

The relationship of vesicular-arbuscular
mycorrhizal root colonization and growth
of Acacia saligna and Acacia cyclops
growing in Clovelly and Fernwood soils
of the South-Western Cape.

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Abstract

Plants of Acacia saligna and Acacia cyclops were potgrown both in competition and also with two members of a species in a single pot in Fernwood and Clovelly soils. Dry masses, shoot P concentration, mycorrhizal infection and nodulation was determined in each. The Fernwood soil from a west coast Strandveld community had higher levels of Bray no. 2 P. than did Clovelly soil from a Sandplain lowland Fynbos community (47.7 VS 3.3 $\mu\text{g P g}^{-1}$ dry mass). A. cyclops showed a greater capacity to utilize higher levels of soil nutrients than did A. saligna in that growth rates were higher in Fernwood than Clovelly soil. A. saligna showed a greater accumulation of P in the tissues, suggesting that it is unable to efficiently utilize high levels of P. A. saligna generally had higher root dry mass and root : shoot ratios than A. cyclops, whilst A. cyclops showed a greater potential for infection by vesicular-arbuscular mycorrhizal (VAM) fungi. It is suggested that this indicates a different 'strategy' to the acquisition of nutrients in the 2 species. A. saligna may be better adapted to the low soil nutrient levels in the Clovelly soil than is A. cyclops (further evidence for this coming from its ability to outcompete A. cyclops when growing in the same pot). There may thus be an ecophysiological basis for the differential distribution of A. cyclops mainly on mesotrophic coastal sands and A. saligna mainly on oligotrophic soils in the SW Cape.

Several types of VAM fungi were found in association with the roots of both soil types, but infection potential being far

higher in the Clovelly soil. Types 'A' and 'B' Gigaspora auxilliary cells were found in both soil types, while the type 'C' form was only found in Clovelly soil. A non-staining, smooth walled auxilliary cell not described by Hoffman & Mitchell (1986) was observed in Fernwood soil. All 4 types of auxilliary cells were only found on A. cyclops in this study. Glomus chlaⁿrydospores and ^azygospores of Gigaspora were also found in association with the roots.

<u>Contents</u>	<u>Page</u>
<u>Introduction</u>	3
1. Identification and characterization of VAM fungi	3
2. The role of VAM fungi in P uptake	5
3. Alien plant invasions in the SW Cape	8
<u>Study areas</u>	9
<u>Materials and methods</u>	10
1. Chemical characteristics of the soils	10
1.1 pH determination	10
1.2 Organic content	10
1.3 Phosphorus determination	10
1.3.1 Total phosphorus	10
1.3.2 Bray no. 2 phosphorus	11
2. Growth response experiment	11
2.1 Shoot total phosphorus determination	12
2.2 Mycorrhizal infection intensity	13
2.3 Intensity of root nodulation	14
3. Competition experiment	14
<u>Results</u>	15
1. Comparison of Fernwood and Clovelly soils	15
2. Growth response experiment	15
2.1 Root & shoot dry mass in Clovelly and Fernwood soils	15
2.2 Plant total P content	23
2.3 Fungal associations with the roots	23

2.3.1	Mycorrhizal infection intensity	23
2.3.2	Identification of fungi in association with the roots	25
2.4	Degree of nodulation	32
3.	Competition experiment	32
3.1	Root and shoot dry masses	32
3.2	Quantifying mycorrhizal infection	37
3.3	Root nodulation intensity	37
	<u>Discussion</u>	40
	<u>Conclusions</u>	45
	<u>Acknowledgements</u>	47
	<u>References</u>	48
<u>Appendix I</u>	A	53
	B	54
<u>Appendix II</u>	A	55
	B	56

INTRODUCTION

The symbiotic endomycorrhizas can be divided into 3 main categories: ericoid, orchidaceous and vesicular-arbuscular mycorrhizas (VAM). The VAM fungi may be found in nearly all soils and are characterized by a lack of host specificity (barring a few plant families which are rarely infected by mycorrhizal fungi) (Harley & Smith, 1983). There has been a considerable increase of research in recent years emphasizing the role these ubiquitous soil fungi play in the nutrition of higher plants as well as in intra- and interspecific plant competition.

1. Identification and characterization of VAM fungi

VAM fungi are characterized by usually possessing aseptate hyphae in the external soil medium, but most importantly by intracellular formation of arbuscules and also vesicles in some cases in the cortical cells of the host (Trappe & Schenck, 1982). There is generally very little alteration of host root anatomy after infection (Harley & Smith, 1983) and root hairs may be retained. After penetration of the host epidermis has occurred, intracellular hyphae develop. The arbuscule (which remain surrounded by host plasmalemma) is believed to be the site of transfer of nutrients from symbiont to host and of carbon metabolites from host to symbiont (first suggested by Harley, 1969).

Despite recent work on the ecophysiology of VAM fungi, knowledge of their taxonomy is sparse. Peyronel in 1923 recognised that VAM fungi are members of the Endogonales (all being members of

the family Endogonaceae of the Zygomycotina assemblage). During the next 3 decades, very little taxonomic work was performed on these fungi, because spores were rarely encountered (Trappe & Schenck, 1982) and also possibly owing to the difficulty with which these fungi are cultured; this is despite the fact that they are amongst the most common of the soil fungi. All the Endogonaceae were originally placed in the genus Endogone. In 1974 this was divided into 7 genera viz. Endogone, Gigaspora, Glomus, Acaulospora, Glaziella, Sclerocystis and Modicella (Gerdemann & Trappe, 1974). Since then, new minor genera have been found and the number of known species has doubled. (Trappe & Schenck, 1982). Genera were designated primarily according to the manner of spore formation. The type genus Endogone forms zygosporangia and has not been known to form VAM association. (Trappe & Schenck, 1982). The other genera all display the criteria for VAM infection described above. Two types of spores have been suggested for VAM fungi.

Of the most widespread genera, Acaulospora and Gigaspora form azygosporangia, whilst Glomus and Sclerocystis form chlamydospores (Trappe & Schenck, 1982), these being the soil resting structures in the absence of a suitable host. The genus Gigaspora is also characterized by the extracellular development of 'vesicles' or auxiliary cells borne singly or in clusters (Trappe & Schenck, 1982). Because these structures are not always accompanied by intracellular penetration, they may not be used as a criterion for host infection. A further feature of this genus is that it does not generally form intercellular vesicles (Gerdemann & Trappe, 1976).

2. The role of VAM fungi in P uptake

Phosphorus is an element of primary importance to the functioning of the plant, performing numerous roles, most notably via ATP utilized in active transport and synthesis of organic compounds. If mycorrhizas are capable of increasing P uptake, they must be having a marked effect on metabolic processes within the plant, owing to their widespread distribution in most soils.

Indirect evidence that mycorrhizal roots are more efficient in P uptake than non-mycorrhizal roots comes from the fact that mycorrhizal plants frequently have far higher concentrations of phosphorus in their tissues than uninfected plants (Harley & Smith, 1983; Stribley et al. 1980). Concomitant increase in growth rates have also been shown to occur (Gianinazzi-Pearson & Gianinazzi, 1981). Mycorrhizas are of particular importance in supplying P to nodules of N-fixing legumes (Green et al, 1983).

In discussing how mycorrhizal fungi may increase P uptake, it is necessary to outline reasons for the frequently limiting levels of phosphorus present in the soil. Phosphate anions become strongly bound ^{to} ~~by chelation agents such as Fe, Al and Ca,~~ ^{and} especially under conditions of low pH (Mengel & Kirkby, 1982), resulting in low availability of inorganic orthophosphate (Pi). The labile P fraction is significantly lowered by low pH, (the labile fraction being the portion in rapid equilibrium with the soil solution with Fe, Al, clay minerals and apatites). In addition where parent rock material is low in nutrients, nutrient deficient soils will develop, as will occur where rates of decomposition are

are slow. Organic complexes may also bind P (up to 80% in some soils (Harley & Smith, 1980)). Slow diffusion of phosphates through the soil medium results in the development of a zone of depletion in the rhizosphere of roots capable of rapid P absorption (Harley & Smith, 1983). Dry soils would further increase P-limitation due to slow diffusion (Fitter, 1985). The combination of these factors frequently results in soils where nutrients are present in micromolar, rather than millimolar concentrations (Harley & Smith, 1983).

Ericoid and ectomycorrhizal fungi have been shown to have the capacity to 'mineralize' phosphate present in organically bound form, rendering it available for uptake (Bartlett & Lewis, 1973; Shaker & Mitchell, unpublished). However, Gianinazzi-Pearson & Gianinazzi (1976) found that soluble phosphatase activity was not significantly increased by VAM fungi, and rock-phosphate is not released either (Harley & Smith, 1983). It therefore appears that the most important means whereby VAM increase P uptake is by overcoming limitation of P diffusion through the soil medium. At very negative water potentials, under conditions where plant uptake is minimal, nearly all P is taken up by mycorrhizal hyphae (Fitter, 1985). In Australia and the SW Cape, the Mediterranean climate results in approximately 6 months of every year being hot and dry. Soils are also strongly leached and parent rock is infertile (Lamont, 1983); it is therefore likely that mycorrhizas play an important role in both of these regions, where over 90 genera of 50 families have been found to be infected to date (Lamont, 1983).

By rapid growth and maintenance of a large surface area in contact with undepleted soil, the mycorrhizal hyphae may further increase P uptake, being a further reason for greater P uptake in VA infected plants (Harley & Smith, 1983).

The relationship of mycorrhizal infection intensity to P uptake has not been found to be linear, but depends primarily on P requirement by the host (Harley & Smith, 1983). Increases in P uptake by VAM have been found to be especially important in soils of low nutrient status (Hetrick et. al. 1984). Cress et al. (1979) found that there are two phases to uptake of P - operating at low and high concentrations. The high affinity uptake system of the mycorrhizal fungus appears to be more efficient than the host root at P uptake (Abbot & Robson, 1977). This further emphasises the importance of VAM in enhancing P nutrition of the plant.

After being taken up by the hyphae, P is transformed into inorganic polyphosphate (polyP) by polyP kinase (Harley & Smith, 1983) which maintains an equilibrium with P_i in solution. P in solution moves passively down a concentration gradient into the host which acts as a 'sink'. In exchange, hexoses are actively taken up by the fungus from the host under the control of polyP hexokinase in the mycorrhizal hyphae (Capaccio & Callow, 1982). Thus it can be seen that VAM fungi are playing an important role in the P-nutrition of higher plants.

3. Alien plant invasion in the SW Cape

The South-western Cape (SW Cape) is presently being extensively invaded by alien plant species (Boucher, 1984). Several possible reasons have been suggested for the success of alien plant species in the SW Cape (Macdonald, 1984). Perhaps the most important of these is the long history of disturbance by unnaturally high fire frequencies (Shaughnessy, 1980 in Weiss, 1983), making the vegetation inherently susceptible to invasion. Two species which have been especially successful as invaders are Acacia saligna (Labill.) Wendl and Acacia cyclops. A. Cunn, ex G. Don (Shaughnessy, 1980), both of which originate from SW Australia, possess type IV roots according to the classification of Cannon (1949) (i.e. they have a long primary root with extensive branching laterals, particularly near the soil surface). A. cyclops has tended to predominate on coastal calcareous sands, whilst A. saligna has been in lowland fynbos (Milton, 1980). Very little research has been conducted on the reasons for the present distribution of these species within the SW Cape. Appendix I A & B shows the distribution of past planting of A. cyclops and A. saligna in the Cape Peninsula. It is evident that extensive spread of these species has been caused directly by seed dispersal by man. However, ecophysiological factors may also have contributed to their differential distribution ranges.

This project aims to assess seedling growth rates of A. saligna and A. cyclops in two different soil types. Mycorrhizal infection intensity and nodulation in roots of the two species grown on

different soils shall also be assessed. Phosphorus uptake may be influenced by mycorrhizal infection intensities. Plants of A. saligna and A. cyclops grown in competition on the two soil types may indicate that one species will have a growth advantage.

By understanding the above factors it may be possible to suggest reasons for the differential distribution of A. cyclops and A. saligna in the SW Cape.

STUDY AREAS

Pella, situated 33°31'S, 18°32'E is dominated by Sandplain Lowland Fynbos, having an open to closed (25-90%) canopy cover and being described by Moll et al. (1984) as being low to mid-high graminoid shrubland. This vegetation type is confined to deep acid sands of the west coast lowlands and also locally occurring on the south coast (Moll et. al. 1984). The Pella site has had a long history of frequent burning and rough grazing described by Brownlie (1982)(cf Appendix IIA). Appendix IIB shows the patterns of encroachment of A. saligna and A. cyclops at Pella, with A. saligna being the more dominant invading species. The soil was classified as having a Clovelly form with an orthic A and yellow-brown apedal B horizon (Macvicar et. al. 1977).

Melkbos (33°43'S, 18°28'E) situated on the west coast is dominated by Strandveld shrublands with a mid-dense to closed canopy cover. Sub-tropical and Cape Fynbos broadleaf species form components of

the vegetation. (Moll et al. 1984). There is a high proportion of semi-deciduous to deciduous shrubs as well as a large succulent component. A. cyclops is becoming an increasingly dominant alien in the coastal shrublands (Milton, 1980). The soil consists of an orthic A horizon overlying regic sand, classified as a Fernwood form (Macvicar et al. 1977).

MATERIALS AND METHODS

1. Chemical characteristics of the soils

Soil was collected and 2mm sieved from the two study sites in early March, 1986.

1.1 pH determination

20g soil samples in 0.01 M Ca Cl₂ were mechanically shaken for 30 minutes (Schofield & Taylor, 1955). pH was determined using a Beckman 20 portable pH meter. 5 replicates were performed for each of the two soil types

1.2 Organic content

Oven-dried soils were muffled at 450⁰C for 16 hours and the change in soil mass was determined. Results were calculated as percentages.

1.3 Phosphorus determinations

1.3.1 Total phosphorus was determined using 2g of 2mm sieved soil that had been muffled at 240⁰C for 90 minutes, 5 replicates

↳ this an accepted word?

for each soil type. 10cm^3 of HCl was used to digest the material at 100°C for 30 minutes. 10cm^3 of distilled water was then added. After 30 minutes samples were allowed to filter through Whatman No. 1 filter paper. The filtrate was then made up to 50cm^3 . A 2cm^3 aliquot was taken to which was added 8cm^3 of Murphy and Riley solution (Murphy & Riley, 1962). After being made up to 50cm^3 , colour was allowed to develop for 30 minutes. Absorbances were read at 882nm on a Bausch & Lomb spectronic 21 spectrophotometer.

2. This is a very unusual wavelength.

1.3.2 Bray no. 2P

This method of P-determination is a measure of the plant-available phosphorus in the soil. 60cm^3 of Bray No. 2 solution was added to 8g of 2mm sieved soil and shaken for exactly 45 seconds (5 replicates being made for each soil type). Soil was filtered through Whatman No. 1 filter paper and a 10cm^3 aliquot of the filtrate was taken. 8cm^3 of Murphey & Riley solution was added to the filtrate. After being made up to 50cm^3 , colour was allowed to develop for 30 minutes. Absorbances were read as for total P.

2. Growth response experiment

A. saligna and A. cyclops seeds collected from litter at Pella and Melkbos respectively had their dormancy broken by scarification of the testa at the micropylar end after being surface-sterilized in 5% sodium hypochlorite. Seeds were allowed to germinate under sterile dark conditions at 20°C for 4 days. Seeds were kept on damp Whatman No. 1 filter paper in glass petri dishes. Seedlings of similar stages of development were potted in 12.5cm pots in fresh 2mm sieved soil, each pot containing

but this is a bit dangerous?

two plants of the same species. Pots were kept in a controlled environment of 16 hr photoperiod. The maximum day temperature was approximately 28°C and minimum night temperature was about 20°C. The plants were watered with \pm 50ml of double deionized water every 2-3 days. Positions of the pots were changed every week so that they would have equal amounts of light. 4 pots of each treatment (i.e. A. cyclops and A. saligna grown in Clovelly and Fernwood soils) were harvested every two weeks by careful root-washing using a 2mm sieve. One of the plants' roots was retained in FAA for later determination of mycorrhizal infection intensity. The other plant was oven-dried at 80°C for 12 hours after which time root and shoot biomasses were determined to 4 decimal places on an Oertling balance. Using this data, root : shoot ratios were calculated for A. saligna grown on Clovelly and Fernwood soil and A. cyclops grown on Clovelly and Fernwood soil.

2.1 Shoot total phosphorus determinations

Dried shoot material of 10-weekold seedlings of A. saligna and A. cyclops from Fernwood and Clovelly soils was milled (4 shoots from each treatment) using a 40 mesh Wiley Mill. Due to lack of plant material for performing replicate plants (since biomasses were too low), determinations on younger seedlings could not be performed. Thus age of seedling could not be correlated to phosphorus content and mycorrhizal infection intensity. 0.1000g of plant material was predigested with 1cm³ of concentrated nitric acid at 170°C for $\frac{3}{4}$ hr. 1cm³ of tri-acid mixture was used for further digestion for $\frac{3}{4}$ hr (Jackson, 1958). The digests were made up to 25cm³. 2.5cm³ aliquots were taken to which was added

8cm³ of Murphy & Riley solution. The colour was allowed to develop for 30 minutes after samples were made up to 50cm³. Absorbances were read as before.

2.2 Mycorrhizal infection intensity

Lateral roots stored in FAA were rinsed and cut into +- 7mm lengths. Segments were cleared in 10% KOH w/v at 90° (for approximately ³/₄ hr (Bevege, 1968). Roots were then rinsed in tap water followed by 1M HCl. Staining in 0.05% trypan blue in lactophenol was carried out for 5 minutes at 90°C (Hayman, 1970). Segments were stored in the dark in lactophenol until examination of the mycorrhizal infection was performed. For 2 and 4-weekold seedling roots, 4 replicates were examined. For the 6-10 weekold plants, 100 root segments were randomly taken from the lateral roots of a single seedling. Segments were mounted in dilute glycerine and were examined under a binocular compound microscope at 40x (or 100x when necessary) magnification. Segments were taken to be infected if arbuscules could be observed. The percentage number of infected segments for each treatment was determined (infection being recorded as either present or absent in a segment).

Fungal structures (whether mycorrhizal or not) were identified and semipermanent slide mounts using nail varnish were made. These slides were later photographed, using a Carl Zeiss large Universal photomicroscope. An eyepiece micrometer was used for measurement of structures.

2.3 Intensity of root nodulation

Roots to be cut and stained for inspection of mycorrhizal infection intensity were first used to determine the number and sizes of the nodules on the rooting systems. Nodules were placed into size classes, the % number in each class being determined.

3. Competition experiment

Two plants (each of a different species) were grown in competition together for 8 weeks; growth conditions were the same as for the growth response experiment, except that the soil was 2 months older.

10 replicate pots were grown for each treatment. In addition, the same number of control pots (using methyl bromide fumigated soil) were grown in the same way. For each treatment, the plants in 5 of the pots were used for dry root and shoot biomasses, whilst the other 5 had their roots retained for analysis of % mycorrhizal infection, as for the growth response experiment. Nodule numbers and size were also determined.

Where relevant, statistical analysis to test the significance of differences in the mean results were carried out. The students' t-test for one-tailed hypotheses was used, which assumes that populations are normally distributed and that variances are approximately equal (Zar, 1982).

RESULTS1. Comparison of Fernwood and Clovelly Soils

Marked differences were found in the properties of soil collected at Melkbos (Fernwood soil) and Pella (Clovelly soil) (cf Table 1). pH of the Clovelly soil was acidic, whilst that of the Fernwood soil was slightly alkaline. The percentage organic content of the Fernwood soil was an order of magnitude higher than that of the Clovelly soil (11.69 \pm 0.03% versus 0.84 \pm 0.02%). Total phosphorus content was also found to be far higher in Fernwood soil, as was Bray no. 2P, a measure of P available for plant uptake.

What about other Coast plants?

2. Growth response experiment2.1 Root and shoot dry mass in Clovelly and Fernwood soils

Figure 1 shows the dry masses of the growth response experiment for A. saligna and A. cyclops plants grown in Fernwood and Clovelly soils. The Clovelly-grown plants showed an initial increase in dry weight (4-6 weeks) which was greater than the Fernwood-grown plants. Total dry mass was significantly higher at 6 weeks in Clovelly soil for both species. However, at 10 weeks, A. cyclops had a significantly higher dry mass in Fernwood soil. (cf Table 2).

~~10-weekold A. cyclops had a significantly higher dry mass than A. saligna in Fernwood soil.~~

Table 1: Differences in the properties of Fernwood and Clovelly soils. The results are the product of 5 replicates, ± 1 SEM.

	Clovelly	Fernwood
pH \pm S.E.	4.62 \pm 0.02	7.03 \pm 0.02
% organic content \pm S.E.	0.84 \pm 0.02	11.69 \pm 0.03
Total P \pm S.E. ($\mu\text{g P g}^{-1}$ dry mass)	12.65 \pm 0.07	195.40 \pm 5.93
Bray no. 2P \pm S.E. ($\mu\text{g P g}^{-1}$ dry mass)	3.29 \pm 0.83	47.66 \pm 1.08

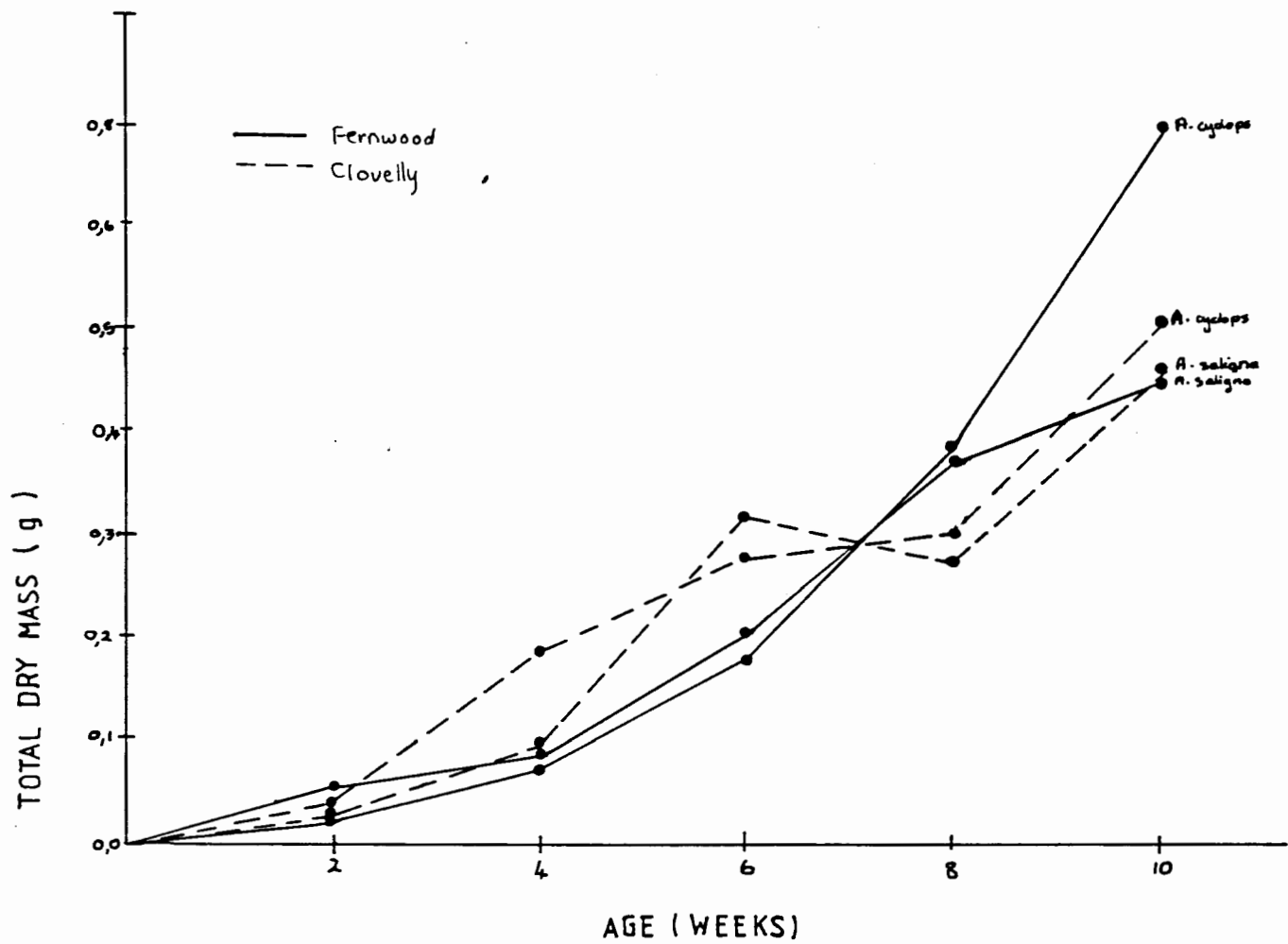


Figure 1: Total dry masses of *A. saligna* and *A. cyclops* grown on Fernwood and Clovelly soils. (2 plants of the same species per pot). Each point is the mean of 4 replicates.

Table 2: Significance of the differences in total plant dry mass of A. cyclops and A. saligna in Fernwood and Clovelly soils, and between species but in the same soil type.

	Age	df	p	t-value
<u>A. saligna</u> in Clovelly & Fernwood soil	6 weeks	6	0.025	2.88
<u>A. saligna</u> in Clovelly & Fernwood soil	10 weeks	6	0.05	NS*
<u>A. cyclops</u> in Clovelly & Fernwood soil	6 weeks	6	0.025	3.28
<u>A. cyclops</u> in Clovelly & Fernwood soil	10 weeks	6	0.025	3.04
<u>A. saligna</u> and <u>A. cyclops</u> in Fernwood soils	10 weeks	6	0.05	2.406

*Not significant

Figure 2A shows that A. saligna shoot increments were not significantly higher in the Fernwood soil, but Figure 2B indicates root dry masses were significantly higher in Clovelly compared to Fernwood soils. At 6 weeks, A. saligna root had a significantly higher dry mass in Clovelly soil ($df = 6$; $p = 0.025$; $t = 2.056$) as well as at 10 weeks ($df = 6$; $p = 0.025$; $t = 2.05$).

After 8 weeks A. cyclops shoots from Fernwood soil had a significantly higher mass ($df = 6$; $p = 0.05$; $t = 2.21$). (cf Plate 1 of A. cyclops seedlings at 10 weeks). A. cyclops root dry mass was highly significantly greater in Clovelly compared to Fernwood soil at 6 weeks although this trend did not continue (figure 2D). The phenomenon of the decrease in root biomass, at 8 weeks is interesting to note since A. cyclops experiments were running 2 weeks behind A. saligna. Thus some uncontrolled environmental factor e.g. lack of water probably did not cause the decrease in dry mass.

A. cyclops root : shoot ratios are consistently higher in Clovelly than in Fernwood soil (Table 3). A. saligna ratios were significantly higher at 2 weeks in Fernwood soils than Clovelly soil ($df = 6$; $p = 0.01$; $t = 3.41$). The older A. saligna plants then followed the same trend as A. cyclops. A. saligna generally had a higher root : shoot ratio than A. cyclops in Clovelly soil, except at 4 weeks when A. cyclops had a significantly higher root : shoot ratio ($df = 6$; $p = 0.01$; $t = 4.12$). The same trends were true for the Fernwood soil where at 4 weeks,



Plate 1: 10-weekold seedlings of *A. cyclops* grown on Fernwood (left) and Clovelly (right) soils.

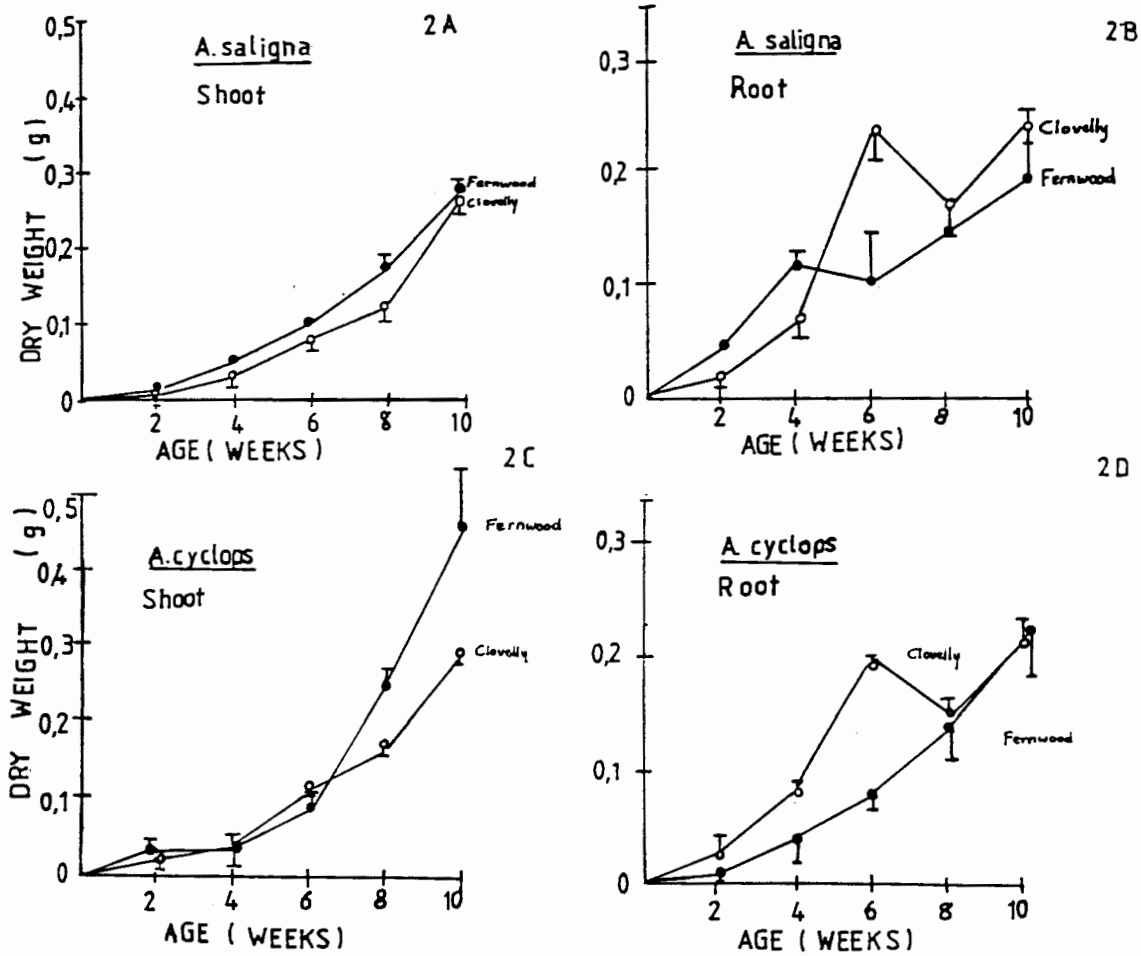


Figure 2: Root and shoot dry masses of *A. saligna* and *A. cyclops* grown on Fernwood and Clovelly soils (2 plants of the same species per pot). Each point is the mean of 4 replicates. (± 1 SEM).

Table 3: Root : shoot ratios of A. cyclops and A. saligna grown on Clovelly and Fernwood soils (each pot containing two plants of the same species, one of which was examined for mycorrhizal infection). Results represent the mean of four ratios \pm 1 SEM.

Age (weeks)	CLOVELLY		FERNWOOD	
	<u>A. saligna</u>	<u>A. cyclops</u>	<u>A. saligna</u>	<u>A. cyclops</u>
2	2.13 \pm 0.16	1.23 \pm 0.20	4.39 \pm 0.66	0.83 \pm 0.19
4	1.815 \pm 0.45	3.20 \pm 0.37	0.83 \pm 0.11	1.04 \pm 0.34
6	2.68 \pm 0.20	1.69 \pm 0.11	1.00 \pm 0.20	0.94 \pm 0.17
8	1.18 \pm 0.11	1.01 \pm 0.04	0.33 \pm 0.07	0.53 \pm 0.08
10	0.96 \pm 0.09	0.69 \pm 0.07	0.79 \pm 0.05	0.49 \pm 0.07

A. cyclops had a higher root : shoot ratio (although not significant at $p = 0.05$) whereas at the other ages A. saligna had a higher root : shoot ratio.

2.2 Plant total P content

10 weekold seedlings of A. saligna had a phosphorus content which was significantly higher at $p = 1.0$ ($df = 6$; $p = 0.05$; $t = 1.92$) than A. cyclops grown in Fernwood soil (cf Table 4).

There was a very marked increase in P content of plants grown in Fernwood soil compared to Clovelly soil.

2.3 Fungal association with the roots

2.3.1 Mycorrhizal infection intensity

The percentage number of root segments infected was highest in A. cyclops in Fernwood soil, except at 4 weeks where it appeared as though infection was undergoing a slight lag phase with respect to A. saligna (cf figure 3). A. saligna showed a very rapid initial infection rate in Fernwood soil with 34% of the root segments being infected at 4 weeks. The infection rate then plateaued off, but increased again although at a lower level than A. cyclops. Infection intensities were consistently lower in roots from Clovelly soil, again with A. cyclops showing the greatest susceptibility to infection. A. saligna had exceptionally low infection intensities in Clovelly soil (at 10 weeks the infection intensity being only 6.9%)(cf figure 3).

Table 4: Plant total P (g g⁻¹ dry mass) +- 1 SEM (mean of 4 replicates) of above - ground plant material grown in Clovelly & Fernwood soils. The samples were taken from 10 - weekold A. cyclops and A. saligna seedling roots.

	<u>Acacia saligna</u> ($\mu\text{g Pg}^{-1}$ dry mass)	<u>Acacia cyclops</u> ($\mu\text{g Pg}^{-1}$ dry mass)	Significance of difference
Clovelly	91.15 \pm 13.56	84.05 \pm 11.32	NS*
Fernwood	306.25 \pm 33.20	213.80 \pm 34.88	at $p \leq 1.0$

*Not significant at $p \leq 1.0$

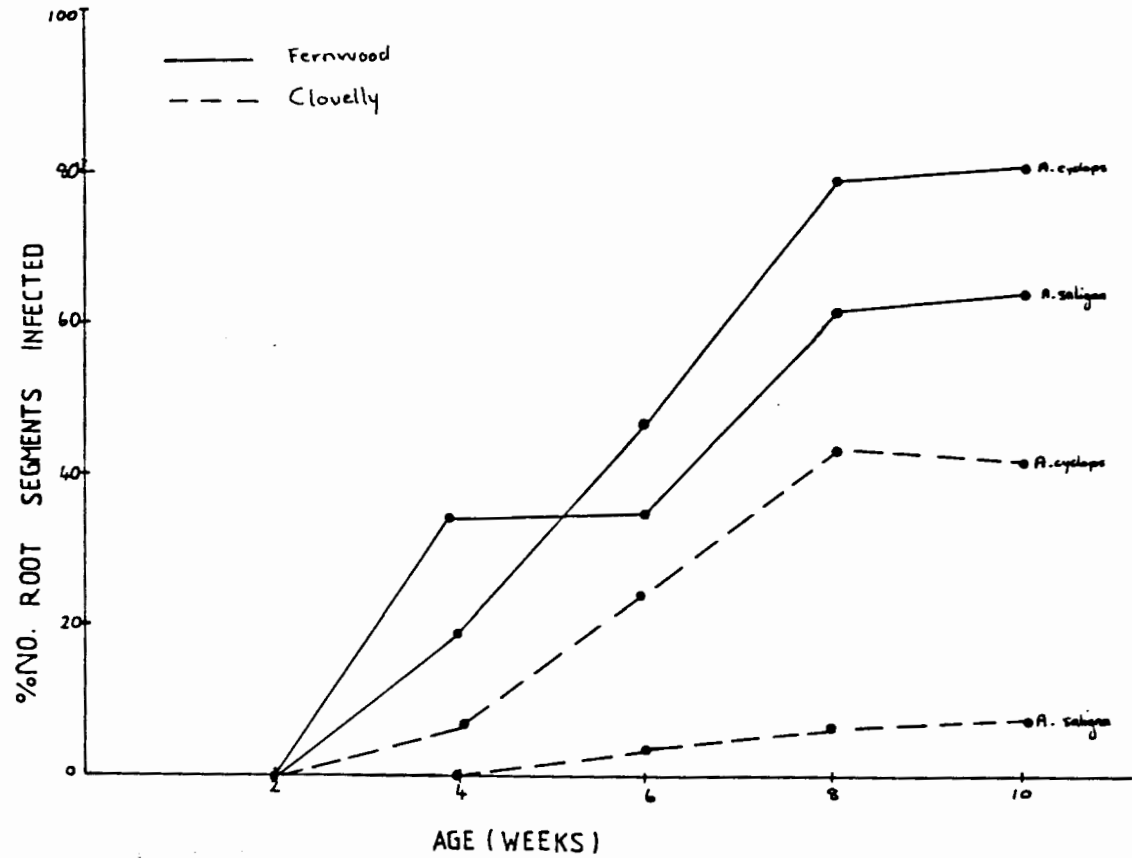


Figure 3: % of Root segments infected with increasing age in *A. cyclops* and *A. saligna* grown on Fernwood and Clovelly soils (2 plants of the same species per pot). 100 segments of each plant were examined.

2.3.2 Identification of fungi in association with the roots

Taxonomy of observed fungi was not attempted to species level; with respect to genus Gigaspora, wet-sieving for isolation of ~~A~~^A/~~zygospores~~^e is required which is to be carried out at a later stage.

Chlamydozoospores of Glomus were observed in A. saligna and A. cyclops in both Fernwood and Clovelly soils. Plate 2A shows a spore of Glomus infecting 8-weekold A. cyclops on Fernwood soil.

Plate 2B shows a region of root of A. cyclops (6 weeks) grown in Clovelly soil which has high infection intensity near the stele in the root cortex.

Vesicles predominated in the roots grown in Fernwood^{so} soil. Plate 3A shows terminal vesicles present in the 8-weekold roots of A. cyclops grown in Fernwood soil.

Relatively few hyphal coils were observed in any of the seedling roots; the structure most closely fitting the description of a hyphal coil (Trappe & Schenck, 1982) is shown in plate 3B, being in the root cortex of A. saligna (8 weeks old) grown in Clovelly soil.

vs. C. Linn. x.

Several types of extramatrical/auxiliary cells belonging to genus Gigaspora were observed on the roots of A. cyclops in both Clovelly and Fernwood soils, but none were found on the roots of A. saligna for the growth response experiment, but some appear

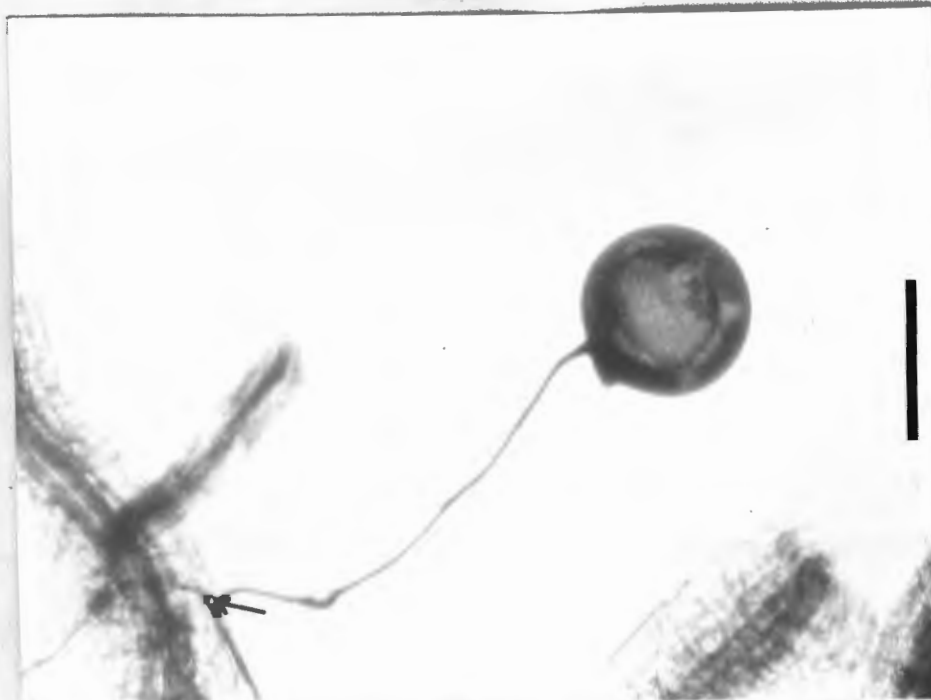


Plate 2A: *Glomus* chlamydospore infecting an 8-weekold *A. cyclops* root in Fernwood soil. Arrow indicates point of hyphal penetration. Scale = 40 μ m.



Plate 2B: Region of root of *A. cyclops* (6 weeks) grown in Clovelly soil with high infection intensity near the ^{ele}state in the root cortex. Scale = 10 μ m.

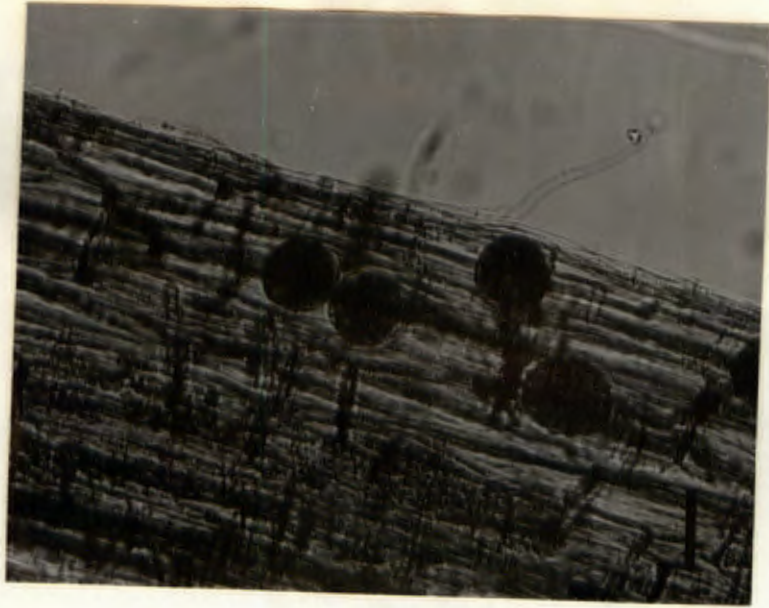


Plate 3A: Terminal vesicles present in 8-weekold roots of A. cyclops grown in Fernwood soil. Scale = 10 μm .

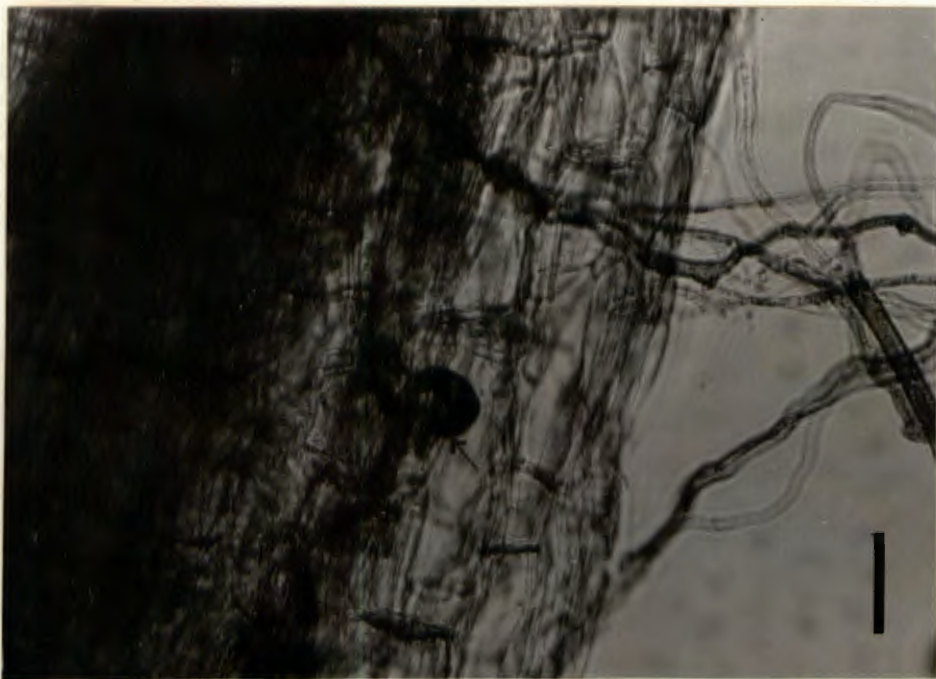


Plate 3B: Hyphal coil in the cortex of the root of A. saligna grown on Clovelly soil (8 weeks old). Scale = 5 μm .

Not clear

for the competition experiment. 'Type A' auxil*i*ary cells characterized by papillate terminal projections were relatively common in both soil types (cf plate 4B). 'Type C' auxil*i*ary cells (non-staining, irregularly shaped lobed structures) were found only in Clovelly soil (cf plate 4B) (Hoffman & Mitchell, 1985). 'Type B' auxil*i*ary cells were found in both soil types. These are characterized by being a clustered group of 'cells' with cone-like projections from the spore surface (Hoffman & Mitchell, 1986). (cf plate 5A). Another type of auxil*i*ary cell not described by Hoffman & Mitchell (1986) was found on the roots of A. cyclops of 8 and 10 weeks. These structures were characterized by being a non-staining (brown-walled) clustered group of small walled 'cells' having aseptate hyphae (cf plate 5B). It is unlikely that this was simply an undeveloped 'type C' auxilliary cell since no mature structures of that type were found in Fernwood soil. In addition, the brown colouration generally only develops in maturing auxil*i*ary cells (Trappe & Schenck, 1982).

Plate 6A shows the azygospore of Gigaspora on A. saligna grown in competition with A. cyclops on Fernwood soil, characterized by having a bulbous 'suspensor' which bears a hyphal projection (not visible in the photomicrograph).

Plate 6B indicates how extensive the root hair development was on A. saligna at 4 weeks grown in Clovelly soil. Root hair development was generally more extensive in Clovelly soil. It appeared that after infection, root hairs did not develop.

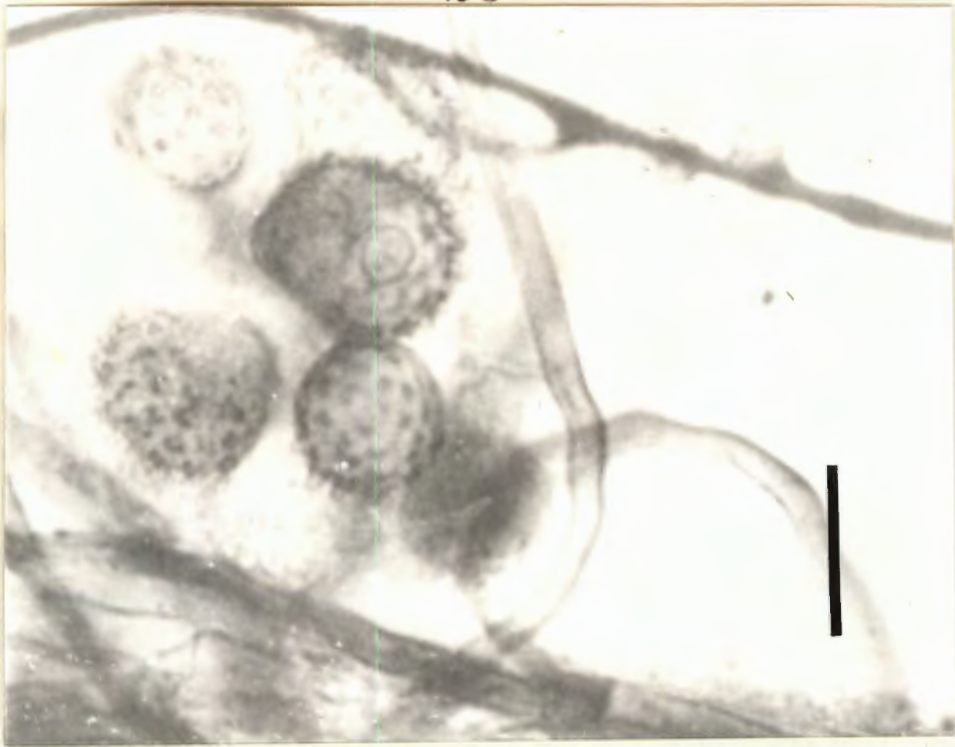


Plate 4A: 'Type A' auxiliary cells of Gigaspora on A. cyclops (8 weeks) grown in Fernwood soil. Scale = 25 μm .



Plate 4B: 'Type C' auxiliary cells of Gigaspora on A. cyclops grown on Clovelly soil (8 weeks). Scale = 10 μm .

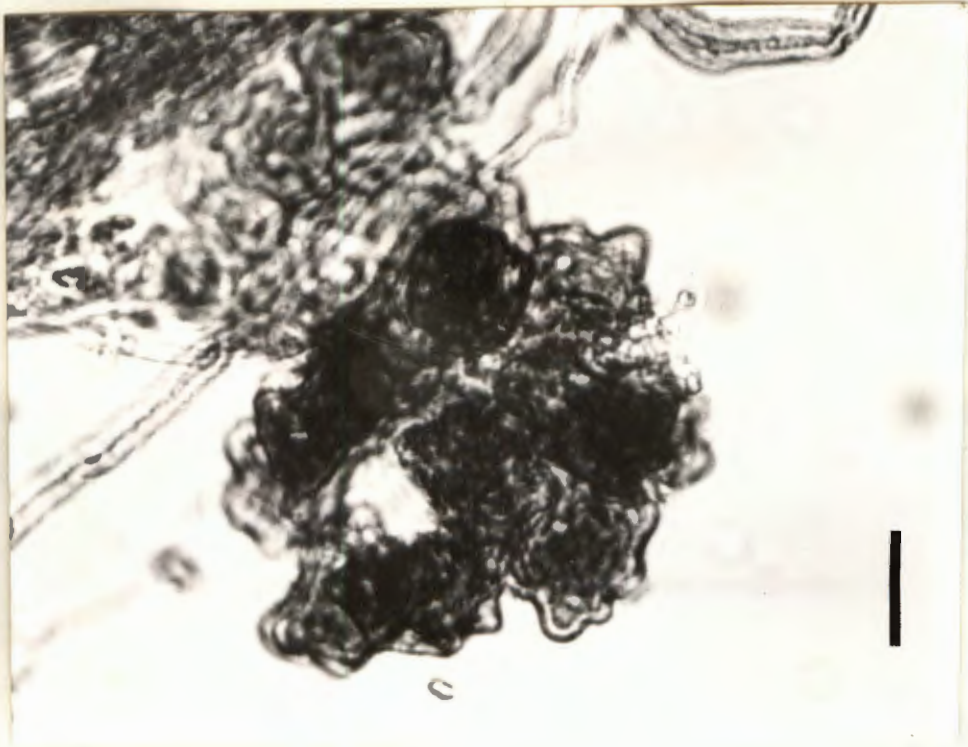


Plate 5A: 'Type B' auxiliary cells of Gigaspora on A. cyclops (6 weeks) grown in Fernwood soil. Scale = $10\mu\text{m}$.

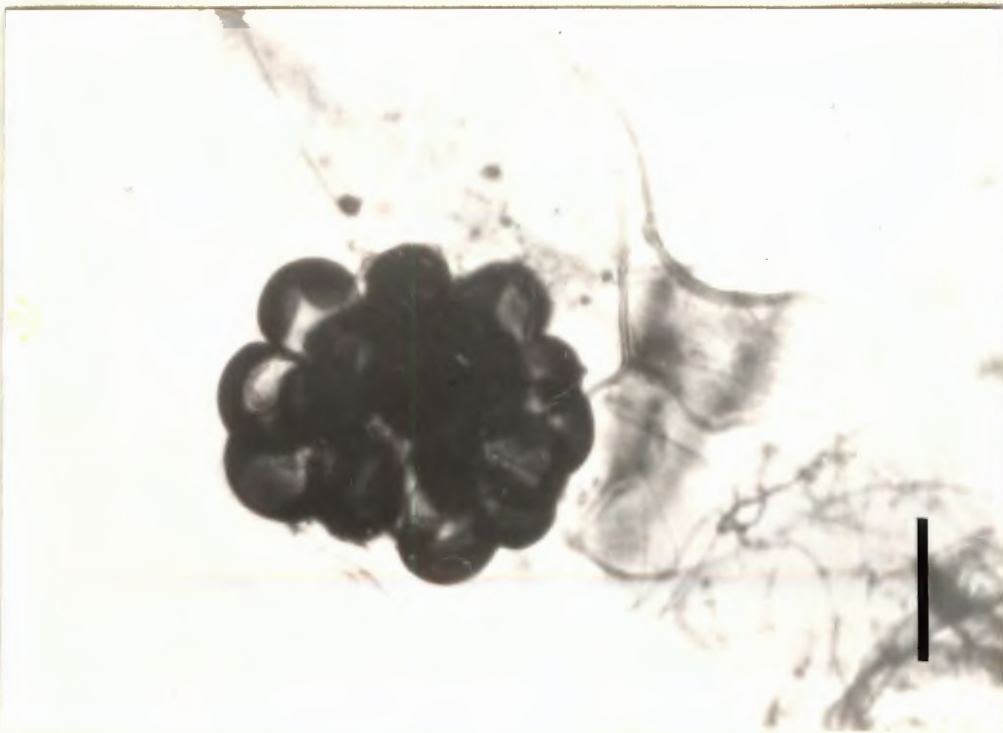


Plate 5B: Non-staining, brown-walled auxiliary cells with smooth walls, on A. cyclops (8 weeks) grown in Fernwood soil. Scale = $20\mu\text{m}$.



Plate 6A: Azygospore of Gigaspora on A. saligna grown in competition with A. cyclops on Fernwood soil (8 weeks). Scale = 100 μm .

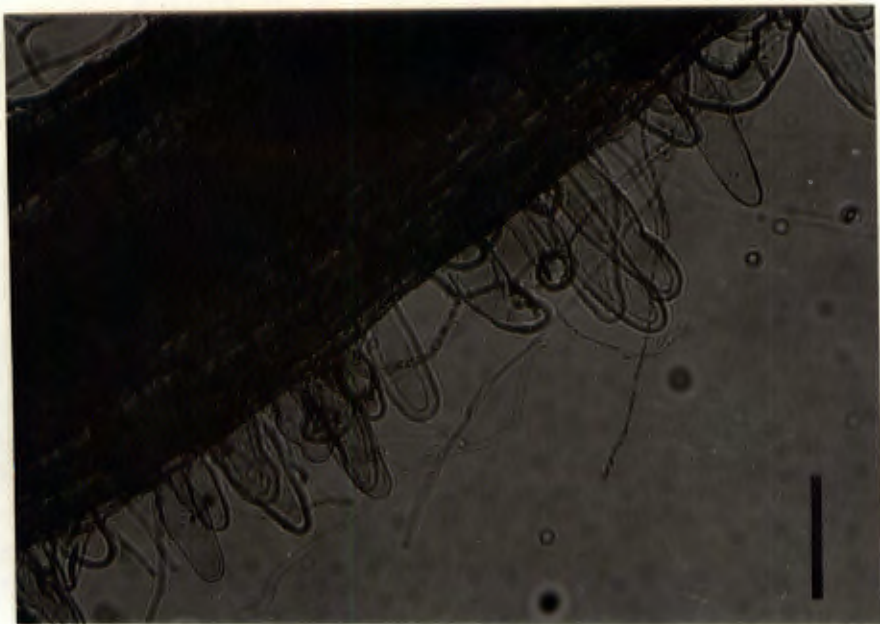


Plate 6B: Extensive root hair development on A. saligna (4 weeks) grown in Clovelly soil. Scale = 40 μm .

for the competition experiment. 'Type A' auxiliary cells characterized by papillate terminal projections were relatively common in both soil types (cf plate 4B). 'Type C' auxiliary cells (non-staining, irregularly shaped lobed structures) were found only in Clovelly soil (cf plate 4B) (Hoffman & Mitchell, 1985). 'Type B' auxiliary cells were found in both soil types. These are characterized by being a clustered group of 'cells' with cone-like projections from the spore surface (Hoffman & Mitchell, 1986). (cf plate 5A). Another type of auxiliary cell not described by Hoffman & Mitchell (1986) was found on the roots of A. cyclops of 8 and 10 weeks. These structures were characterized by being a non-staining (brown-walled) clustered group of small walled 'cells' having aseptate^{te} hyphae (cf plate 5B). It is unlikely that this was simply an undeveloped 'type C' auxiliary cell since no mature structures of that type were found in Fernwood soil. In addition, the brown colouration generally only develops in maturing auxiliary cells (Trappe & Schenck, 1982).

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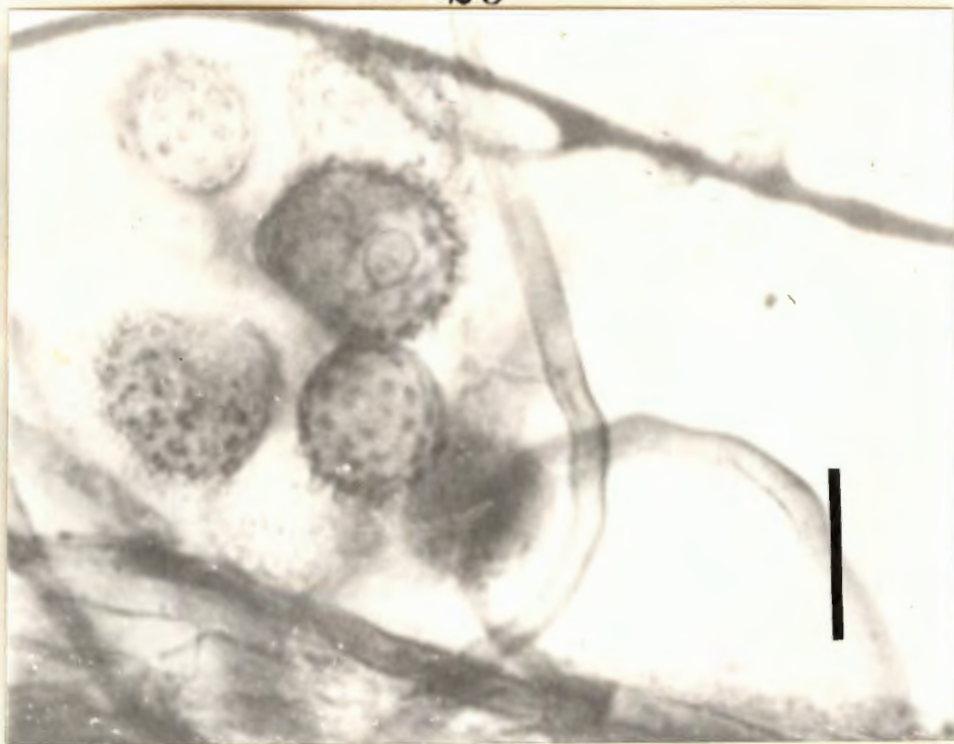


Plate 4A: 'Type A' auxiliary cells of Gigaspora on A. cyclops (8 weeks) grown in Fernwood soil. Scale = 25 μm .



Plate 4B: 'Type C' auxiliary cells of Gigaspora on A. cyclops grown on Clovelly soil (8 weeks). Scale = 10 μm .

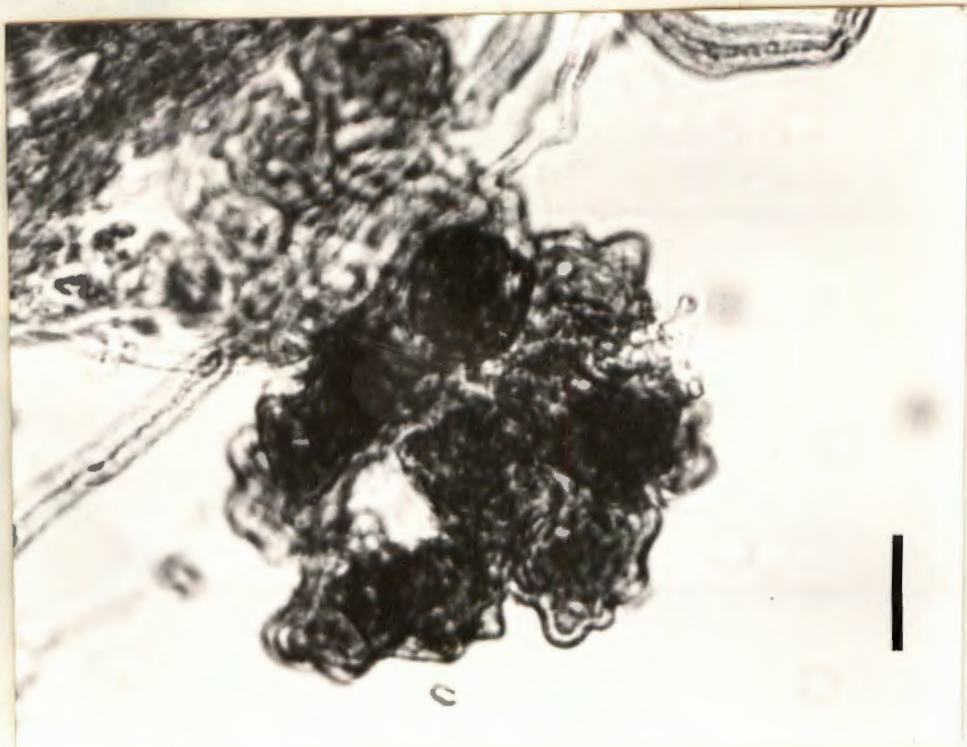


Plate 5A: 'Type B' auxiliary cells of Gigaspora on A. cyclops (6 weeks) grown in Fernwood soil. Scale = 10 μ m.

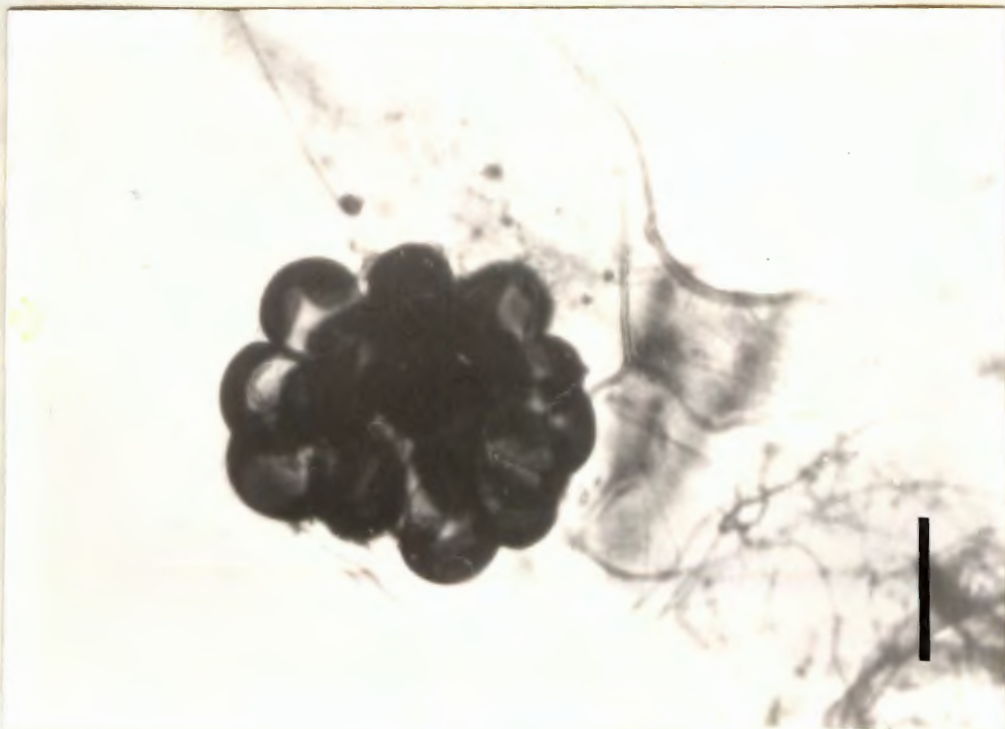


Plate 5B: Non-staining, brown-walled auxiliary cells with smooth walls, on A. cyclops (8 weeks) grown in Fernwood soil. Scale = 20 μ m.



Plate 6A: Azygospore of Gigaspora on A. saligna grown in competition with A. cyclops on Fernwood soil (8 weeks). Scale = 100 μm .

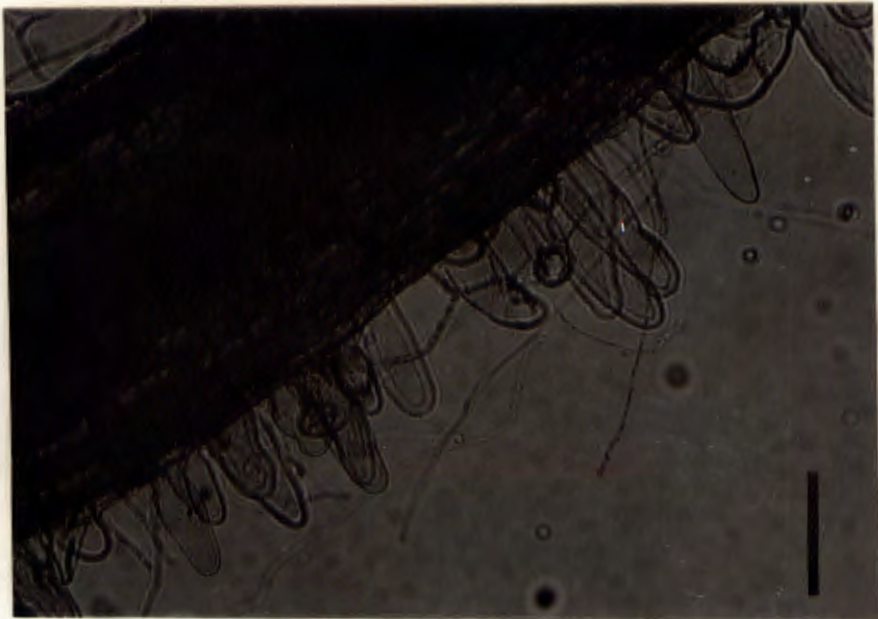


Plate 6B: Extensive root hair development on A. saligna (4 weeks) grown in Clovelly soil. Scale = 40 μm .

The Clovelly-grown plants were particularly infected with fungi other than mycorrhizas. Plate 7A shows the ^{Perithecium} perithecia of Chaetomium (of the Pyrenomycetes) covered with stiff, dark, straight hairs which are septate (Webster, 1980). Lemon-shaped spores were associated with the perithecium, but these do not appear in the photomicrograph. An Oomycete, possibly belonging to the Peronosporales, containing spiny-walled spores was found in the root of a 4-weekold A. cyclops seedling (cf plate 7B).

2.4 Degree of root nodulation

No nodules were found on the roots of plants grown in Fernwood soil. In plants grown in Clovelly soil, the number of nodules generally increased with time, the proportion of larger nodules also generally increasing. Older seedlings of A. saligna had more nodules than A. cyclops in Clovelly soil (Table 5).

3. Competition experiment

3.1 Root and shoot dry masses

The total dry mass of A. saligna was significantly higher than that of A. cyclops in Clovelly soil, the difference mainly contributed by root dry mass. ($df = 8$; $p = 0.005$; $t = 3.35$ for root dry mass) (cf Figure 4, Table 6).

↙ what are these?
The control plants all showed a lower total dry mass, but A. saligna maintained its dry mass advantage in the below ground tissue in both soils. In the Fernwood soil, the root dry mass advantage which A. saligna had (was) reduced.

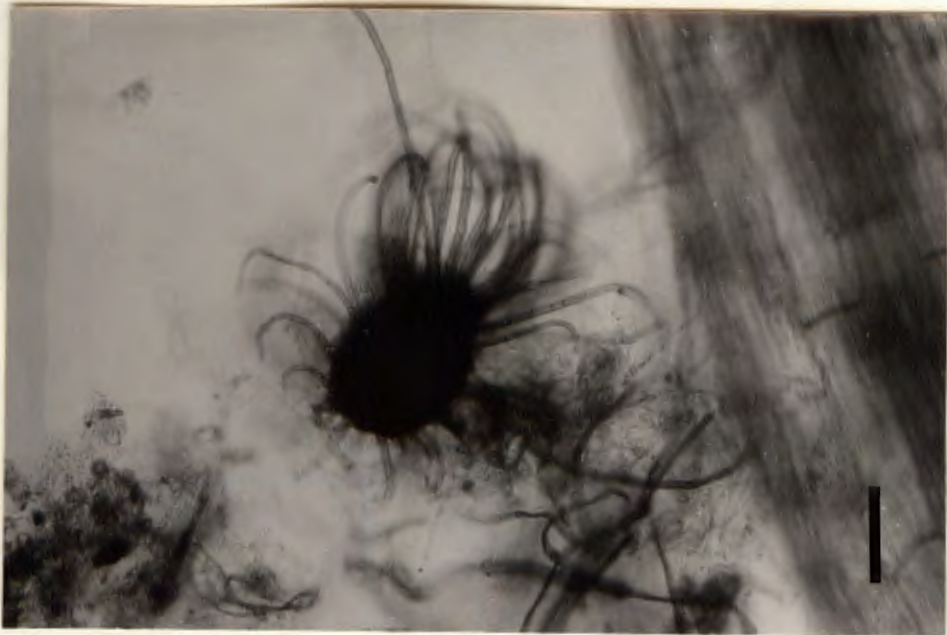


Plate 7A: Perithecium of Chaetomium covered with characteristic stiff hairs, found in Clovelly soil. Scale = 20 μm .

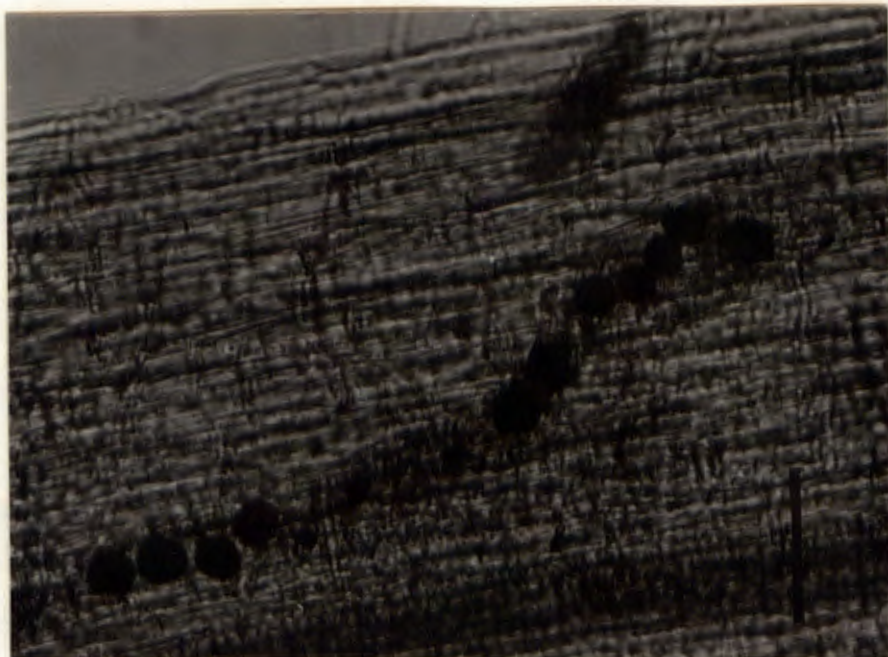


Plate 7B: Oomycete (Peronosporales) on 4-weekold A. cyclops in Clovelly soil. Scale = 10 μm .

Table 5: The number of nodules and % in each size class on A. saligna and A. cyclops roots grown in Clovelly and Fernwood soils. Two plants of the same species were grown in each pot.

per plant?

Clovelly [*]				
<u>Acacia saligna</u> Age of plant	Total number of nodules	% in each size class		
		0-2mm	3-4mm	5-7mm
2 weeks	0	-	-	-
4 weeks	4	100		
6 weeks	0	-	-	-
8 weeks	5	60	20	20
10 weeks	15	66,6	13,3	20,0
<u>Acacia cyclops</u>				
2 weeks	0	-	-	-
4 weeks	0	-	-	-
6 weeks	0	-	-	-
8 weeks	9	100	-	-
10 weeks	7	57,1	42,9	-

^{*}No nodules were found on plants grown in Fernwood soils

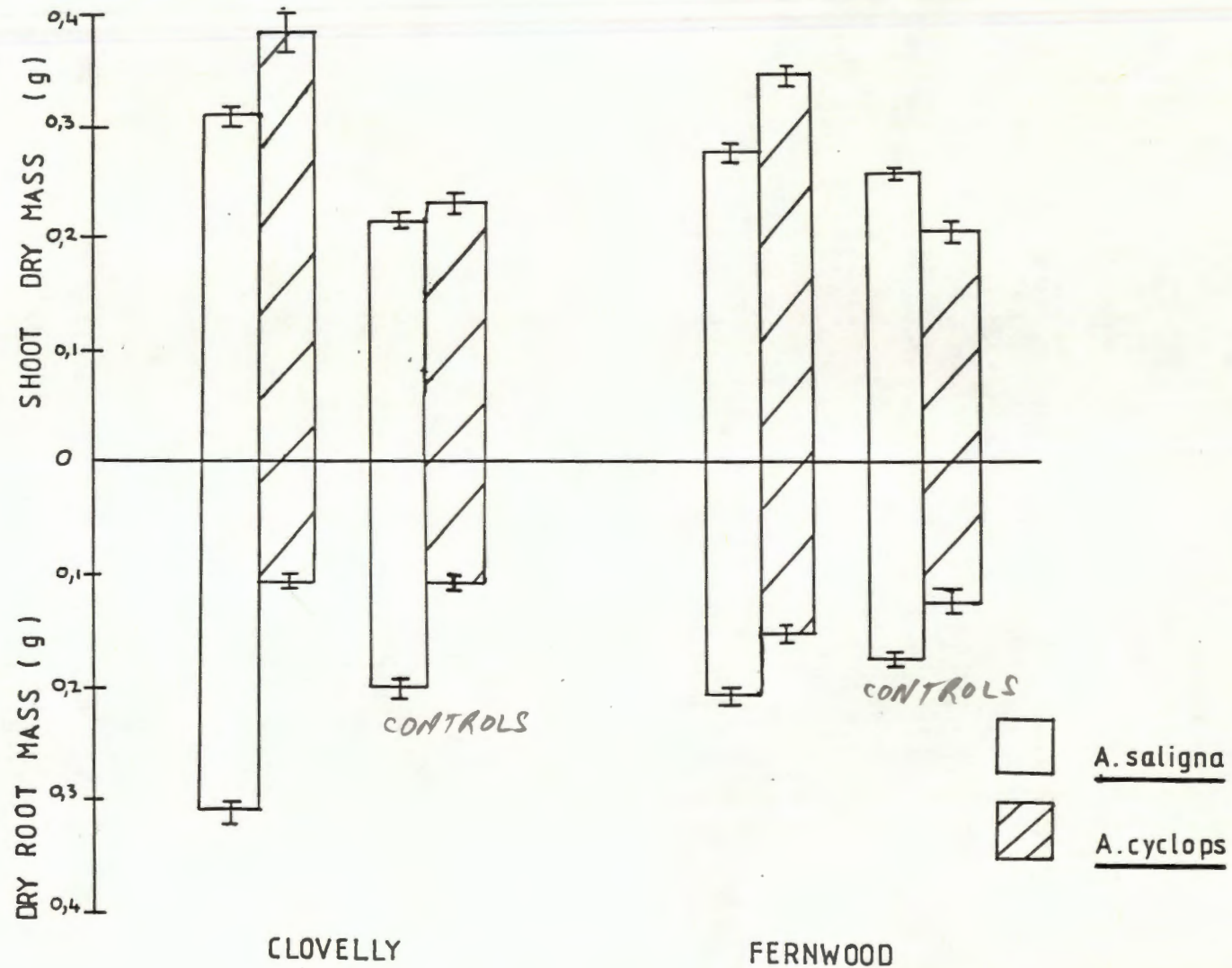


Figure 4: Dry root and shoot masses of *A. saligna* and *A. cyclops* grown in competition in Fernwood and Clovelly soils. The results are the mean of 4 replicates. (± 1 SEM).

One set of soils were fumigated. Which are they?

Table 6: Root : shoot ratios of 8-weekold plants grown in competition. Each result is the mean of 4 replicates \pm 1 SEM. Control plants were grown in sterilized soil.

*↑
fumigated*

	<u>A. saligna</u>	<u>A. cyclops</u>	df	p	t
Clovelly Experiment	1.00 \pm 0.07	0.50 \pm 0.04	6	0.005	6.2
Clovelly Control	1.14 \pm 0.06	0.73 \pm 0.08	6	0.005	4.11
Fernwood Experiment	0.75 \pm 0.03	0.42 \pm 0.12	6	0.025	2.7
Fernwood Control	0.95 \pm 0.05	0.39 \pm 0.07	6	0.005	6.5

The dry masses were approximately equal for plants growing in competition in Fernwood soil. The effect of soil fumigation was more marked in A. cyclops than A. saligna in Fernwood soil. This may be related to greater dependence on soil microorganisms in this species. In both the Clovelly and the Fernwood controls, A. cyclops had significantly lower root : shoot ratios than A. saligna (cf Table 6).

3.2 Quantifying mycorrhizal infection

Results of mycorrhizal infection intensity of the competition experiment are very variable, and not much may be concluded, *not the place for conclusion*. The control plants, although grown in fumigated soil, in some treatments had high levels of infection. Nevertheless, Clovelly experimental results were lower than those of Fernwood-grown plants. A. cyclops maintained a slightly higher infection intensity than A. saligna in both Fernwood and Clovelly soil (Table 7).

3.3 Root nodulation intensity

A. saligna in Clovelly soil showed the highest amount of nodulation, as with the growth response experiment (Table 8). The mean number of nodules is decreased in the controls of A. saligna and A. cyclops growing in Clovelly soil. As expected, the mean number of nodules is decreased in the controls of the Clovelly soil, but in the Fernwood soil, the controls had higher numbers of nodules.

contradiction for previous results.

Table 7: % number of root segments infected of A. saligna and A. cyclops grown in Fernwood and Clovelly soils. Plants were grown in competition.

	<u>A. saligna</u>	<u>A. cyclops</u>
Clovelly Expt.	1.3%	3%
Control	6.0%	1.6%
Fernwood Expt.	50.9%	59.0%
Control	1.9%	22.4%

Table 8: The number of root nodules and % in each size class in 8 weekold Acacia cyclops & Acacia saligna grown in competition in Fernwood and Clovelly soils. Control plants were grown in fumigated soil. The results represent the mean of three replicates.

		Mean number of nodules	% in each size class		
			0-2mm	3-4mm	5-7mm
Clovelly Experiment	<u>A. saligna</u>	10.3	48.5	45.3	9.4
	<u>A. cyclops</u>	5.6	61.1	33.3	5.5
Clovelly Control	<u>A. saligna</u>	4.3	23.0	61.5	15.4
	<u>A. cyclops</u>	4.3	53.8	30.7	15.4
Fernwood Experiment	<u>A. saligna</u>	0	-	-	-
	<u>A. cyclops</u>	1		66.6	33.3
Fernwood Control	<u>A. saligna</u>	1.3		50	50
	<u>A. cyclops</u>	1.6	20	60	60

DISCUSSION

The chemical characteristics of the Fernwood soil collected from Strandveld are very different to those of the ^{Clovelly}soil collected in Sandplain Lowland Fynbos at Pella (Table 1). It is therefore to be expected that plants will be more, or less adapted to these soils, depending on their ability to compete for, and to utilize the available resources. pH of the soil is of primary importance in influencing the availability of nutrients. Low levels of available P in the Clovelly soil (3.29 gPg^{-1} dry mass) may at least in part be due to the low soil pH prevailing (4.62 ± 0.02) and the subsequent chelation of most soil P by Fe (Mitchell et al. 1984), although the parent material, Table Mountain Sandstone, is also low in P and therefore total P is inherently low. The pH results obtained in this experiment for Clovelly soil were slightly higher than those of Mitchell et al. (1984) for Autumn; their pH measurement was $\text{pH } 4.2 \pm 0.1$. Surface total P for autumn was around $40 - 50 \text{ g g}^{-1}$ dry mass, while Bray no. 2 P was found to be about $5 - 7 \text{ g g}^{-1}$ dry mass. Both of these readings are significantly higher than those obtained in this experiment, but this may be accounted for by the fact that P determinations were not carried out immediately after soil collection.

The total and Bray no. 2 P at Melkbos were found to be higher by Witkowski et al. 1984 than the results found in this study (422 gP g^{-1} dry mass versus 195 gPg^{-1} for total P and 72 vs 47 gPg^{-1} dry mass for Bray no. 2 P. The same reasons for lower results

may be used to explain this as for the Pella soil results. Soil pH readings were also slightly higher in the study of Witkowski et. al. 1984 (pH 7.5 vs 7.03).

However, with the large differences in pH, total P and Bray no. 2 P between Fernwood and Clovelly soil, these minor differences in results may be overlooked in this study.

Growth response study

Growth responses to Clovelly and Fernwood soils differed significantly. When the plant species were not grown in competition, A. cyclops had the highest total dry mass at 10 weeks (cf Figure 1) in Fernwood soil. Figure 2C indicates that this was primarily due to a high shoot dry mass, suggesting that A. cyclops is investing ^{more} ~~most~~ carbon resources in shoot biomass production. In Clovelly soil, the higher dry mass (total) that A. cyclops has compared to A. saligna at 10 weeks is not as marked. A. cyclops apparently has a higher potential for mycorrhizal infection than does A. saligna (evidenced by the fact that in both Fernwood and Clovelly soils, A. cyclops has higher infection intensities (cf figure 3). This observation, together with the fact that root : shoot ratios are generally lower in A. cyclops than A. saligna (cf Table 3) indicates that A. cyclops has a greater reliance on VAM fungi. Hardie & Leyton (1981) found that mycorrhizal infection may have been a factor directly contributing to lower root : shoot ratios. Thus, in Clovelly soil where VAM infection potential appears to be lower than in Fernwood soil, A. cyclops may be at a disadvantage. However, lower available nutrients in the soil may have been the direct cause for the drop in A. cyclops biomass.

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A possible cause for the lower mycorrhizal activity in Clovelly soil is the fact that soil organic content is low compared to Fernwood soil (cf Table 1). Hepper & Warmer (1983), found that VAM fungi are able to grow saprophytically and organic content is an important factor in this process. If this is the case, Fernwood soil may inherently be expected to have a high mycorrhizal infection potential since % organic content is high (11.7% compared to 0.8% in Clovelly soil).

A. saligna total dry mass is similar for Clovelly and for Fernwood soils at 10 weeks (cf Figure 1). This suggests that A. saligna may not be able to utilize the higher levels of nutrients available in the Fernwood soil, and it may be specifically adapted to soils of lower nutrient status. Nevertheless, A. saligna has higher shoot P content than A. cyclops in 10 weekold seedlings both from Clovelly and from Fernwood soil. This might suggest that this species is more efficient at taking up P than is A. cyclops. This would be despite the fact that VAM infection intensities are far lower in A. saligna. However, the fact that this species usually has a higher root biomass than A. cyclops especially in Clovelly soil (figures 2B & 2D) and high root : shoot ratio (Table 3) could account for its P uptake efficiency. A large proportion of its carbon resources are thus being partitioned to production of root material. A. saligna therefore appears to have adapted to utilization of root surface area for increasing nutrient uptake, rather than VA fungal hyphae.

However, there may be three major criticisms to this conclusion. Firstly, the fact that shoot P concentrations are higher in

A. saligna than A. cyclops does not necessarily mean that it is more efficient at uptake of nutrients since this is not a direct measure of the rate of P uptake by the plant. Rather, this may be a measure of the inefficiency with which the plant is translating nutrient uptake into growth, since tissue concentrations should remain constant in an efficiently growing plant. Harley & Smith (1983) have suggested that some limiting factor (such as carbon) may also give rise to increased tissue P concentrations. If the former is true for A. saligna, this may be further evidence to suggest that this species is not adapted to soils of higher nutrient status.

The second criticism of the conclusion that A. saligna has a low reliance of VAM comes from the fact that only 100 segments, and not the entire rooting structure was examined for VAM fungi. What may be more important is total fungal biomass infecting the plant. The fact that A. saligna even though low generally has higher root biomass than A. cyclops suggests that its % VAM infection measurements may have been an underestimate, or else that A. cyclops infection was overestimated.

Finally, even though the infection intensities of A. saligna may be low, this is not necessarily a direct measure of the potential of the VAM fungi for nutrient uptake. The work of Hetrick et al. (1984) showed that at low P concentrations in the soil, uptake of P may be more efficient (the high uptake affinity system of Cress et al. 1979 & Staker, 1986).

Although VAM may be playing an important role in P uptake from the soil, both A. saligna and A. cyclops generally have higher root : shoot ratios in Clovelly compared to Fernwood soil (Table 3). This suggests that root surface area remains an important factor in soils of low nutrient status. This would also effectively increase the root surface area which may be infected by VAM.

The fact that no nodulation occurred in plants growing in Fernwood soil may have been due to higher levels of nutrients present in the soil; that low levels of soil nutrient may be important in stimulating root nodulation. In Clovelly soil, higher nodule numbers in A. saligna (cf Table 4) compared to A. cyclops may have been a result of higher root-surface area and therefore larger potential for infection by Rhizobium. This is despite the fact that A. saligna (at least according to the method employed in this experiment) had lower % VAM infection. This is in contrast to the finding of Green et/ al.(1983) that VAM infection is closely related to and increases nodule formation.

Competition experiment

The control plants (grown in fumigated soils) all showed lower dry masses than the experimental plants (cf figure 4) which suggests that soil microbial activity is having an important effect in stimulating plant growth. However, it is not possible to ascertain what effect the fumigant (methyl bromide) may be having on the plant itself. It also is not completely effective in eliminating all VAM fungal propagules in the soil (Linderman & Hendrix, 1982). A further problem with soil fumigation is

I would have thought that the methyl bromide would have disappeared.

that all soil micro-organisms are affected; thus the experiment did not have a true control. Explain?

The most notable result from the competition experiment is the high root dry mass and therefore significantly higher total dry mass of A. saligna when grown in competition with A. cyclops on Clovelly soil. In addition, A. saligna shows higher levels of nodulation than A. cyclops on Clovelly soil (Table 8). Thus A. saligna appears to have a competitive advantage over A. cyclops in Clovelly soil.

In Fernwood soil, total dry masses of A. saligna and A. cyclops are similar (figure 4), although the root : shoot ratios differ (Table 6), A. saligna maintaining a higher ratio than A. cyclops. From the parameters studied, no conclusion may be drawn as to which species has an advantage in Fernwood soil when the plants are grown in competition.

CONCLUSIONS

The most apparent result from this study has been that differential growth response occurs in A. saligna and A. cyclops grown in Fernwood and Clovelly soils. A. saligna generally tends to be better-adapted to growth in Clovelly soil, evidenced by the fact that when grown in competition with A. cyclops, total dry mass of this species was higher, as was root nodulation. Further support for the suggestion that A. saligna is better-adapted to a low-

nutrient soil comes from the fact that total dry mass did not increase when plants were supplied with higher nutrient levels i.e. grown in Fernwood soil. Accumulation of phosphorus in the tissues and high root biomasses of A. saligna also suggest that this is the case. A. saligna appears to have a low potential for being infected by VAM fungi, but invests more energy into the production of high root dry mass.

The higher potential for mycorrhizal infection in the Fernwood soil may have resulted from a higher organic content of this soil. The resultant high levels of VAM fungi on the roots of A. cyclops may have contributed to the high dry mass of this species when not grown in competition. This species appears to have adopted a strategy of having low root biomass, associated with a high VAM infection intensity. A large proportion of carbon metabolites appear to be portioned for the production of shoot material.

Shaughnessy (1980) suggested that the non-occurrence of a species under consideration at a given site does not mean that it is unable to exist there, since this idea would assume that there is an equal probability of a plant species reaching all sites. However, this study has shown that there may well be an ecophysiological basis for the differential distribution of A. cyclops and A. Saligna at Melkbos and at Pella respectively. However, more extensive investigations are required before this can be conclusively stated, such as the effects of the different soil types on the reproductive potential of the two species.

Acknowledgments

I would first of all like to thank Prof. Mitchell for his supervision and constant interest in this project. I am also indebted to Ed Witkouski for advice on phosphorus analyses. I am especially grateful to Niki Allsopp for her help and advice on methodology, as well as for valuable discussion and provision of a number of references.

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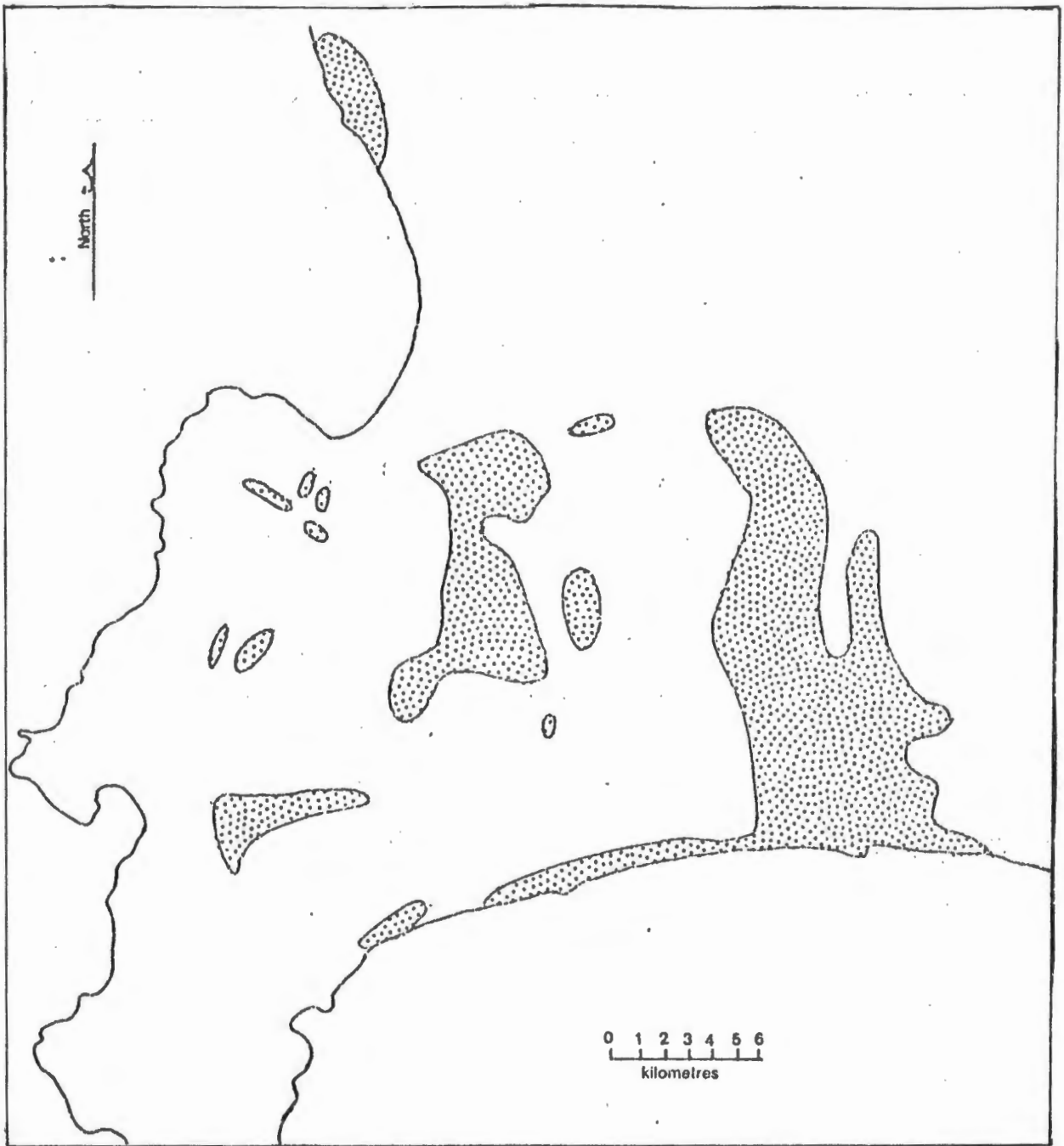
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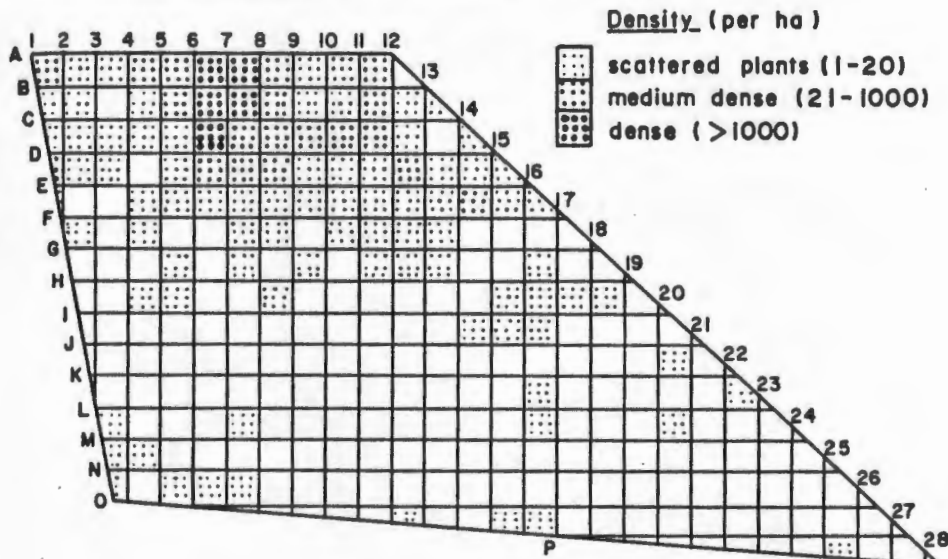
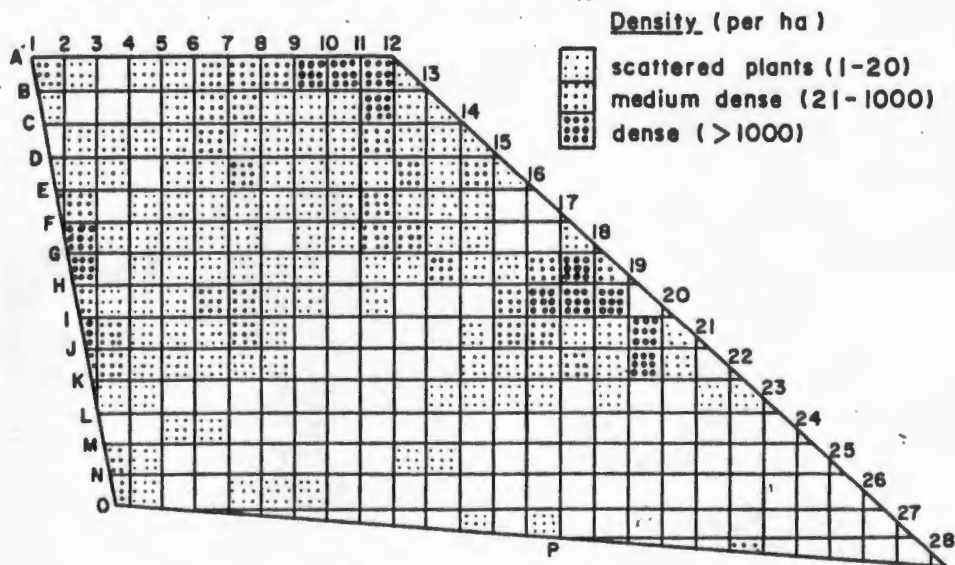
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Areas where planting of *Acacia saligna* is recorded
in this report.

(Boundaries are approximate.

After Shaughnessy,
1980.

1984 ALIEN DENSITYAcacia cyclopsInfestation density of Acacia cyclops on PRS (1984).1984 ALIEN DENSITYAcacia salignaInfestation density of Acacia saligna on PRS (1984).

