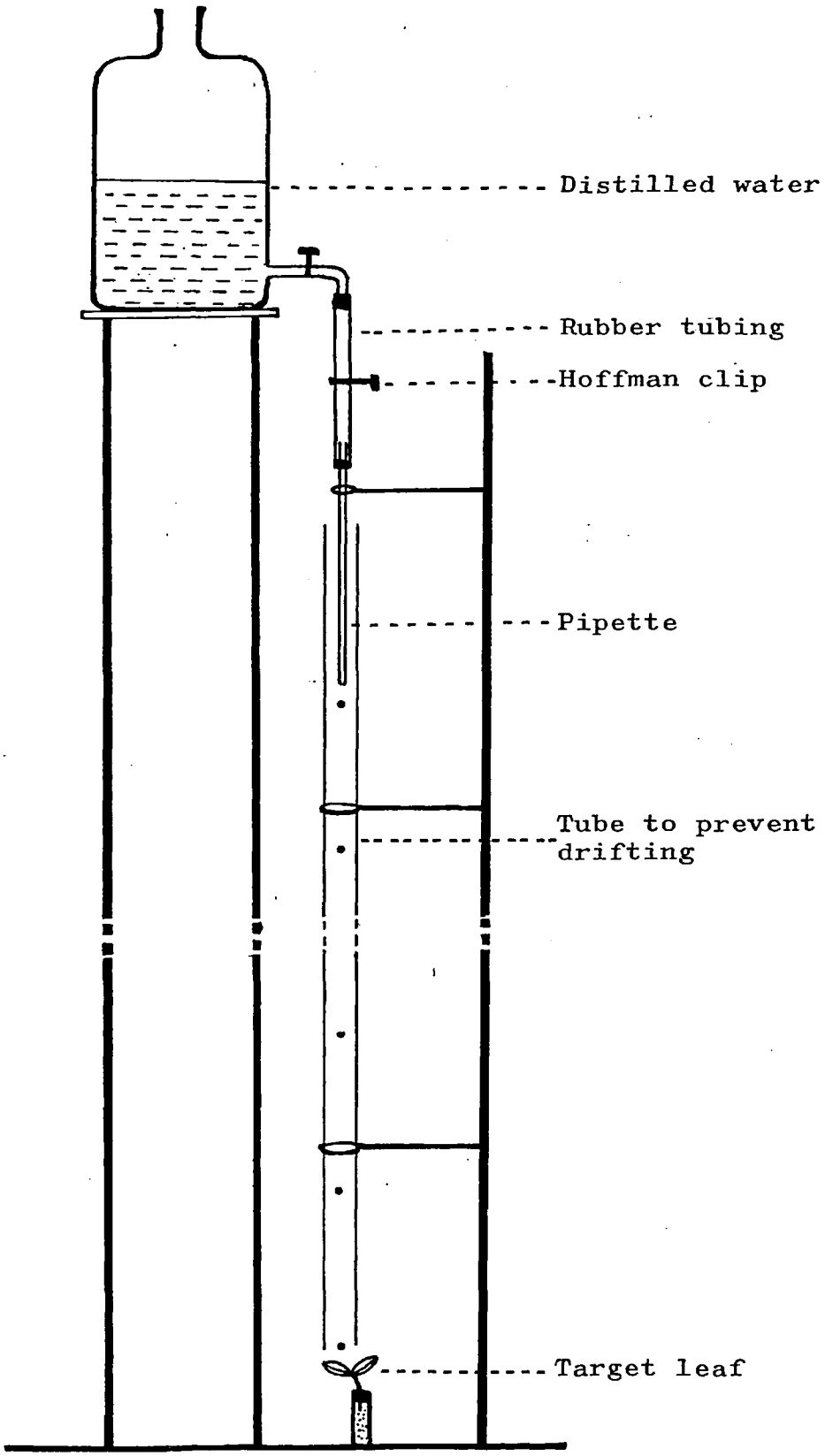


Fig. 3.2 Apparatus to generate droplets of water

5 sec. Treatments consisted of 1, 10 or 20 drops applied immediately after inoculation of leaves with conidia of E.graminis and there were 5 replicate leaves for each treatment and the control. After treatment, the leaves were allowed to dry and conidia counted on celloidin peels covering the target area.

The results (Table 3.6) indicate that more conidia are removed by the larger drops but that even a single small drop (2 mm) can remove some 30% of the conidia within a circle of 1 cm diameter. The examination of celloidin peels also showed that a single drop pushed away conidia to the periphery of the target area and that subsequent drops then eroded these conidia.

The second experiment examined the effect of increasing the height of fall of a single 2 mm drop and combinations of 5, 10 and 20 drops when applied to barley leaves immediately after inoculation with E.graminis. The methods were otherwise similar. The results are presented in Table 3.7. Increasing the height of a single drop markedly increased the number of conidia removed. The effect of height was less pronounced where several drops were applied in sequence. Even 5 drops at 0.5 m removed nearly 80% of the conidia.

In a third experiment of this type, the effects of a single 4 mm drop and combinations of 5, 10 and 20 drops from 2.5 m were examined when applied to leaves of barley, pea and rose immediately after inoculation with their respective

Table 3.6 Effect of droplet size on the removal of conidia of E.graminis immediately after inoculation.

	*Conidia/ mm^2 leaf		
Leaves subjected to....	1	10	20 drops
Droplet size: 2mm	94	12	8
4mm	61	5	0

On leaves not wetted (control): 138 conidia/mm^2

*Mean of 3 assessments on each of 5 leaves (Appendix Table 3.6).

Table 3.7 Effects of height above target leaf on the removal of conidia of *E.graminis* immediately after inoculation (droplet size 2mm).

	*Conidia/mm^2 leaf			
Leaves subjected to....	1	5	10	20 drops
Height above target leaf: 0.5m	96	36	11	6
1.0m	85	31	5	0
1.5m	73	21	5	0
2.0m	48	20	3	0
2.5m	42	17	2	0

On leaves not wetted (control): 176 conidia/mm^2

*Mean of 3 assessments on each of 5 leaves (Appendix Table 3.7).

mildews. The results (Table 3.8) show that the impaction of drops affects the conidia of all three mildews in basically a similar way but with some indication that few drops are less able to remove conidia from pea leaves than they are from rose and barley. Twenty drops were enough to remove all conidia so this number of 4 mm drops at 2.5 m formed a standard for other experiments.

(ii)

The second series of experiments was concerned with the effects of impacting drops on conidia that had germinated on leaves.

Single leaves of barley, pea and rose were inoculated with conidia of their respective mildews, floated on water in 17 x 11 x 4 cm polystyrene boxes and incubated in an illuminated cabinet at 20±1°. Leaf samples were removed at 1h intervals from 0-10h after inoculation and subjected to droplet impaction (twenty, 4 mm drops from 2.5 m). A set of samples was also treated at 24h after inoculation. The number of conidia left per mm^2 of the target area was determined.

The results (Table 3.9) indicate that with all three mildews conidia were readily removed from host leaves during the first three hours after inoculation. Thereafter the ability of the conidia to resist washing increased with incubation time. This was less marked at 24h with E.graminis than with other two mildews, probably because at this stage this

Table 3.8 Effect of droplet impaction (4 mm) on the removal of mildew conidia immediately after inoculation.

	*Conidia/mm^2 leaf			
Leaves subjected to....	1	5	10	20 drops
Conidia of: *E.graminis*	30	9	4	0
E.pisi	58	21	8	0
S.pannosa	18	3	1	0

On leaves not wetted (control): *E.graminis* 126 conidia/mm^2
E.pisi 152 conidia/mm^2
S.pannosa 61 conidia/mm^2

*Mean of 3 assessment on each of 5 leaves (Appendix Table 3.8).

Table 3.9 Effects of water droplets on mildew conidia after different periods of incubation at 20°.

Hours between inoculation and impaction	Reduction in conidia/mm^2 leaf (as % of control)*		
	E.graminis	*E.pisi*	*S.pannosa*
0	100	100	100
1	100	100	100
2	100	100	100
3	100	100	100
4	96	98	97
5	91	92	89
6	87	88	87
7	85	86	84
8	83	81	81
9	81	79	79
10	78	73	78
24	74	56	45

*Mean of 3 assessments on each of 5 leaves (Appendix Table 3.9).

species usually has only one germ-tube whereas the others have 2-3 germ-tubes, usually at opposite ends of the conidium.

A microscopic examination of leaves subjected to impacting drops showed that most of the conidia retained had germinated, indicating the adhesive nature of the germ-tubes. However, there was also evidence of some damage with exudation of the contents of some conidia (Plate 7) and in some instances remnants of germ-tubes and appressoria with no conidia attached.

The latter phenomenon was studied quantitatively. Inoculated barley, pea and rose leaves were incubated at 20° for 24h when germination of conidia was assessed on half of them. The other leaves were subjected to the standard treatment of twenty, 4 mm drops from 2.5 m. The assessment of germination and damage are shown in Table 3.10.

The results again show that E.graminis conidia are more vulnerable to impacting water drops compared to other two mildews. The germ-tubes tend to adhere to the leaf surface, probably by appressoria, and withstand the impaction of water.

(iii)

The immediate and long term reflects of impaction of water drops on young colonies were next examined. In the first instance mildew colonies were allowed to develop to

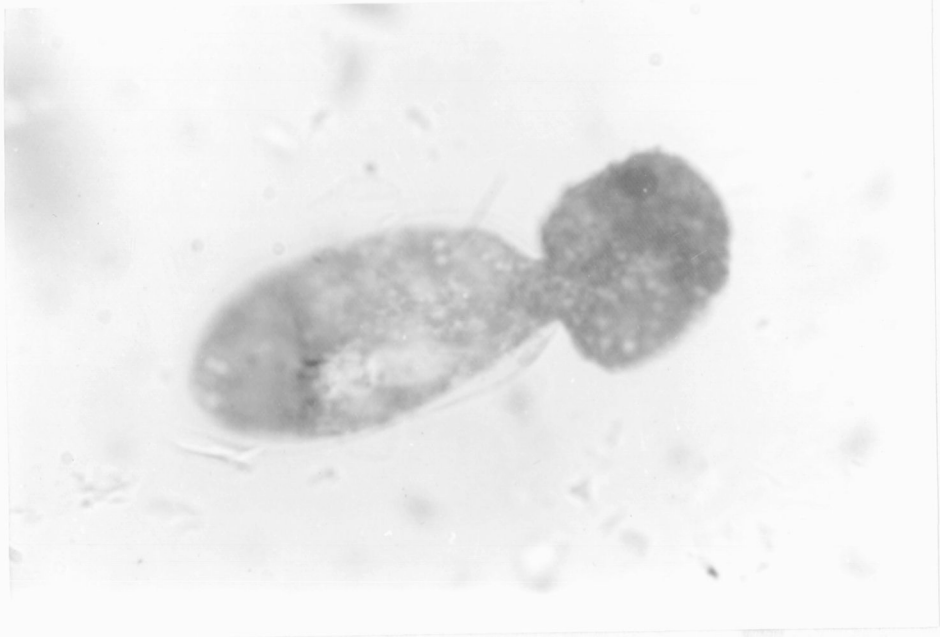


Plate 7 Exudation of contents of conidia of E.graminis caused by impacting water drops (x 1000).

Table 3.10 Damage to germinating conidia by impacting water drops applied 24h after inoculation.

	*Conidia/mm^2 leaf		
	E.graminis	E.pisi	S.pannosa
Control:			
Ungerminated conidia	37	22	23
Germinated conidia	96	119	57
Total	133	141	80
Treated:			
Ungerminated conidia	0	0	0
Germinated conidia			
(i) conidium intact	43	76	42
(ii) conidium removed	37	33	10
Total	80	109	52

*Mean of 3 assessments on each of 5 leaves (Appendix Table 3.10).

various stages, they were subjected to water drops and the resulting damage was assessed immediately by comparing the total mycelial length of 25 colonies with that of a similar number on untreated leaves. Table 3.11 shows the results of such an experiment.

In absolute terms the amount of mycelium lost increased with colony size but after 24h the proportion lost, relative to the control varied with the mildew involved. Thus with E.graminis some 40-45% mycelium was lost compared with 30-38% for E.pisi and S.pannosa. This difference may reflect the frequencies with which appressoria are formed along the respective mycelia. Until 24h apparently no mycelium of E.graminis was removed, probably because the short, single germ-tube allowed the conidium to break away clearly when impacted with water drops. With other two mildews, the presence of 2-3 germ-tubes probably made mycelial growth as such more vulnerable to the detachment of the conidium.

Some of the effects of water drops were examined microscopically and are illustrated in Figs. 3.3-3.5. In many instances the parent conidium appeared more vulnerable than the rest of the colony though often mycelia became detached and aggregated into clumps.

To examine the long term effects, inoculated leaves were subjected to water drops at 24, 36, 48 and 60h after inoculation and, after air drying were re-incubated.

Table 3.11 Direct effects of impacting water droplets on mycelial growth.

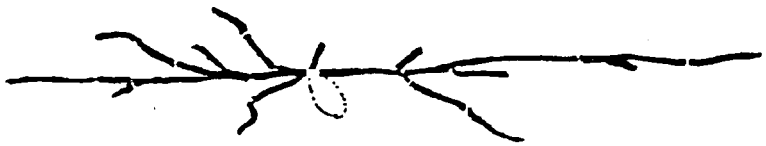
Mildew	Hours between inoculation and impaction	*Mycelial length (mm)		Mycelium lost(mm)	as % of control
		T	C		
E.graminis	24	0.03	0.03	0.0	0
	36	0.76	1.36	0.60	44
	48	1.41	2.36	0.95	40
	60	2.92	5.34	2.42	45
E.pisi	24	0.28	0.31	0.03	10
	48	1.67	2.41	0.74	31
	72	4.48	7.28	2.80	38
S.pannosa	24	0.37	0.39	0.02	5
	36	0.92	1.45	0.53	37
	48	1.80	2.70	0.90	33
	60	4.91	6.97	2.06	30

T - treated, C - control

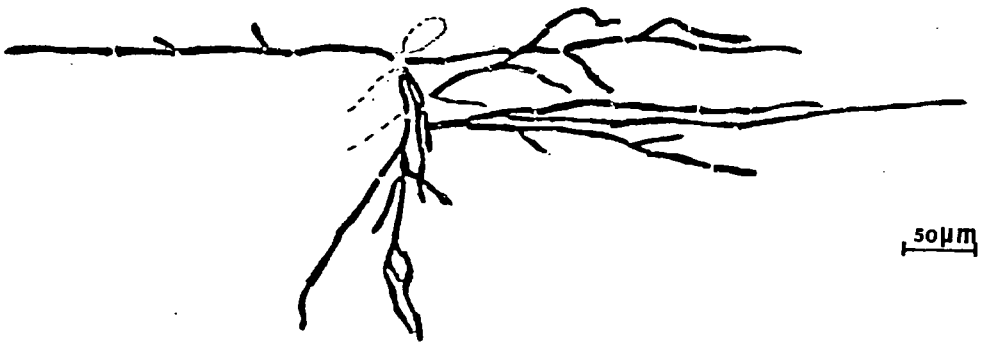
*Mean of 25 colonies (Appendix Table 3.11).

Fig. 3.3 Camera lucida drawings of the various stages of development of E.graminis showing damage caused by impacting water drops (broken lines indicate areas affected).

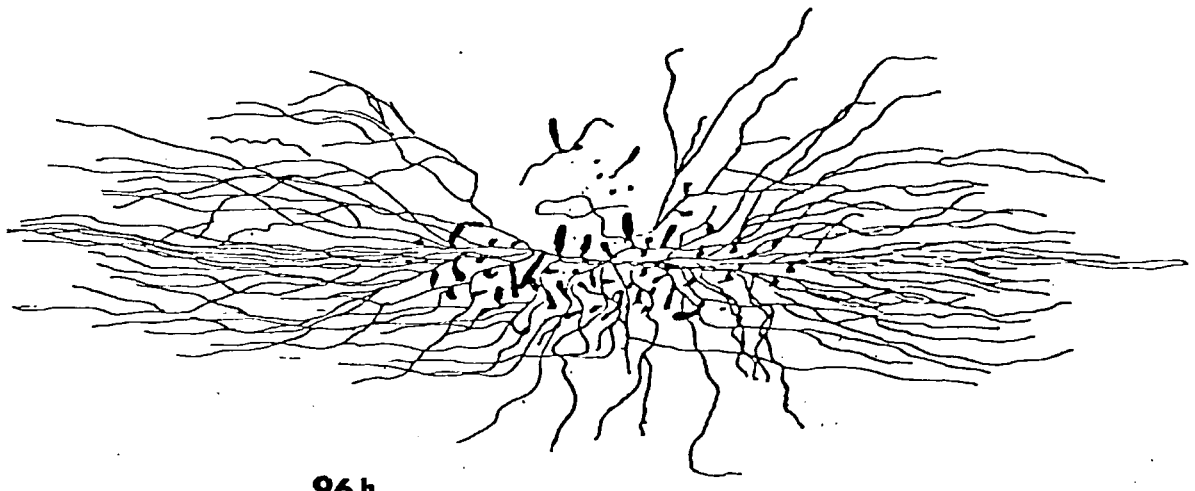
6h 24h 30h



36h



48h



96h

Fig. 3.4 Camera lucida drawings of the various stages of development of E.pisi showing damage caused by impacting water drops (broken lines indicate areas affected).

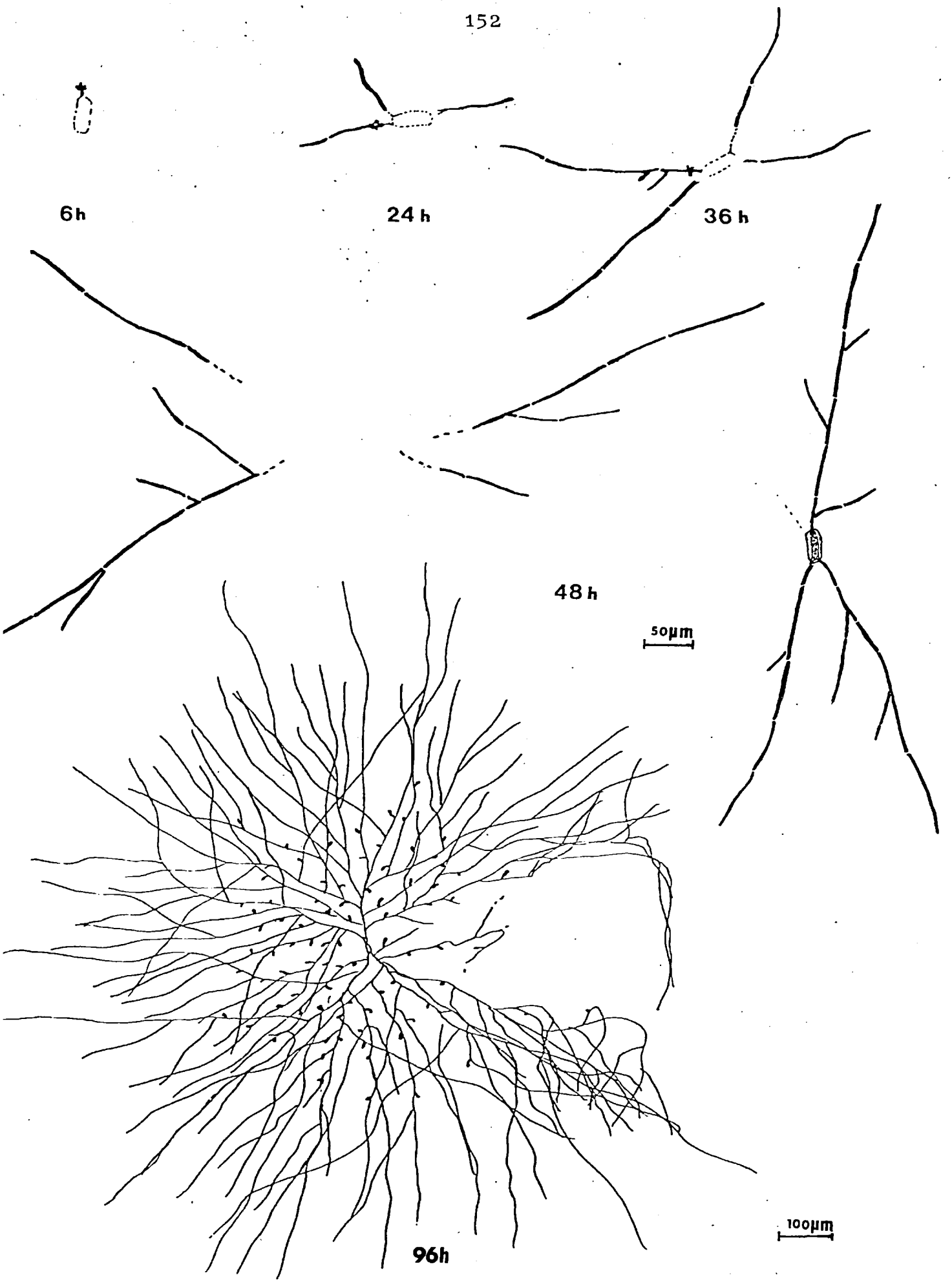
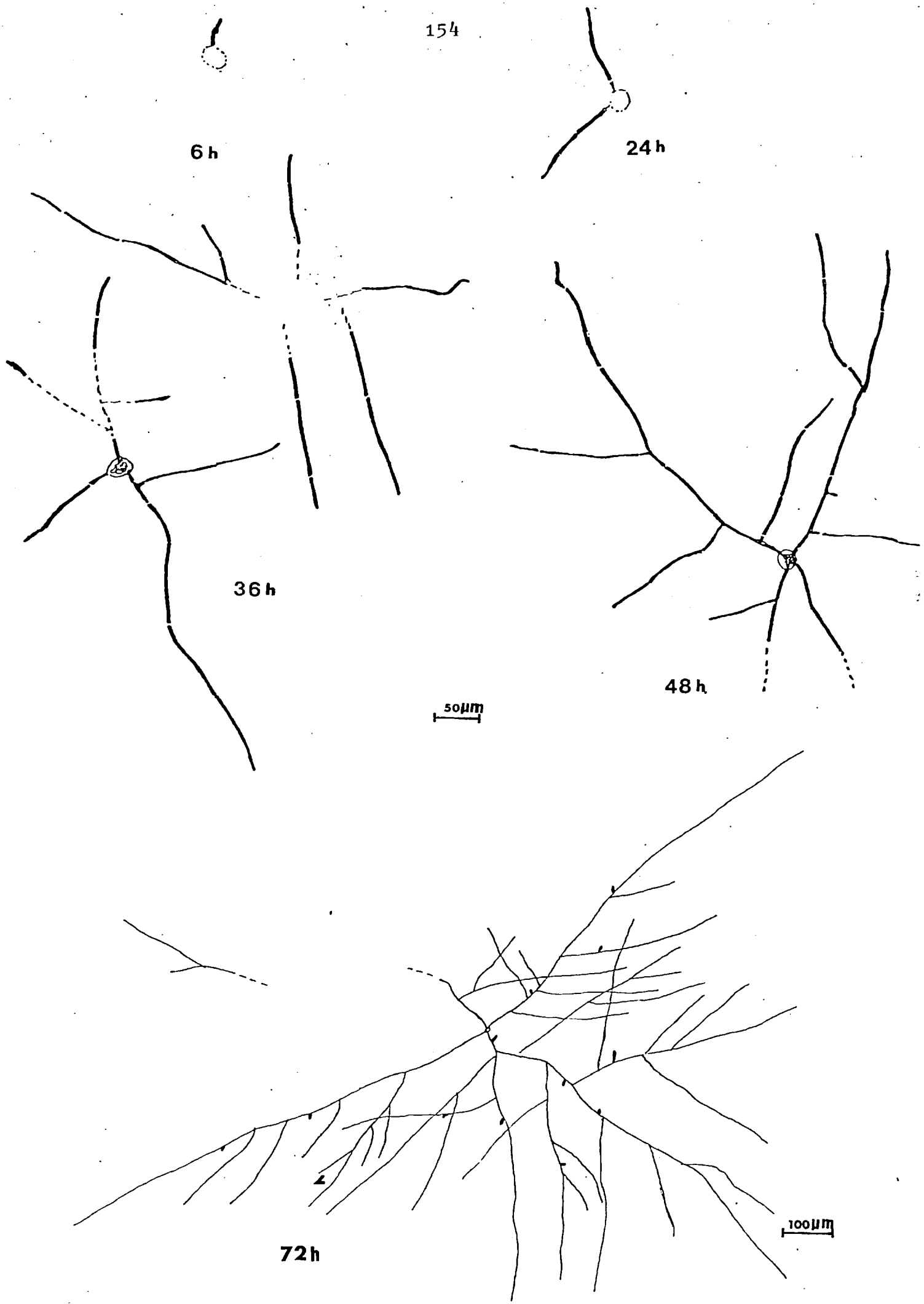

6h
24 h
36 h
48 h
50µm
96h
100µm

Fig. 3.5 Camera lucida drawings of the various stages of development of S.pannosa showing damage caused by impacting water drops (broken lines indicate areas affected).


6h
24h
36h
48h
50µm
72h
100µm

Mycelial growth on these and appropriate controls was assessed at 60h or 72h after inoculation. The results (Table 3.12) suggest that more damage is caused by water drops 24h after inoculation than is apparent from the previous table (3.11, p.148). Thus on inoculated leaves treated at 24h and then re-incubated for a further 36h, the reduction in mycelial growth was c. 70% for all three mildews, whereas the direct effects were assessed as nil, 10 and 5% reduction for E.graminis, E.pisi and S.pannosa respectively (Table 3.11). Similar comparisons for periods after 24h also suggest that the damage to E.pisi and S.pannosa is more extensive than immediate observations indicate, whereas with E.graminis they reflect more accurately the true position. Generally, the effects were proportionally less severe with increasing age of the colony.

Similar experiments were carried out to study the direct and indirect effects of impacting water drops on conidiophore development. In the first of these, inoculated leaves were treated at 24, 36, 48, 60, 72 and 96h after inoculation and the number of conidiophores per mm^2 was assessed on all treatments at 96h. The results (Table 3.13) show that the direct effects of impaction of water drops (at 96h) were most severe with S.pannosa. Conidiophores of this fungus tend to develop over the entire colony surface and this probably increases the chances of them being hit by a succession of impacting drops. With the other two

Table 3.12 Indirect effects of impacting water droplets on mycelial growth.

Hours between inoculation and impaction	Growth assessed	Reduction in mycelial length (as % of control)		
		E.graminis	E.pisi	S.pannosa
24	60	69.1	69.2	71.0
36	60	44.6	42.4	58,8
48	60	28.4	50.4	47.8
60	72	-	53.8	-

Detail results are given in Appendix Table 3.11.

Table 3.13 Direct effects of impacting water droplets on conidiophores at 96h.

Mildew	*Conidiophores/mm^2 colony		Reduction in conidiophore no. (as % of control)
	T	C	
E.graminis	57	77	26.9
E.pisi	83	138	39.9
S.pannosa	25	58	56.9

T - treated, C - control

*Mean of 15 replicates (Appendix Table 3.12)

mildews, especially E.graminis, conidiophores are produced at the cetre of colonies and possibly relatively fewer drops reach this particular area. With all three mildews, the indirect effects on conidiophore production of impacting water, especially early in the life of the colony (24 and 36h) are well marked (Table 3.14). Some of this may reflect a delay in the recovery of mycelial growth.

This study was completed by observing the impaction of water drops on 7-8 day old, sporulating colonies of the three mildews. Usually when leaves just inoculated with conidia or leaves with very young colonies were treated, the impacting water drops rolled over them because of the non-wettable surface and in doing so dislodged conidia. With sporulating colonies, it was different. The first drop by its impaction caused conidia to be released but then wetted the colony. Subsequent drops shattered on impact on this water film into smaller drops and mature conidia were soon removed. This left only the conidiophore of E.pisi or broken conidial chains of E.graminis and S.pannosa.

(iv)

The final series of experiments examined the effects of naturally occuring rain on pea plants inoculated with E.pisi and on field grown roses at Silwood Park during an epidemic of S.pannosa.

Table 3.14 Indirect effects of impacting water droplets on conidiophores.

	Hours between inoculation and impaction					
	24	36	48	60	72	96
E.graminis						
Conidiophores/mm^2*	27	32	39	42	47	57
Reduction(% control)	65	58	49	46	39	26
E.pisi						
Conidiophores/mm^2*	39	57	73	78	78	83
Reduction(% control)	72	59	47	44	44	40
S.pannosa						
Conidiophores/mm^2*	15	21	22	26	30	25
Reduction(% control)	74	64	62	55	48	57

*Assessed at 96h (Appendix table 3.12)

(a) E.pisi/pea

Pea plants, raised singly in 7.5 cm pots in J.I. no.1 compost, were maintained in an 'open' glass house where they were exposed to the natural environment but not rain. Seed was sown so that a succession of 2 wk-old plants were obtained that could be inoculated with E.pisi on both leaf surfaces, thus providing plants with different stages of mildew development on any one day. On 16 September 1980, a batch of such plants were placed outdoors for 24h and were exposed to 9.6 mm rain. The plants were returned to the glass house, their leaf surfaces were allowed to dry and mildew development on both surfaces of uppermost leaves was compared with that on plants that were not exposed.

The assessments were:

(i) No. conidia/mm^2 leaf on plants inoculated on the day with rain (0h) and on previous day (24h)

(ii) Germ-tube or mycelial length of colonies on plants inoculated 24, 48 and 72h before the day with rain

(iii) Conidiophores/mm^2 colony on plants inoculated 4 days or 5 days before the day with rain

The results for exposed plants are summarized in Table 3.15 as percetages of the appropriate controls to allow for the differences in inoculum. Conidia were completely removed from the upper leaf surface of plants inoculated immediately before exposing them to rain but c. 34% of the

Table 3.15 Effects of rain on E.pisi.

Growth stage	Rain applied (h after inoculation)	Reduction (as % of control)	
		upper surface	Lower surface
(a) *Conidia/mm^2 leaf	0	0	34
	24	22	86
(b) *Germ-tube(µm)	24	44	88
(c) *Total mycelium(mm)	48	50	91
	72	43	97
(d) *Conidiophores/ mm^2 colony	96	42	88
	120	59	97

*Figures are based on counts of conidia in 15 areas, germ-tubes of 25 conidia, total mycelial length of 15 colonies and no. conidiophores in 25 areas.

conidia were retained on the lower surface. With plants inoculated 24h earlier, c. 22% of the conidia were retained on the upper surface and c. 86% on the lower surface.

This substantial retention of conidia on the lower leaf surface is paralleled in the results for mycelial growth. While some 43%-50% of the mycelium was lost from the upper surface when exposed to rain, most of the mycelium on the lower leaf surface was retained.

The effects on conidiophore production were similar. On the lower leaf surface this was this was relatively little affected compared with that on the upper leaf surface. Plates 8 and 9 illustate visually some results of exposing infected plants to this amount of rain.

(b) S.pannosa/rose

A few rose bushes within a planting of the cultivar Frensham were protected from rain by covering them with transparent, corrugated sheets, 1.5 m above ground level. Other marked bushes were designated controls.

Initially the number of conidia deposited on leaves was examined. From 1 August 1980, five leaflets were taken daily at random from the last fully expanded leaves of both protected and exposed bushes and the number of conidia per mm^2 leaf was assessed from celloidin peels of the upper leaf surface. Usually the samples were taken in the afternoon.

Plate 8 Damaging effect of rain on colonies of E.pisi on pea seedlings, A - exposed to rain, B - protected from rain and C - uninoculated control.

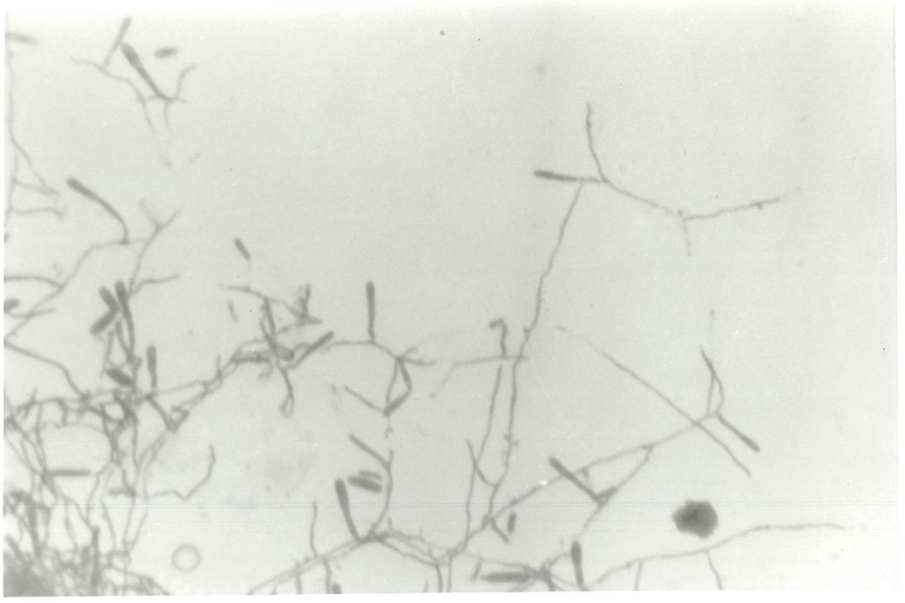


Plate 9 A portion of colony of E.pisi showing damages to mycelia and conidiophores (x 100).

The counts obtained in relation to rainfall (Fig.3.6) clearly show the washing effect of rain in removing conidia from the leaves.

Subsequently, the development of mildew was studied on four separate days, two of which immediately followed days with rain and two followed dry days. On each occasion, leaflets were sampled from both protected and unprotected bushes. Celloidin peels were taken from both leaf surfaces on which the following measurements were made; number of conidia deposited, no. of germinated conidia, mycelial length of colonies and conidiophore production. The results are shown in Fig. 3.7. On days following rain there were fewer conidia remaining on the leaves, fewer conidia have germinated and both mycelial length and sporulation were reduced. Plates 10 , 11 and 12 show some of the effects of rain on S.pannosa.

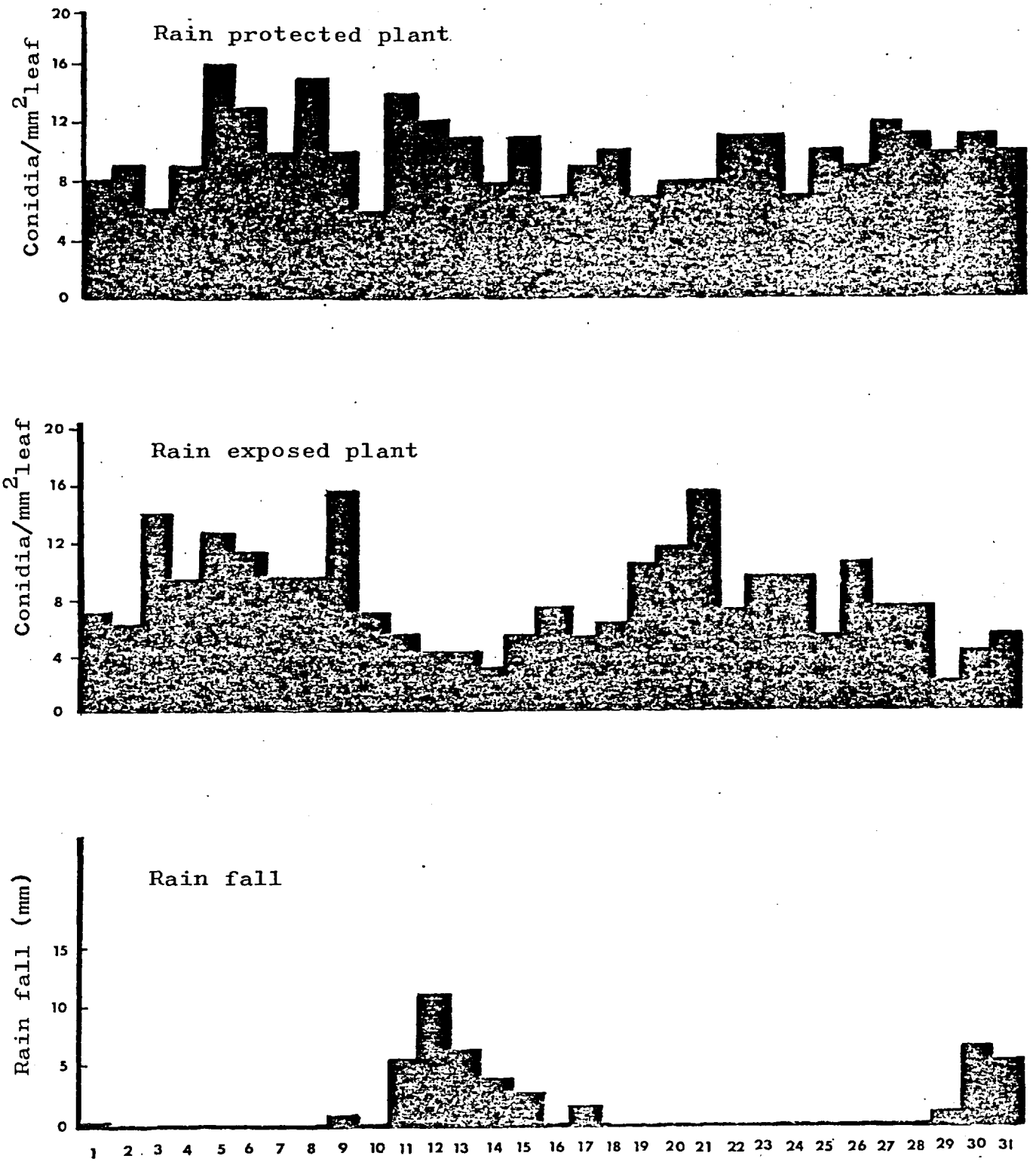


Fig. 3.6 Daily deposition of conidia of S.pannosa on rose leaves(Frensham) in relation to rain fall.

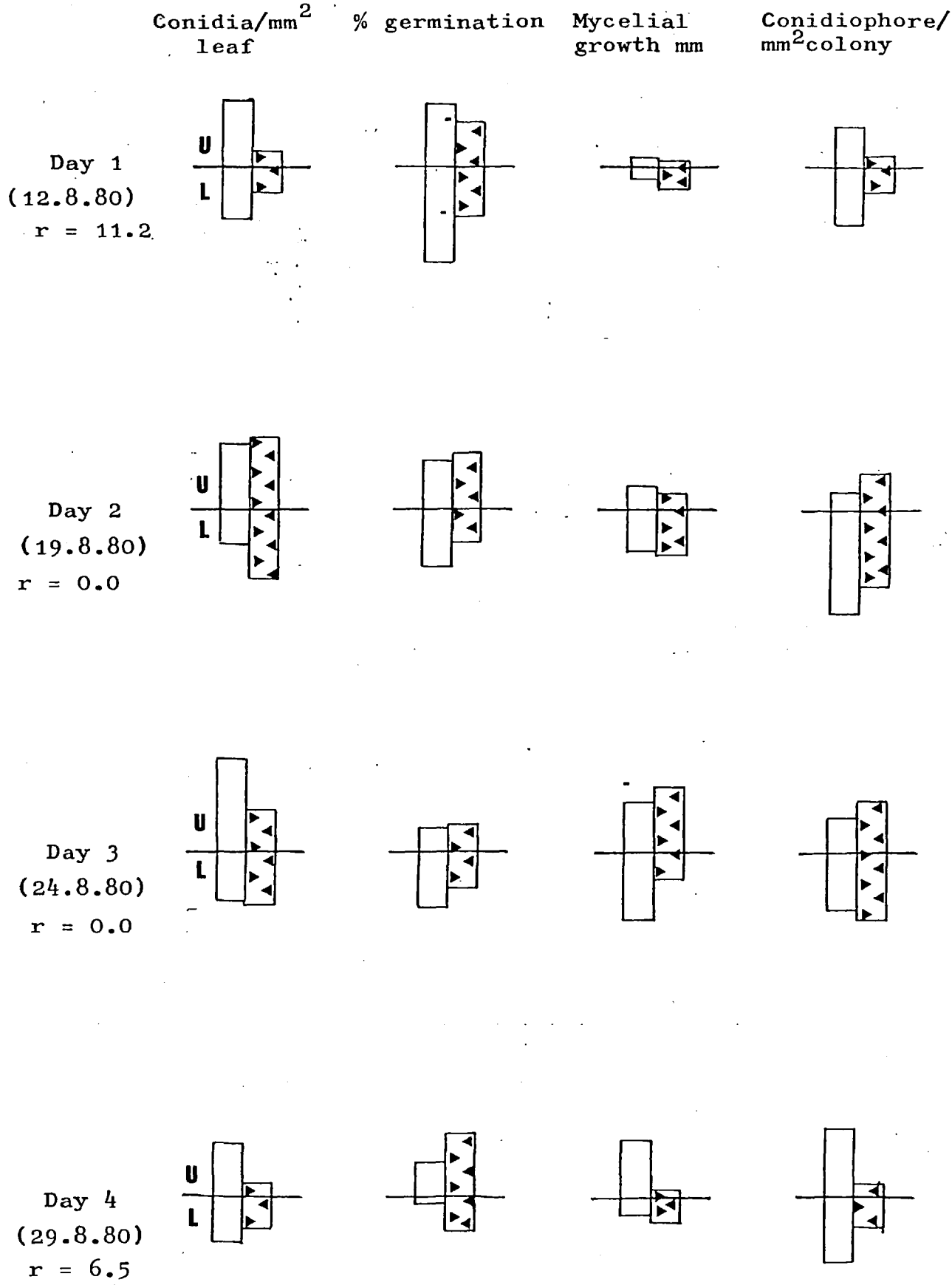
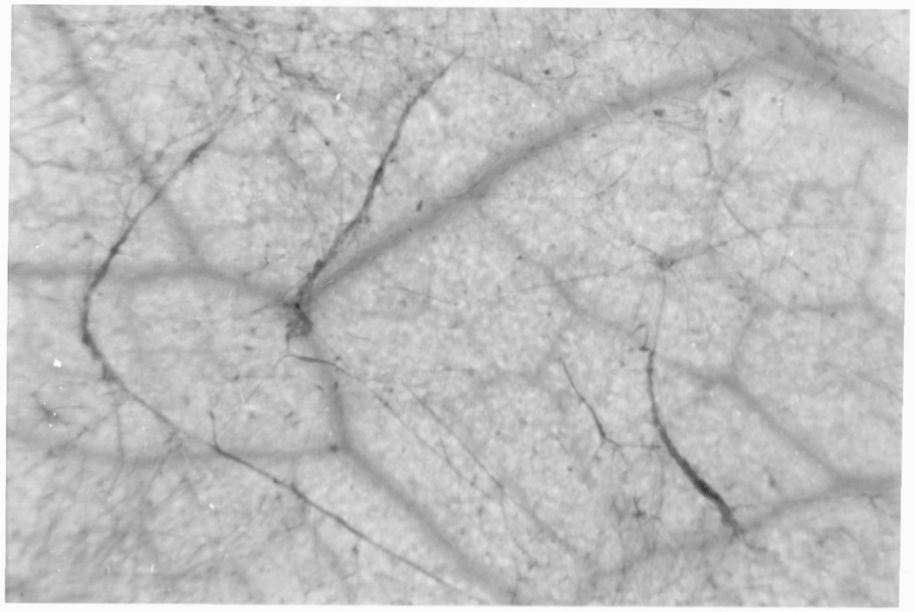


Fig. 3.7 Effect of rain on the development of S.pannosa on rain protected ▭ and rain exposed ▶◀ rose plants. U - upper and L - lower leaf surfaces. r = amount of rain on the day preceeding the day of assessment.

Plate 10 Effect of rain on S.pannosa on rose leaves. A and B - lower and upper surfaces of rain exposed plants, C and D - upper and lower surfaces of rain protected plants (note the low intensity of mildew on B).



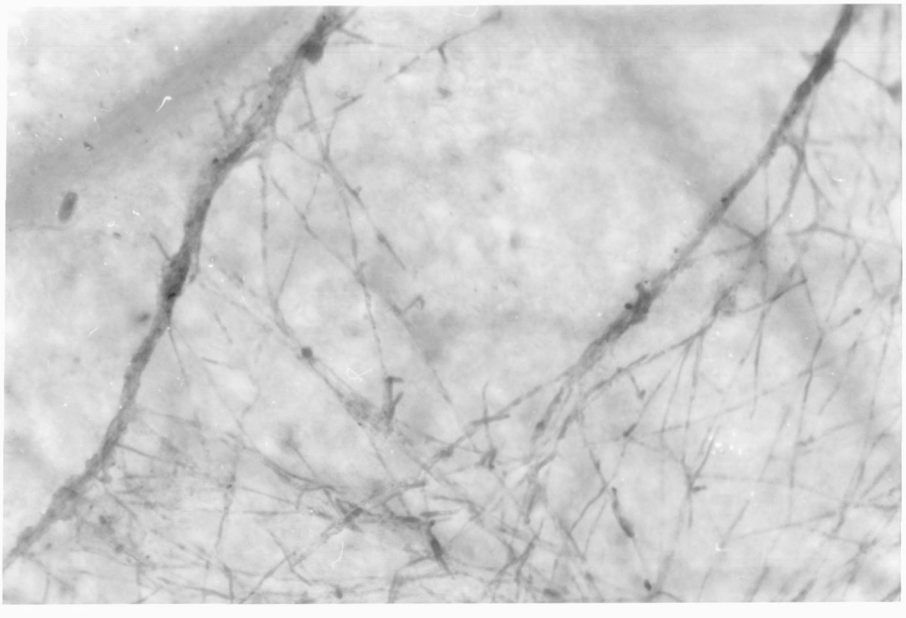


Plate 11 Effect of rain on S.pannosa. Note the aggregation of detached mycelia caused by impacting rain drops (x 100)
Plate 12 same as above (x 400).

IV. MILDEW GROWTH ON WASHED LEAVES

Rain washing over leaves removes materials from the leaf surface and this has been shown to affect the growth of Erysiphe cruciferarum on swede (Purnell & Preece, 1971) and Podosphaera clandestina on hawthorn (Khairi & Preece, 1979). The effects on mildew growth of washing leaves of barley, pea and rose before inoculating them with their respective mildew fungi was examined in the following experiment.

Plants of the three hosts in pots (p.124) were subjected to simulated rain for 1h and then dried under a fan. Leaf segments or discs cut from these plants together with similar materials from unwashed plants were inoculated with conidia and mildew development from conidial germination to conidiophore production was assessed.

The germination of conidia was similar on washed and unwashed leaves (Table 4.1), but subsequently there were differences in growth which varied with the mildew species. Germ-tube growth at 24h of E.graminis and E.pisi were very much reduced on washed leaves of barley and pea whereas that of S.pannosa on washed rose leaves increased. The values were significantly different from those on unwashed leaves. At 48h mycelial growth of E.graminis was significantly less on washed barley leaves, but mycelial growth of E.pisi and S.pannosa was significantly greater on washed leaves of

Table 4.1 Mildew growth on washed (W) and unwashed (UW) leaves.

		E.graminis	E.pisi	S.pannosa
(a)% germination* at 24h	W	78.6	84.6	66.9
	UW	80.3	88.4	69.2
(b)Germ-tube growth* (µm) at 24h	W	34 } sig.	53 } sig.	73 } sig.
	UW	44	67	56
(c)Mycelial growth* (mm) at 48h	W	1.58 } sig.	3.10 } sig.	3.36 } sig.
	UW	2.30	2.28	2.65
(d)Conidiophores/mm^2* colony at 96h	W	37	59 } sig.	19
	UW	39	41	13

*Figures are means of 10 replicates (germination), 25 germinated conidia (germ-tube), 25 colonies (mycelial length) and 15 replicates (no.conidiophores).

sig.- means differ significantly ($P \leq 0.05$)

pea and rose respectively. At 96h more conidiophores of E.pisi were produced per mm^2 colony on washed pea leaves than on unwashed ones but E.graminis and S.pannosa produced similar amounts on both types of leaf.

V. EFFECTS OF WATER STRESS ON MILDEW DEVELOPMENT

Recent investigations indicate that powdery mildews develop more slowly on water stressed plants. Thus Ayres (1977) found that there was less growth of E.pisi on water stressed pea leaves and Ayres & Woolacott (1980) showed that germination of E.graminis and elongation of secondary hyphae were inhibited on water stressed barley especially on adult plants. The experiments in this section determined the effect of water status of the host on the development of E.graminis on barley (cv. Zephyr), E.pisi on pea (cv. Kelvedon Wonder) and S.pannosa on rose (cv. Perle d' Alcanada).

These plants were grown in pots as described previously and additionally, barley and pea plants were grown in nutrient solution (Hewitt, 1966). Water stress was achieved by not watering potted plants or by replacing nutrient solutions with polyethylene glycol 4000 (PEG) in amounts determined from the calibration curves of Lowlor (1970). Water potentials of excised leaves were determined in a pressure bomb (Scholander et al., 1965). Samples were removed when mildew was assessed and during the middle of the light period.

The effect of water stress on conidial germination was examined first. With plants grown in compost, water stress was imposed by stopping watering at different times prior

to inoculation. Nutrient solutions were replaced by various strengths of PEG, 24h before inoculation to allow equilibration. After inoculation, plants were kept for 24h at 20±3°, then samples were taken to assess germination and leaf water potential. Germination was similar at all levels of water stress that were obtained (Table 5.1).

A similar experiment investigated the growth of mycelium 48h after inoculation. Watering of plants in pots was stopped as before but nutrient solutions were replaced by PEG 24h after inoculation. The results (Table 5.2) clearly indicate a decrease in the amount of hyphal growth as leaf water potential decreased. At low water potentials most germinated conidia ceased to grow and only a few grew to small colonies.

There was a parallel decline in conidiophore production, assessed at 120h after inoculation (Table 5.3). A final experiment examined the infectivity of conidia produced on water stressed plants. Mildews were allowed to develop and sporulate on plants and water stress was imposed 6 days after inoculation. Old conidia were removed by shaking the plants and 24h later they were used as source of inoculum for leaf segments and discs cut from plants under a normal watering regime. This leaf material was incubated at 20° for 48h when the number of conidia producing ESH was determined to

Table 5.1 Effects of water stress on germination of conidia at 24h after inoculation.

A. Plants in pots (water stress by cessation of watering)

E.graminis

Leaf water potential (bar)	-2.8	-6.2	-7.9	-9.0	-14.1
% germination*	78.7	74.6	77.7	75.9	76.9

E.pisi

Leaf water potential (bar)	-4.8	-6.9	-9.7	-10.7	-12.4
% germination*	90.9	92.4	92.7	93.2	91.6

S.pannosa

Leaf water potential (bar)	-3.5	-4.9	-6.7	-9.3
% germination*	71.3	69.8	67.2	69.3

B. Plants in nutrient solution (water stress by PEG)

E.graminis

Leaf water potential (bar)	-2.1	-4.1	-5.2	-7.2	-11.4
% germination*	80.5	83.0	82.1	84.2	80.0

E.pisi

Leaf water potential (bar)	-3.8	-5.5	-6.9	-9.3	-11.0
% germination*	94.1	94.8	93.8	93.5	92.0

*Figure is the mean of 10 replicates of 100-200 conidia (Appendix Table 5.1)

Table 5.2 Effects of water stress on mycelial growth at 48h after inoculation.

A. Plants in pots (water stress by cessation of watering)

E.graminis					
Leaf water potential (bar)	-2.8	-5.2	-7.2	-9.7	-12.9
Total mycelial length (mm)*	2.61	2.08	1.52	0.72	0.51
E.pisi					
Leaf water potential (bar)	-3.8	-5.9	-8.3	-10.3	-12.4
Total mycelial length (mm)*	2.53	2.01	1.60	0.96	0.64
S.pannosa					
Leaf water potential (bar)	-1.7	-4.5	-6.2	-9.1	
Total mycelial length (mm)*	1.85	1.62	0.94	0.59	

B. Plants in nutrient solution (water stress by PEG)

E.graminis					
Leaf water potential (bar)	-1.1	-4.3	-7.1	-9.7	-13.3
Total mycelial length (mm)*	2.09	1.66	1.35	0.82	0.57
E.pisi					
Leaf water potential (bar)	-3.5	-6.2	-7.6	-8.6	-12.1
Total mycelial length (mm)*	2.45	2.27	1.58	1.10	0.44

*Figure is the mean of 25 colonies (Appendix Table 5.2)

Table 5.3 Effects of water stress on conidiophore production at 120h after inoculation.

A. Plants in pots (water stress by cessation of watering)

E.graminis

Leaf water potential (bar)	-2.1	-3.1	-5.2	-6.6	-8.3
Conidiophores/mm^{2}colony*	52	38	32	15	5

E.pisi

Leaf water potential (bar)	-1.4	-5.5	-9.7	-13.1	-13.8
Conidiophores/mm^{2}colony*	128	63	21	3	0

S.pannosa

Leaf water potential (bar)	-2.1	-5.2	-9.0	-11.4
Conidiophores/mm^{2}colony*	31	20	12	0

B. Plants in nutrient solution (water stress by PEG)

E.graminis

Leaf water potential (bar)	-2.1	-4.5	-5.2	-7.2	-10.3
Conidiophores/mm^{2}colony*	59	41	22	14	4

E.pisi

Leaf water potential (bar)	-2.4	-3.8	-9.0	-11.0	-15.2
Conidiophores/mm^{2}colony*	122	75	29	10	0

*Figure is the mean of 25 replicates (Appendix Table 5.3)

measure infectivity. The results (Table 5.4) showed that conidia from water stressed and non-stressed plants had similar potentials for infection.

Table 5.4 Effects of water stress on the infectivity of conidia

A. Plants in pots (water stress by cessation of watering)

E.graminis

Leaf water potential (bar)	-3.2	-5.4	-8.0	-10.8	-14.3
% ESH*	60.5	60.3	58.4	57.1	56.0

E.pisi

Leaf water potential (bar)	-2.1	-4.0	-6.2	-8.4	-10.0
% ESH*	73.2	75.4	73.3	76.6	71.1

S.pannosa

Leaf water potential (bar)	-2.2	-5.2	-9.7	-12.9
% ESH*	61.1	58.9	54.4	54.4

B. Plants in nutrient solution (water stress by PEG)

E.graminis

Leaf water potential (bar)	-3.2	-6.3	-9.8	-12.1	-14.7
% ESH*	65.7	62.1	65.2	60.0	56.8

E.pisi

Leaf water potential (bar)	-1.7	-3.5	-8.3	-10.3	-13.4
% ESH*	74.6	75.6	77.2	78.4	78.2

*Figure is the mean of 10 replicates (Appendix Table 5.4)

DISCUSSION

Much of the controversy surrounding the effects of leaf surface wetness and rain on the development of powdery mildews stems from a lack of precise experimental data. The primary aim of this investigation was to provide such data.

It has been repeatedly emphasized that water is harmful to mildew conidia. The evidence in this investigation however, suggests that mildew conidia differ widely in their ability to germinate in water (Table 2.2). Germination of conidia in water is poor with a wide range of mildews and this contrasts markedly with the behaviour of other fungi, many of which require a film of water. Several suggestions have been made to explain the poor germination of powdery mildew conidia in water, including plasmoptysis, lack of oxygen, the leaching out of a self-inhibitor and increased hydration leading to disruption of the cell membrane and cytoplasm.

Although many workers have reported the occurrence of plasmoptysis, bursting of conidial wall was rarely observed in this study. Also,the fact that even the conidia floating on water in some mildew fungi germinated poorly suggests that lack of oxygen may not be the only factor that cause loss of germinability. There is no direct evidence here or elsewhere to support the possible role of a self-inhibitor.

As reported by some workers (eg. Zaracovitis,1964) changes

in the internal structure of the conidium were observed with many mildews when they were placed in water, the vacuoles coalesced and the contents became granular but the extent to which this occured varied. These events support the explanation given by Mitchell & McKeen (1970) for the collapse of conidia in water. Absorption of water causes uneven pressure by vacuoles of varying sizes which are separated only by thin strands of cytoplasm. They swell and break. This breaking up of vacuoles and subsequent dispersal of cytoplasmic fragments may be the cause for granular appearence of contents. Once the cytoplasmic integrity is lost, the conidium can not germinate. Somers & Horsfall (1966) provided evidence that conidia of E.graminis from oat were more effective than those of E.cichoracearum from squash in both sorbing and retaining water. Such differences might affect their response to water and thus partly explain the different levels of germination obtained in the presence of water with conidia of various mildew fungi. It might also partly explain the relatively higher levels of germination on water than in water.

Indeed, conidia of many mildews germinate well on water. In this respect the water may only be providing a surface and contact because of the relative non-wettability of the conidium, may be minimal. Also, there is a tendency for the germ-tubes to arise vertically away from the water. This or the nature of the surface does not provide the right stimulus for appressoria formation.

The fate of conidia on leaves depends in part on the wettability of leaves and the ways in which these become wetted. Dews or fine rain result in deposition of small droplets in which some conidia will become embeded or will float. They will either be rendered non-viable or will germinate abnormally and exhaust their food reserves without forming appressoria that are necessary pre-requisites for infection. Thus claims that dews increase mildew intensity (eg. Peries,1973) seem inappropriate.

Water deposition immediately after inoculation causes more drastic reduction in mildew, a finding in this investigation agrees with that of Perera & Wheeler (1975). However, when the water droplets evaporate the conidia could be lowered to the surface of leaves and become dried. Schnathorst (1958) suggested that these conidia would eventually infect leaf tissue. Evidence in this investigation supports his view. The results of experiments (Tables 2.4-2.7) show that conidia do not lose their ability to germinate or infect leaves entirely when they are kept on or in water. They can grow on leaves, although more slowly, when they are transferred from water. This largely depends on the length of time the conidia are in contact with water and the extent to which mildew conidia respond in this way varies with species. For those mildew conidia that are readily affected by water even relatively short periods of exposure may be sufficient reduce germination. eg. E.graminis (Fig. 1.4). Also, conidia are vulnerable to

impacting rain drops which rapidly removes them before they germinate (Table 3.1).

Although water affects the germination process, experimental evidence using E.graminis shows that successful infections by conidia suspended in water can be obtained if such a suspension is used soon after preparation. However, the infectivity will drop sharply if inoculation is delayed (Fig. 2.5). In this connexion the observations agree with those of Yarwood (1978b). The failure to obtain infection by aquous suspension of conidia of Leveillula taurica on pepper by Reuveni & Rotem (1973) might be due to the greater sensitivity of this fungus to water.

Once conidia have germinated the effects of water films appear to be less drastic (Table 1.4) provided that they are not too prolonged. Indeed, there is some evidence that once dry again, mycelial growth might be even enhanced (Figs 1.7-1.9 and 2.9). This apparent stimulatory effect caused by water might partly provide explanation for the positive correlation in intensity of Sphaerotheca fuliginea with periods of leaf wetness as observed by Reuveni & Rotem (1974) and stimulation of growth of this fungus by exposing it to water (Yarwood, 1978a). However, the claim made by Yarwood (1978a) that submerging an inoculated leaf immediately after inoculation enhanced mildew development seems unacceptable, as conidia could be removed during immersion (Table 2.8).

Impaction of water at the early growth stages appears

generally to be adverse since it involves the physical removal of the conidium and some of the ESH (see Tables 3.9 and 3.11). The extent of damage appears to depend on the form of the early growth. Thus with E.graminis the conidia usually possess s single germ-tube at 24h which could be removed easily by impacting drops whereas the conidia of E.pisi and S.pannosa are held more firmly by 2-3 germ-tubes. However, the proportion of germ-tube lost during such impaction appears to be more in E.pisi and S.pannosa (Table 3.11).

The effect of water films on later mycelial development to conidiophore initiation is mainly one of slowing growth but development otherwise proceeds normally. Strikingly, development can occur, though more slowly, on leaves immersed in water. Although the system is a purely artificial one it raises interesting questions such as how the fungus succeeds in growing at all in a system where oxygen might be thought limiting. It also suggests that the adverse effects of water on powdery mildews have been over emphasized.

Conidiophore production and formation of conidia appear to be the other stages of development which are most adversely affected by water either as films or as impacting rain (see Tables 1.12 and 3.13). Conidiophores as erect structures could be easily detached by rain drops.

Water films causes adherance of conidiophores and conidial chains (Plate 1) thus preventing the release of conidia. However, the wetted colonies could resume to normal sporulation by about 72h after wetting (Table 1.13). The effect of impacting drops on conidial release seems to be more pronounced. Thus sporulating colonies that are hit by rain fail to sporulate normally even after 72h (Table 3.5). There is thus a loss of conidia and a delay before a colony again becomes productive.

Rain washing of leaves prior to inoculation also affects mildew development. The effect could be due to interaction of substances on washed leaves as proposed by Khairi & Preece (1979) or it could be due to an enhanced flow of nutrients caused by removal of surface waxes. The effect of these factors might be responsible for the differing ability of germ-tube growth and mycelial extension of E.graminis, E.pisi and S.pannosa on washed leaves (Table 4.1).

While many of the effects of rain appear to affect mildew adversely, in the field these effects may be partly offset by the development of pustules on the lower leaf surface where they are protected and by the enhanced growth in periods of high humidity following rain. Indeed, intermittent periods of light rain may overall be beneficial. Long periods without rain which might impose water stress on the host might be detrimental since all experiments on

water stress indicated, like those of Ayres (1977) and Ayres & Woolacott (1980) a reduction in mildew growth on stressed plants.

In many instances, the effects of leaf surface wetness and rain on mildew development are less drastic than might have been supposed and the role of these factors in the epidemiology of powdery mildews needs to be re-appraised.

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Appendix Table 1.1 Effect of 6h wet period applied immediately after inoculation on the development of E.graminis.

1.% germination(24h)

	1	2	3	4	5	6	7	8	9	10	Mean(S.E) $t_{.05}$
T	28.3	28.2	40.3	28.7	47.8	44.4	26.7	36.1	24.1	19.3	32.4(4.1)
C	69.3	75.0	73.6	75.2	68.1	66.4	65.2	61.8	68.6	68.5	69.3(1.9)

2.Total mycelial growth(mm)(48h)

TL1	1.20	1.10	1.15	0.70	1.40	1.65	1.15	1.75	1.80	1.55	
L2	1.10	1.30	1.15	1.10	1.15	0.85	1.35	1.05	1.30	1.10	
L3	2.00	2.05	1.50	1.55	1.35	1.10	1.00	1.05	1.50	2.10	
L4	1.45	0.45	1.75	0.90	0.55	0.70	1.60	0.75	1.95	1.30	
L5	1.60	1.95	1.20	2.15	0.80	1.80	1.95	1.00	0.40	1.10	1.31(.13)
CL1	1.75	2.25	2.30	2.50	2.05	1.90	1.90	1.80	2.55	2.90	
L2	1.65	1.80	2.45	1.50	1.85	1.60	2.30	1.85	1.45	2.65	
L3	3.65	2.55	1.70	2.10	2.95	3.00	2.45	1.30	1.65	2.20	
L4	2.25	2.25	2.30	1.85	2.50	1.85	3.30	1.80	1.70	2.45	
L5	1.50	2.15	2.30	1.85	2.15	2.50	2.50	0.75	2.35	2.10	2.14(.15)

3.Conidiophore production(72h)

TL1	a	.69	.90	.69	.66	.28	.49	.39	.42	.40	.36	
	c	13	8	18	41	28	14	6	19	24	20	
L2	a	.26	.32	.34	.62	.54	.39	.42	.48	.72	.29	
	c	39	4	21	19	34	23	20	4	21	16	
L3	a	.48	.52	.64	.39	.48	.50	.64	.38	.39	.42	
	c	17	8	20	13	36	24	23	16	37	11	
L4	a	.52	.60	.51	.44	.39	.74	.36	.52	.69	.60	
	c	20	14	10	23	13	26	39	8	16	10	
L5	a	.64	.72	.64	.53	.44	.60	.63	.70	.69	.70	
	c	6	10	25	42	18	40	42	9	28	10	20(6)
CL1	a	1.48	1.57	1.19	1.24	1.27	1.34	1.20	1.18	1.32	1.40	
	c	108	69	80	106	89	79	142	39	81	64	
L2	a	1.53	1.40	1.61	1.20	1.14	1.30	1.28	1.16	1.10	1.80	
	c	49	82	63	94	103	84	36	62	94	85	
L3	a	1.72	1.14	1.20	1.22	1.32	1.40	1.28	1.14	1.16	1.33	
	c	69	54	146	52	163	49	84	103	96	102	
L4	a	1.32	1.31	1.70	1.60	1.39	1.44	1.62	1.33	1.19	1.55	
	c	72	96	110	138	82	94	139	162	148	94	
L5	a	1.14	1.30	1.26	1.52	1.33	1.26	1.27	1.30	1.42	1.60	
	c	93	62	49	99	84	61	70	82	98	131	90(9)

Appendix Table 1.1 contd.

4.Conidiophores/colony(96h)

TL1	i	206,	172,	116,	268,	319,	392,	246,	268,	242,	246
	m	68	73	29	92	134	66	85	90	76	43
L2	i	349,	390,	214,	313,	370,	302,	143,	217,	282,	309
	m	114	48	28	72	120	54	128	110	80	80
L3	i	218,	213,	265,	290,	334,	206,	342,	305,	314,	163
	m	90	68	91	68	110	91	79	91	134	30
L4	i	310,	281,	332,	384,	293,	252,	264,	286,	363,	312
		98	86	85	93	128	63	83	112	76	88
L5	i	268,	294,	286,	318,	392,	197,	280,	343,	394,	380
	m	92	94	99	68	55	85	49	93	69	81

i 285(19)
m 83(7)

CL1	i	126,	139,	119,	208,	195,	210,	160,	183,	218,	260
	m	318,	211	193	278	325	264	292	320	383	260
L2	i	214,	119,	214,	219,	210,	242,	262,	196,	200,	213
	m	314	192	201	263	284	291	263	280	240	263
L3	i	273,	214,	208,	220,	245,	254,	243,	162,	181,	142
	m	241	330	233	280	114	139	263	291	243	301
L4	i	210,	239,	190,	188,	138,	137,	201,	167,	191,	140
	m	283	193	321	168	330	268	296	288	243	297
L5	i	178,	210,	195,	164,	151,	90,	143,	101,	163,	202
	m	153	291	192	280	314	138	283	204	211	178

i 189(12)
m 256(17)

T - treated, C - control, L1...leaf no.

a - area of colony(mm^2)

c - no.conidiophores

i - no.conidiophore initials

m - no.mature conidiophores

Figures in brackets are standard errors(analysis based on angular transformation of data for germination)

Appendix Table 1.2 Effect of 6h wet period applied 24h after inoculation on the development of *E.graminis*

1.Total mycelial length(mm)(48h)

			Mean(SE)
T	L1	0.72,1.32,1.01,0.70,0.46,0.68,1.42,0.61,0.56,0.66	
	L2	1.32,0.62,0.70,0.68,0.80,0.68,0.81,0.50,0.40,1.10	
	L3	0.95,1.10,1.21,0.80,0.62,0.83,1.13,0.35,0.55,1.45	
	L4	1.25,0.65,0.93,0.85,0.93,0.60,0.50,0.40,0.60,0.98	
	L5	0.68,0.93,0.53,1.28,1.10,1.26,0.92,0.62,0.91,0.84	0.83(.08)
C	L1	1.10,1.02,1.36,0.80,0.92,1.42,0.71,0.62,1.52,0.60	
	L2	1.34,0.68,0.92,0.52,0.70,1.10,1.28,1.34,1.72,1.60	
	L3	1.21,1.41,1.02,1.48,1.80,0.93,1.00,1.23,1.55,2.00	
	L4	1.53,0.90,0.98,1.13,1.53,1.10,0.53,1.35,1.30,1.35	
	L5	1.23,1.13,1.25,1.15,0.98,1.14,1.21,1.13,1.15,1.17	1.16(.09)

2.Conidiophore production(72h)

T	L1	a	.51	.87	.67	.48	.63	.38	.59	.72	.62	.90	
		c	10	8	3	25	5	6	9	4	3	9	
	L2	a	.61	.42	.81	.93	.43	.61	.52	.64	.74	.6	
		c	9	17	6	2	19	10	4	2	0	6	
	L3	a	.70	.39	.89	.55	.46	.38	.92	.64	.52	.80	
		c	26	12	14	17	6	2	0	17	4	2	
	L4	a	.59	.60	.72	.65	.63	.41	.72	.80	.53	.56	
		c	19	13	20	26	0	0	8	6	18	10	
	L5	a	.61	.54	.64	.50	.67	.72	.63	.81	.55	.48	10(2)
		c	28	21	33	6	19	3	4	2	19	4	
C	L1	a	.61	.94	.88	1.04	1.21	1.08	1.12	.72	.82	.94	
		c	68	44	36	22	21	36	14	21	46	28	
	L2	a	.64	.82	1.14	1.68	1.72	1.50	.92	.68	.72	1.2	
		c	34	56	10	26	12	24	10	18	3	16	
	L3	a	1.59	.62	.80	.69	.70	.72	1.42	1.20	1.60	.52	
		c	10	39	26	50	14	12	7	6	51	20	
	L4	a	.86	.93	1.21	1.60	1.20	1.10	.68	1.21	.80	.6	
		c	19	35	22	22	19	10	28	53	18	16	
	L5	a	1.12	1.80	1.60	.61	.71	1.20	1.00	1.02	.74	.84	21(5)
		c	24	51	20	13	46	68	33	27	14	37	

Appendix Table 1.2 contd.

3.Conidiophores/colony(96h)

T	L1	i	124,	171,	230,	141,	160,	146,	182,	122,	214,	226
		m	114	120	90	68	91	62	96	114	23	81
	L2	i	191,	127,	136.	194,	163,	138,	114,	98,	219,	180
		m	68	126	114	98	126	29	68	90	116	120
	L3	i	211,	240,	207,	227,	100,	132,	152,	103,	172,	168
		m	81	60	83	46	28	92	96	68	94	39
	L4	i	196,	231,	217,	211,	221,	116,	194,	128,	190,	226
		m	120,	72	91	80	106	46	88	43	82	80
	L5	i	147,	169,	190,	129,	213,	197,	94,	128,	211,	201
		m	92	68	110	90	58	79	80	124	146	93
C	L1	i	121,	136,	98,	126,	81,	134,	126,	198,	132,	69
		m	190	148	110	122	192	213	172	184	180	117
	L2	i	76,	122,	69,	157,	128,	148,	124,	86,	92,	60
		m	123	109	154	162	114	119	155	169	193	111
	L3	i	42	98,	119,	135,	182,	110,	142,	116,	149,	124
		m	126	159	181	130	170	210	164	175	121	130
	L4	i	128	81	72	122	114	160	183	130	193	103
		m	128	90	94	100	193	199	173	139	181	110
	L5	i	142,	99	189,	72,	89,	173,	91,	76,	67,	144
		m	126	132	158	105	160	149	122	140	129	176

i 172(12)
m 85(8)

i 119(11)
m 148(9)

4.Conidia/cm^2leaf(10^{-3})(120h)

T	L1	L2	L3	L4	L5
	4.4	5.0	6.3	6.4	4.2

C	L1	L2	L3	L4	L5
	12.6	11.0	9.3	10.4	11.2

T - treated, C - control, L1....leaf no.

a - area of colony(mm^2) c - no.conidiophores

i - conidiophore initials, m - mature conidiophores

Figures in brackets are standard error($t_{0.05}$)

Appendix Table 1.3 Effects of 6h wet period applied 48, 72 and 96h after inoculation on conidia production by E.graminis.

Time of assessment (h after inoculation)	Conidia x 10^{-3} /cm^2 leaf	
1.Wetted at 48h		
	Treated	Control
96	1.9,1.9,1.8,1.4.1.9	2.3,2.4,2.5,2.7,2.0
120	9.2,9.6,9.0,8.2,10.4	12.9,13.1,10.4,12.8,12.9
144	16.4,17.6,14.9,16.2,17.3	22.0,21.4,20.2,20.6,20.3
2.Wetted at 72h		
96	2.2,2.4,2.6,1.9,1.8	3.8,3.1,3.6,3.9,3.4
120	7.8,8.4,7.2,7.1,7.0	12.4,11.2,11.3,12.5,12.6
144	13.8,12.9,13.4,13.4,13.6	18.1,17.2,17.4,18.9,18.6
168	20.3,19.4,19.1,21.4,20.2	24.3,26.7,24.4,26.6,25.2
3.Wetted at 96h		
120	10.8,12.3,12.4,11.6,14.1	17.0,16.2,19.4,17.2,18.0
144	23.6,23.4,20.8,20.2,21.1	29.4,33.3,30.2,31.4,33.2
168	28.7,29.4,26.6,30.1,29.8	51.2,56.4,48.4,52.3,54.8
192	44.0,44.2,40.4,46.2,43.2	58.4,56.5,60.2,56.0,54.0

Appendix Table 1.4 Effect of 6h wet period applied immediately after inoculation on the development of E.graminis after different incubation periods.

			Mean(SE)
1.% germination			
T	24h	56.0,44.0,33.0,41.0,39.0,34.0,36.0,40.0,44.0,45.0	41.2(2.8)
	30h	50.0,44.0,47.0,46.0,42.0,41.0,49,0,40.0,50.0,57.0	46.6(2.2)
C	24h	74.0,71.0,76.0,73.0,70.0,68.0,73.0,78.0,57.0,79.0	71.9(2.8)
2.Total mycelial length(mm)			
T	48h		
	L1	1.05,0.05,1.20,1.30,1.70,1.00,1.00,1.95,0.90,0.45	
	L2	0.90,1.40,1.25,0.80,1.00,1.10,1.00,1.30,1.05,1.05	
	L3	0.80,o.7o,1.20,1.65,1.30,1.05,1.75,0.90,1.70,1.30	
	L4	1.25,1.05,0.95,1.95,0.80,0.65,1.00,0.90,0.65,1.55	
	L5	1.75,1.05,0.65,1.25,0.75,1.20,1.25,1.40,1.20,1.60	1.14(0.1)
T	54h		
	L1	1.25,1.50,3.10,1.95,2.30,2.65,1.60,1.40,2.50,1.10	
	L2	1.80,0.80,1.65,1.90,1.80,3.00,2.80,2.20,1.75,1.60	
	L3	1.80,2.30,1.80,0.70,1.50,1.40,2.65,2.10,2.05,1.05	
	L4	1.80,1.70,1.05,0.85,1.65,2.95,2.10,1.85,1.65,1.80	
	L5	2.70,1.75,1.65,1.75,1.90,1.70,2.65,2.70,1.40,2.00	1.87(.17)
C	48h		
	L1	1.50,1.20,1.80,1.70,1.95,1.25,1.90,1.80,2.60,1.70	
	L2	1.20,2.00,2.05,1.10,1.85,1.15,1.80,2.00,1.50,1.50	
	L3	1.60,1.70,0.90,2.40,1.70,1.40,1.45,1.60,1.85,1.70	
	L4	1.30,1.15,2.25,0.80,2.55,1.80,1.75,0.85,1.95,1.15	
	L5	1.60,1.60,1.45,2.20,2.20,1.35,1.50,1.75,2.50,2.10	1.67(.12)

3.Conidiophore production

T	72h										
	Li	a	.35	.38	.34	.39	.46	.23	.18	.52	.28	.39
		c	0	2	0	0	0	0	0	0	2	8
	L2	a	.28	.26	.36	.45	.30	.41	.45	.50	.52	.29
		c	0	0	3	2	0	0	2	0	0	0
	L3	a	.30	.42	.29	.33	.40	.23	.55	.43	.30	.42
		c	0	3	2	4	0	0	6	2	5	0
	L4	a	.42	.56	.21	.47	.34	.26	.46	.41	.20	.25
		c	6	4	0	8	2	5	0	8	0	0
	L5	a	.38	.22	.48	.50	.32	.42	.49	.33	.45	.67
		c	8	0	6	0	2	5	0	8	0	0

2(1)

Appendix Table 1.4 contd.

T 78h											
L1	a	.41	.46	.43	.46	.57	.39	.53	.40	.40	.54
	c	12	20	0	8	4	16	3	8	14	9
L2	a	.50	.43	.46	.72	.40	.39	.50	.56	.38	.67
	c	8	7	0	12	18	16	13	4	8	1
L3	a	.48	.49	.31	.37	.40	.45	.54	.36	.73	.61
	c	19	21	0	0	28	3	4	6	7	9
L4	a	.40	.45	.42	.31	.37	.56	.29	.30	.33	.54
	c	4	3	29	33	4	26	18	4	3	31
L5	a	.52	.50	.46	.48	.56	.57	.39	.34	.47	.52
	c	6	38	16	22	0	45	8	15	7	10

12(3)

C 72h											
L1	a	.50	.56	.44	.57	.42	.28	.66	.43	.47	.56
	c	2	9	3	0	17	4	3	0	8	6
L2	a	.60	.48	.53	.76	.50	.39	.46	.51	.60	.81
	c	16	10	21	0	3	21	3	6	0	12
L3	a	.36	.36	.30	.56	.50	.40	.87	.55	.61	.67
	c	11	0	18	32	8	16	0	8	7	6
L4	a	.52	.46	.45	.64	.60	.48	.41	.39	.51	.53
	c	5	2	7	17	14	7	0	8	0	0
L5	a	.70	.51	.23	.55	.45	.46	.67	.61	.48	.62
	c	5	6	3	26	16	0	4	16	5	9

8(2)

T-treated, C-control, L1....leaf no.
a-area of colony(mm^2), c-no. conidiophores
i-conidiophore initials, m-mature conidiophores
Figures in brackets are standard error($t_{0.05}$), values for germination based on angular transformation of data.

Appendix Table 1.5 Effect of 6h wet period applied immediately after inoculation on germination of conidia of *E.graminis* after different incubation periods.

		% germination	Mean
T	24h	33.0,33.0,30.0,33.0,34.0,26.0,33.0,32.0,30.0,27.0	31.1
	30h	43.0,39.0,44.0,38.0,38.0,33.0,34.0,37.0,36.0,34.0	37.6
	48h	39.0,33.0,49.0,43.0,35.0,36.0,40.0,38.0,37.0,38.0	38.8
	54h	44.0,39.0,42.0,39.0,38.0,39.0,44.0,39.0,35.0,40.0	39.9
	72h	39.0,48.0,38.0,42.0,39.0,50.0,38.0,37.0,44.0,43.0	41.8
	78h	44.0,41.0,37.0,39.0,33.0,48.0,45.0,51.0,43.0,42.0	42.3
C	24h	69.0,75.0,71.0,64.0,72.0,72.0,71.0,72.0,75.0,75.0	71.6
	48h	69.0,72.0,73.0,69.0,75.0,72.0,75.0,71.0,76.0,75.0	72.7
	72h	74.0,68.0,69.0,73.0,73.0,76.0,78.0,75.0,70.0,75.0	75.1

T-treated, C-control, 24h....assessed after inoculation.

ANOVA

Factor	SS	DF	MS	F
Treatment	8316.32	8	1039.54	209.58*
Residual	401.75	81	4.96	
Total	8718.07	89		

SE = 0.70

33.9 37.8 38.5 39.2 40.3 40.6 57.8 58.5 58.8

Means not underscored by the same line are significantly different ($P \leq 0.05$)(Analysis based on angular transformation of data).

Appendix Table 1.6 Distribution of water droplets and conidia when leaves inoculated with E.graminis were mist sprayed.

Replicate	A*	B*	C*
1	49.7	86.9	46.9
2	52.1	81.8	46.1
3	45.9	83.7	45.1
4	47.9	79.0	46.9
5	50.4	79.8	47.8
6	52.9	78.1	43.8
7	53.0	80.2	45.7
8	47.3	76.7	46.0
9	50.0	82.8	44.8
10	50.3	78.6	45.7
Mean	49.7	80.8	45.9
**$SE_{0.05}$	1.0	1.6	0.5

*Percentage valuesfor germination on leaves wetted with water for 6h (A),on unwetted leaves(B)and no. conidia stained with neutral red(C).

**Analysis based on angular transformation of data

Appendix Table 1.7 Effects of different periods of wetness applied immediately after inoculation on conidial germination of E.graminis (Ref.Fig.1.3)

Treated	% germination										Mean
1h	45.1	55.3	44.3	46.1	31.3	47.8	59.4	57.6	47.1	44.2	47.8
2h	41.9	33.6	58.6	40.5	34.3	44.1	47.5	40.6	54.3	36.8	43.2
3h	40.1	46.3	50.4	27.9	40.3	51.4	36.7	49.2	45.3	31.9	41.9
4h	43.8	42.9	39.5	39.0	39.2	32.1	45.9	35.3	43.2	36.2	39.7
5h	41.3	45.8	37.8	32.1	31.8	37.1	40.3	38.5	40.2	36.0	38.1
6h	44.8	37.1	33.8	45.7	40.7	38.8	37.4	31.3	43.6	25.2	37.8
7h	38.0	38.1	34.9	40.0	35.3	42.1	34.3	38.2	37.7	35.7	37.1
8h	29.3	36.6	37.9	28.0	31.8	34.5	39.2	45.2	41.5	39.5	36.3
9h	36.8	32.1	37.8	37.0	34.3	37.8	36.3	37.3	31.3	34.5	35.5
10h	39.8	33.8	36.5	35.2	31.9	33.9	31.5	38.8	38.4	35.2	35.2
Control	79.0	74.0	70.0	74.0	80.0	79.0	70.0	69.0	81.0	72.0	74.8

ANOVA

Factor	SS	DF	MS	F
Treatment	477.86	9	53.10	4.70
Residual	1015.62	90	11.28	
Total	1493.48	99		

SE = 1.06

36.6 36.6 37.0 37.5 37.9 38.1 39.0 40.3 41.1 43.7

Means underscored by the same line are not significantly different ($P \leq 0.05$)(Analysis based on angular transformation of data)

Appendix Table 1.8 Effects of different periods of wetness applied immediately after inoculation on conidial germination of E.graminis.

(Ref.Fig.1.4)

Treated	% germination										Mean
5 min	76.2	79.4	77.2	74.6	77.1	74.8	74.8	71.1	79.5	80.2	76.5
15 min	69.8	73.1	66.0	65.1	73.0	71.0	69.1	72.1	70.1	68.3	69.7
30 min	63.6	67.0	59.0	61.1	59.4	62.9	59.8	61.8	65.3	62.0	62.2
45 min	54.0	57.0	53.3	54.9	59.9	54.2	54.7	53.2	53.8	55.2	55.0
60 min	53.8	51.4	47.4	50.3	52.1	51.2	54.4	46.0	53.6	57.0	51.7
Control	78.4	79.1	84.5	86.3	81.2	81.2	80.9	85.3	79.2	83.1	81.9

ANOVA

Factor	SS	DF	MS	F
Treatment	2734.80	5	546.96	178.16
Residual	165.52	54	3.07	
Total	2900.32	59		

SE = 0.55

46.0	47.9	52.1	56.7	61.0	64.8

Means underscored by the same line are not significantly different ($P \leq 0.05$)(Analysis based on angular transformation of data)

Appendix Table 1.9 Effect of 6h wet period applied immediately after inoculation on germination of conidia of E.pisi and S.pannosa.

E.pisi	% germination										Mean(SE)
T	76.3	79.9	79.0	77.8	76.7	75.8	77.3	77.8	78.2	76.0	77.4(0.7)
C	91.9	93.3	93.3	92.7	93.6	94.5	94.7	92.4	95.8	95.3	93.8(1.1)
S.pannosa											
T	53.1	56.6	53.9	55.3	59.8	52.5	56.6	60.4	53.3	61.0	56.3(2.0)
C	81.1	80.0	88.9	78.6	85.9	86.8	83.1	80.3	86.3	81.2	83.2(1.3)

T - treated, C - control

Appendix Table 1.10 Effect of 6h wet period applied immediately after inoculation on the establishment of infection.

E.graminis											Mean(SE)
A. T	63.9	62.8	64.0	64.4	67.6	62.4	61.7	61.5	64.8	60.4	63.3(0.9)
C	88.2	90.3	89.1	90.2	88.0	88.3	87.0	86.5	90.3	88.1	88.6(0.9)
B. T	55.7	48.6	55.6	56.2	54.6	57.6	51.9	52.2	57.5	56.2	54.6(1.2)
C	72.1	75.2	75.7	76.3	71.9	72.3	74.9	75.6	75.7	71.0	74.1(0.9)
E.pisi											
A. T	78.1	76.1	76.1	75.1	76.0	76.0	76.0	78.1	77.1	76.1	76.5(0.5)
C	94.3	92.1	93.2	95.5	95.1	92.0	95.2	94.1	94.0	95.0	94.0(1.1)
B. T	52.1	55.8	48.9	52.7	56.3	50.9	54.6	50.2	50.5	55.9	52.8(1.1)
C	91.1	89.2	87.5	89.3	88.5	88.6	91.2	91.1	92.0	90.4	89.9(1.0)
S.pannosa											
A. T	55.8	58.8	52.5	54.4	55.9	56.6	57.9	55.6	55.7	55.7	55.9(0.7)
C	85.5	83.2	85.2	85.2	81.5	80.1	86.0	85.4	85.3	83.3	84.1(1.1)
B. T	44.8	45.9	45.6	48.7	47.9	46.9	45.6	47.6	49.1	49.7	47.2(0.7)
C	74.1	75.2	76.4	70.0	76.3	72.2	75.3	69.8	73.1	73.1	73.6(1.1)

A - % germination, B - % ESH production, T - treated, C - control
Figures in brackets are standard errors ($t_{0.05}$) based on angular transformation of data.

Appendix Table 1.11 Effect of 6h wet period applied immediately and 24h after inoculation on the development of E.graminis.

											Colonies/cm^2 leaf Mean(SE)
1.Wetted immediately after inoculation											
P1	a	13.0	12.9	15.0	14.9	17.0	13.9	12.7	8.7	9.6	14.0	
	ad	56	0	2	2	0	34	0	35	5	8	
	ab	31	101	24	8	151	3	32	3	1	6	
P2	a	8.1	11.0	11.2	7.7	13.6	10.4	13.2	12.3	17.6	14.8	
	ad	0	26	174	26	18	0	22	17	1	27	
	ab	56	4	0	13	79	6	9	20	43	61	
P3	a	10.2	13.6	15.5	14.2	12.1	11.2	9.9	14.0	11.7	15.0	
	ad	32	69	36	0	0	0	0	33	20	19	
	ab	30	26	6	6	9	50	19	14	40	0	
P4	a	17.8	14.6	12.7	13.8	14.5	12.0	13.2	12.0	14.5	17.4	
	ad	11	20	8	6	21	18	8	34	43	98	
	ab	21	54	40	17	61	4	52	0	3	4	
P5	a	12.0	13.6	12.3	9.2	11.3	11.2	12.1	13.5	15.8	11.8	
	ad	96	21	103	0	44	52	42	27	3	26	
	ab	28	17	57	40	8	81	6	7	103	8	4.3(0.9)
2.Wetted 24h after inoculation											
P1	a	14.1	9.4	14.0	11.2	13.0	7.1	12.8	10.0	11.6	8.2	
	ad	25	272	151	49	99	50	150	116	30	72	
	ab	144	78	18	31	11	65	48	156	270	207	
P2	a	11.5	11.9	10.8	11.1	10.3	9.0	8.6	9.7	9.5	9.8	
	ad	90	206	101	16	122	31	78	40	161	178	
	ab	25	5	42	114	76	61	18	29	77	1	
P3	a	7.5	9.3	7.4	7.5	6.9	11.5	9.1	9.9	9.0	10.0	
	ad	130	3	15	172	116	260	137	214	32	117	
	ab	106	236	35	36	13	25	62	44	40	42	
P4	a	9.5	13.5	10.9	11.0	11.4	12.0	11.7	7.9	11.4	8.3	
	ad	108	234	207	137	15	4	181	263	102	132	
	ab	41	46	44	54	100	113	98	104	77	48	
P5	a	6.8	9.6	9.8	6.8	9.9	10.3	14.3	11.5	9.9	10.8	
	ad	17	126	15	226	119	94	370	292	68	118	
	ab	348	35	135	53	16	30	106	46	298	96	20.6(3.0)

Appendix Table 1.11 contd.

3. Unwetted(control)

P1	a	12.3	11.9	9.3	14.1	11.7	7.6	8.0	11.5	9.5	8.8	
	ad	43	16	156	204	17	48	34	4	152	52	
	ab	217	238	6	76	328	24	20	167	27	55	
P2	a	11.3	11.7	13.2	11.7	12.1	9.3	9.9	9.7	8.6	13.2	
	ad	82	198	160	358	50	36	41	46	54	402	
	ab	49	45	58	19	36	58	68	98	116	158	
P3	a	6.9	10.1	11.5	11.8	11.0	10.8	9.5	8.8	9.3	10.8	
	ad	96	78	203	364	2	231	145	164	16	18	
	ab	86	50	136	136	290	118	68	28	108	107	
P4	a	11.6	11.2	10.2	10.7	10.6	8.3	8.4	10.7	10.2	13.6	
	ad	76	102	64	30	178	14	124	6	3	59	
	ab	103	90	152	300	35	43	16	192	281	159	
P5	a	12.1	10.6	11.7	11.2	9.9	10.5	11.5	10.2	9.7	12.6	
	ad	274	282	3	132	3	68	10	11	26	90	
	ab	144	48	111	148	159	43	138	38	212	70	19.5(2.5)

P1, P2..... pot no.

a - area of leaf (both surfaces)

ad - no. of colonies on adaxial surface of leaf

ab - no. of colonies on abaxial surface of leaf

Appendix Table 1.12 Effect of wetting leaves for 6h before or after inoculation on the development of E.graminis.

1.Wetted before inoculation

P1	a	12.7	12.4	11.7	13.5	10.7	12.9	11.1	11.7	10.5	10.6
	ad	14	83	33	169	51	80	71	45	142	25
	ab	18	26	14	6	114	27	34	130	3	26
P2	a	11.6	9.9	11.5	9.9	12.6	12.1	11.5	12.5	12.9	14.1
	ad	12	73	68	26	56	96	130	16	3	5
	ab	20	156	60	14	16	69	14	61	80	84
P3	a	12.4	11.4	10.0	11.6	10.9	11.2	5.7	9.6	11.8	11.2
	ad	1	6	22	171	17	16	36	2	62	137
	ab	79	55	81	31	216	64	133	117	45	44
P4	a	11.5	9.9	13.4	9.1	9.8	15.4	9.8	12.2	9.0	12.4
	ad	112	30	110	69	33	68	49	5	30	75
	ab	20	34	33	11	32	50	16	34	18	14
P5	a	11.1	11.3	13.1	9.7	10.7	9.3	12.6	10.3	13.0	11.4
	ad	118	3	107	43	19	150	121	2	1	117
	ab	19	132	18	9	139	13	4	179	83	93

2.Wetted after inoculation

P1	a	11.7	14.2	10.7	14.1	14.1	11.9	12.3	11.4	11.9	9.2
	ad	4	15	14	5	3	25	13	6	8	5
	ab	10	28	6	8	10	3	5	8	7	6
P2	a	9.1	12.7	9.3	11.1	10.0	12.0	14.0	9.6	9.8	11.9
	ad	15	7	49	70	34	18	21	1	15	23
	ab	23	96	26	45	27	91	7	105	20	4
P3	a	13.3	11.3	13.0	12.7	14.1	14.1	10.9	12.9	12.3	10.4
	ad	4	3	3	8	26	45	45	13	6	6
	ab	16	20	21	25	4	2	11	19	3	4
P4	a	13.0	11.7	9.3	11.4	8.5	12.8	11.9	8.3	10.0	11.7
	ad	39	20	31	38	20	2	35	9	47	13
	ab	68	88	20	4	2	110	94	10	22	27
P5	a	15.1	10.6	8.7	11.7	16.3	12.1	13.9	11.3	13.0	10.5
	ad	4	6	5	3	12	24	9	8	12	48
	ab	36	12	108	29	28	7	19	63	66	32

Appendix Table 1.12 contd.

3.Unwetted (control)

P1	a	12.1	12.3	10.6	8.7	14.2	13.6	9.8	12.4	15.4	13.3
	ad	64	183	72	115	40	6	44	71	268	102
	ab	3	10	6	18	76	77	7	25	11	18
P2	a	9.1	7.6	13.3	9.0	7.7	13.4	14.0	11.7	13.4	10.2
	ad	238	135	179	234	12	308	10	238	58	296
	ab	6	3	15	10	112	7	236	88	170	3
P3	a	13.6	12.2	12.1	15.4	14.6	10.9	9.2	9.8	11.5	12.0
	ad	155	148	158	286	39	310	148	187	56	108
	ab	88	6	4	2	286	46	19	12	88	2
P4	a	13.5	16.1	12.3	12.3	12.2	15.2	14.2	14.1	10.0	13.2
	ad	52	11	155	130	59	112	357	64	45	328
	ab	86	278	113	12	28	158	57	101	51	39
P5	a	10.0	7.8	10.9	9.4	11.8	9.8	9.8	10.7	13.7	13.0
	ab	21	92	129	102	19	100	119	178	130	38
	ab	61	4	123	82	302	59	41	117	49	228

P1,P2....pot no.

a - area of leaf (both surfaces)

ad - no.of colonies on adaxial surface of leaf

ab - no. of colonies on adaxial surface of leaf

Appendix Table 1.13 Effect of 6h wet period applied 24h after inoculation on mycelial growth.
(Ref.Figs.1.7-1.9)

Total mycelial length (mm)

E.graminis	Treated					Control				
	[1]	[2]	[3]	[4]	[5]	[1]	[2]	[3]	[4]	[5]
at 30h	0.46	0.35	0.24	0.46	0.46	0.40	0.46	0.46	0.42	0.22
	0.30	0.26	0.32	0.40	0.32	0.53	0.48	0.40	0.32	0.42
	0.35	0.25	0.26	0.22	0.24	0.36	0.40	0.44	0.34	0.56
	0.40	0.20	0.32	0.42	0.38	0.54	0.36	0.52	0.36	0.44
	0.30	0.25	0.28	0.35	0.35	0.44	0.42	0.38	0.48	0.32
at 36h	0.44	0.66	0.72	0.56	0.36	1.06	1.18	0.96	0.96	0.92
	0.84	0.72	0.64	0.76	0.72	0.94	0.66	0.94	0.90	0.88
	0.52	0.76	0.42	0.64	0.88	1.22	0.72	0.82	0.72	0.72
	0.62	0.62	0.66	0.44	0.65	0.98	0.90	1.06	0.74	1.16
	0.54	0.46	0.76	0.68	0.56	1.18	0.82	1.20	1.12	0.92
at 42h	1.18	1.16	1,32	1.12	0.92	1.54	1.70	1.92	1.98	1.44
	0.98	0.88	1.16	1.02	1.12	1.72	1.64	1.86	1.72	1.62
	0.92	0.62	1.28	1.04	1.74	1.66	1.92	1.96	1.42	1.90
	0.36	1.14	1.54	1.72	1.22	1.62	1.86	1.68	1.86	1.36
	1.22	1.32	1.96	1.56	1.28	1.92	1.98	1.72	1.78	1.96
at 48h	1.78	2.30	2.18	2.46	1.72	2.72	3.22	2.22	1.62	2.72
	1.66	2.58	1.76	1.94	1.76	3.26	1.86	2.12	2.92	2.22
	1.82	2.16	1.94	1.92	1.94	2.24	1.94	3.36	2.38	1.96
	1.96	2.06	1.94	1.84	1.92	1.68	1.68	2.02	3.42	2.42
	1.64	2.68	2.32	1.86	2.74	2.82	2.24	1.96	2.26	2.56
at 54h	4.56	3.92	3.62	3.52	3.88	3.76	4.22	4.12	4.38	3.62
	4.10	2.76	2.82	2.72	3.64	3.94	4.34	3.56	3.52	3.56
	3.56	3.16	3.16	2.92	2.98	4.12	3.66	4.36	3.74	4.02
	2.76	4.24	3.02	2.62	3.04	4.18	3,82	3.98	4.06	4.24
	3.22	3.28	3.16	3.78	3.26	3.82	4.12	4.14	3.08	3.76
at 60h	6.12	6.66	5.44	6.12	5.22	6.36	5.22	6.92	5.12	6.46
	5.66	6.32	6.82	6.28	6.18	6.94	6,92	6.04	4.76	5.26
	6.32	5.72	6.84	5.22	5.84	6.32	6.44	6.66	6.62	6.18
	5.38	5.10	6.36	6.62	5.18	5.84	5.92	6.24	6.34	6.82
	5.04	6.22	4.98	4.78	5.26	5.68	6.88	5.25	6.22	6.34
E.pisi										
at 30h	0.48	0.52	0.36	0.40	0.40	0.30	0.28	0.42	0.46	0.52
	0.52	0.52	0.28	0.50	0.56	0.28	0.32	0.36	0.52	0.36
	0.48	0.48	0.42	0.52	0.54	0.40	0.42	0.40	0.42	0.32
	0.52	0.42	0.54	0.56	0.60	0.28	0.28	0.28	0.40	0.40
	0.30	0.28	0.60	0.58	0.36	0.36	0.40	0.28	0.28	0.56
at 36h	1.24	1.30	1.26	1.22	0.80	0.76	0.56	0.58	0.64	0.62
	1.28	0.80	1.16	1.14	0.84	0.68	0.78	0.66	0.66	0.74
	1.18	1.26	1.02	1.08	0.98	0.84	0.62	0.56	0.76	0.68
	1.14	1.24	1.12	1.06	1.22	0.60	0.84	0.78	0.68	0.52
	1.20	1.04	0.96	1.24	1.30	0.68	0.62	0.58	0.64	0.76

Appendix Table 1.13 contd.

at 42h	1.86	1.86	2.22	1.96	2.26	1.02	1.06	1.14	1.08	1.12
	1.94	2.20	2.16	1.96	1.88	1.12	1.00	1.08	1.18	1.06
	2.14	2.16	2.10	1.84	1.28	1.06	1.14	1.00	1.08	1.10
	2.04	1.92	1.88	1.94	1.96	1.18	1.18	1.08	1.00	1.14
	2.18	2.12	1.84	2.18	1.96	1.24	1.12	1.08	1.16	1.18
at 48h	2.84	2.86	2.70	2.90	2.60	2.02	1.74	1.86	2.02	1.78
	2.92	2.95	2.65	2.80	2.82	1.96	2.12	2.06	1.92	2.12
	2.64	2.92	2.92	2.92	2.88	1.88	1.72	1.82	1.72	1.80
	2.62	2.64	2.64	2.86	2.60	2.06	1.66	2.16	2.12	2.06
	2.74	2.82	2.82	2.52	2.78	1.94	1.80	2.02	1.96	1.78
at 54h	3.76	3.80	3.48	3.48	2.78	3.76	2.62	4.02	3.18	3.68
	3.64	3.82	3.92	3.52	3.86	2.84	3.70	3.92	2.80	3.28
	4.52	4.80	3.60	3.82	3.64	2.66	2.92	2.62	3.80	3.52
	3.68	3.62	3.58	3.58	3.58	3.94	3.68	2.98	2.90	3.70
	4.28	3.39	3.40	3.70	3.42	2.88	3.28	2.96	2.70	3.78
at 60h	4.92	5.38	5.20	5.98	6.24	5.26	5.20	5.26	4.82	5.68
	5.12	6.42	5.24	5.90	5.22	4.90	4.99	4.62	4.92	5.31
	5.88	5.28	5.22	6.06	6.08	4.80	4.72	5.36	4.94	4.66
	6.20	4.96	5.26	6.14	5.30	5.22	5.18	5.40	5.18	5.98
	5.18	4.88	6.34	5.18	5.12	4.76	4.74	4.59	4.60	4.96
S.pannosa			Control					Treated		
at 30h	0,60	0.60	0.56	0.58	0.60	0.48	0.46	0.24	0.34	0.28
	0.56	0.60	0.58	0.58	0.54	0.40	0.54	0.28	0.40	0.28
	0.58	0.52	0.56	0.56	0.54	0.32	0.24	0.40	0.36	0.60
	0.58	0.54	0.52	0.60	0.60	0.28	0.60	0.32	0.26	0.42
	0.54	0.56	0.52	0.60	0.42	0.36	0.60	0.30	0.26	0.24
at 36h	0.98	1.00	0.98	1.14	0.94	o.84	0.72	0.82	0.68	0.82
	0.98	1.06	1.04	0.96	1.08	0.68	1.02	0.86	0.72	0.68
	0.96	1.08	0.96	1.08	1.06	0.72	0.68	0.94	0.74	0.84
	0.90	0.90	1.14	0.88	1.08	0.96	0.94	0.98	0.74	0.90
	0.98	1.02	1.08	1.18	0.94	0.74	0.88	0.72	1.04	0.86
at 42h	1.94	1.90	1.88	1.82	1.88	1.24	1.42	1.48	1.30	1.40
	1.82	1.96	1.80	2.10	1.88	1.28	1.60	1.60	1.38	1.28
	1.98	2.14	1.92	1.98	1.92	1.42	1.32	1.36	1.42	1.26
	1.96	1.80	1.94	1.94	1.80	1.18	1.40	1.30	1.26	1.40
	1.74	2.04	2.14	1.92	2.16	1.50	1.36	1.44	1.30	1.28
at 48h	2.82	2.82	2.84	3.26	2.84	2.32	1.90	2.24	1.56	2.30
	2.72	3.28	2.90	3.40	2.78	2.18	2.38	1.76	1.20	2.22
	3.18	2.86	3.28	3.24	3.52	2.40	2.40	2.32	1.16	2.34
	3.24	2.84	2.68	2.80	3.26	2.52	2.20	1.62	2.42	2.24
	3.12	3.86	3.26	2.72	3.46	2.70	1.42	2.18	2.18	2.42
at 54h	4.60	4.68	4.14	4.54	4.62	3.18	3.86	4.26	3.36	3.40
	4.72	4.56	4.02	4.00	4.32	3.62	4.02	3.90	4.40	3.68
	3.84	4.72	4.48	4.54	4.80	3.40	3.54	3.84	4.54	3.38
	4.20	4.64	4.70	4.42	4.30	4.72	4.36	4.42	4.72	4.40
	3.80	4.68	4.68	4.46	4.22	3.18	4.18	3.92	4.32	4.60
at 60h	6.40	6.08	5.86	6.72	6.04	6.72	6.40	6.62	6.02	6.26
	5.02	6.70	6.32	6.62	5.64	5,54	6.18	5.68	6.20	6.36
	6.72	6.08	6.36	6.96	5.94	6.18	6.12	5.66	6.26	6.04
	6.92	5.82	6.10	5.98	6.00	5.62	5.72	6.54	5.70	6.42
	6.06	6.90	5.94	6.04	6.68	5.22	6.12	6.40	6.30	6.12

Appendix Table 1.14 Effect of 6h wet period on the initiation of conidiophores

No. Conidiophores/ mm^2 colony

E.graminis

leaf	Treated										Control									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
1	15	17	34	17	14	22	27	12	36	22	51	45	43	37	47	53	50	40	39	35
2	11	32	40	17	26	12	32	11	11	15	31	48	36	38	44	48	49	49	44	26
3	14	33	47	40	16	15	40	16	11	11	33	49	44	36	45	40	44	42	49	21
4	12	22	33	45	11	25	36	28	16	19	44	57	36	33	66	44	36	46	56	35
5	28	16	14	13	33	38	11	41	44	40	30	50	37	44	36	34	38	35	24	60

E.pisi

1	37	30	33	38	36	33	43	25	41	32	49	53	72	34	29	66	81	70	31	90
2	37	34	30	42	35	26	41	34	29	28	48	49	26	24	30	51	43	49	52	62
3	30	41	24	26	29	37	29	34	36	36	44	37	40	39	28	46	47	32	29	80
4	36	36	34	20	25	40	37	41	36	39	50	28	82	39	92	70	23	54	29	43
5	34	35	33	35	42	37	33	23	33	41	44	52	63	73	81	60	48	40	80	74

S.pannosa

1	14	31	9	11	14	7	12	11	22	9	26	11	23	40	17	11	32	11	19	10
2	5	7	28	15	7	30	16	6	4	15	16	50	11	19	28	17	11	11	28	30
3	6	5	11	9	15	15	8	6	15	10	47	13	32	22	16	41	19	32	36	33
4	11	38	21	29	28	6	30	10	36	20	34	27	12	19	33	45	13	17	22	30
5	21	10	5	36	10	8	12	19	5	18	18	14	10	29	40	50	41	19	10	33

Appendix Table 1.15 Effect of 6h wet period on the production of conidia.

(Ref.Figs.1.10-1.12)

E.graminis

		Treated					Control				
		1	2	3	4	5	1	2	3	4	5
Day 6	a	1.16	1.24	1.20	1.22	1.13	1.26	1.31	1.27	1.28	1.26
	c	2.1	2.3	2.0	3.4	2.1	2.9	3.1	3.3	3.1	3.0
Day 7	a	1.41	1.40	1.34	1.41	1.41	1.60	1.68	1.59	1.55	1.55
	c	4.4	4.7	4.2	4.1	4.4	4.6	5.0	4.4	4.8	4.5
Day 8	a	1.66	1.75	1.71	1.78	1.70	1.96	2.07	2.00	1.98	1.89
	c	7.0	6.3	6.7	6.2	6.0	6.7	6.3	6.4	6.8	7.6
Day 9	a	2.39	2.33	2.33	2.32	2.30	2.50	2.43	2.39	2.38	2.55
	c	7.3	7.8	7.6	7.3	7.7	7.8	8.3	8.1	8.1	7.6
Day 10	a	2.81	2.87	2.84	2.89	2.84	2.94	2.89	2.97	2.78	3.00
	c	8.0	7.5	8.7	9.0	8.7	8.4	8.1	7.7	9.2	8.7

E.pisi

Day 6	a	1.72	1.61	1.63	1.72	1.72	1.39	1.37	1.43	1.29	1.33
	c	3.2	4.0	3.9	2.8	2.9	3.2	2.4	3.0	2.9	2.8
Day 7	a	2.32	2.27	2.43	2.22	2.38	1.99	2.01	1.94	1.99	1.86
	c	3.8	4.2	3.0	3.5	3.8	3.1	3.2	3.2	3.3	3.1
Day 8	a	3.11	3.02	3.24	2.99	3.11	2.78	2.75	2.81	2.78	2.75
	c	4.1	4.4	4.0	4.4	4.6	3.8	4.2	4.5	3.7	4.2
Day 9	a	3.50	3.40	3.53	3.53	3.37	3.27	3.30	3.33	3.43	3.37
	c	5.1	5.0	4.7	4.7	5.0	5.3	4.3	4.6	4.7	4.5
Day 10	a	3.66	3.70	3.77	3.80	3.77	3.94	4.01	4.08	3.80	3.84
	c	5.4	5.4	5.0	5.2	5.2	4.8	5.2	5.0	6.0	5.4

S.pannosa

Day 6	a	2.24	2.19	2.24	2.16	2.24	2.01	2.04	2.04	2.09	2.14
	c	1.7	2.0	1.5	1.7	1.7	1.1	0.9	1.0	0.9	1.0
Day 7	a	2.57	2.57	2.54	2.63	2.69	2.11	2.27	2.22	2.30	2.14
	c	2.6	3.0	2.8	2.7	2.9	2.1	2.2	1.9	2.2	2.5
Day 8	a	2.99	2.90	3.02	3.08	3.11	2.84	2.84	2.72	2.78	2.75
	c	3.3	3.7	4.0	3.5	3.4	2.8	2.7	3.2	2.9	3.3
Day 9	a	3.30	3.14	3.17	3.14	3.30	3.17	3.14	3.05	3.02	3.02
	c	4.2	4.4	4.4	3.9	3.7	3.9	4.4	4.3	3.8	3.8
Day 10	a	3.60	3.53	3.46	3.40	3.27	3.40	3.33	3.27	3.20	3.17
	c	4.4	4.2	4.1	4.3	4.4	4.4	4.9	4.2	4.0	4.6

a - area of colony (mm^2) c - conidia/mm^2colony(10^{-2})

Appendix Table 1.16 Effect of 6h wet period on the production of viable conidia.

Plants used as source of inoculum

pot	Treated ad	Treated ab	Treated leaf area*	Control ad	Control ab	Control leaf area*
1.immediately after inoculation						
1	22	15	13.5	40	78	12.3
2	8	13	13.2	60	73	12.7
3	9	9	11.8	116	65	11.8
4	20	8	11.7	50	74	11.8
5	14	13	11.6	104	66	13.4
2.6h later						
1	50	13	12.7	67	53	12.0
2	36	47	12.3	113	60	12.0
3	52	59	12.3	101	73	10.4
4	25	35	12.7	133	128	12.2
5	62	42	13.5	120	35	12.8
3.24h later						
1	101	107	12.4	70	163	12.3
2	34	104	11.6	83	172	12.2
3	73	99	11.3	119	182	12.2
4	98	93	12.2	102	167	12.4
5	70	97	12.1	127	116	12.7
4.48h later						
1	75	76	13.2	55	144	12.3
2	19	110	11.5	60	105	12.2
3	76	95	12.3	64	204	12.3
4	54	114	11.8	62	90	12.3
5	50	69	11.4	60	108	10.2
5.72h later						
1	33	138	12.9	53	93	11.5
2	36	115	12.6	64	105	11.0
3	44	103	11.6	100	55	10.0
4	59	110	12.4	107	73	13.0
5	68	101	12.6	67	85	10.9

ad-no.colonies on adaxial surface
ab-no.colonies on abaxial surface
*area of both surfaces

Each figure is a mean of assessment on 10 seedlings

Appendix Table 2.1 Percentage conidia germinated when transferred from water to host leaf.

E. graminis

						Mean
After 24h on leaf only:	87.2	88.6	89.4	86.4	89.5	88.2
on water only:	55.2	54.1	56.0	54.5	57.2	55.4
in water only:	45.0	44.0	44.8	40.1	47.2	44.2

After 24h following period of contact with water of:

	on water						in water					
*0h	86.5	85.5	85.6	87.2	88.4	86.7	85.8	88.9	89.6	88.0	87.1	87.9
2h	84.2	82.3	82.4	84.5	84.9	83.6	81.7	81.4	79.8	82.5	80.8	81.3
4h	76.2	73.7	75.0	72.4	75.0	74.5	71.5	74.5	76.6	75.4	72.2	74.1
6h	71.4	69.7	70.9	73.5	72.1	71.5	64.5	62.8	65.0	63.5	63.9	63.9
8h	65.5	66.4	67.6	68.2	65.8	66.7	57.5	55.7	58.5	58.1	59.1	57.8
10h	62.8	63.7	62.7	61.4	64.0	62.9	50.8	52.6	53.2	55.3	56.5	53.7
24h	57.7	56.1	57.0	56.6	58.1	57.1	45.3	45.2	45.4	44.7	45.5	45.2
48h	55.4	54.6	55.3	57.4	55.8	55.7	44.7	45.6	45.5	45.2	45.3	45.3

E. pisi

						Mean
After 24h on leaf only:	91.7	90.1	92.2	93.0	90.1	91.4
on water only:	72.5	70.2	76.2	75.0	75.7	73.9
in water only:	66.7	68.7	70.0	66.2	68.4	68.0

After 24h following period of contact with water of:

*0h	90.4	90.4	93.0	90.1	90.3	90.8	89.4	92.5	90.4	90.9	89.2	90.5
2h	90.5	90.3	91.4	89.1	92.3	90.7	87.7	86.9	86.7	86.0	87.9	87.0
4h	89.3	88.3	89.2	87.3	89.2	88.7	85.4	82.9	83.8	81.2	83.2	83.3
6h	87.9	87.4	85.5	86.4	86.1	86.0	83.0	80.9	79.6	81.5	79.8	81.0
8h	84.7	83.6	84.5	83.9	83.5	84.0	77.7	78.1	77.7	78.0	80.0	78.3
10h	83.6	83.2	82.2	82.3	82.4	82.7	75.7	73.3	73.7	72.7	75.8	74.3
24h	79.4	79.4	80.0	81.4	80.4	80.1	67.3	68.6	68.2	70.5	71.2	69.2
48h	77.1	76.3	76.3	78.2	78.4	77.2	67.9	68.3	66.3	66.7	66.7	67.2

*Conidia removed immediately after contact with water.

Appendix Table 2.2 Percentage conidia producing ESH when transferred from water to host leaf.

E.graminis

After 48h on leaf only: 77.6 78.8 80.2 80.6 77.2 Mean 78.9

After 48h following period of contact with water of:

*	on water					Mean	in water					Mean
0h	79.7	80.8	78.5	78.6	79.8	79.5	73.3	73.6	74.2	76.4	74.3	74.5
2h	71.7	72.4	69.7	70.6	72.2	71.3	69.0	65.9	65.4	68.3	67.3	67.2
4h	61.4	60.0	59.7	62.5	61.3	61.0	59.0	57.7	58.4	56.3	55.7	57.4
6h	54.4	55.2	51.3	51.3	52.1	52.9	45.4	44.8	45.2	45.7	42.3	44.7
8h	44.7	45.6	42.5	43.0	45.0	44.2	37.1	35.2	36.0	35.6	32.5	35.3
10h	32.8	32.8	30.6	28.4	33.3	31.6	25.7	25.9	25.2	26.2	24.8	25.6
24h	4.0	3.5	2.4	3.4	1.7	3.0	1.5	1.6	2.1	1.9	0.9	1.6
48h	0	0	0	0	0	0	0	0	0	0	0	0

E.pisi

After 48h On leaf only: 80.4 81.2 82.5 82.7 82.0 81.8

After 48h following period of contact with water of:

*												
0h	80.4	78.4	80.0	80.4	82.2	80.3	80.0	79.7	81.6	82.6	81.4	81.1
2h	75.0	73.3	70.3	75.2	75.4	73.9	67.5	66.4	68.7	69.8	65.7	67.6
4h	68.1	65.1	65.2	64.1	67.4	66.0	58.3	58.2	57.3	57.6	60.2	58.3
6h	59.1	60.1	60.1	61.6	60.3	60.3	52.6	49.5	51.5	47.9	49.1	50.2
8h	51.5	52.9	55.9	50.5	48.0	51.7	44.0	41.7	41.9	42.5	43.3	42.5
10h	42.2	41.7	37.5	38.8	38.4	39.7	34.0	34.3	36.9	33.7	33.3	34.4
24h	23.2	28.6	25.5	28.7	24.0	26.0	20.8	22.2	21.2	20.3	23.8	21.7
48h	1.7	4.6	2.6	3.1	1.8	2.8	0.8	1.8	1.8	0.9	0.8	1.2

*Conidia removed immediately after contact with water.

Each figure represents the mean of 5 assessments on a single leaf.

Appendix Table 2.3 Mycelial growth (mm) of conidia when transferred from water to host leaf.

E.graminis

After 48h on leaf only: 2.64 2.62 2.71 2.81 2.70 Mean 2.70

After 48h following period of contact with water of:

	on water					Mean	in water					Mean
*0h	2.70	2.73	2.76	2.56	2.85	2.72	2.54	2.81	2.70	2.66	2.67	2.68
2h	2.43	2.43	2.55	2.40	2.44	2.45	2.18	2.45	2.39	2.43	2.41	2.37
4h	2.09	2.31	2.20	2.29	2.21	2.22	2.06	2.21	2.19	2.28	2.08	2.16
6h	1.91	1.82	1.88	1.84	1.65	1.82	1.73	1.68	1.95	1.69	1.69	1.75
8h	1.54	1.65	1.66	1.53	1.66	1.61	1.45	1.60	1.57	1.43	1.68	1.53
10h	1.48	1.51	1.32	1.41	1.28	1.40	1.26	1.48	1.41	1.42	1.33	1.38
24h	0.90	0.80	0.61	0.29	1.15	0.75	0.72	0.43	0.62	0.39	0.81	0.59

E.pisi

After 48h on leaf only: 2.75 2.62 2.71 2.83 2.81 Mean 2.74

After 48h following period of contact with water of:

*0h	2.85	2.81	2.79	2.55	2.71	2.74	2.84	2.85	2.69	2.71	2.66	2.75
2h	2.59	2.68	2.70	2.66	2.59	2.63	2.60	2.60	2.61	2.63	2.54	2.60
4h	2.43	2.35	2.41	2.56	2.39	2.43	2.44	2.41	2.39	2.30	2.47	2.40
6h	2.05	2.29	2.21	2.19	2.05	2.16	2.11	2.14	2.05	2.12	2.30	2.14
8h	1.88	1.89	1.91	2.03	1.94	1.93	1.68	1.85	1.93	1.88	1.76	1.82
10h	1.76	1.74	1.75	1.68	1.64	1.71	1.40	1.52	1.54	1.55	1.59	1.52
24h	1.17	1.08	1.09	1.30	1.26	1.18	1.07	1.01	1.00	1.14	1.18	1,08
48h	0.75	0.63	0.54	0.53	0.73	0.64	0.66	0.38	0.64	0.51	0.43	0.52

*Conidia removed immediately after contact with water.

Each figure represents mean of 5 assessments on a single leaf.

Appendix Table 2.4 Conidiophore production/mm^2 colony when conidia were transferred from water to leaf.

E.graminis:

											Mean
After 96h on leaf only:											
	64	42	57	39	82	76	33	80	86	92	65
After 96h following period of contact with water of:											
on water											
*0h	54	93	83	49	80	64	38	55	80	90	69
2h	42	32	50	63	38	24	27	49	36	44	41
4h	19	30	29	40	33	26	18	19	40	21	28
6h	14	28	31	8	18	20	26	16	13	18	19
8h	2	4	11	0	14	0	2	3	4	0	4
10h	0	0	0	0	0	0	0	0	0	0	0
24h	0	0	0	0	0	0	0	0	0	0	0
in water											
*0h	37	43	68	72	84	59	66	74	55	93	65
2h	48	33	40	52	32	29	18	38	19	43	43
4h	24	10	12	31	23	34	14	18	16	12	19
6h	12	17	8	4	9	17	4	19	16	22	13
8h	0	0	0	0	0	0	0	0	0	0	0
10h	0	0	0	0	0	0	0	0	0	0	0
24h	0	0	0	0	0	0	0	0	0	0	0

E.pisi

												Mean
After 96h on leaf only:												
	83	94	113	29	86	43	91	89	114	120		86
After 96h following period of contact with water of:												
on water												
*0h	37	49	98	113	126	44	38	96	110	133		84
2h	54	29	48	72	18	29	72	93	82	36		53
4h	43	61	54	32	21	19	43	52	64	33		42
6h	40	32	0	26	14	37	54	12	23	25		26
8h	29	12	0	17	10	19	34	27	18	24		19
10h	7	0	16	32	4	0	0	18	26	9		12
24h	0	0	0	0	0	0	0	0	0	0		0
48h	0	0	0	0	0	0	0	0	0	0		0
in water												
*0h	76	98	110	29	93	58	79	82	103	94		82
2h	42	54	68	39	14	48	52	78	86	18		50
4h	50	29	18	28	42	53	55	39	19	29		36
6h	53	26	14	42	40	38	0	0	18	7		24
8h	34	12	21	0	0	7	4	16	7	3		10
10h	0	19	12	7	28	10	0	14	0	0		9
24h	0	0	0	0	0	0	0	0	0	0		0
48h	0	0	0	0	0	0	0	0	0	0		0

*Conidia removed immediately after contact with water.

Appendix Table 2.5 Development of E.graminis on barley when conidia were applied as aquous suspension.

A. aquous suspension

	0h				.5h				1h				2h			
ad	111	108	133	144	93	90	86	76	74	66	60	66	63	54	57	72
ab	117	135	133	147	91	90	94	111	64	60	74	65	52	46	40	32
	4h				6h				8h				10h			
ad	35	35	42	39	17	14	18	19	10	6	10	2	5	4	5	4
ab	50	38	43	42	15	24	14	14	6	11	8	15	0	3	1	6

B.aquous suspension + Tween 80

	0h				.5h				1h				2h			
ad	78	84	95	61	48	44	44	27	27	27	21	19	15	15	16	13
ab	30	43	39	43	36	37	30	37	16	21	21	18	17	15	11	6
	4h				6h				8h				10h			
ad	7	12	10	11	5	5	6	1	2	0	0	4	0	0	0	0
ab	4	4	1	7	2	0	0	5	0	2	1	1	0	0	0	0

Each figure represents the total no. of colonies on 10 seedlings

ad ab refer to the number of colonies on adaxial and abaxial leaf surfaces

Oh, .5h....refer to period of immersion of conidia.

Appendix Table 2.6 Effect of submerging leaves immediately after inoculation on the number of conidia retained.

E.graminis:	Conidia/mm^2 leaf															Mean
T	14	36	12	20	36	48	23	44	44	36	26	53	18	24	57	33
C	51	57	24	48	22	22	38	49	57	63	54	43	62	49	40	45
E.pisi																
T	48	21	14	10	26	38	19	64	28	36	59	43	12	29	39	32
C	68	33	59	49	30	22	75	47	61	61	58	61	50	63	56	53
S.pannosa																
T	12	21	40	26	14	29	3	32	24	9	19	24	31	34	20	23
C	29	42	26	34	33	43	26	45	14	32	36	27	29	39	28	32

Each treatment involved 3 assessments from each of 5 leaves
C - control, T - treated

Appendix Table 2.7 Effect of submerging inoculated leaves immediately after inoculation on germination and production of ESH by conidia.

E.graminis	% germination(24h)						% ESH production(48h)					
						Mean						Mean
T	59.3	64.2	58.5	50.6	48.2	56.2 (4.1)	40.2	45.1	42.9	40,6	38.5	41.5 (1.8)
C	85.9	83.1	88.1	89.0	89.7	87.3 (2.8)	76.0	73.7	69.8	70.8	75.8	73.2 (2.3)
E.pisi												
T	76.4	78.8	73.1	79.8	75.7	76.8 (2.2)	42.5	46.4	44.5	48.4	40.0	44.5 (2.5)
C	89.5	88.4	92.0	89.8	90.5	90.0 (1.6)	89.0	81.3	86.0	86.5	85.3	85.6 (2.8)
S.pannosa												
T	68.3	64.1	54.7	62.3	57.3	61.3 (4.0)	50.5	49.6	42.1	43.4	40.4	45.2 (3.3)
C	83.3	84.4	88.0	83.8	78.1	83.5 (3.4)	72.6	69.6	75.2	76.3	68.3	72.4 (2.8)

T - treated, C - control.

Figures in brackets are standard errors(analysis based on angular trasformation of data).

Appendix Table 2.8 Effect of submerging leaves immediately after inoculation on germination and production of ESH by conidia.

	% germination (24h)						% ESH production (48h)					
E.aquilegiae						Mean						Mean
T	88.2	88.3	91.1	91.3	94.9	90.8	a. 63.2	68.8	62.9	58.7	65.9	63.9
							b. 71.4	72.6	79.3	70.4	65.2	72.4
C	95.8	95.5	94.7	95.9	92.1	94.8	73.3	70.7	75.5	79.6	75.7	75.0
E.depressa												
T	84.2	76.8	77.4	78.3	74.9	78.3	a. 0.0	0.0	0.0	0.0	0.0	0.0
							b. 50.4	48.3	64.6	54.6	58.3	55.2
C	78.5	81.2	86.7	72.3	79.4	79.6	62.7	58.4	54.5	53.7	57.8	57.4
E.verbasci												
T	54.0	60.3	64.3	58.7	62.7	60.0	a. 43.7	50.8	45.8	42.8	40.5	44.7
							b. 54.5	62.0	53.4	58.1	57.0	57.0
C	68.9	68.8	63.8	67.5	65.8	66.9	52.6	50.2	55.2	58.3	54.2	54.1
M.alphitoides												
T	92.9	95.7	96.0	90.9	95.2	94.2	a. 15.4	8.0	10.5	8.8	4.5	9.4
							b. 89.7	89.4	88.9	88.6	88.9	89.1
C	97.9	97.2	96.4	96.9	97.3	97.1	82.3	86.4	88.3	81.6	87.3	85.2

C - control, T - treated a and b refer to assessment of ESH production on leaves submerged at 0h and 24h respectively.

Appendix Table 2.9 Effect of submerging leaves on mycelial growth

	Total mycelial length (mm)											Mean
E.graminis												
T Oh	1.42	1.20	1.08	1.22	1.16	1.52	1.02	1.36	1.60	1.58	1.40	
	1.56	1.48	1.12	1.80	1.02	1.42	1.12	1.20	1.20	1.86	1.06	1.33
	1.32	1.04	1.48									
24h	2.04	1.98	2.25	2.20	1.76	1.68	2.12	1.54	1.94	1.78	1.82	
	2.02	1.88	1.64	2.12	1.58	1.46	1.48	2.06	1.42	2.22	2.12	1.88
	2.10	2.06	1.86									
C	2.96	2.84	2.90	2.28	2.36	2.88	2.42	2.32	2.78	2.26	2.56	
	2.72	2.64	2.34	2.42	2.82	2.52	2.36	2.68	2.46	2.40	2.32	2.55
	2.28	2.62	2.70									
E.pisi												
T Oh	1.88	1.88	1.82	1.76	1.78	1.92	1.46	1.10	1.52	1.68	1.72	
	1.48	1.82	1.64	1.75	1.22	1.42	1.32	1.80	1.62	1.38	1.42	1.59
	1.26	1.38	1.40									
24h	2.08	2.42	2.21	2.26	2.16	2.21	2.34	2,27	2.31	2.22	2.28	
	2.26	2.04	2.32	2.44	2.18	2.12	2.28	2.40	2.31	2.30	2.29	2.27
	2.46	2.18	2.34									
C	2.82	2.94	2.64	2.78	2.64	2.66	2.46	2.68	2.84	2.82	2.92	
	2.96	2.82	2.80	2.76	2.86	2.62	2.66	2.48	2.40	2.98	2.70	2.74
	2.62	2.78	2.86									
S.pannosa												
T oh	2.40	2.50	2.52	2.56	2.44	2.28	2.26	2.46	2.32	2.36	2.60	
	2.52	2.38	2.36	2.52	2.62	2.40	2.46	2.48	2.28	2.42	2.40	2.43
	2.32	2.48	2.42									
24h	2.62	2.74	2.50	2.54	2.66	2.64	2.76	2.62	2.82	2.76	2.68	
	2.80	2.54	2.66	2.72	2.72	2.48	2.70	2.52	2.82	2.78	2.56	2.65
	2.62	2.58	2.48									
C	3.02	3.16	3.20	3.12	3.28	3.08	3.20	3.12	3.22	3.12	3.26	
	3.10	3.28	3.22	3.14	3,26	3.30	3.32	3.32	3.20	3.22	3.18	3.19
	3.16	3,20	3.06									

C - control, T - treated, Oh and 24h refer to time of immersion after inoculation.

Each treatment involved 5 measurements on each of 5 leaves.

Appendix Table 2.10 Effect of submerging inoculated leaves on the production of conidiophores at 96h.

E.graminis		Conidiophores/mm^2 colony															Mean
T	Oh	15	13	16	8	7	7	13	11	15	16	5	12	6	8	19	11
	24h	27	25	33	26	22	32	28	30	33	37	36	26	30	24	40	30
	48h	47	39	49	34	56	53	30	46	52	62	50	52	54	57	39	48
	72h	62	45	85	30	66	66	71	61	67	44	80	63	61	70	48	61
C		84	71	98	48	83	87	57	94	62	77	71	87	97	54	79	77

E.pisi																	
T	Oh	4	0	7	0	0	9	0	0	0	11	3	2	0	2	0	3
	24h	8	4	7	0	14	12	8	9	8	11	4	12	6	7	6	8
	48h	20	15	36	6	15	23	19	17	13	18	33	24	11	12	17	19
	72h	38	22	18	18	25	12	30	26	27	30	19	20	23	33	26	24
C		34	35	44	24	48	39	45	25	41	54	17	33	41	28	35	36

S.pannosa																	
T	Oh	2	0	5	7	0	0	8	0	0	0	0	1	7	6	10	3
	24h	8	11	21	4	10	13	9	11	10	17	6	16	0	0	12	10
	48h	11	21	17	12	14	27	15	13	16	8	17	10	13	16	25	16
	72h	18	24	27	43	9	21	23	21	30	11	42	20	17	19	21	23
C		21	37	28	32	36	30	36	38	26	32	24	30	36	32	27	31

C - control T- Oh, 24h.... h-leaves submerged after inoculation.

Appendix Table 2.11 Effect of submerging leaves immediately after inoculation on germination of conidia when removed from water.

		% germination (24h)										Mean
E.graminis												
T	6h	62.2	66.6	68.7	70.4	58.4	66.6	64.3	62.4	68.5	66.7	65.5
	12h	60.7	68.5	64.2	62.8	66.5	53.3	58.8	61.3	55.6	66.4	61.8
	24h	64.3	58.8	52.3	60.6	59.3	55.4	50.6	51.6	57.8	54.3	56.5
C		69.7	78.2	81.4	68.6	72.7	74.6	74.5	73.3	84.3	79.4	75.7
E.pisi												
T	6h	89.3	80.3	78.2	82.1	79.1	80.8	84.3	86.5	82.4	79.8	82.3
	12h	70.2	78.9	79.3	78.4	80.2	78.7	79.5	74.0	77.7	76.0	77.3
	24h	78.1	72.2	68.2	73.6	76.5	73.6	71.4	71.8	78.9	75.4	74.0
C		93.7	96.3	90.2	89.1	90.4	94.6	93.9	95.8	90.6	88.8	92.3
S.pannosa												
T	6h	72.2	73.8	60.9	68.4	74.6	73.3	76.1	74.3	70.2	75.1	71.9
	12h	59.2	64.1	68.4	66.2	60.9	70.5	59.3	58.6	56.0	67.2	63.0
	24h	56.2	49.1	60.7	54.3	58.7	52.2	57.5	56.6	54.5	49.3	54.9
C		84.3	82.1	78.5	76.5	89.7	80.0	87.3	85.3	80.4	78.2	82.2

C - control, T 6h, 12h .... h in water after inoculation.

Appendix Table 2.12 Effect of submerging leaves immediately after inoculation on mycelial growth when removed from water.
(ref.Fig.2.7)

	Total mycelial length (mm)(48h)										Mean
E.graminis											
T 6h	2.28	2.74	1.08	1.20	2.20	2.17	1.90	1.35	2.64	2.51	2.01
12h	1.42	1.68	2.21	1.68	1.09	1.78	2.40	1.80	2.30	2.29	1.87
24h	1.73	2.29	2.76	1.36	1.55	1.19	1.58	1.35	1.60	1.31	1.67
48h	1.72	1.64	1.28	1.70	0.92	1.44	1.56	0.68	0.49	0.75	1.22
C	2.80	2.62	2.07	2.92	1.42	2.98	2.13	2.24	2.62	2.78	2.78
E.pisi											
T 6h	1.93	2.47	1.93	1.60	1.73	1.73	2.00	2.46	2.73	2.53	2.11
12h	1.53	1.67	2.06	1.07	1.60	1.67	1.53	2.00	1.86	1.67	1.67
24h	1.43	1.73	2.00	1.60	2.20	1.47	1.20	1.60	1.47	0.93	1.56
48h	1.07	0.87	1.27	1.47	1.53	1.20	1.00	1.27	1.67	2.00	1.34
C	1.73	2.23	1.86	2.27	2.53	2.20	2.07	2.33	2.80	2.47	2.26
S.pannosa											
T 6h	1.60	2.22	1.48	1.83	1.64	2.38	2.15	1.95	1.87	1.99	1.91
12h	1.60	1.82	1.39	0.68	1.74	1.24	2.36	2.30	1.01	2.09	1.62
24h	1.39	2.21	1.78	0.92	0.86	0.94	1.43	1.68	2.04	1.35	1.46
48h	1.72	1.48	1.33	1.44	1.01	0.90	0.93	0.78	0.98	0.90	1.15
C	3.32	2.22	2.96	2.11	2.34	2.50	2.26	2.61	3.00	2.11	2.53

C - control, T 6h, 12h ....h in water after inoculation.

Appendix Table 2.13 Effect of submerging leaves immediately after inoculation on conidiophore production when removed from water.

(ref.Fig.2.8)

E.graminis	Conidiophores/mm^2 colony										Mean
T 6h	167	257	74	169	118	210	46	94	98	109	134
12h	49	54	86	134	123	73	149	176	118	29	99
24h	12	85	99	124	84	0	111	106	29	80	73
48h	38	74	39	0	124	0	84	36	13	21	43
72h	45	7	0	0	0	0	19	24	0	0	10
96h	0	0	0	0	0	0	0	0	0	0	0
C	214	144	105	148	262	100	141	136	246	206	170

E.pisi											
T 6h	62	81	39	92	114	41	77	40	92	60	70
12h	68	20	34	46	21	78	51	32	99	40	49
24h	34	29	45	29	60	44	28	40	24	18	35
48h	19	26	14	49	27	14	8	20	61	0	24
72h	0	0	0	0	0	24	8	4	0	0	4
96h	0	0	0	0	0	0	0	0	0	0	0
C	98	79	42	68	74	81	52	108	141	62	81

S.pannosa											
T 6h	7	31	11	26	32	8	58	39	41	29	28
12h	0	7	16	30	24	13	14	29	1	12	15
24h	21	4	0	18	0	14	19	8	12	7	10
48h	0	7	0	3	10	2	0	8	0	0	3
72h	0	1	0	0	0	0	0	0	0	0	1
96h	0	0	0	0	0	0	0	0	0	0	0
C	11	48	0	72	43	14	2	68	45	59	36

C - control, T 6h, 12h ...h in water after inoculation.

Appendix Table 2.14 Effect of submerging leaves for 6h, 24h after inoculation on mycelial growth.
(ref.Fig. 2.9)

Total mycelial length(mm)

E.graminis

	Treated					Mean	Control					Mean
30h	0.78	.034	.068	.052	.048	.054	.112	0.88	0.14	0.15	1.08	0.12
36h	0.58	0.84	0.72	0.69	0.37	0.64	1.07	0.68	0.70	0.92	1.38	0.95
42h	0.82	0.69	1.07	0.82	1.90	1.06	1.94	1.23	1.45	1.92	1.68	1.64
48h	2.44	1.43	2.08	2.24	2.31	2.10	2.45	3.50	2.27	2.01	3.42	2.73
54h	2.23	3.20	3.81	3.62	2.69	3.11	3.13	3.88	3.84	3.94	3.21	3.60
60h	5.51	4.02	5.60	5.79	5.13	5.21	5.83	5.57	5.34	4.49	5.62	5.37

E.pisi

30h	0.97	0.94	0.57	0.51	0.51	0.70	0.93	0.72	0.90	0.62	1.08	0.85
36h	1.03	1.79	0.74	1.13	1.06	1.15	1.00	1.42	1.44	1.25	1.39	1.30
42h	1.93	1.30	1.59	1.65	1.78	1.65	2.29	1.84	2.36	2.42	1.14	2.01
48h	3.14	2.60	2.59	2.26	2.66	2.65	3.17	3.50	3.02	2.64	2.32	2.95
54h	3.79	3.84	3.28	3.92	3.42	3.65	3.26	3.99	4.40	4.83	4.27	4.15
60h	5.22	5.41	5.54	5.10	5.48	5.35	6.18	6,02	6.08	5.67	6.30	6.05

S.pannosa

30h	0.39	0.57	0.14	0.46	0.34	0.38	0.63	0.57	0.51	0.39	0.30	0.48
36h	0.83	0.40	0.68	0.74	0.60	0.65	1.31	0.68	1.11	0.51	0.74	0.87
42h	1.41	1.31	1.14	0.97	1.82	1.33	1.30	1.33	1.44	1.78	1.55	1.48
48h	2.33	2.18	2.66	1.78	1.70	2.13	2.66	2.33	2.22	2.44	2.00	2.33
54h	3.00	4.00	3.44	2.63	4.33	3.48	3.79	3.21	3.42	2.97	3.41	3.36
60h	4.21	4.48	5.71	4.08	5.62	4.82	5.43	4.60	4.55	5.01	3.96	4.71

Figures are means of 5 assessments on a single leaf.

Appendix Table 2.15 Effect of submerging leaves for 6h, 84h aftr after inoculation on conidiophore production.

h assessed (after inoc.)	Conidiophores/ mm^2 colony					
	E.graminis		E.pisi		S.pannosa	
	T	C	T	C	T	C
90	14	18	6	13	1	5
96	22	27	19	28	8	11
102	33	38	24	33	13	16
108	46	54	28	49	19	25
114	67	71	53	64	40	39

C - control, T - treated. Each figure is the mean of 10 assessments.

Appendix Table 2.16 Effect of submerging sporulating colonies on the production of viable conidia.

		% ESH production					Mean	SE*
E.graminis	T	62.2	68.6	47.7	53.1	54.6	57.2	6.0
	C	65.6	61.8	65.5	62.6	59.2	62.9	2.0
E.pisi	T	79.6	70.5	71.6	65.5	67.4	70.9	4.4
	C	67.6	71.9	70.4	77.1	80.9	73.6	4.4
S.pannosa	T	59.4	56.2	66.0	68.3	69.4	63.9	4.3
	C	69.4	66.3	64.9	72.7	74.1	69.5	3.1

C - control, T - treated.

*Analysis based on angular transformation of data.

Appendix Table 3.1 Effect of rain on mildew conidia immediately after inoculation.

Conidia/mm^2 leaf

E.graminis

C.1.ab	24	116	92	113	49	6.122	104	79	44	39
ad	16	42	34	29	82	9	14	23	78	43
2.ab	25	29	32	44	93	7.96	92	49	86	102
ad	116	92	78	86	60	11	49	92	46	19
3.ab	17	12	59	43	29	8.92	73	68	91	42
ad	74	96	34	66	115	29	24	96	48	114
4.ab	99	83	24	29	65	9.39	89	101	173	141
ad	18	54	99	86	72	86	39	4	11	6
5.ab	79	49	77	26	49	10.49	123	146	112	119
ad	52	72	66	91	29	69	4	23	12	3
T.1.ab	12	6	9	14	4	6.21	4	6	3	33
ad	0	3	6	13	0	2	1	0	4	4
2.ab	12	4	2	1	12	7.17	2	6	9	14
ad	13	16	23	4	2	6	29	3	4	23
3.ab	23	6	9	12	22	8.22	12	17	16	29
ad	5	11	9	24	4	9	31	4	3	0
4.ab	33	14	29	22	12	9.12	13	14	6	0
ad	4	2	1	3	3	2	4	2	9	3
5.ab	2	9	3	4	29	10.21	4	19	23	22
ad	16	19	14	13	2	6	4	2	1	4

ab-abaxial, ad-adaxial surface

E.pisi

C.1.	107	158	169	149	114	5.	199	166	154	174	131	8.	199	203	147	174	153
2.	216	189	202	192	149	6.	174	177	166	152	149	9.	141	176	139	181	141
3.	145	167	134	169	172	7.	129	114	126	161	144	10.	193	149	174	203	165
4.	120	132	116	172	141												
T.1.	0	1	0	0	1	6.	0	2	4	0	0	8.	2	0	0	0	0
2.	2	1	4	0	0	7.	4	2	0	0	0	9.	2	0	1	2	1
3.	0	0	1	0	1	8.	0	2	0	1	1	10.	0	0	1	0	0
4.	1	0	1	1	0												

S.pannosa

C.1.	109	116	64	101	109	T.1.	0	0	4	2	3
2.	46	83	84	121	94	2.	0	4	1	0	0
3.	89	119	102	122	104	3.	4	2	0	0	0
4.	68	96	112	74	105	4.	0	1	3	2	1
5.	99	124	113	114	131	5.	0	0	4	2	1

C control, T-rain subjected, 1,2.... leaf sample each with 5 assessments.

Appendix Table 3.2 Effect of rain on E.graminis during its initial development on barley.

Rain applied:

1.immediately after inoculation

a.	11.2	11.9	10.7	11.7	11.8
ab	7	12	10	13	10
ad	18	7	9	14	16

Unwetted(control)

a.	12.3	11.1	11.3	11.2	11.0
ab	101	121	86	79	68
ad	62	67	98	85	113

2.2h later

a.	11.5	11.1	11.5	12.1	11.1
ab	7	4	19	11	14
ad	14	18	4	19	15

3.4h later

a.	10.7	11.6	11.8	10.9	11.1
ab	25	21	15	16	27
ad	20	14	26	21	16

4.6h later

a.	10.7	11.3	12.1	11.0	11.0
ab	49	46	24	50	58
ad	25	20	48	32	26

5.8h later

a.	11.7	13.2	11.7	11.6	11.4
ab	58	65	29	42	50
ad	33	42	63	54	49

Ecah figure is the mean of assessment on 10 seedlings
a - area of leaf (both surfaces), ab and ad refer to the no. of colonies on abaxial and adaxial leaf surfaces.

Appendix Table 3.3 Effect of rain applied immediately (0), 24h and 48h after inoculation on mildew development.

	E.graminis					E.pisi					S.pannosa				
Rain applied															
1. immediately after inoculation															
a.	11.1	12.7	12.9	13.1	12.9	4.2	5.8	3.9	4.6	5.3	0	0	0	0	0
ad	6	7	3	4	10	0	0	0	0	0					
ab	13	12	10	9	8										
2. 24h later															
a.	12.5	12.9	11.5	11.2	12.0	4.6	4.7	5.4	4.6	5.0	2	4	2	4	3
ad	59	62	92	74	46	3	4	5	3	2					
ab	87	45	73	63	64										
3. 48h later															
a.	11.2	12.5	11.9	13.1	13.3	4.2	3.0	2.6	4.6	4.6	6	6	8	4	7
ad	99	94	87	105	66	16	14	10	13	12					
ab	79	76	98	72	113										
4. Unwetted (control)															
a.	11.7	13.0	11.8	11.6	13.3	4.6	4.4	6.2	2.7	3.8	8	6	9	7	8
ad	156	168	114	120	115	20	20	21	13	14					
ab	118	109	150	150	124										

Each figure is the mean of assessments on 10 seedlings.
a - area of leaf (both surfaces of barley and upper surface of pea) ad and ab refer to the no. of colonies(adaxial and abaxial leaf surfaces)
Mildew was rated on a scale of 0-10 in the case of S.pannosa.

Appendix Table 3.4 Effect of several periods of rain on the development of *E.graminis*.

Plants subjected to rain at:

1. 0, 24 and 48h after inoculation

a.	9.5	9.5	9.0	11.6	11.1
ad	2	0	6	9	9
ab	5	4	1	8	2

2. 24, 48 and 72h after inoculation

a.	9.9	9.5	8.2	8.5	9.9
ad	37	21	21	19	37
ab	15	31	40	22	25

3. 48, 72 and 96h after inoculation

a.	9.1	8.9	7.1	7.9	9.3
ad	43	42	32	35	60
ab	47	35	42	43	32

4. Unwetted (control)

a.	9.8	9.3	10.4	9.3	9.8
ad	89	60	88	55	78
ab	36	62	34	62	62

Each figure is the mean of assessments on 10 seedlings.
a - area of leaf, ad and ab refer to the no. of colonies on the adaxial and abaxial leaf surfaces.

Appendix Table 3.5 Effect of rain on the production of viable conidia.

E.graminis	Treated					Control				
h after which rain subjected plants used as source of inoculum										
1. immediately after wetting										
a.	11.3	11.7	12.0	10.9	10.8	12.0	11.3	12.1	12.4	11.3
ad	13	13	8	11	11	97	88	81	108	77
ab	6	7	8	9	7	127	126	141	120	116
2. 24h later										
a.	10.4	10.2	10.4	9.7	10.5	10.1	10.3	10.0	10.0	10.5
ad	32	36	29	31	35	84	93	109	118	101
ab	49	39	41	40	36	108	123	95	100	87
3. 48h later										
a.	10.5	9.8	9.9	10.5	9.9	9.4	10.9	9.8	10.3	10.4
ad	60	41	36	44	56	125	91	101	87	139
ab	47	56	65	61	46	80	104	130	138	78
4. 72h later										
a.	11.2	11.0	10.6	10.8	11.0	10.7	11.2	11.3	11.8	10.4
ad	65	80	103	51	74	60	120	107	83	109
ab	55	43	36	83	45	125	85	67	117	57

a- area of leaf ad and ab refer to no.of colonies on adaxial and abaxial leaf surfaces.

E.pisi										
1. immediately after wetting										
a.	4.2	5.0	4.9	3.8	4.4	4.6	5.0	5.3	4.9	4.7
ad	0	0	0	0	0	24	24	26	21	23
2. 24h later										
a.	5.5	4.8	4.8	4.8	5.1	5.3	4.0	4.4	5.2	5.2
ad	2	2	1	3	2	25	29	32	20	19
3. 48h later										
a.	5.0	4.0	4.9	5.0	5.3	4.5	5.4	5.2	5.2	5.1
	6	6	4	7	3	14	26	19	12	26
4. 72h later										
a.	5.4	4.3	5.2	5.3	5.6	6.2	4.3	5.7	5.6	4.4
ad	13	11	10	16	14	18	33	29	28	25

a and ad refer to leaf area and no. of colonies on adaxial leaf surface respectively.

Appendix Table 3.5 contd.

S.pannosa (mildew score)

1. immediately after wetting

0	0	0	0	0		3.3	9.4	2.8	6.2	1.4

2. 24h later

1.0	2.5	2.0	2.0	1.8		7.2	4.8	6.1	9.3	3.8

3. 48h later

4.3	3.0	4.0	3.4	1.5		6.4	5.2	8.3	9.8	9.4

4. 72h later

5.8	4.8	6.3	4.0	3.3		6.4	9.2	8.2	4.7	9.8

Mildew scored on 1-10 scale

Each figure is the mean of 10 assessments

Appendix Table 3.6 Effect of droplet size on the removal of conidia of E.graminis immediately after inoculation.

Treated:

Droplet size 2 mm: Conidia/mm^2 leaf

drops no.																Mean
1	94	69	150	89	74	132	48	108	120	53	114	103	126	92	39	94
10	0	1	16	24	19	5	3	8	22	0	17	20	30	6	2	12
20	9	0	16	2	0	13	10	0	6	18	2	19	0	22	4	8

Droplet size 4 mm:

drops no.																
1	84	35	42	76	59	109	23	39	59	49	72	10	105	117	28	61
10	2	5	2	0	1	5	0	1	1	2	0	0	6	0	0	5
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Control :

145	108	182	100	149	121	128	143	155	120	130	142	108		138
133	200													

Each treatment involved 15 assessments (3 from each of 5 leaves)

Appendix Table 3.7 Effect of different height of fall on the removal of conidia of E.graminis immediately after inoculation.

Treated:

Height of fall 0.5 m drops no.	Conidia/mm^2 leaf	Mean
1	108 100 71 95 91 102 97 89 112 103 119 84 75 96 103	96
5	30 36 40 37 22 36 24 33 37 29 41 42 39 43 48	36
10	12 14 10 19 8 23 0 12 11 4 9 11 13 8 6	11
20	7 6 9 0 8 6 4 1 9 6	6
Height of fall 1.0 m		
drops no.		
1	92 96 74 72 69 99 84 92 94 85 102 84 81 65 87	85
5	27 27 33 24 25 41 26 33 35 30 26 29 34 37 39	31
10	8 6 0 9 2 7 5 6 0 7 8 6 7 2 9	5
20	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0
Height of fall 1.5 m		
drops no.		
1	79 81 84 72 75 69 64 81 62 71 72 66 74 69 75	73
5	24 23 26 21 18 18 16 14 14 16 18 29 21 26 17	21
10	4 6 2 9 2 3 5 2 6 2 6 9 4 3 9	5
20	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0
Height of fall 2.0 m		
drops no.		
1	52 49 56 42 41 46 54 69 51 29 72 32 46 51 44	48
5	24 31 18 19 16 13 14 21 26 14 19 23 24 19 13	20
10	6 5 0 4 0 4 0 0 0 6 4 0 9 2 8	3
20	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0
Height of fall 2.5 m		
drops no.		
1	49 42 52 29 34 32 61 36 31 34 47 42 46 42 51	42
5	19 17 21 18 16 12 18 19 16 13 14 16 21 14 14	17
10	6 4 5 0 6 3 0 0 0 0 3 0 0 0 2	2
20	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0
Control:		
	197 176 164 183 202 172 167 182 181 167 165 182 149 169 180	176

Each treatment involved 15 assessments(3 from each of 5 leaves)

Appendix Table 3.8 Effect of water droplets on mildew conidia immediately after inoculation.

E.graminis

Treated: drops no.	Conidia/mm^2 leaf	Mean
1	26 41 32 22 29 43 28 29 34 32 29 30 24 26 27	30
5	4 6 7 11 9 14 10 8 9 6 8 9 11 12 7	9
10	3 0 6 4 2 10 0 7 2 2 4 6 3 2 2	4
20	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0
Control:	129 148 107 99 145 168 114 100 137 126 121 144 107 119 123	126

E.pisi

Treated: drops no.		
1	53 70 64 51 70 49 69 59 23 74 54 60 62 61 55	58
5	18 19 22 24 21 9 26 22 14 12 19 28 39 18 20	21
10	7 18 12 6 6 0 0 12 14 9 9 6 5 11 7	8
20	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0
Control:	176 136 123 145 162 179 141 147 161 152 135 125 174 149 171	152

S.pannosa

Treated: drops no.		
1	20 10 24 19 13 16 26 12 24 18 25 11 14 19 21	18
5	6 4 3 0 3 2 4 5 0 2 5 1 2 7 3	3
10	5 0 0 2 1 2 1 2 3 0 2 1 0 0 0	1
20	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0
Control:	79 52 45 50 64 63 74 54 77 63 64 65 72 49 46	61

Each treatment involved 15 assessments (3 from each of 5 leaves)

Appendix Table 3.9 Effects of water droplets on mildew conidia after different periods of incubation at 20°.

Conidia/mm^2 leaf

	E.graminis						E.pisi						S.pannosa					
Treated at:						Mean						Mean						Mean
0h	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1h	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2h	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3h	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4h	4	3	44	3	1	3	2	0	1	3	2	2	2	1	2	2	2	2
5h	7	6	8	5	10	7	4	5	7	8	7	7	6	6	6	7	6	6
6h	10	9	11	12	12	11	10	15	12	13	12	12	8	9	6	9	7	8
7h	13	14	11	9	12	12	15	18	14	15	15	15	9	12	10	11	10	10
8h	14	15	15	10	16	14	18	18	21	20	24	20	11	12	13	12	12	12
9h	16	18	12	14	17	15	20	23	19	26	22	22	12	11	13	13	16	13
10h	15	19	23	14	20	18	27	34	30	30	24	29	13	13	15	12	16	14
24h	22	18	25	17	25	21	41	52	46	46	50	47	37	28	36	28	34	33
Control:																		
	79	91	88	70	81	82						106						63

Each figure represents assessment on single leaf (mean of 3 assessments per leaf)

Appendix Table 3.10 Damage to germinating conidia by impacting water droplets applied 24h after inoculation.

	Conidia/mm^2 leaf																	
	E.graminis						E.pisi						S.pannosa					
Control:						Mean						Mean						Mean
Ungerminated conidia	25	40	30	42	49	37	22	20	25	18	24	22	25	22	22	23	13	23
Germinated conidia	87	89	94	99	113	96	129	99	115	108		119	54	49	52	64	76	57
Total							146											
Treated:																		
Ungerminated conidia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Germinated conidia																		
1.conidiun intact	41	39	45	43	49	43	75	58	79	84	86	76	47	41	53	38	29	42
2.conidium removed	38	34	32	41	42	37	35	23	38	34	34	33	12	15	9	5	7	10

Each figure represents assessment on a single leaf (mean of 3 assessment per leaf).

Appendix Table 3.11 Effects of water drop impaction on mycelial growth.

	Total mycelial length (mm)					Mean
E.graminis						
A. Direct effect of impaction						
1. impaction at 24h						
T	0.031	0.032	0.030	0.031	0.030	0.031
C	0.031	0.030	0.032	0.029	0.031	0.031
2. impaction at 36h						
T	0.86	0.92	0.72	0.65	0.66	0.76
C	1.28	1.22	1.63	1.24	1.42	1.36
3. impaction at 48h						
T	1.39	1.33	1.16	1.43	1.75	1.41
C	2.29	2.44	2.22	2.51	2.34	2.36
4. impaction at 60h						
T	2.85	2.97	2.77	2.63	3.39	2.92
*C	5.73	5.50	5.37	5.27	5.24	5.34
B. Indirect effect of impaction						
1. impaction at 24h/assessment at 60h						
	1.07	1.10	2.08	1.79	2.20	1.65
2. impaction at 36h/assessment at 60h						
	2.92	3.85	3.06	2.93	2.04	2.96
3. impaction at 48h/assessment at 60h						
	2.61	3.92	2.05	3.12	4.68	3.29

*Control as above

E.pisi						
A. Direct effect of impaction						
1. impaction at 24h						
T	0.28	0.31	0.18	0.35	0.27	0.28
C	0.33	0.30	0.29	0.30	0.32	0.31
2. impaction at 48h						
T	2.28	1.30	2.19	1.16	1.11	1.67
C	2.46	2.33	2.51	2.19	2.57	2.41

Appendix Table 3.11 contd.

3.impaction at 72h

*T	3.89	3.03	6.38	2.86	6.23	4.48
C	7.24	7.71	7.36	6.77	7.33	7.28

B. Indirect effect of impaction

1.impaction at 24h/assessment at 72h

T	1.62	3.07	0.93	2.64	2.94	2.24
C						

2.impaction at 36h/assessment at 72h

	4.22	2.95	4.75	2.99	6.05	4.19

3.impaction at 48h/assessment at 72h

	3.23	4.64	2.15	4.14	3.89	3.61

4.impaction at 60h/assessment at 72h

	3.17	3.15	4.40	1.72	4.36	3.36

*Control as above

S.pannosa

A. Direct effect of impaction

1.impaction at 24h

T	0.35	0.38	0.40	0.33	0.38	0.37
C	0.40	0.37	0.38	0.40	0.40	0.39

2.impaction at 36h

T	1.45	0.85	0.75	0.84	0.71	0.92
C	1.38	1.49	1.47	1.48	1.45	1.45

3.impaction at 48h

T	1.83	1.41	2.34	2.20	1.03	1.80
C	2.68	2.69	2.77	2.62	2.73	2.70

4.impaction at 60h

*T	2.51	5.88	4.13	6.54	5.50	4.91
C	6.12	7.64	5.94	7.23	7.92	6.97

B. Indirect effect of impaction

1.impaction at 24h/assessment at 60h

	2.25	0.33	3.80	2.63	1.11	2.02

2.impaction at 36h/assessment at 60h

	2.35	3.31	1.31	2.56	5.01	2.91

3.impaction at 48h/assessment at 60h

	3.65	4.24	3.52	4.82	1.99	3.64

*Control as above

Each figure is the mean of 5 assessments on a single leaf.

T - treated, C - control.

Appendix Table 3.12 Direct and indirect effects of impacting water droplets on conidiophore production at 96h.

E.graminis

	Conidiophores/mm^2 colony	Mean
Control:		
	76 79 81 78 76 72 67 84 70 74 66 76 81 74 83 83 80 76 84 78 74 78 78 82 77	77
Impaction at:		
24h	0 0 0 78 76 68 0 74 0 0 46 63 0 0 70 10 0 63 54 0 20 0 51 0	27
36h	0 73 55 0 0 69 51 0 68 0 0 61 0 48 41 39 0 68 0 65 72 70 12	32
48h	12 34 31 32 26 14 33 10 42 43 62 61 54 62 37 48 34 16 34 33 72 64 25 41 48	39
60h	21 65 43 54 28 26 24 29 57 64 51 42 35 26 27 29 33 45 61 54 63 52 48 51 36	42
72h	53 43 34 21 55 60 61 51 22 45 24 22 62 18 37 42 16 43 21 40 19 17 45 44 27	47
96h	64 68 58 48 49 72 74 49 55 62 44 66 88 51 53 65 51 43 40 58 59 34 61 56 49	57

E.pisi

Control:		
	169 156 122 98 121 140 181 84 149 148 151 132 121 144 174 148 155 164 151 114 76 157 102 157 142	138
Impaction at:		
24h	19 49 0 28 25 47 128 31 32 22 131 0 18 33 34 39 21 37 29 37 36 143 0 6 28	39
36h	43 131 71 68 74 0 78 110 114 38 113 0 51 10 72 63 104 6 41 53 2 41 48 32 71	57
48h	5 102 146 85 40 108 0 121 6 93 83 9 11 88 72 98 85 124 84 32 114 64 96 81 70	73
60h	97 164 0 125 67 3 138 15 86 80 12 113 123 106 7 1 114 138 75 43 129 18 93 64 132	78
72h	70 118 3 0 150 149 54 79 45 121 129 18 152 47 96 27 101 68 58 143 44 66 104 88 26	78
96h	138 0 14 158 163 7 121 52 140 113 0 0 113 104 108 88 32 0 7 122 148 155 107 64 108	83

S.pannosa

Control:		
	84 13 42 73 163 68 38 69 76 41 68 55 21 33 85 62 3 79 18 42 173 9 116 24 7	58

Appendix Table 3.12 contd.

Impaction at:

24h	13 14 0 27 14 26 0 1 25 18 31 21 6 22 3 2 26 18 5 35 4 21 26 4 11	15
36h	18 2 33 16 28 41 0 3 26 39 35 47 13 14 7 25 40 16 20 5 13 18 19 24 31	21
48h	12 34 2 44 51 29 43 14 29 43 17 4 16 12 0 12 0 7 60 3 34 2 54 4 18	22
60h	42 16 28 14 31 12 0 17 46 19 33 0 61 36 37 22 0 7 27 42 35 64 15 19 27	26
72h	61 0 72 0 14 29 33 54 21 18 59 16 31 49 42 51 49 7 2 0 38 64 32 17 1	30
96h	80 0 0 12 8 24 49 2 36 0 48 10 0 0 19 22 76 12 77 26 34 22 6 19 8	25

Each treatment involved 5 assessments on each of 5 leaves

Appendix Table 3.13 Effects of rain on E.pisi.

																	Mean
1.a. Conidia/mm^2 leaf (0h)																	
T	U	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	L	12	8	13	8	9	10	13	9	7	16	11	14	17	11	21	12
C	U	33	35	53	30	30	24	36	25	23	30	26	37	41	33	30	32
	L	29	42	52	33	27	48	45	23	28	36	19	24	38	34	46	35
b.Conidia/mm^2 leaf (24h)																	
T	U	29	4	8	12	19	10	2	9	13	8	17	21	4	0	2	11
	L	38	54	40	62	36	54	28	32	23	38	42	48	34	53	49	42
C	U	67	62	47	39	43	42	34	46	30	48	47	70	67	64	65	51
	L	52	39	64	29	72	49	44	38	43	48	51	46	63	54	36	49
2. Germ-tube length (µm)(24h)																	
T	U	14	10	7	6	10	44	3	7	28	51	3	16	54	62	5	10
		39	21	27	4	2	6	14	28	24							19.8
	L	42	39	44	34	19	30	38	35	48	44	62	51	68	28	19	60
		45	32	30	28	48	54	62	31	20							40.4
C	U	49	46	53	43	65	27	42	51	43	47	43	41	38	42	27	50
		42	49	49	43	41	51	46	41	46							44.6
	L	52	41	29	39	43	64	29	52	29	41	62	54	41	49	50	46
		35	51	47	30	51	45	40	39	54							46.1
3a.Total mycelial length(mm)(48h)																	
T	U	0.17	1.31	0.23	0.17	0.09	0.27	0.11	1.14	1.31							
		0.40	1.60	1.08	1.14	0.86	0.17										0.67
	L	1.31	0.97	1.14	1.20	1.08	1.25	1.14	1.14	1.14							
		1.43	1.20	1.03	1.14	1.31	1.20										1.18
C	U	1.37	1.65	1.02	1.15	1.37	1.65	1.65	1.31	1.14							
		1.20	1.48	1.37	1.31	1.25	1.25										1.34
	L	1.68	1.14	1.37	1.29	1.14	1.25	1.48	1.25	1.72							
		0.88	0.97	1.31	1.20	1.48	1.20										1.29
b.Total mycelial length(mm)(72h)																	
T	U	1.56	0.50	0.63	3.68	1.00	2.56	0.56	0.63	1.38							
		0.88	0.13	5.19	3.25	0.31	3.75										1.73
	L	5.13	4.38	4.06	3.12	2.88	4.00	3.75	3.31	2.56							
		4.69	3.75	3.31	2.69	4.00	4.12										3.72

Appendix Table 3.13 contd.

C	U	4.44	4.94	4.19	3.88	3.63	3.38	3.63	4.56	5.50	4.13	
		3.69	4.00	3.75	2.81	3.44						4.00
	L	3.06	3.31	2.81	4.69	3.81	3.75	4.13	3.43	3.88	3.88	
		4.69	4.19	3.81	4.50	3.86						3.85

4a. Conidiophore/mm^2 colony(96h)

T	U	29	42	24	00	14	0	0	7	31	62	18	0	0	2	8	14	29
		28	34	0	9	27	34	12	43									19
	L	45	3	35	30	53	21	31	43	31	14	43	57	54	61	44	17	52
		33	34	56	64	12	43	38	35									38
C	U	48	46	42	35	45	34	24	8	36	62	41	60	85	82	64	62	67
		44	21	0	46	27	45	29	68									45
	L	39	54	68	13	29	44	54	60	3	80	56	52	60	29	63	54	19
		62	43	38	52	16	18	23	50									43

b. Conidiophore/mm^2 colony(120h)

T	U	101	0	71	57	0	0	50	0	99	9	102	47	176	25	0	0	0
		0	131	80	126	33	115	71	142									57
	L	97	113	77	85	46	119	38	61	119	75	85	107	108	97	94	116	
		57	31	129	77	99	108	116	53	75								87
C	U	108	108	66	97	112	105	101	102	68	113	96	58	105	97	157		
		90	135	82	93	60	112	28	97	108	105							96
	L	83	78	103	69	117	38	96	72	98	67	82	114	67	113	76	80	84
		128	39	92	109	107	88	79	163									90

C - control, T - treated, U - upper leaf surface, L - lower leaf surface.

Appendix Table 4.1 Effect of washing leaves on mildew development.

1. % germination(24h)

											Mean
A.	W	84.4	78.9	80.5	71.2	83.8	77.9	75.8	78.7	71.6	82.7	78.6
	UW	80.2	84.6	79.1	72.4	86.4	72.0	86.5	82.7	76.6	82.8	80.3
B.	W	92.5	91.8	79.9	80.6	82.4	79.1	86.8	91.9	78.9	82.0	84.6
	UW	89.4	92.1	92.6	84.7	81.3	89.6	92.0	80.1	91.2	90.9	88.4
C.	W	59.3	66.8	60.1	59.2	63.3	74.3	70.2	71.0	69.1	75.2	66.9
	UW	64.0	61.9	71.5	70.7	69.5	71.4	71.7	68.6	70.4	71.8	69.2

2. Germ-tube length(µm)(24h)

																		Mean
A.	W	30	26	16	40	24	46	28	34	26	44	42	26	32	42	34	30	40	34
		38	46	40	30	28	38	30	38										
	UW	56	26	52	38	32	54	60	28	30	38	44	28	42	32	34	48	60	44
		56	30	62	46	50	62	48	62										
B.	W	48	60	42	56	58	66	44	68	30	80	58	30	40	42	62	50	46	53
		50	82	78	58	28	36	50	58										
	UW	66	66	72	70	46	80	66	72	54	46	60	72	76	66	80	62	36	67
		74	82	54	62	78	72	72	80										
C.	W	80	92	78	60	72	58	96	94	54	96	84	60	48	98	60	94	94	73
		82	68	54	42	28	74	64	86										
	UW	60	54	68	78	74	64	60	54	48	42	68	74	46	52	50	68	50	56
		86	48	60	52	48	36	22	50										

3. Mycelial growth(mm)(48h)

																		Mean
A.	W	1.26	1.68	2.26	1.68	1.05	1.68	1.89	1.47	2.68	1.89	1.05	1.26	1.26	1.68	1.47	1.08	1.58
		2.18	1.68	1.05	1.31	1.47	1.47	1.28	1.68	2.08								
	UW	2.52	1.15	2.52	2.73	2.52	2.10	2.10	1.94	2.73	2.73	3.15	2.10	2.52	1.31	1.31	2.94	2.30
		2.73	1.52	1.73	2.94	2.73	2.52	2.94	1.62	2.34								
B.	W	3.78	2.20	3.78	2.41	3.20	3.20	4.41	3.99	2.21	2.20	3.78	3.20	3.78	3.20	2.99	3.78	3.10
		2.20	2.68	2.79	3.12	2.72	3.48	2.92	2.89	2.64								
	UW	2.52	3.36	1.94	2.57	2.57	2.92	2.36	2.78	2.57	1.68	3.57	2.36	2.52	2.36	1.94	1.36	2.28
		1.78	3.78	1.99	1.72	1.64	2.36	1.24	1.26	1.95								

Appendix Table 4.1 contd.

C. W	3.54	3.82	4.44	2.46	4.00	3.30	2.58	3.92	3.20	3.76	3.36
	2.94	2.92	2.28	3.74	3.66	3.76	3.92	4.26	3.70	4.12	
	3.76	2.42	2.68	2.12	2.70						
UW	2.30	3.04	4.12	2.36	2.98	2.64	3.08	3.22	2.12	2.22	2.65
	2.80	3.38	1.86	3.20	2.92	1.92	2.42	2.36	2.92	1.68	
	2.82	2.78	2.48	2.88	1.80						

4. Conidiophores/mm^2 colony (96h)

A. W	47	29	18	73	26	54	24	25	41	33	52	19	34	50	24	37
UW	63	24	21	40	20	43	68	30	26	51	45	33	32	62	24	39
B. W	52	68	74	29	90	20	21	33	86	49	74	31	61	98	92	59
UW	81	22	44	61	29	14	64	38	23	26	49	43	23	55	41	41
C. W	23	28	7	16	9	0	39	18	0	0	63	25	31	0	40	19
UW	3	17	12	49	3	9	24	11	0	13	29	24	2	0	0	13

A - E.graminis, B - E.pisi, C - S.pannosa

W - washed leaf, UW - unwashed leaf.

Appendix Table 5.1 Effect of water stress on germination of conidia.

A.Water stress by cessation of watering

E.graminis	% germination										Mean (SE)*
-2.8	82.5	75.6	79.2	76.7	80.6	81.6	74.1	77.4	78.3	80.7	78.7 (1.4)
-6.2	80.8	62.7	81.1	74.4	75.4	66.1	79.5	78.3	66.1	81.3	74.6 (3.3)
-7.9	82.4	84.3	76.3	72.6	74.4	74.1	78.3	75.4	79.0	80.4	77.7 (1.9)
-9.0	72.7	76.5	74.5	80.4	81.5	72.6	74.6	72.7	74.2	79.2	75.9 (1.6)
-14.1	76.7	75.8	78.0	79.4	76.9	79.1	78.5	70.5	79.2	72.6	76.9 (1.4)
E.pisi											
-4.8	93.8	91.0	89.4	92.3	90.2	83.9	94.9	82.3	96.7	94.9	90.9 (3.3)
-6.9	95.1	92.9	86.7	92.2	96.8	93.8	93.5	87.2	93.6	91.7	92.4 (2.4)
-9.7	87.9	97.2	93.6	93.0	94.3	92.6	93.6	88.0	87.8	97.4	92.7 (2.8)
-10.7	94.2	95.3	91.5	88.9	93.8	94.2	86.6	94.4	97.2	96.3	93.2 (2.6)
-12.4	93.0	94.4	84.3	95.3	5.8	92.6	85.6	94.2	94.5	84.8	91.6 (3.4)
S.pannosa											
-3.5	75.0	70.9	69.4	73.9	71.9	67.8	75.6	72.1	73.8	62.1	71.3 (1.8)
-4.9	76.0	70.0	63.1	73.5	69.9	74.8	60.5	70.9	71.0	67.9	69.8 (2.1)
-6.7	74.4	69.2	60.4	67.3	60.8	74.5	63.2	71.4	72.0	58.6	67.2 (2.6)
-9.3	71.4	61.4	72.7	72.4	74.5	58.7	70.8	74.6	65.4	72.7	69.3 (2.5)

B.Water stress by PEG

E.graminis											
-2.1	75.8	82.4	79.6	82.7	80.4	76.0	79.1	78.3	84.6	86.1	80.5 (1.8)
-4.1	82.6	84.8	88.1	78.2	82.1	85.2	76.2	84.2	83.7	85.2	83.0 (1.6)
-5.2	84.6	88.6	75.3	82.0	86.0	79.4	85.8	78.3	86.6	74.8	82.1 (2.6)
-7.2	88.4	73.0	85.2	86.7	89.2	86.5	85.4	86.3	80.9	80.5	84.2 (2.6)
-11.4	85.7	70.8	82.0	75.8	75.8	84.5	85.9	81.5	70.0	88.2	80.0 (3.3)
E.pisi											
-3.8	93.5	96.5	94.6	94.1	96.2	95.8	85.8	96.5	97.1	91.3	94.1 (2.7)
-5.5	94.4	96.7	95.1	87.1	96.6	96.9	90.5	96.5	98.2	86.3	94.8 (3.5)
-6.9	95.7	95.6	88.8	94.5	96.2	95.2	90.5	93.2	93.5	94.5	93.8 (1.9)
-9.3	95.6	90.1	91.6	94.8	92.8	94.9	95.6	95.0	97.7	87.0	93.5 (2.6)
-11.0	96.7	94.1	90.6	96.1	91.6	94.5	96.3	90.9	86.5	82.3	92.0 (3.4)

*Analysis based on angular transformation of data.

Appendix Table 5.2 Effect of water stress on mycelial growth.

Total mycelial length(mm)(48h)

A.Water stress by cessation of watering							B.Water stress by PEG						
						Mean							Mean
E.graminis													
-2.8	2.05	2.90	2.60	2.80	2.70	2.61	-1.1	1.05	2.15	2.35	2.50	2.40	2.09
-5.2	1.20	2.35	2.40	2.35	2.10	2.08	-4.3	1.20	1.75	2.45	1.20	1.70	1.66
-7.2	1.80	1.60	1.45	1.50	1.25	1.52	-7.1	1.45	1.55	1.20	1.60	0.95	1.35
-9.7	0.90	0.80	0.80	0.60	0.50	0.72	-9.7	0.60	0.85	0.45	1.15	1.05	0.82
-12.9	0.55	0.60	0.45	0.30	0.65	0.51	-13.3	0.30	0.70	0.75	0.35	0.75	0.57
E.pisi													
-3.8	2.70	2.30	2.35	2.85	2.45	2.53	-3.5	2.40	2.50	2.70	2.40	2.25	2.45
-5.9	2.10	2.05	1.90	2.65	1.35	2.01	-6.2	2.40	2.15	2.25	2.40	2.15	2.27
-8.3	1.95	1.15	1.90	1.25	1.75	1.60	-7.6	1.40	1.30	1.65	1.60	1.95	1.58
-10.3	0.65	1.05	1.10	1.25	0.75	0.96	-8.6	0.95	1.05	1.15	1.10	1.25	1.10
-12.4	0.45	0.60	0.75	0.50	0.90	0.64	-12.1	0.40	0.70	0.25	0.45	0.40	0.44
S.pannosa													
-1.7	2.15	1.80	1.75	2.00	2.55	1.85							
-4.5	1.35	2.05	2.10	1.60	1.00	1.62							
-6.2	0.90	0.90	0.70	1.20	1.00	0.94							
-9.1	0.70	0.60	0.90	0.25	0.50	0.59							

Each figure represents the mean of 5 assessments on a single leaf.

Appendix Table 5.3 Effect of water stress on conidiophore production.

Conidiophores/mm^2 colony

A. Water stress by cessation of watering

E. graminis						Mean
-2.1	49	48	59	50	54	52
-3.1	49	30	35	45	33	38
-5.2	21	36	27	40	38	32
-6,6	12	18	8	12	24	15
-8.3	0	6	9	0	9	5
E. pisi						
-1.4	136	143	127	138	96	128
-5.5	77	53	48	63	72	63
-9.7	27	19	18	23	18	21
-13.1	0	4	8	1	0	3
-13.8	0	0	0	0	0	0
S. pannosa						
-2.1	21	40	27	37	30	31
-5.2	21	29	17	25	10	20
-9.0	3	9	11	17	20	12
-11.4	0	0	0	0	0	0

B. water stress by PEG

E. graminis						Mean
-2.1	55	60	63	51	65	59
-4.5	48	36	39	41	42	41
-5.2	16	13	26	31	25	22
-7.2	14	13	16	7	19	14
-10.3	4	8	0	0	10	4
E. pisi						
-2.4	137	74	122	127	150	122
-3.8	85	61	44	92	93	75
-9.0	35	19	22	28	40	29
-11.0	0	10	21	9	10	10
-15.2	0	0	0	0	0	0

Each figure represents mean of 5 assessments on a single leaf.

Appendix Table 5.4 Effect of water stress on infectivity of conidia

% ESH production (48h)

A. Water stress by cessation of watering

E.graminis											Mean(SE)*
-3.2	54.2	52.9	68.0	65.6	65.0	60.9	54.9	59.0	54.0	70.9	60.5(2.8)
-5.4	64.6	69.6	58.5	58.4	64.6	56.1	59.1	61.5	58.5	51.9	60.3(2.1)
-8.0	54.8	67.0	60.1	52.7	53.9	73.6	54.5	59.2	52.3	55.7	58.4(3.0)
-10.8	58.5	53.7	63.8	67.1	67.2	55.2	50.3	55.5	55.4	54.1	57.1(2.5)
-14.3	54.8	42.9	66.1	59.3	54.1	47.8	69.6	60.1	54.1	50.7	56.0(3.4)
E.pisi											
-2.1	73.8	73.6	70.4	75.6	73.3	73.3	77.9	75.8	71.3	66.7	73.2(1.4)
-4.0	75.1	72.1	76.1	77.6	77.8	72.1	79.0	78.5	73.9	71.5	75.4(1.4)
-6.2	75.5	70.4	73.6	76.8	76.2	72.4	72.7	63.7	73.8	77.6	73.3(1.8)
-8.4	78.0	75.8	77.5	73.7	71.8	76.8	78.7	78.3	77.0	78.3	76.6(1.1)
-10.0	70.0	68.7	70.9	71.1	72.3	68.4	75.7	71.5	70.5	72.2	71.1(0.9)
S.pannosa											
-2.2	45.2	67.9	69.4	53.3	62.6	54.9	68.2	68.0	65.6	55.5	61.1(3.5)
-5.2	63.2	54.7	58.7	48.7	64.5	52.7	57.7	66.4	58.5	64.2	58.9(2.4)
-9.7	52.9	68.6	52.2	53.7	46.6	45.7	68.8	60.1	49.8	45.7	54.4(3.6)
-12.9	48.4	63.5	55.2	59.2	55.3	50.9	52.3	52.8	48.5	57.4	54.4(2.0)

B. Water stress by PEG

E.graminis											
-3.2	63.6	67.5	62.4	72.4	67.9	60.8	68.9	64.0	63.0	66.7	65.7(1.5)
-6.3	63.9	62.4	59.2	60.2	57.7	64.4	65.3	65.2	59.6	62.9	62.1(1.2)
-9.8	65.5	60.4	68.4	64.7	65.0	67.2	67.0	65.8	65.0	63.1	65.2(1.0)
-12.1	62.4	55.2	55.9	56.2	58.7	64.5	62.2	63.6	64.4	57.3	60.0(1.6)
-14.7	66.0	59.0	50.4	50.7	44.2	65.0	66.4	52.5	51.7	61.9	56.8(3.3)
E.pisi											
-1.7	70.7	74.5	74.3	76.4	72.5	71.8	80.7	71.9	78.5	74.5	74.6(1.5)
-3.5	81.4	74.3	77.5	75.4	75.5	74.6	72.8	75.4	74.3	75.2	75.6(1.2)
-8.3	77.3	78.5	84.1	87.0	83.4	68.8	74.8	75.3	71.8	75.8	77.2(3.3)
-10.3	74.1	74.4	82.3	87.4	81.2	78.3	75.2	79.6	77.2	74.3	78.4(2.2)
-13.4	74.9	76.1	81.3	74.5	82.1	74.7	79.5	81.8	81.2	76.1	78.2(1.6)

*Analysis based on angular transformation of data.