2) Malachite green - Acid Fuchsin - Martius Yellow (Pianeze IIIB stain for differentiating fungus and host cells. From Gurr, 1965).

The resin sections on slides were immersed for three to five minutes in a saturated solution of sodium hydroxide in absolute ethanol to remove the resin. The slides were then immersed for five minutes each in 100 percent, 10 percent and 50 percent alcohol and then stained with Pianeze IIIB stain (1 percent aqueous malachite green; 1 percent acid fuchsin, 1 percent Martius yellow in 95 percent alcohol and distilled water (W/V)) for sixty minutes. The excess stain was washed away with a few drops of 95 percent alcohol for one to two minutes, and the slides transferred to acified alcohol (1 percent acetic acid in 95 percent alcohol) for half a minute. The slides were then washed with a few drops of 95 percent alcohol followed by a wash in absolute alcohol, and then mounted in Permount. The fungal mycelia stain bright pink, and the host cells green/brown.

3) Aniline blue - safranin (Vágás and Maácz, 1960)

The resin was removed with saturated sodium hydroxide in absolute ethanol for five minutes and passed through a graded alcohol series. The sections were stained in Safranin O (1g/100mℓ distilled H_2O) for five minutes, flooded with aniline blue (2.5g/25mℓ distilled H_2O in saturated aqueous picric acid) and heated for a few minutes. After rinsing off the excess stain, the sections were differentiated in a few drops of NaOH (1g/100mℓ). After washing in distilled water and 90 percent alcohol, the sections were mounted in Permount for viewing in the light microscope. Hyphae appear dark violet in contrast with the pale light blue/purple ground tissue.

6.4 RESULTS

4.1 Autoradiography

4.1.1 Feeding *D. eriantha* leaves with D - (6 - ^{3}H) glucose before spore inoculation

Oblique transverse sections taken through inoculated leaves, 4h after incubation (Fig. 96A) indicated that the spores (arrows) had not yet germinated. The uredospores only germinated after 16h (Fig. 96B), with the germ tubes staining a purple colour. This delay in fungal development could be due to the lack of ideal germination conditions in the growth cabinets. Figs. 97-100 represent a serial section series through inoculated *D. eriantha* leaf tissue. Evidence of fungal structures in the epidermal cells can be observed in Figs. 98-100. It is possible that penetration does occur directly through the epidermis, since continuity of the 'infection peg', in the inter-cellular space, (Fig. 100) with the 'hyphal-like' structures in the epidermal cells (Figs. 98 & 99), was observed. Penetration was observed through stoma in some cases (Fig. 101). Note the violet stain taken up by the penetration structure (Fig. 101). Even though these intracellular fungal mycelia (Figs. 98-100) did not take up the stain as in the case of the germ tubes, further fungal differential staining with malachite green - acid fuchsin - martius yellow, revealed the presence of bright pink mycelia in the epidermal cells (Fig. 102). Further support for these being fungal structures arises from the fact that mature epidermal cells of *D. eriantha* do not possess cellular contents, and therefore the possibility of these intracellular structures being plasmolysed cell contents is unlikely. The irregular appearance of these intracellular structures may be explained by the plane of sectioning through the branched mycelia.

The 'penetration peg' (Fig. 100) wall stains blue/purple and the cellular contents stain red-brown. This staining pattern was also observed in 'intracellular bodies' (open arrows, Figs. 98, 100, 104) in leaf cells. It is possible that these 'intracellular bodies' are haustoria since their cell walls are too thick to be any cellular organelle.

The variability in stain uptake between intracellular mycelia, 'penetration pegs' and germ tubes may be due to lack of stain penetration once the fungus enters the leaf tissue, especially in resin-embedded sections. However, the stains employed in this study (3.3) have, in the past, only been utilized for differentiating general fungal mycelia from host cells. Differences in the staining properties of infection processes at different stages of penetration have not been investigated. Indeed, it is possible that changes in cellular chemistry and cell wall components of the fungal infection processes, which occur during differentiation, may lead to variability in the staining patterns.

In some cases, four infection hyphae (Fig. 103) were observed to occur without the formation of a sub-stomatal vesicle.

Each autoradiograph was examined under bright and dark-field illumination. Labelled glucose was incorporated in both healthy (Figs. 105 B and 106 B) and infected (Figs. 105 A and 106 A) *D. eriantha* leaf tissue. Since most of the soluble glucose was leached out during fixation and dehydration, the radioactive tracer is incorporated into insoluble starch in the mesophyll and bundle sheath (Fig. 105 A) chloroplasts; polysaccharides in the cell wall, and unidentified cellular components. Quantitative counts were not made in this study. Where label occurred, it could be readily located against the low background, and in most cases the granulation was too dense to allow accurate counting. The distribution of silver grains in infected tissue changed in comparison to healthy leaf tissue. In infected tissue ^{3}H - glucose accumulated in the mesophyll cells (Fig. 105 A, and 107 A, 108 A) in the areas of infection.

LEGENDS

bsc - bundle sheath cell
E - epidermis
ih - infection hyphae
ip - infection peg
H - haustorium
m - mesophyll
p - pustule
sh - sclerenchyma
ssv - substomatal vesicle
u - uredospore
Vb - vascular bundle
my - intracellular mycelium
N - nucleus

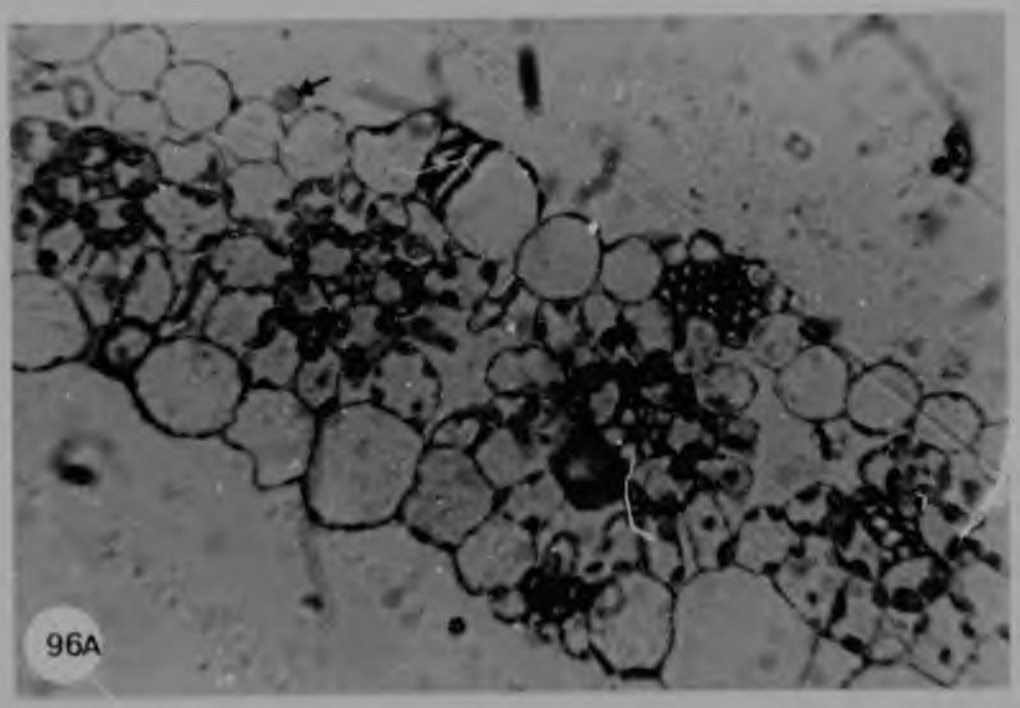


Fig.96A Transverse section (LM) through a *D. eriantha* leaf 4h after uredospore inoculation. The spores (arrow) had not yet germinated.

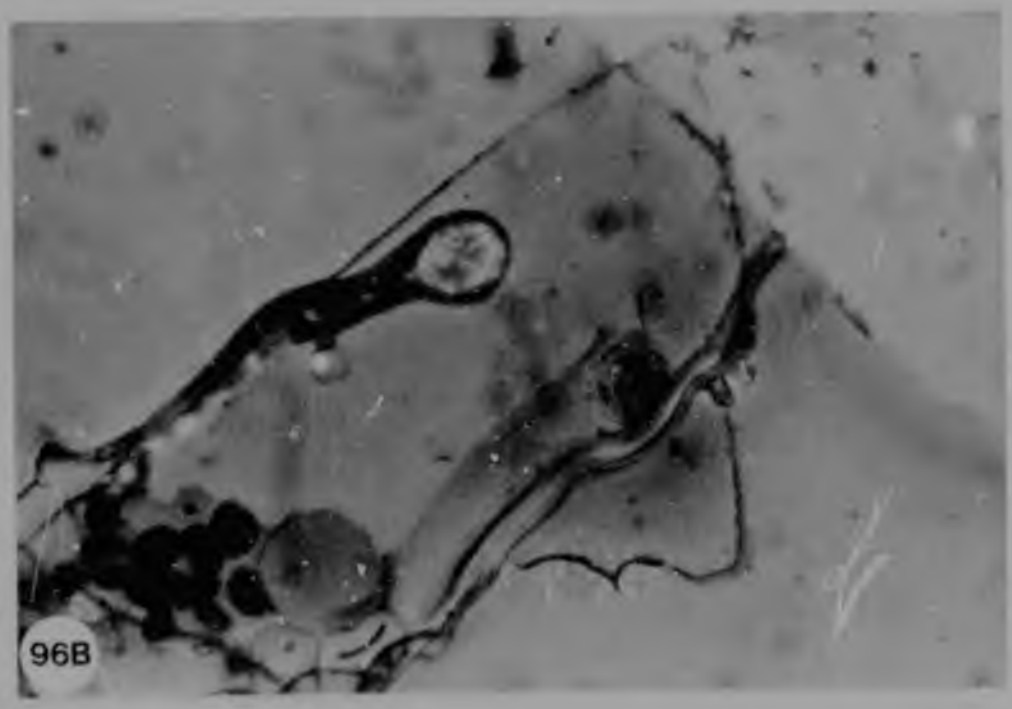
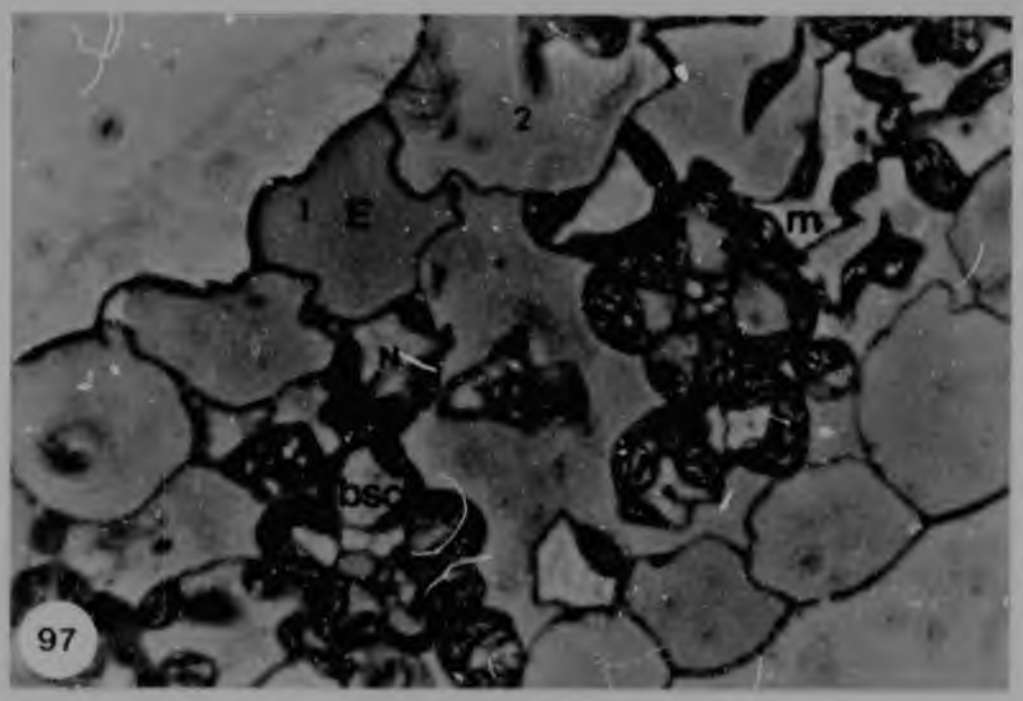


Fig. 96 B. Germinating uredospore on leaf surface, with erm tube staining purple.



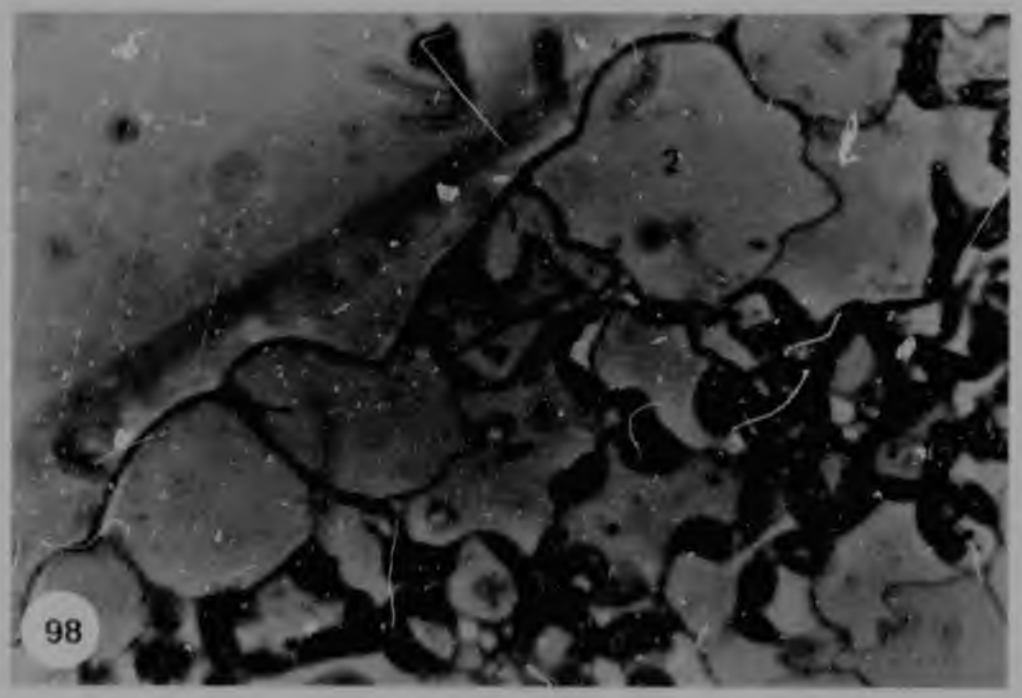
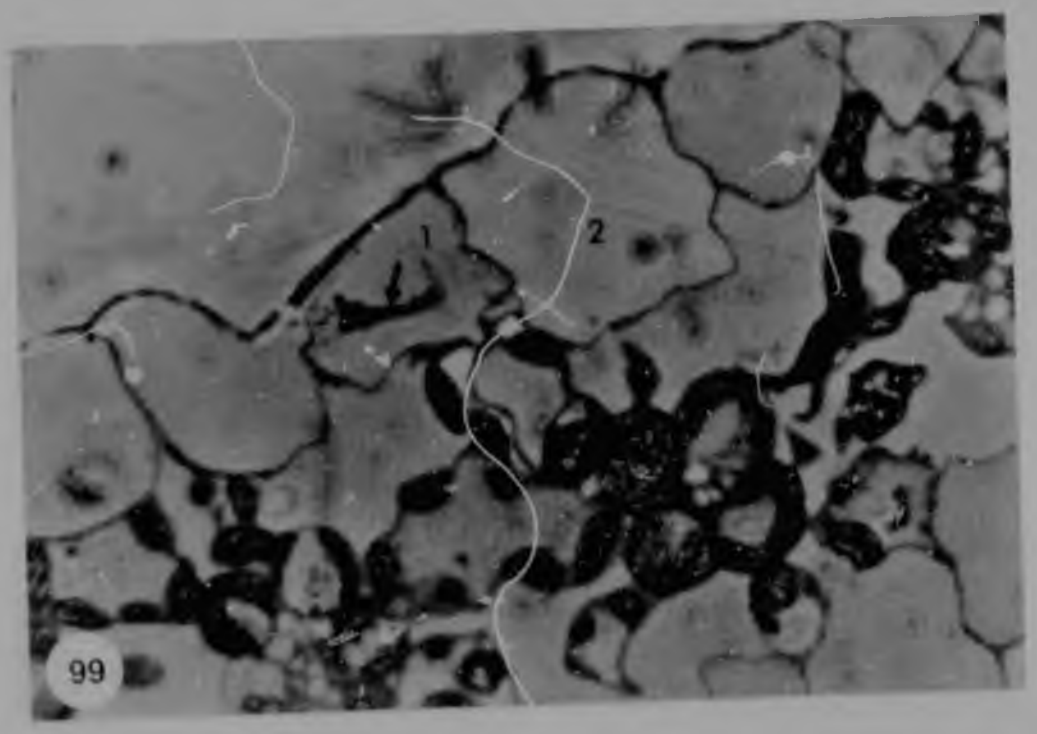


Fig.97 Aniline blue-safranin stained transverse section through *H. erianthus* leaf tissue 21h after uredospore inoculation. This figure is part of the serial section series Figs.97-100. Fig.98 Possible penetration of rust fungus, through the epidermis by means of intracellular mycelia, and between the epidermal cells (arrow). The purple stain of the structure between the cells appears similar to that of the germ tube (Fig. 96B).



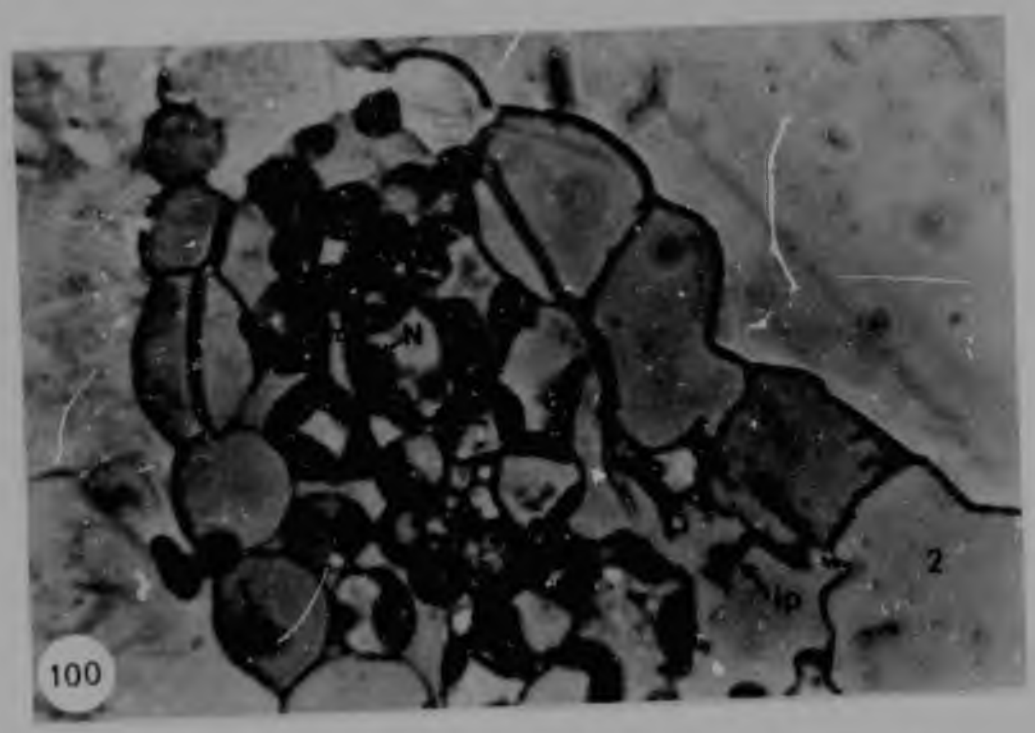
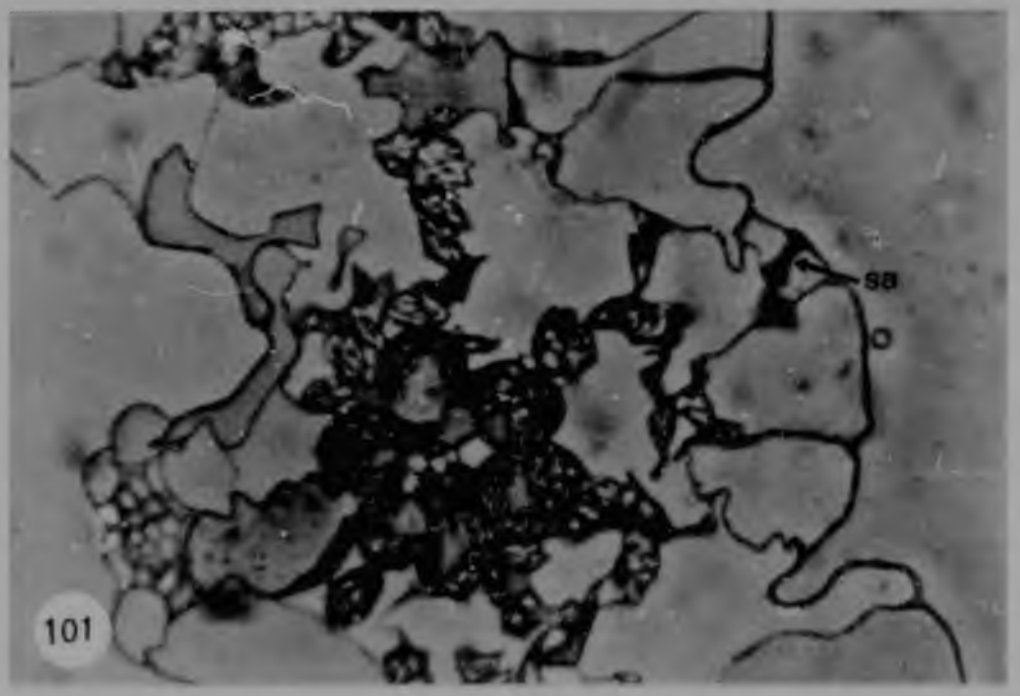


Fig. 99 Evidence of fungal material in epidermal cells of *D. eriantha*. Fig. 100 Apparent 'penetration peg' in the intercellular space below the epidermis. Note the blue wall and red-brown contents of this process, which resembles the structure (open arrow) lying adjacent to the nucleus (N).



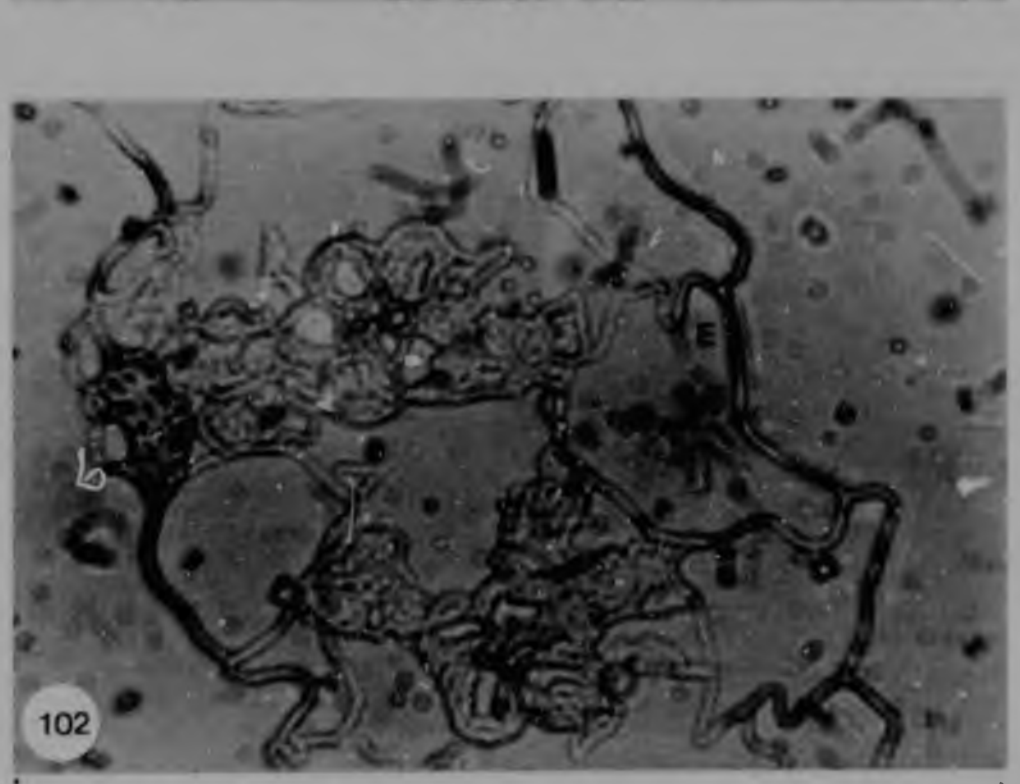
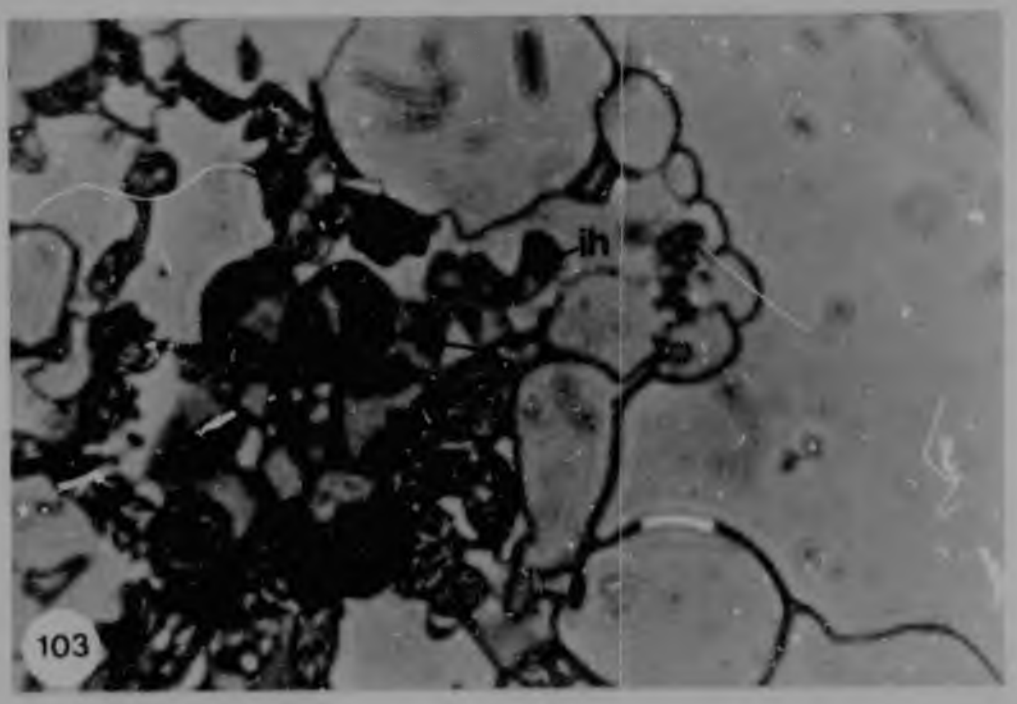


Fig.101 Penetration through stomata of *D. eriantha* by *P. digitariae*. Note the violaceous stain of the penetration process.
Fig.102 Malachite green-acid fuchsin-martius yellow stained section through *D. eriantha* leaf tissue. The fungal mycelia stain pink.



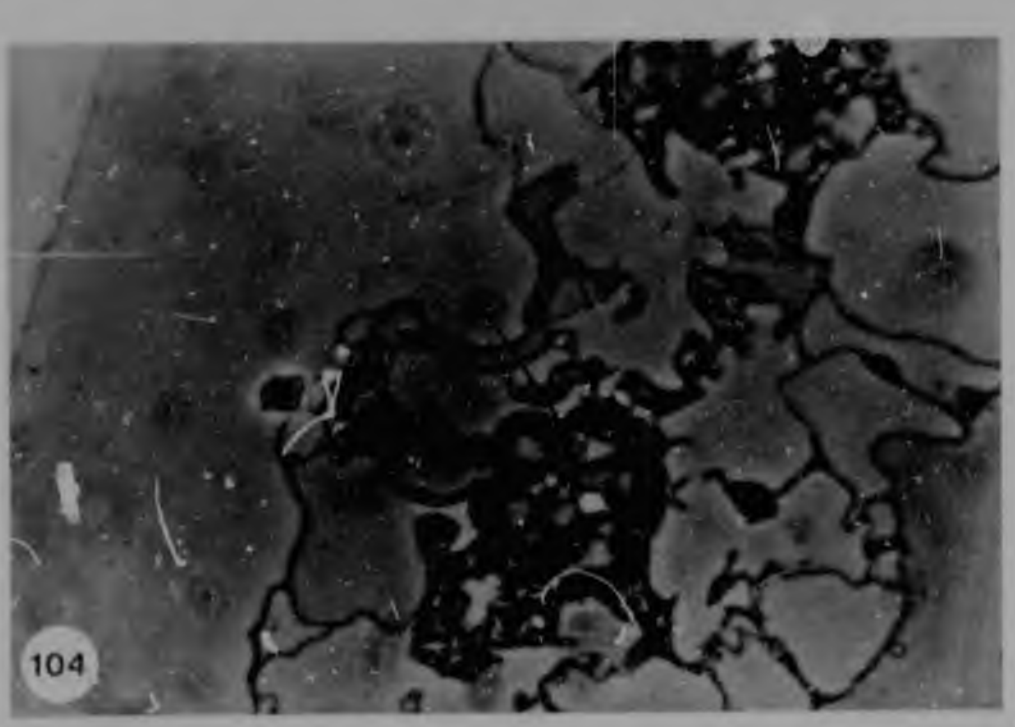
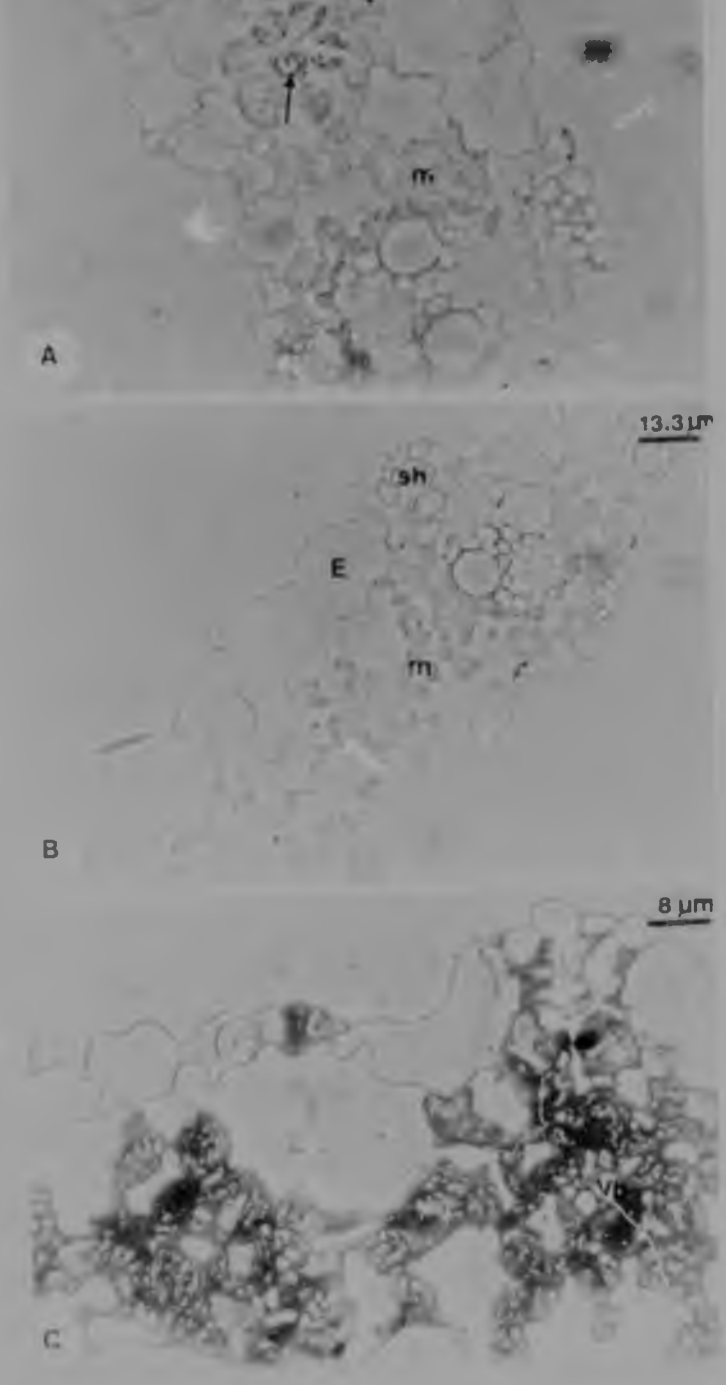


Fig.103 Transverse section through *D. eriantha* leaf tissue depicting the infection hyphae closely adhering to host mesophyll cells.
Fig.104 Possible haustoria, with the contents staining red-brown and the walls blue-purple.



Figs.105 A-C. Phase contrast autoradiographs of transverse sections through *D. eriantha* fed with labelled glucose. A. Rust-infected leaf tissue exhibiting intense labelling in mesophyll and bundle sheath cells. B. Healthy leaf tissue with less label incorporated than A. C. Control leaf tissue fed with non-radioactive glucose. No label is visible.

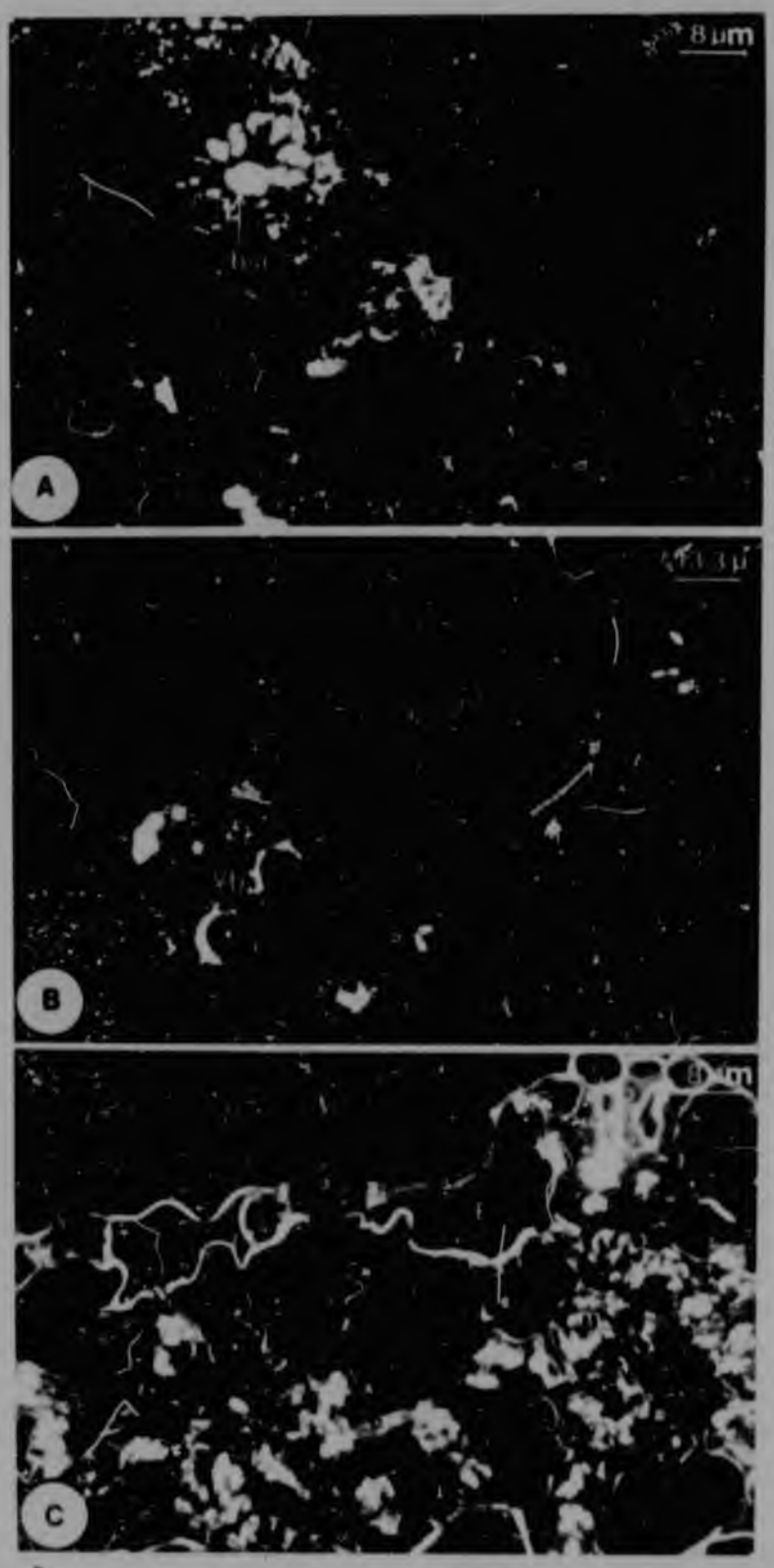


Fig.106 A-C. Dark field autoradiographs of Fig.105 A-C. A. Low power of ^{3}H-glucose labelled rust-infected *D. eriantha*. Silver grains were concentrated in the mesophyll and chloroplasts in bundle sheath cells in areas of infection. B. Label in healthy leaf tissue. C. Control leaf tissue fed with unlabelled glucose. Autofluorescence is detected for lignin, suberin and starch accumulation in the chloroplasts.

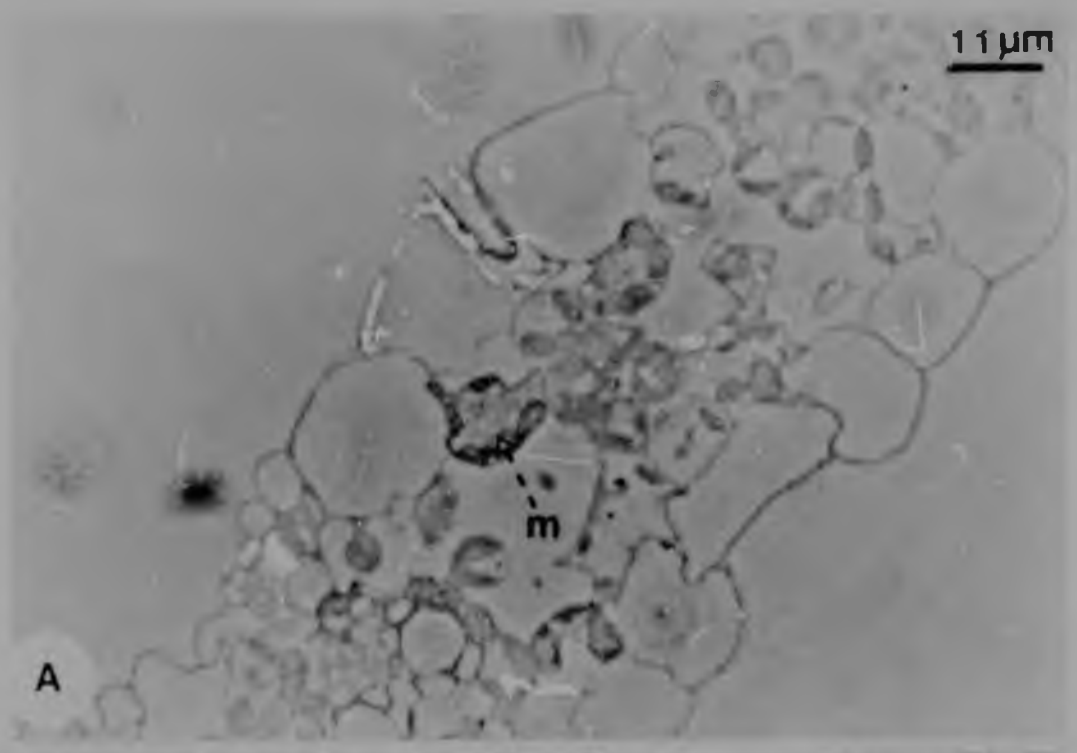


Fig.107 A. LM autoradiograph of rust-infected *D. eriantha* leaves, exhibiting intense label accumulation in mesophyll cells. B Incorporation of ^{3}H-glucose into structures resembling fungal haustoria. Note heavy label in the cell walls (arrow).

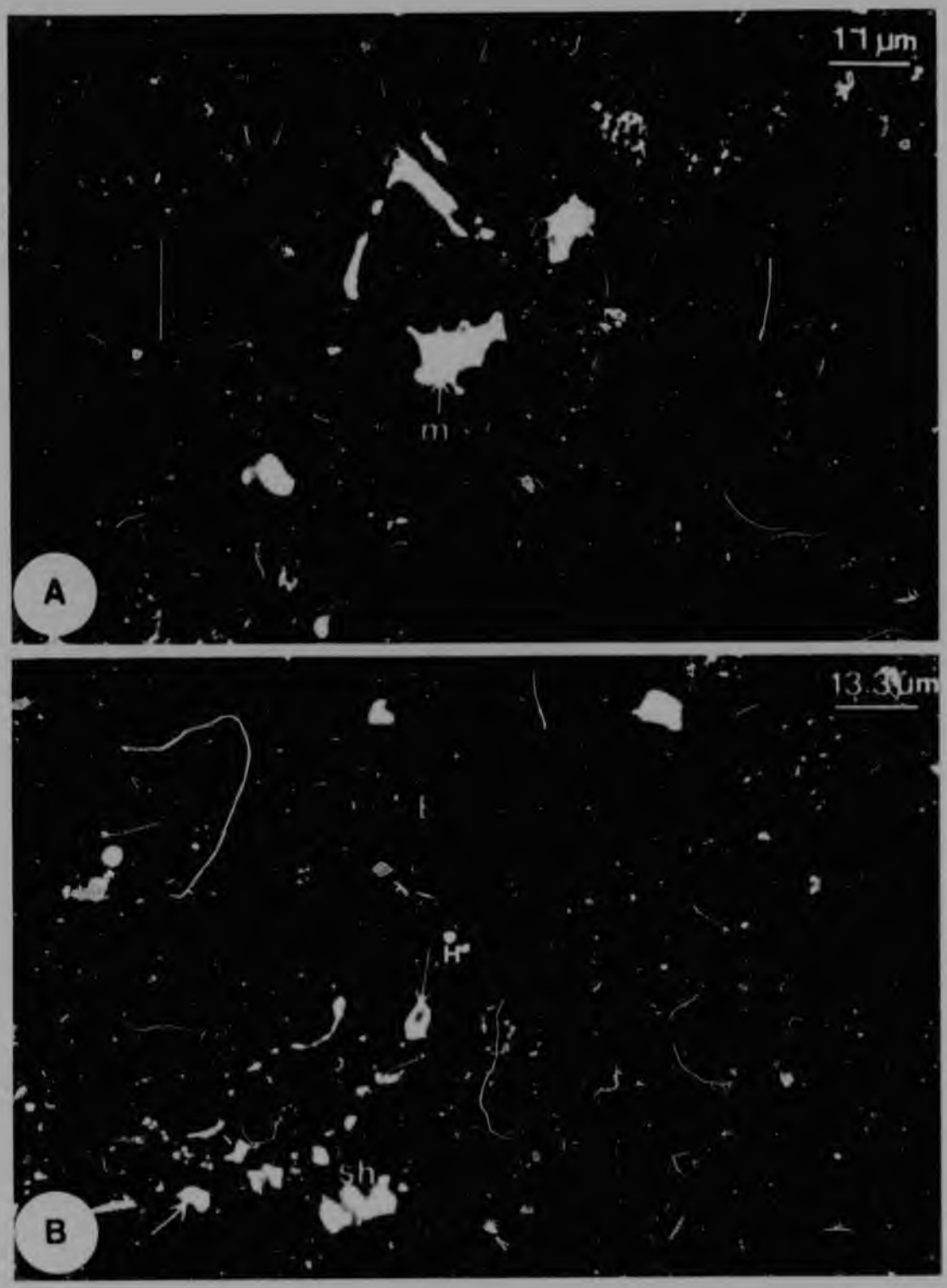


Fig.10B Dark field autoradiographs of Fig 10A. A. Label accumulated in mesophyll cells in the areas of rust-infection. B d-glucose observed to be incorporated into fungal haustorial cells (arrows).

especially in the cells below the epidermis, whilst in healthy leaf tissue markedly fewer silver grains were observed. with the majority of label being incorporated into sclerenchyma and vascular bundle cell walls (Figs. 105 B, 106 B). No silver grains were detected in control leaf tissues fed with unlabelled glucose (Figs. 105 C, 106 C).

Fungal haustoria cell walls were heavily labelled with ^{3}H - glucose (arrows Figs. 107 B and 108 B) whilst silver grains were detected over the penetration peg, sub-stomatal vesicle (Figs. 109 B and 110 B) and infection hyphae (Figs. 109 A and 110 A). Intensity of labelling was greatest in the sub-stomatal vesicle and infection hyphae. These autoradiographs establish that *P. digitariae* incorporates label from ^{3}H - glucose extensively before haustorial penetration of the mesophyll cells, as well as after penetration.

4.1.2 Feeding *D. eriantha* leaves, exhibiting mature pustules, with ^{3}H - glucose

Leaves, exhibiting pustules, that were fed with ^{3}H - glucose and left for eight hours, exhibited smaller amounts of tracer in the leaf mesophyll below the pustule (Fig. 111 B) in comparison to the healthy areas adjacent to the lesion (Figs. 111 C and 112 B). The healthy tissue appeared to incorporate the label mainly into the cell walls. Leaves fed with non-radioactive glucose contained no silver grains (Fig. 111 A). Only a few silver grains were observed in the uredospores (Figs. 111 B and 112 A).

4.2 Sugar analysis

Recovery of sugars from the leaf samples was estimated to be 91%. Percentage sugar content in healthy and infected leaves are presented in Table 25. In *D. eriantha* leaves during the pre-sporulation period, levels of fructose, glucose and sucrose increased markedly compared to healthy leaves (Fig. 113). Sucrose was influenced to a greater extent than either fructose or glucose, with levels increasing from 4% in healthy leaves to 9.5% in sporulating leaves (50 - 75% infected). T-tests showed little significant difference between healthy leaves and leaves exhibiting

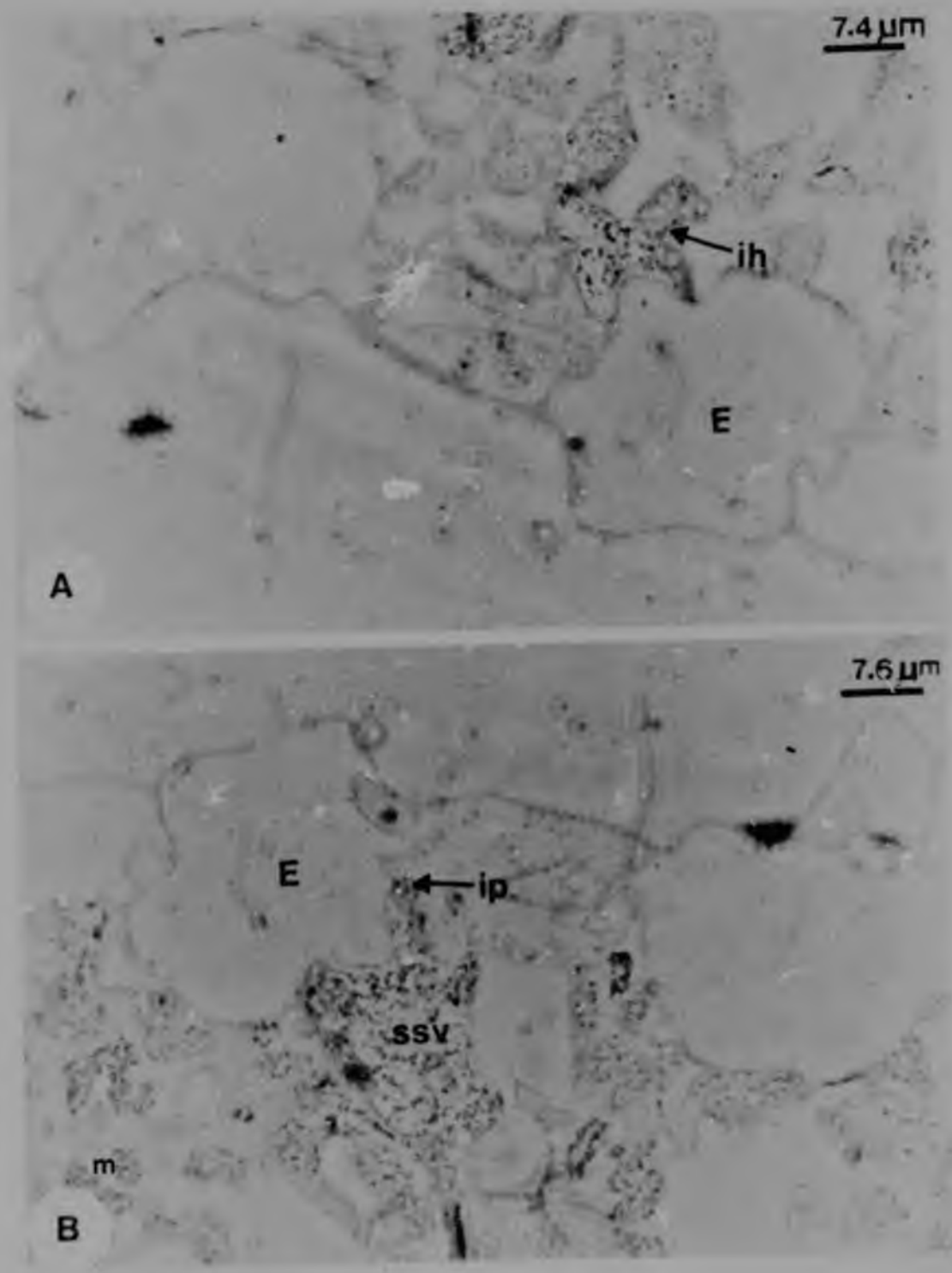


Fig.109 A. LM autoradiograph illustrating the intense silver grains in the infection hyphae of the penetrating rust *P. digitatiae*. B. Incorporation of ^{3}H-glucose can be detected in the infection peg and sub-stomatal vesicle in rust-infected tissue.

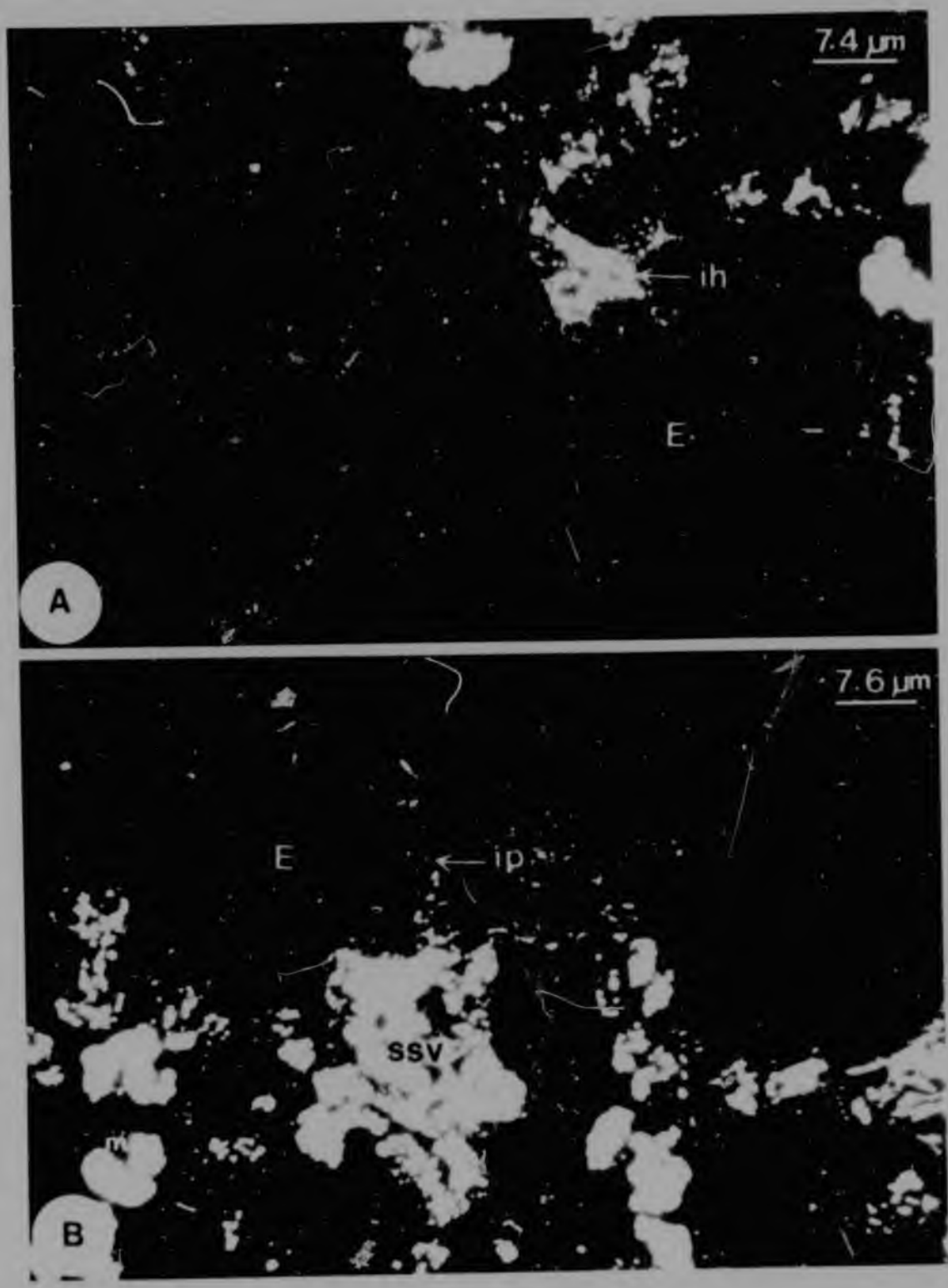


Fig.110 A and B. Dark field autoradiographs of sections through penetrating structures of *P. digitariae* infecting *D. sanguinalis*. A. Silver grains can be seen in the infection hyphae. B. ^{3}H-glucose incorporation into the infection peg and sub-stomatal vesicle is visible.

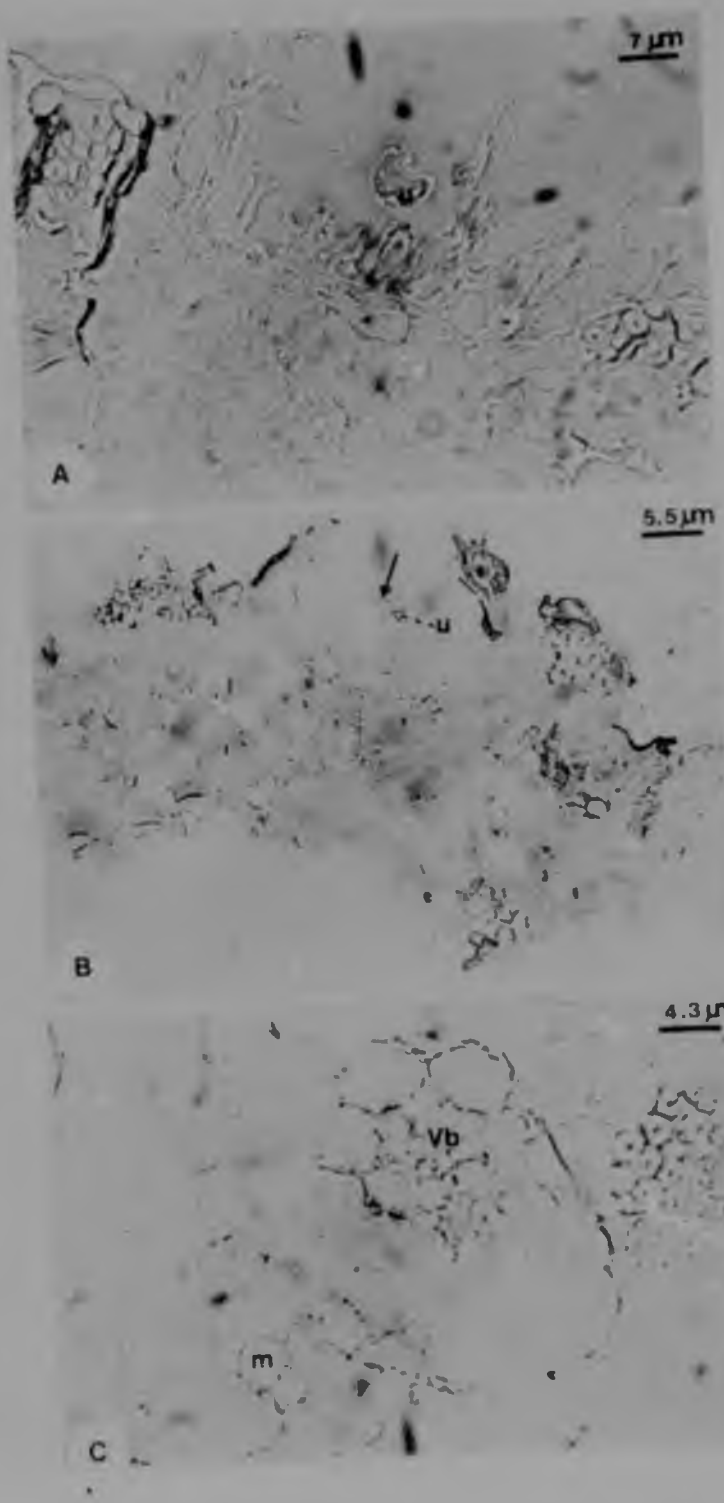


Fig.111 B-C. Phase contrast autoradiographs of rust-infected *D. eriantha* leaves fed with ^{3}H-glucose. A. Section cut through a pustule fed with non-radioactive glucose. B. Pustule fed with labelled glucose. Only a few silver grains are visible. C. Healthy leaf tissue fed with ^{3}H-glucose. Incorporation is mainly in the cell walls of mesophyll and vascular bundle cells.

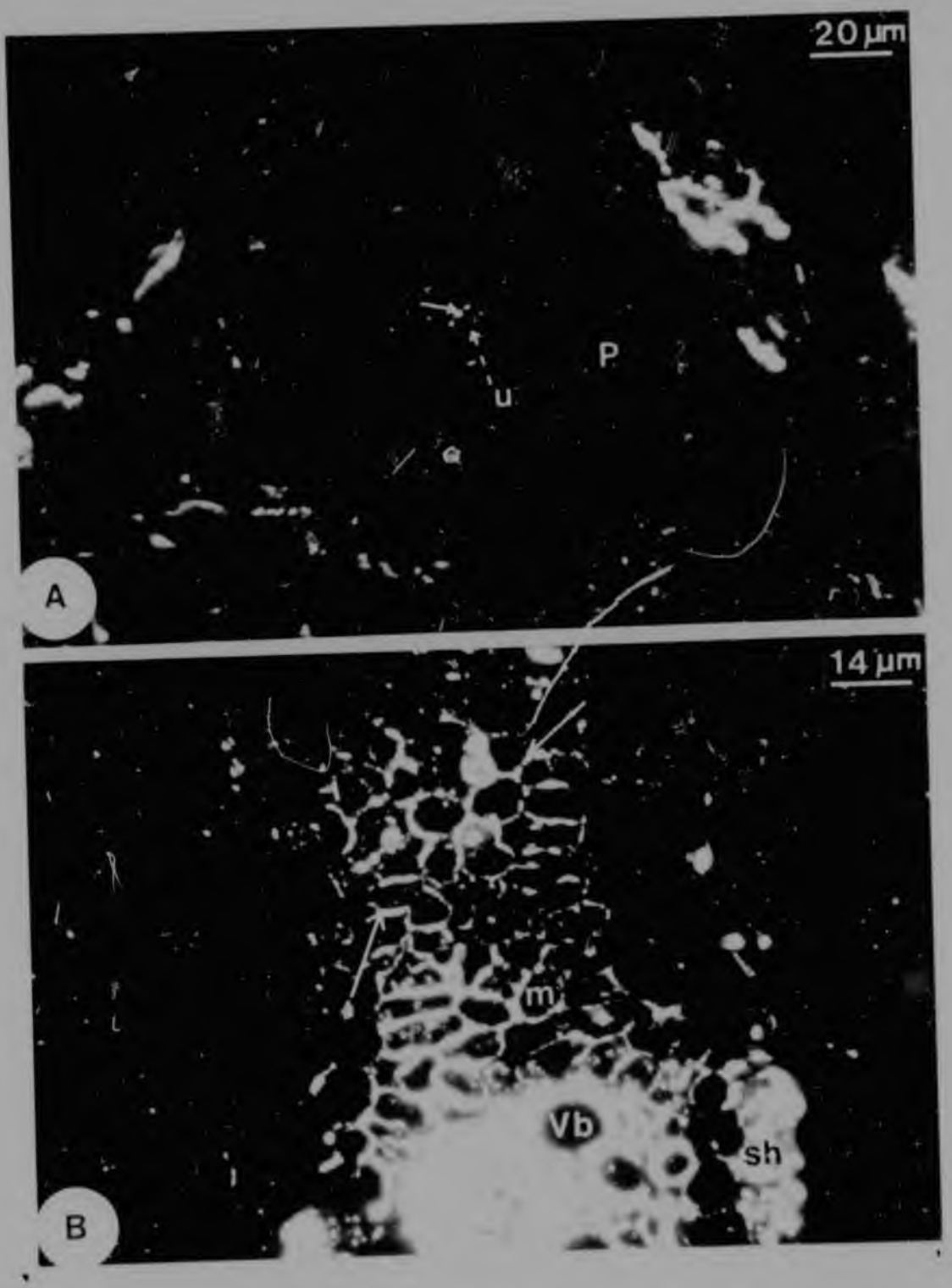


Fig.112 A. Dark field autoradiograph of a rust pustule fed with ^{3}H-glucose, and exhibiting a few silver grains in the uredospore. B. Healthy *D. eriantha* leaf tissue showing greater incorporation of label into mesophyll and vascular bundle cells.

Table 25 Average percentage sugar content of healthy and fungal-infected leaves of *D. eriantha* and *P. maximum* (1981/82)

SPECIMEN	FRUCTOSE	GLUCOSE	SUCROSE
D. eriantha HEALTHY	0.5 ± 0.03	0.8 ± 0.04	4.3 ± 0.1
INFECTED			
10% Flecking	1.0 ± 0.1	1.1 ± 0.05	4.5 ± 0.8
50% Sporulating	-	-	9.5 ± 1.0
Post-sporulation	1.2 ± 0.05	1.3 ± 0.01	4.70 ± 1.0
P. maximum HEALTHY	1.6 ± 0.06	1.5 ± 0.08	5.2 ± 0.3
INFECTED 25%	1.7 ± 0.02	1.8 ± 0.04	12.4 ± 1.1
Estimated % recovery = 91			

Table 25 Average percentage sugar content of healthy and fungal-infected leaves of *D. eriantha* and *P. maximum* (1981/82)

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INFECTED			
10% Flecking	1.0 ± 0.1	1.1 ± 0.05	4.5 ± 0.8
50% Sporulating	-	-	9.5 ± 1.0
Post-sporulation	1.2 ± 0.05	1.3 ± 0.01	4.70 ± 1.0
P. maximum HEALTHY	1.6 ± 0.06	1.5 ± 0.08	5.2 ± 0.3
INFECTED 25%	1.7 ± 0.02	1.8 ± 0.04	12.4 ± 1.1
Estimated % recovery = 91%			

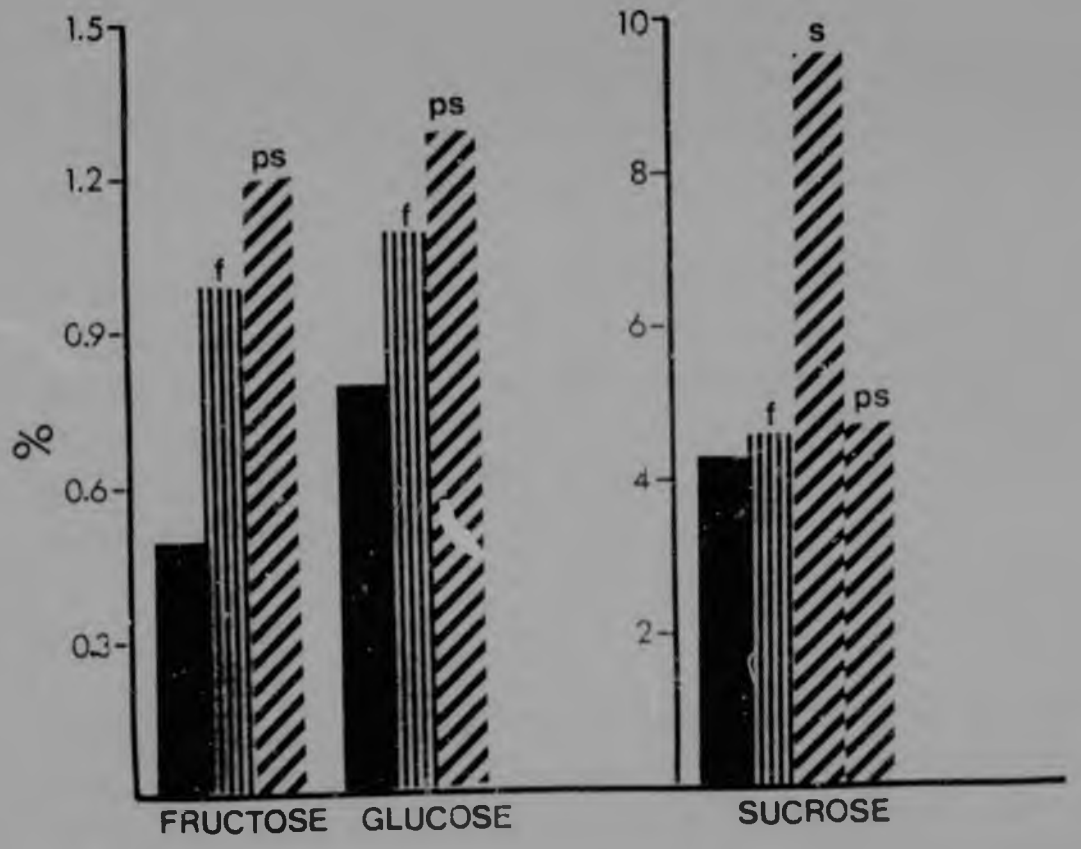

Fig.113 Sugar content in healthy and rust-infected *D. eriantha* leaves (1981/82)

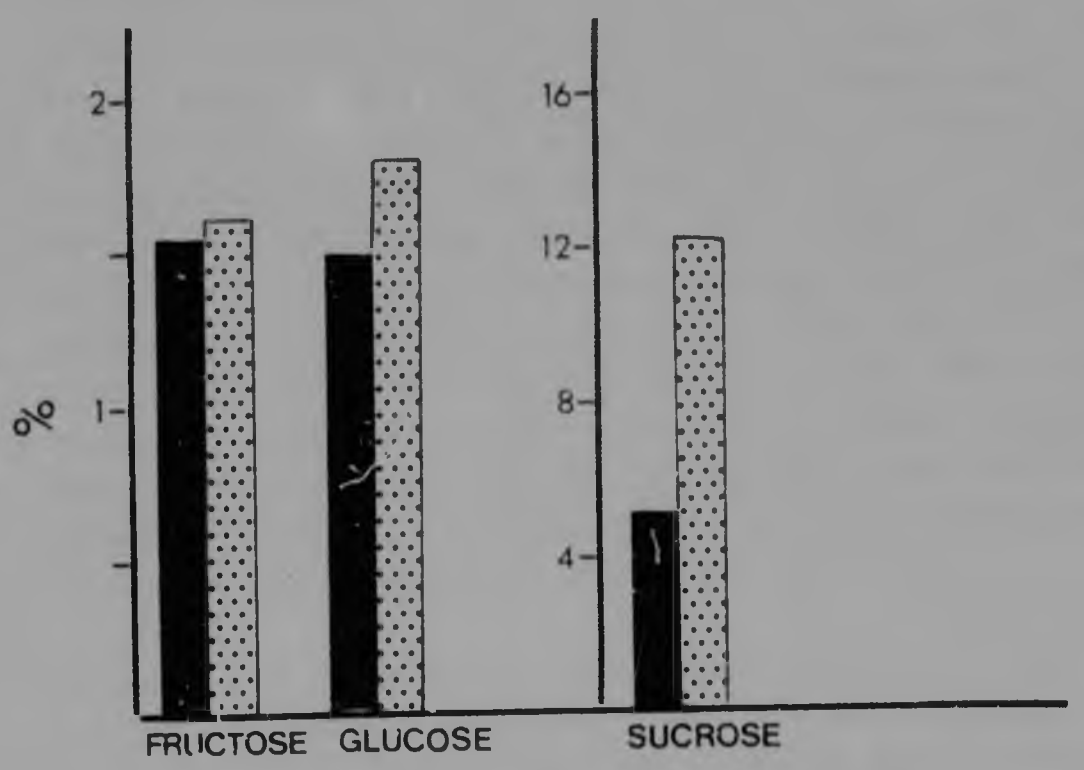

Fig.114 Sugar content of healthy and tarspot-infected *P. maximum* leaves (1981/82)

a low degree (10%) of infection, whereas at the 50 - 75% infection level, the differences became highly significant. During the post-sporulation period, sucrose dropped to 4.7% in infected leaves.

Tarspot-infected *P. maximum* leaves exhibiting mature fruiting bodies (clypei) appeared to have a similar fructose and glucose content as healthy leaves (Fig. 114). However sucrose levels increased dramatically from 5.2% in healthy leaves to 12.4% in infected leaves. The difference between healthy and infected (25%) leaves proved significant at $p = 0.05$.

3.5 DISCUSSION

Light microscopy

Despite variability in staining, evidence presented in the results (4.1.1) strongly supports the suggestion that the structures observed in the inoculated leaf tissue sections are indeed fungal. It is possible that penetration does occur directly through the epidermis since this has been demonstrated previously (Hunt, 1968).

Autoradiography

Autoradiographic results in this study seem to suggest that glucose is absorbed from host cells by the rust fungus and converted into insoluble fungal metabolites, probably storage glycogen, since most soluble sugars are lost into the fixation and dehydration media. Many studies have been carried out on the nutritional relationship between biotrophs and autotrophs (Livne and Daly, 1966; Daly et al., 1967; Smith et al., 1969; Mendgen, 1981) but most experiments have involved macro-autoradiographic techniques where infected leaves containing pustules were fed with labelled compounds or $^{14}CO_2$ (Wang, 1961; Holligan et al., 1974; Manners and Gay, 1978; Takahashi et al., 1977), or feeding leaves with labelled spores (Ehrlich and Ehrlich, 1970). These workers show the incorporation of $^{14}CO_2$ into host soluble sugars such as sucrose, glucose and fructose or into starch, and conversion of these substances into fungal metabolites such as polyols and trehaloses.

The experiments performed with the host-parasite system *D. eriantha* - *P. digitariae* indicate the uptake of soluble sugars by this rust fungus, and confirm the findings of other workers that obligate biotrophs such as the rusts depend upon an exogenous supply of sugars. For example,

Pfeiffer et al. (1969) (in Mendgen, 1981) illustrated the uptake of ^{14}C - glucose by rust in wheat leaves. In contrast to the reports that labelled glucose is taken up by uredia eg. uredia of *Uromyces trifolii* in leaves of *Trifolium subterraneum* (Thrower, 1965), little incorporation of ^{3}H - glucose into pustules or uredospores was observed in this study. This may possibly be due to the fact that the pustules were in an advanced stage of development. Von Sydow and Durbin (1962) reported the assimilation of ^{14}C in immature uredospores and hypae comprising the spore bed in stem rust-infected wheat leaves fed with $^{14}CO_2$. The uredospores in this experiment had already matured, possessing thick walls, and it is possible that during the earlier stages of uredosori development, when the immature uredospores are attached to their sporophores, ^{3}H - glucose can indeed be absorbed by the developing uredospores of *P. digitariae*.

Despite the demonstration of ^{14}C uptake by fungal mycelia of powdery mildew (Edwards and Allen, 1966) and by intercellular hyphae and haustoria in downy mildew (Takahashi et al., 1977), little is known about the nutritional relationship between host and parasite during the initial stages of germination and penetration. Studies have shown the accumulation of sugars such as glucose, sucrose and fructose formed during $^{14}CO_2$ assimilation, at the infection sites and in host tissues around the pustules (Holligan et al., 1974). Workers have also noted that translocation of soluble sugars to infected leaves from healthy parts of the plants or retention of assimilates also takes place in certain biotroph infections. (Doodson et al, 1965; Thrower and Thrower, 1966; Billett and Burnett, 1978). However virtually no work has been done on the accumulation or retranslocation of substances at the early stages of fungal germination.

The results from this study indicate that even at the initial stages of penetration, sugars accumulate in the mesophyll cells at the sites of penetration (Figs. 105, 107 A; 108 A). The mesophyll cells of *D. oriantha* below the epidermis appeared in some cases to be swollen, with the cytoplasm appearing granular and staining a blue/purple colour to a greater extent than other mesophyll cells (Figs. 101 and 104). This finding is in agreement with the work of Peyton and Bowen (1963) who noted increases in the volume of cytoplasm around fungal haustoria. The cytoplasm often appeared granular, having a high concentration of ribosomes. These features reported

by Peyton and Bowen (1963) and also demonstrated in this study, may be associated with increases in protein synthesis for the benefit of the parasite.

Glucose was found to be absorbed by fungal structures such as the penetration peg, sub-stomatal vesicle and infection hyphae (Figs. 109 and 110). This observation of early incorporation of sugars has not been demonstrated previously in rust fungi, but has been reported by Andrews (1975) in *Bremia lactucae*. He showed the incorporation of ^{3}H - glucose into the primary and secondary infection vesicles, appressoria and germ tubes. Therefore despite contrary reports to this early utilization of sugars (Sargent et al., 1973), it appears that *P. digitariae* derives nutrition from the host during the early stages of penetration and formation of the sub-stomatal vesicle or primary infection hyphae.

The possible role of glucose or other sugars in fungal germination and penetration is not surprising in view of the diversity of plant exudates (Preece and Dickinson, 1971). Kosuge and Hewitt (1964) have also pointed out the significance of grape berry exudates on the germination of conidia of *Botrytis cinerea*. Since rust fungi rely on endogenous rather than exogenous substrates during uredospore germination (Shaw, 1963) the finite reserve in uredospores is most likely depleted by the time host penetration occurs. Germ tube extension involves rapid utilization of sugar alcohols. It would therefore appear that a ready source of carbohydrate available to the penetrating rust fungus to replace or supplement the endogenous reserve is necessary in biotrophic infections including the pathosystem which has been investigated here.

Autoradiographs of the *D. eriantha* - *P. digitariae* pathosystem illustrate incorporation of glucose to a large extent into starch grains in the chloroplasts. This starch may be stored, ready to be utilized by the pathogen. Even though incorporation into specific cytoplasmic organelles, with the exception of chloroplasts, could not be distinguished in these autoradiographs label from ^{3}H - glucose has been observed in mitochondria and vacuoles in mesophyll

and epidermal cells of lettuce (Andrews, 1975). Labelling was also observed in structures resembling haustoria (Figs. 107 B and 108 B). The thickness of the walls of these structures, and evidence of silver grain accumulation into cell wall components (Fig. 107 B and 108 B), suggest that these may be haustoria, but TEM is needed to confirm this hypothesis. In view of the fact that these structures resemble haustoria, the incorporation of ^{3}H - glucose into haustorial walls would imply that *P. digitariae* may utilize host-derived sugars in the production of cell wall polysaccharides. In fact fungal mycelia are capable of converting sugars into compounds such as glutamine, amino acids and chitin (Howes and Scott, 1972). These results would agree with the findings of both Manners and Gay (1970), who demonstrated the uptake of photosynthetic products by mycelia and haustoria of *Erysiphe pisi* in *Pisum sativum*, and Takahashi et al., (1977) who obtained similar results in downy mildew (*Pseudoperonospora cubensis*) of cucumbe .

It is difficult to ascertain whether the original metabolite is absorbed by the fungus, or whether it is metabolized into a different form before reaching the parasite. Nevertheless this research along with previous work, indicates that glucose is utilized in one form or the other by rust fungi. The results of these autoradiographic studies in addition demonstrate the requirement for exogenous nutrients even at the initial germination and penetration stages of rust diseases, and confirm similar results obtained by Andrews (1975) in *P. lactucae*. It is possible that the conversion of a large proportion of assimilates to insoluble compounds may maintain the concentration gradient of soluble translocates.

Sugar studies

In the current study gross changes ir sucrose, fructose and glucose were found in rust-infected *D. eriantha* leaves during presporulation. In *P. maximum* however little change was observed in glucose and fructose levels, although sucrose did increase in tarspot-infected leaves. *Phyllachora* species are considered to be less dramatic in their effect on host plants than rust fungi, and this is reflected in the smaller changes which occurred in *P. maximum*. Sucrose levels increased to a greater extent than fructose and glucose in both *D. eriantha* and *P. maximum*, and this is not

surprising in view of the fact that sucrose is utilized readily by most fungi. Sucrose is thought to be inverted by acid invertase before being absorbed by the fungal parasites (Long et al., 1975). although Roberts and Mitchell (1979) reported no accumulation of carbohydrates and stimulation of acid invertase in rust infected areas of poplar infected with *Melampsora aecidiodes* (D.C.) Schroeter and hence concluded that this infection was fairly benign.

The increase in sugars in infected leaves of *D. eriantha* and *P. maximum* are in agreement with the results of many workers (Inman, 1962; Holligan et al., 1973) who have reported an increase in glucose, sucrose, fructose in biotrophic infections, although several investigators such as Hodges and Robinson (1977) have reported a decrease in sugar content in infected leaves. There may be several reasons for the increase in sugars in leaves during presporulation periods. The first possible cause may be the stimulation of host synthesis. This seems possible since soluble sugars especially sucrose are the first products formed during $^{14}CO_2$ assimilation (Holligan et al., 1974). It is thought that sucrose is hydrolysed before absorption by the pathogen. This is supported by the increased incorporation of radioactivity into hexoses in infected regions of *Tussilago farfara* infected by *Puccinia poarum* (Holligan et al.,1973). Carbon dioxide fixation was observed to be slightly stimulated in rust-infected leaves of *D. eriantha* during early necking and presporulation (5.4.1.2) and stimulation of CO_2 fixation enzymes was also revealed (5.4.1.3). Similar results were found for *P. maximum*, but to a lesser degree (5.4.1.2 and 5.4.1.3). These findings, along with the fact that sucrose is generally not considered to be synthesized by fungi, and may be transported into infected leaves at the expense of healthy leaves or plant parts, may be responsible for the increased sucrose levels in infected *D. eriantha* and *P. maximum* leaves during the presporulation stages.

Some of the imported sucrose and glucose may be synthesized into and stored as starch in the chloroplasts in areas adjacent to the lesions, ready to be released by some pathogen-induced activation. This is supported by the observation of large starch grains noted

in mesophyll cells in areas adjacent to pustules (4.4.2). During infections by biotrophic pathogens, patterns of translocation have been found to be altered so that sites of infection accumulate photosynthetic products at the expense of other regions of the plant (Smith et al., 1969; Lewis, 1973). The movement to infection sites of sucrose has been demonstrated to occur in both light and dark (Holligan et al., 1974). For example, in plants infected by *Puccinia poarum*, export of photosynthate from rusted leaves has been reported to be inhibited (Holligan et al., 1974). When infection was slight (pustules <10% surface area of leaf) little import to the infected leaves was observed, whereas in severe infections (pustules >25% surface area) infected mature leaves imported up to 20% of the photosynthate from healthy younger leaves.

This may possibly explain the smaller increases in sugars in infected leaves of *D. sorghina* and *P. maydinum* at lower severities of infection (pustules <25% surface area of leaf) shown in Table 25.

Taking into account the nutritional requirements of obligate parasites at various stages of disease development it is understandable that metabolites would be required for extensive synthesis of fungal tissue especially during sporogenesis. Recently synthesized photosynthates and starch (in the early stages of flecking and presporulation) are utilized in the dark and products pass to the fungus where they are transformed into glucomannan, polyols, glycogen and lipids. This is strongly supported by the rise in dark respiration (5.4.1.4.1) in rust-infected *D. sorghina* at the onset of sporulation. With the increasing age of the pustules many sugars are transformed into fungal sugar alcohols or other insoluble metabolites and a drop in host sugars would seem inevitable. This is certainly evident in *P. maydinum* and especially in *D. sorghina* where sucrose levels dropped drastically during the post-sporulation period, and continued to do so until senescence occurred (Table 25).

The results from this study indicate that the Basidiomycete (rust fungus) and the Ascomycete (tarspot fungus) utilize sugars derived

from their hosts. In view of the fact that these host-derived nutrients are converted into fungal components, it appears as if host plants lose much of their carbohydrates through sporulation of their fungal parasites. This research has demonstrated the gross changes in sugars in infected leaves and the exchange of glucose between *P. digitariae* and *D. eriantha*. It does not however indicate the distribution changes between host and pathogen on a quantitative basis. The changes in tarspot-infected *P. maximum* are not as remarkable as in the case of *D. eriantha*, but it is nevertheless interesting to note that *P. paspalicola*, being a biotroph, behaves in a similar manner to the more severe rust fungus *P. digitariae*. It is also of interest with respect to the view that *Phyllachora* species are considered economically unimportant, that significant changes were indeed detected in heavily infected *P. maximum* leaves.

The following concluding chapter will reconsider the host-pathogen concept as a distinct energy unit within a natural population. With the results presented from the previous chapters kept in mind, the significance of carbohydrate content and other nutritional aspects of crops will be discussed not only with respect to the grazing potential of foliage for the herbivorous populations in the reserve, but also with respect to the concepts of energy flow and exchange within a natural ecosystem.

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CHAPTER SEVEN FINAL DISCUSSION

7.1 General discussion

1.1 Identification of the pathogens

The pathogens occurring at Nylsvley had not been identified before this research was initiated. Before one can study the influence of disease on a host plant, it is necessary to identify the pathogen and describe the nature of its infection processes. The foliar pathogen on *D. eriantha* was identified as a rust *Puccinia digitariae* Pole Evans and the tarspot fungus on *P. maximum* was identified as *Phyllachora pasvalicola*. The nature of the necrotic lesions on *B. africana* is suspected to be of a viral origin introduced by insect vectors. Mechanical and vector transmission experiments failed, as did the attempts to graft *B. africana* tissue onto *Vinca* species. However transmissions from woody species are difficult to obtain, and may in some cases take up to one year. Therefore unless transmission of the suspected infective agent is achieved, the precise nature of the lesions cannot be established.

1.2 Epidemiology

The increase of incidence and severity of lesions on *B. africana* (Figs. 15 and 16) appears to increase throughout the season, although levels are not as high as in the case of the fungal diseases on *D. eriantha* and *P. maximum*. Since the lesions are initiated by insect wounding, the pattern of lesion spread is dependent on emergence of the leaves and insect population buildup. Both these parameters are strongly influenced by the first spring rains and are probably the principle factors influencing the relative growth rate and pattern of lesion development. Defoliation of *B. africana* by caterpillars in the 1979/80 season (Fig. 16) is responsible for the decline in lesions in January 1980 which was followed by a new flush of leaves and renewed lesion development. It may also be speculated that if a virus was involved, that *B. africana* may function as a virus reservoir in the reserve.

The relative growth rates of rust on *D. eriantha* and *P. maximum* exhibit an epidemiological increase throughout the growing seasons (Figs. 17-20). The principle controlling factors appear to be host susceptibility at the time of infection (as was the case in *P. maximum* in the 1979/80 season), host tissue availability, initial leaf flush emergence, and host development through the season. The two primary factors influencing these aspects discussed above are rainfall and temperature. Rainfall is important not only with respect to leaf emergence and growth, but dictates the moisture available for pathogen germination processes. Certainly moisture and temperature regimes were suitable at Nylsvley (Figs. 3-J) and allowed for disease increases to take place throughout the season.

1.3 Ultrastructural studies

1.3.1 Morphological changes

The changes which pathogen initiate in their hosts are important with respect to the ultrastructural and physiological functions which the host plant exhibits. Research was undertaken to study the effects of the infective agents on the ultrastructure of the hosts, and where possible relate them to physiological disturbances. The fungal diseases on the grasses are obligate parasites and require nutrients from their hosts. This dependence of the rust and tarspot fungus upon their hosts, dictates the pattern of morphological and physiological processes of *D. eriantha* and *P. maximum* in response to infection. Whatever the origin of the necrotic lesions is, the areas of necrosis developing on *B. africana* leaves will also affect the morphology of the leaves.

B. africana

Lesion formation in *B. africana* appears to be a hypersensitive reaction, similar to that described in many virus infections (Israel and Ross, 1967; Hiruki and Tu, 1972). However the formation of a zone of necrotic cells around virus infection sites may also occur in non-specific hypersensitive reactions due to wounding or heat treatment (Faulkner and Kimmins, 1975).

Therefore it is possible that the lesion formation on *B. africana* leaves may be a hypersensitive response induced as a result of insect feeding. The detection of lignin in the necrotic and semi-necrotic areas (Figs. 32 and 33) in this study of *B. africana* resembles the lignin deposition in resistant zones of *Nicotiana glutinosa* infected with a mild strain of TMV (Wu, 1973). The transmission electron microscopical studies confirm the presence of electron dense deposits along the cell walls of semi-necrotic mesophyll cells (Fig. 28A) and demonstrate the presence of plasmalemmasomes (Fig. 28C) and paramural bodies (Fig. 28B) which have been associated with virus infections (Shulka and Hiruki, 1975). Degradation of the chloroplasts (Fig. 29C and D) and other cellular organelles forming membraneous vesicular bodies, was noted in necrotic *B. africana* leaf tissue (Fig. 27B).

The presence of 'virus-like' particles and crystalline inclusions are detected in semi-necrotic mesophyll cells (Fig. 9A and B). These ultrastructural studies appear to suggest that a virus is involved, but until conclusive evidence is obtained through transmission of the infective agent, the precise nature of the lesions cannot be illucidated.

D. eriantha

The uredosorus formation on rust-infected *D. eriantha* leaves is similar to that described for rust fungi by many workers (Littlefield and Heath, 1979). The haustoria or feeding structures resemble those described by several authors (Calonge, 1969; Coffey et al., 1972a; Manocha and Shaw, 1967) where the haustorium is surrounded by an extra haustorial matrix (Fig. 38A). Ultrastructural changes are observed in the nuclei, chloroplasts and mitochondria of rust-infected mesophyll cells as has been demonstrated in many rust infections studied in the past (Manocha and Shaw, 1966; Heath, 1974b; Abu-Zinada et al., 1975). These changes however only occur at the onset of sporulation and increase in magnitude after sporogenesis. Of particular interest is the degradation of chloroplasts (Fig. 38A) and swelling of

mitochondria (Fig. 41B) in infected cells, with reference to physiological parameters. The degradation of chloroplasts and chlorophyll decline appears to be partially responsible for the decrease in photosynthetic rates during post-sporulation (4.4.2). The swelling of the mitochondria suggests an increase in the surface membrane area and may be partly associated with the stimulation of dark respiration in sporulating *D. eriantha* leaves (5.4.1.4).

The formation of perithecia on *P. maximum* is similar to that reported in *P. paspalicola* on other grass species (Parberry, 1967). This fungus produces intercellular and intracellular haustoria. The intracellular penetration of hyphae occurs through the cell wall in the manner of many penetrating feeding structures (Fig. 49C), and the presence of a wall aposition layer can be detected. However these intracellular hyphae do not exhibit the high degree of specializa ion observed in rust haustorial formation (Fig. 38A).

P. maximum

The morphological changes which took place in *P. maximum* were similar to those described for *D. eriantha* with respect to chloroplast disruption (Fig. 48B and C). However these changes did not reflect as severe physiological effects as the rust on *D. eriantha*. This is not suprising since tarspot does not appear to have such a high degree of specialization in terms of sporogenesis and infection processes. However it was interesting to note the similarity between the two obligates parasites, since *P. paspalicola* has not been previously studied at the electron microscope level.

1.3.2 Uredospore ontogeny

During the course of the transmission electron microscopical studies, the unusual development of the uredospores of *P. digitariae* was noted and studies were undertaken to establish the nature of this phenomenon. Further work revealed that uredospore ontogeny

exhibits an'annellophoric-type' development where collars form as a result of new growth from the inner sporophore cell wall, which forces the old sporophore walls to be laterally displaced as the new uredospores develop at the apex (Figs. 43 A-E and 44 A-D). This type of ontogeny has not been documented at the electron microscopical level and only once at the light microscope level in *Kernkampella breyniae-patensis* where the actual mechanism was not demonstrated (Rajendren, 1970). Rijenkenberg and Truter (1974) have shown that pycnial ontogeny of *Puccinia sorghi* is annellophoric and it is possible that this type of development in uredospores occurs elsewhere.

1.4 Photosynthesis, and related processes

The effect of *E. africana* on photosynthetic metabolism proved to be insignificant (5.4). This is due to the fact that the lesions are localized and the surrounding tissue is not affected. Areas of chloroses were not observed frequently as in the case of the rust and tarspot infection. As the proportion of necrotic to non-necrotic tissue increases so the loss in green photosynthetic tissue is greater and this explains the more marked effects observed in leaves exhibiting a high severity of lesions.

The studies on the rust and tarspot infections reveal that photosynthetic rates are slightly stimulated in the very early stages of infection, but as sporulation occurs the gross and net photosynthetic rates decline. This has been previously demonstrated in obligate parasite infections Doodson et al., 1975). As sporulation proceeds and during the post-sporulation period photosynthesis declines rapidly due to the destruction of chloroplasts, disintegration of mitochondria (Fig.41 D), decline in chlorophyll content (5.4.1.5) and decrease in C_4 photosynthetic enzyme activities (5.4.1.3). There also appears to be a positive correlation between intensity of infection and the parameters mentioned above. This may be explained in view of the fact that as the degree of diseased tissue increases so the effects become more noticeable. The patterns in both rust and tarspot fungi are similar, except that in the case of the rust on *D. eriantha* three distinct spore stages can be distinguished, namely

early and late flecking; sporulation; and post sporulation. The changes in photosynthesis seem to be governed by the stage of disease development and pathogen requirement. This is significant since both *P. digitariae* and *P. paspalicola* are obligate parasites requiring nutrients from their hosts.

The unique nature of C_4 photosynthesis provides a useful tool in elucidating the effects of parasites on host carboxylation processes. From the work accomplished in this study it appears that rust and tarspot are capable of directly influencing the metabolism of *D. eriantha* and *P. maximum*. The carboxylation enzymes RuBP and PEP carboxylase are stimulated in *D. eriantha* (Figs. 74 and 76) and *P. maximum* (Fig. 78). *P. maximum* exhibits a less severe change compared to *D. eriantha* in C_4 enzymes. NADP-malic enzyme and aspartate aminotransferase activity decreases whilst NADP-malic dehydrogenase activity remains unchanged. This suggests that malate is formed (Fig. 51) as NADP-malic dehydrogenase activity is unaffected, but may be removed by the pathogen since NADP-malic enzyme activity is lost in tarspot-infected leaves. The most remarkable change demonstrated in this study is the increase in aspartate aminotransferase, PEP carboxykinase and alanineaminotransferase in rust-infected *D. eriantha* leaves (Figs. 75 and 77) and a simultaneous decline in NADP-malic enzyme and NADP-malic dehydrogenase activity (Figs. 74 and 76). This indicates a shift from the malate to the alanine forming pathway and suggests that alanine is utilized predominantly by *P. digitariae*.

Stimulation of the carboxylation enzymes prior to sporulation contradict the apparent decrease in gross and net photosynthesis rates. The research undertaken in this study puts forward the suggestion that true photosynthetic rates are masked due to several reasons. The compartmentation of C_4 photosynthesis in C_4 grasses would allow for a refixation by RuBPC of high CO_2 concentrations generated in infected areas. The presence of a high CO_2 concentration may result from stimulated host respiration (5.4.1.4) and fungal respiration which would mask true photosynthesis. In addition the high internal CO_2 concentration whilst stimulating the carboxylation enzymes may engender a high CO_2 diffusion resistance gradient

which would lead to an apparent decline in gross photosynthesis. Evidence for the existence of this high internal CO_2 gradient in *D. eriantha* is provided by the experiments (Fig. 71 B) where the CO_2 concentration was increased from 100-500 ppm to overcome the resistance effects. A greater stimulation of photosynthetic activity was recorded in infected relative to healthy leaves.

1.5 Nitrogen metabolism

No significant differences can be noted in levels of total nitrogen between necrotic and non-necrotic *B. africana* and again this reflects the small impact the lesions have on *B. africana*.

Nitrate (5.4.2.1) and total nitrogen (5.4.2.2) levels increase in rust and tarspot infected leaves, prior to sporulation especially at high intensities of infection. Nitrogen metabolism is important due to its association with photosynthetic metabolism and protein synthesis. Increases in nitrates have been shown to stimulate photosynthesis and C_4 enzyme activities (Cresswell et al., 1974; Amory, 1982) and the high level of nitrates in infected leaves before sporulation may partially be responsible for the increases in photosynthetic metabolism discussed previously. Increases in total nitrogen have been reported by several workers e.g. Calonge (1967) reported stimulation in barley infected with *Puccinia hordei* Otth and this may be a result of stimulated host metabolism and translocation of soluble nitrogen into infected areas at the expense of other plant parts. Total nitrogen and nitrates decline however during post-sporulation since most nitrogenous compounds utilized by the pathogen are no longer required and leaf senescence occurs. The fluctuations in nitrogen in infected leaves is best intepreted as changes between leaf and pathogen components and between infected and non-infected areas at different stages of disease development.

1.6 Sugar analysis

The current study reveals increases in sucrose, fructose and glucose in rust-infected *D. eriantha* leaves (Fig. 113) whilst in *P. maximum* leaves infected with tarspot small changes in fructose and glucose are noted, although sucrose levels increase remarkably

(Fig. 114). Sucrose levels increase to a greater extent prior to sporulation, and this is not suprising in view of the fact that sucrose is utilized readily by most obligate fungi. Long et al. (1975) illustrate that sucrose is inverted by acid invertase before being absorbed. Sugar levels then drop during post-sporulation due to removal by pathogens. These studies indicate that rust and tar-spot fungi derive sugars from their hosts, and the sugars are converted into fungal components. Therefore it appears that even though sugar content initially increases in infected leaves, finally the host plants lose some of their carbohydrates through sporulation of their fungal parasites. The initial increases in sugar content corresponds with the previously mentioned findings where photosynthetic and nitrogen metabolism was also stimulated. However a decline in all physiological parameters after sporulation occurs and is attributed to a slowing down or senescing process of the leaves.

1.7 Autoradiography

In terms of competition for nutrients between host and pathogen and loss of sugars to parasites, it was interesting to note in the study of rust-infected *D. eriantha* that ^{3}H-glucose is absorbed at the early stage of penetration by the fungus. Incorporation of labelled glucose was observed in the sub-stomatal vesicle, penetration peg and infection hyphae (Figs. 109 and 110) and this indicates that glucose is required by the pathogen and removed from the host even at the initial stages of disease development. This has not been demonstrated previously in rust fungi, although Andrews (1975) reported glucose incorporation into the primary infection structures of *Bremia lactucae*. Autoradiographs also illustrate the accumulation of glucose in the mesophyll cells in the infection sites (Figs. 105 A and 106 A) and this confirms the sugar studies where glucose, sucrose and to a smaller extent fructose, were observed to increase in infected leaves. Incorporation of label is also observed in fungal cell walls (Fig. 108 B) which suggests that much of the glucose is utilized for cell wall synthesis and production of infection structures.

Having viewed the physiological consequences of infection by rust and

tarspot in this study many results reported by other worker have been confirmed, whilst new light has been shed on some of the influences of pathogens on their hosts. What is clear is that there is a fluctuating balance between synthetic and breakdown processes depending on the stage of disease development, and a competition for carbon and nitrogen between host and parasite.

7.2 A perspective of plant disease in a natural ecosystem

2.1 Introductory note

This study has achieved its objectives with respect to the influence of naturally occurring pathogens at Nylsvley on their respective hosts. It has also indicated that the patterns of disease development on *D. eriantha* and *P. maximum* follow an epidemiological course, and that reductions in primary production in terms of carbon dioxide fixation do occur in infected leaves at high intensities of infection or at the onset of sporulation. The similar effects of both obligate parasites on their hosts were demonstrated, and a point of particular interest which emerged was the changes which the fungus *P. paspalicola* initiated since this parasite has not been studied with respect to physiological aspects. However many other interesting questions arose during the course of this study. Since the significance of plant disease in natural populations has been largely ignored the postulations which emerged may be of interest for the future, and need to be looked at greater depth.

2.2 Co-evolution of the rusts

Pathogen evolution

Because of the wide-spread heteroecism in rusts evolution of host relationships in the Uredinales is interesting but difficult to study. Because of host alternation, plant associations have largely governed rust evolution (Savile, 1971). Members of the Gramineae throughout the world harbor rust populations representing a wide range of morphological and biological heterogeneity (Anikster and Wahl, 1979). By being obligate parasites the rusts have evolved hand in hand with their hosts. Younger rusts of more recent origin, *Puccinia* and *Uromyces*, are of worldwide distribution on dicotyledons and monocotyledons. The transference of the rust from primary to secondary hosts proceeds in heteroecious organisms by moving to the new host either the haploid or the dikaryotic generation, but never by simultaneous transfer of both generations

(Leppik, 1967). Aecial spores have not been identified as yet in *P. digitariae*, but the presence of teliospores in some cases suggests the common presence of an alternate host. However since the life-cycle of this rust has not been fully established, one can only speculate as to the origin of *P. digitariae* on *D. eriantha*. It is possible that expansion occurred from a primary aecial (dikaryotic) host to the grass. This has been shown to occur in *P. graminis* where tion occurred from *Berberis* to Gramineae (Klebahn, in Aniksta and Wahl, 1979).

Adverse environmental conditions can exert preferential selection pressure favoring the evolution of microcyclic rusts (reduced life-cycle forms) (Saville, 1953). The microcyclic rusts innabit th alternate hosts which frequently possess a higher survivability than the main host. This is especially true of rusts attacking members of the Gramineae, alternating with woody or geophytic plants. Most microcyclic rusts lack pycnidia. No pycnia in *P. digitariae* have been observed and it is possible that this fungus is a microcyclic rust on the alternate host *D. eriantha*, and that the other host is an agricultural crop grown in the extensive farming area around Nylsvley in the Northern Transvaal. Alternatively, *P. digitariae* may follow a similar pattern to *P. graminis* in South Africa where the rust becomes disassociated from the aecial host and its survival and development are dependent on the uredial stage. Certainly no telia were observed on *D. eriantha* at Nylsvley, but this does not imply that they are never produced. The uredial stage appears to be predominant, and the survival of the fungus may rely mainly on the uredospores and dikaryotic mycelia whilst other spore forms become functionless, or even disappear. However, until more is known about the hosts of this rust, its life cycle, origin and its hosts evolution, these speculations will continue.

Host defense and rust virulence

Having discussed rust evolution, the question arises as to the evolution of host defense. As an outcome of correlated evolution of host and pathogen, natural host populations contain a multi-

tude of distinct types and levels of resistance matched by broad spectra of virulence in pathogens (Nelson, 1978). Wild relatives of cultivated crops in the centres of their origin do not necessarily possess total immunity. Ordinarily fungi attack only some areas of the plants, inducing necrosis and producing lower spore yields. Mode (1958) postulated that in balanced host-parasite systems moderate resistance prevails which is more stable and has substituted for populations of high resistance and shorter duration. Van der Plank (1975) labeled diseases in natural ecosystems to be in an endemic balance which can be viewed as the 'evolutionary endpoint'.

However selection pressures can change this endpoint in terms of epidemic proportions. For example environmental selection pressures can cause phenotypic changes in the hosts which may influence disease levels. Similarly if these selection pressures act over a long period, genotypic changes may possibly occur. Genotypic adaptation has certainly been demonstrated in grasses where a heavy-metal tolerant ecotype in *Agrostis tenuis* developed over 20-30 years (Antonovics et al., 1971). Snaydon and Davies (1982) also demonstrated genetic divergence in the grass *Anthoxanthum odoratum* L. under changing soil conditions. Mildew and rust scores amongst many other attributes measured showed a significant difference between populations from unlimed and limed pots.

The incidence of *P. digitariae*, although by no means reaching significant epidemiological proportions, is unexpectedly higher than one would expect in a natural environment. It is possible that disease levels may have increased due to increased host susceptibility. This could have come about as a result of mans interference. The introduction of cattle into the reserve together with the existing herbivore population may have led to an increase in the grazing pressure on the grasses especially *D. eriantha* (Owen-Smith, 1982). This would lead to a decrease in vigour and changes in phenotypic characteristics would certainly occur. Consequently the weakening of certain grasses may have increased susceptibility to disease, and accelerated epidemic growth rates.

Another factor which may play a role in the changes of rust disease on *D. eriantha*, is the reproductive nature of this grass. *D. eriantha* produces many races or varieties which indicates extensive hybridization and an unusually marked response to habitat (Chippindall, 1955). The genetic heterogeneous nature of this grass tends to suggest genetic flexibility and therefore one would expect greater host ability to develop resistance to rust infection. However it may be speculated that since *D. eriantha* also reproduces extensively by vegetative means (stolons) that many offspring are identical to the 'mother' plants and this would lead to a greater degree of homogeneity. Therefore unless sexual reproduction takes place, the potential development of resistance to disease would be reduced. However another interesting speculation is the influence of the pathogen selective pressure exerted on the host. Since *D. eriantha* leaves do become more susceptible to rust as they age compared to the early stages of leaf development, it is possible that the selective pressures exerted by the rust on its host to develop resistance is weak. This would result in a more stable relationship. The linkage of genes for host resistance may in some situations lead to a stable state in a host-pathogen system where the host population is of intermediate resistance, capable of being maintained over long periods of time. Should this equilibrium be disturbed, increased susceptibility to disease may occur.

P. maximum and tarspot

Little is known about the life-cycle of *P. paspalicola* or host-resistance. However *P. maximum* certainly exhibits partial resistance to the fungal disease, and explosive epidemiological rates do not occur. It is interesting to note that *P. maximum* and most other members of the Panicae exhibit asexual (agamospermic) seed production, which is significant with respect to the possibility of a new ecotype arising in a single generation and maintaining itself. The wide genetic heterogeneity in *P. maximum* may speculatively be responsible for the resistance to tarspot. Further resistance was also demonstrated by the less severe effects this obligate parasite had in comparison to the rust, on the physio-

logical aspects discussed in 5.4. However this fungus has lacked attention in the past, and it is apparent that further studies on this parasite are required.

2.3 Photosynthesis, primary production and pathogens

Having looked at the rust and tarspot fungi on their respective hosts at Nylsvley, it is obvious that the definition of a pathogen as applied to an agrosystem is not appropriate for natural ecosystems. Perhaps the host-parasite system can be regarded as more of a coexistance than pathogenicity in natural undisturbed populations. The host-pathogen can be regarded as a discrete energy unit within the entire energy cycle of the ecosystem as a whole.

Due to the heterogeneity of natural ecosystems it is extremely difficult to assess the overall effect of diseasc on primary or dry matter production. Photosynthesis is the biophysical and biochemical background for primary production and hence from single leaf studies it is possible to extrapolate to tufts and then to the entire grass population as was demonstrated previously (5.4.3 and 5.4.4). However production of dry matter by plant cover depends on many other factors besides the specific photosynthetic capacity of the single leaves of the plants (Larcher, 1969). These include respiration; effects of internal and environmental variables during the entire production period; morphological characteristics of the individual plant; leaf area distribution in the plant cover; losses of plant material and translocation and storage of carbohydrates. Thus the influence of pathogens should not be looked at in isolation but rather in association with these factors.

Several important parameters, which need to be taken into account when attempting to study the overall impact of disease on primary production in the herbaceous layer at Nylsvley on a long-term basis, are proposed below:

1. Total CO_2 fixed by the herbaceous layer.

2. Estimate of percentage CO_2 fixed which is incorporated into dry matter production.
3. Estimate of the reduction in CO_2 fixed due to pathogens on a single leaf and whole plant basis.
4. Incidence and severity of disease on a monthly basis for the growing season since this will influence the changes in photosynsis.
5. Above ground biomass of the herbaceous layer.
6. The individual contributions of the diseased grasses to total biomass.
7. Pathogen effects on depletion and retranslocation of reserve carbohydrates.
8. Stage of host plant development when the disease occurs since the impact of disease may be greater if attack corresponds to the critical point of maximum dry matter accumulation.
9. Necromass.

Mineral cycling, defoliation and translocation

Leaf pathogens, even though they remove part of the energy fixed by their hosts and accelerate respiration, leaf senescence and necromass accumulation, may play a beneficial role in the energy cycle of the ecosystem. For example parasites may stimulate leaf size and thickness. El Hammady et al. (1968) demonstrated an increase in leaf size and dry matter production in broad bean infected with *Uromyces phas[illegible]li* and *Uromyces fabae*, and attributed this to a process similar to cytokinin stimulation. Other important aspects which have to be considered are the effects of gradual defoliation by pathogens on regrowth and reserve carbohydrate storage and retranslocation.

One has not only to take into account the effect of nutrient retranslocation to the roots at the end of the growing season, but also the translocation of nutrients to infected leaves during the earlier stages of infection (prior to sporulation after which the leaves senesce). Infected leaves act as nutrient sinks. Photosynthesis is initially stimulated and nitrates and sugar levels increase in infected leaves prior to sporulation. Total nitrogen

or protein nitrogen increases occur simultaneously. These nutrients are used for the synthesis of amino acids and other substances for the obligate fungal parasites. After sporulation the leaves begin to senesce and total nitrogen or protein nitrogen and sugar levels drop drastically (as does photosynthesis). Therefore part of the photosynthate products would be lost to the system due to pathogen utilization and consequently less would be retranslocated to the roots for storage. The amount of storage would in turn influence new growth the following season. At the same time however the pathogen is stimulating translocation of nutrients and minerals into the leaves and is accelerating metabolic processes and consequently senescence occurs sooner than in healthy plants. The amino acids and sugars which are not utilized by the pathogen are retranslocated into the roots. The remainder is left behind in the leaf/pathogen complex. Consequently when senescence of the infected leaves occurs, some of the nutrients are recycled into the system and new flushes can be accelerated. New growth results in renewed photosynthate production and further retranslocation to the roots at the end of the plants growth cycle. In this way the pathogen is actually accelerating growth whilst at the same time removing some of the host's energy for its own use. There seems to be two simultaneous processes occurring, one beneficial to the ecosystem, and the other detrimental to the plant.

What is of greatest significance is the influence of the short-term stimulation of growth on the long-term storage carbohydrate reserves ie. the loss of reserve carbohydrates retranslocated for growth during the season should not exceed the newly synthesized and retranslocated storage products at the end of the growth season. Billet and Burnett (1978) for example illustrated the import of organic material into infected leaves at the expense of other plant parts. However the infection caused a net reduction of carbon import into the roots and this would have a long-term detrimental effect. The consequence of stimulation of new flushes may not be visible above ground, but may be below ground, and may influence new tiller or seed production. It would therefore appear that unless one could determine

the relative importance or influence of these two processes (which could be achieved by measuring differences in growth between seasons following infection, under identical environmental conditions) one would not be able to assess the overall effect of plant disease on biomass accumulation on a long term basis.

Leaf senescence and removal by pathogens can be regarded as a gradual defoliation process and may have some similar effects as grazing (immediatie defoliation) has on leaf growth. Defoliation as an initial effect will reduce the photosynthetic leaf area of the plant, but can stimulate regrowth and dry matter production providing the frequency and intensity is not too high. Quantification of net above-ground production in a perennial sward is confounded by residual or 'carry-over' biomass from a previous to a current year. In addition as residual biomass dies it flows to necromass. This is complicated further by death of the current years biomass before peak production is attained. Hence it is difficult to measure the effects of pathogens on biomass accumulation in a natural environment, without taking these considerations into account.

7.3 Concluding remarks

Improved knowledge of plant disease epidemics will help identify where man can interfere in population dynamics and will permit the development of more efficient methods for disease management. Studies on the mechanisms of disease tolerance in epicenters where host and pathogen co-evole may provide useful material for crop improvement. An adequate knowledge of growth patterns in grasses and the effects of pathogens on yield and quality of the herbage is a prerequisite for the rational utilization of pastures for animals or of natural vegetations which support a variey of consummers.

In agrosystems the most important objective is to produce maximum crop quantity or yield and quality above ground for consumption. In ecosystems however a balance between different plant populations or between consumer and producer components is required. Control-

ling factors are necessary to ensure that changes in the competitive ability of one species does not result in the introduction or dominance of an undesirable species. Pathogens may play a minor part in the mosaic of important factors operating at Nylsvley and other natural ecosystems.

APPENDIX

Nutrient solution

Chemical	g/l
$NaH_2PO_4.2H_2O$	0.21
$MgSO_4.7H_2O$	0.37
$MnSO_4.H_2O$	0.0023
$CuSO_4.5H_2O$	0.003
$ZnSO_4.7H_2O$	0.0003
H_3BO_3	0.002
$(NH_4)_6Mo_7O_{24}.4H_2O$	0.0003
$CoSO_4.7H_2O$	0.0002
Na Cl	0.005
KNO_3	0.50
$Ca(NO_3)_2$	0.82
FeEDTA	0.30
$CaCl_2$	0.50
K_2SO_4	0.44
$(NH_4)_2SO_4$	1.05

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