

---

HONOURS THESIS

---

THE EFFECT OF FOUR INVASIVE ALIEN  
SPECIES ON VARIOUS SOIL FACTORS &  
IMMEDIATE POST-FIRE VEGETATION -  
IN MOUNTAIN FYNBOS

H.R.ENGLEDOW  
B.Sc.  
1989

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.



### Abstract

The impact of four invasive alien species (*Hakea gibbosa*, *Pinus pinaster*, *Acacia cyclops* and *Acacia saligna*) and an indigenous proteoid (*Leucospermum conocarpodendron*) on a mountain fynbos site (Millers Point, near Simonstown) were studied. Their effect on various soil factors, viz. pH, phosphorus, organic matter and nitrogen content, and immediate post-fire vegetation were determined. The results of the soil analysis indicated that pH was not significantly different between the species, while the *Acacia* spp. were having some effect on soil organic matter and nitrogen content, below their canopies. Phosphorus content of soil below the canopies were only significantly different between the *Acacia* spp.. With respect to the post-fire vegetation, the *Acacia* spp. were found to have the greatest effect on diversity and relative abundance. It would appear that the *Acacia* spp. are having an effect on soil nutrients and immediate post-fire vegetation, which could affect the future structure and composition of the fynbos.

## Introduction

The fynbos biome forms the world's smallest and richest floristic kingdoms, viz. Flora Capensis (Hall 1978), which is situated at the southern tip of Africa. Over the last 150 years, a number of alien species have been introduced into this area for various reasons e.g. stand stabilization, fuel, timber, etc. (Stirton 1978; MacDonald & Richardson 1986). Some of these introduced species however, have become invasive and are presently threatening the survival of the fynbos biome (MacDonald & Jarman 1984). According to Vitousek (1986) if an invader differs sufficiently in its effect on soil properties, resource requirements and phenology, then it has the potential to alter the collective properties of the ecosystem. In this study the effect of four woody invasive alien species and an indigenous proteoid (to act as a comparator) on various soil components and immediate post-fire vegetation of a mountain fynbos site, were assessed.

The four alien species, viz. *Hakea gibbosa*, *Pinus pinaster*, *Acacia cyclops* and *Acacia saligna*, would appear to possess mechanisms to enhance nutrient uptake, and therefore the potential to alter the soil chemistry of fynbos. *H.gibbosa* has extensive proteoid roots (twice that of indigenous Proteaceae - Low 1980), while the other three alien species have mycorrhizal associations (Marais & Kotze 1977, Langkamp & Dalling 1982, Barrow 1977).

The two *Acacia* spp. are also able to fix nitrogen (Roux & Warren 1963), and have been found to enrich soil nitrogen in their native habitat (Hansen et al. 1987). Since fynbos is relatively nutrient poor, especially in nitrogen and phosphorus (Kruger et al. 1983), such an increase could have a profound effect on vegetation structure and composition (Kruger et al. 1983, Witkowski & Mitchell 1987).

This study will attempt to answer two main questions:

- (i) Do these alien species have an effect on various soil components ?
  - And if so, would a mature fynbos community be able to tolerate the change ?
- (ii) Do the alien species have an effect on the immediate post-fire fynbos community ?

The purpose of the study is to provide insight into the effect of invasive aliens on the invaded environment; and to highlight the necessity for control and removal measures of these noxious weeds.

## METHOD

The study site was at Millers Point ( $34^{\circ}18'S$ ,  $18^{\circ}27'E$ ), Cape peninsula, South Africa (Fig.1). This area was recently burnt (2 May 1988). The previous fire occurred in 1974 (Bond & Stock 1989), therefore making the burnt vegetation 14 years old, just prior to the fire. The soil is coarse and is derived from a mixture of Table Mountain Sandstone and granite (Bond & Stock 1989).

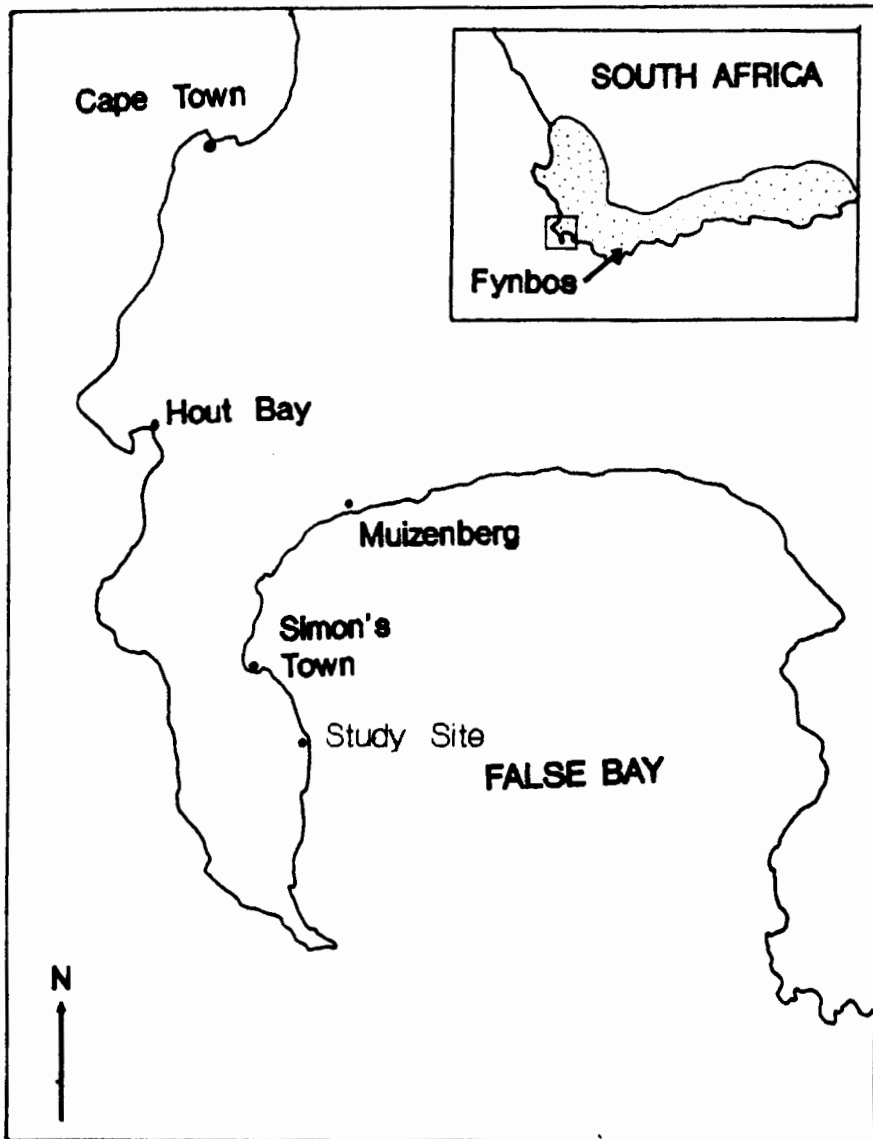


Fig.1: Map showing the position of the studied area, in relation to the rest of the biome.

The study area is relatively heterogeneous, with respect to the vegetation, with dominant patches of various invasive alien species scattered on the mountain side. However, the study site, in particular, consists of a relatively homogeneous 'patch' of the five species examined. Four invasive tree species and one indigenous shrub species were investigated, viz. *Hakea gibbosa*, *Pinus pinaster*, *Acacia cyclops* (1), *Acacia saligna* (2) and *Leucospermum conocarpodendron* respectively.

### Soil Sampling

Paired soil samples were obtained from under the burnt remains of the plants and from the open areas adjacent to them. Each soil sample consisted of four 5 cm cores (3 cm diameter) collected at 90° to one another and within 50 cm of the burnt stem (under canopy samples) or 100 cm outside of the burnt canopy (open area samples). The reason for mixing the four core samples was to reduce any effects that may be caused by a patchy distribution of nutrients. Ten paired samples (i.e. under the canopy and in the adjacent open area) were taken from under each of the five species, mentioned above. The plants were randomly chosen using a wandering quarter method, providing the plants were roughly the same size as their conspecifics. This size varied between species, however, the initial plant of comparison for each species was generally one of the larger plants in the population. By keeping a relatively constant size for each species and a general criterion (i.e. the larger individuals) for all the species, one reduces the variables (eg. different age plants, organic returns to the soil, etc.).

### Soil Analysis

The samples were taken to the laboratory where they were air dried and sieved through a 2 mm sieve. pH was determined as follows: 25 g of sieved soil was added to 50 cm<sup>3</sup> of 0,01 M CaCl<sub>2</sub> and shaken for 30 minutes. The pH of the suspension was then determined using a pH-meter (No.29 Radiometer, Copenhagen).

To ascertain the percentage organic matter, 5-10 g (2 mm sieved) oven dried (at 80°C) soil was weighed together with a pre-weighed oven dried crucible. The crucible and soil sample were then transferred to a muffle furnace at 450°C for 16 hours. The soil containing crucible was then reweighed and the percentage organic matter calculated.

The samples were tested for nitrogen and phosphorus content, using the Kjeldahl Digestion method for nitrogen (Stock 1985) and total phosphorus analysis for phosphorus (Jackson 1958, Murphy & Riley 1962) (See Appendix 1 & 2 for details).

### Vegetation Survey

As in the soil sampling above, samples were taken from under the 'burnt' canopies and adjacent open areas of the five study species. Similar criteria were used for randomization and plant size, as those used in soil sampling above. Ten samples were taken of *Pinus* and *Acacia 1*, and eight for the remaining three species. Each sample consisted of three 1 m ruler lines placed



at 120° to one another. Any plants that was encountered on the 10 cm intervals along the 1 m line were recorded. Equitability was then calculated using the following formula:  $E = \sum P_i^2$

E - Equitability

Pi - Frequency of the species (i.e. No. of times species encountered / Total No. of points surveyed)

### Statistics

Two-Way ANOVA's were performed on the results obtained from soil analysis and the vegetation survey, with respect to canopy/open positions and between study species. Since, there were highly significant differences among the species for soil comparisons, but no significant differences between under/open areas (Table 1), an Analysis of Covariance was used. Analysis of Covariance was performed on the soil analysis and vegetation survey data, with open areas serving as the covariate. In this way, the effect of shrub canopies on soil nutrients could be separated from other local spatial variations in soil nutrients. If the covariate was not significant, a One-Way ANOVA was performed on the open area samples, to see if they were significantly different. If they were not, then the below canopy samples were compared. A Multiple Range Test (95 % Confidence limits) of homogeneous groups was also performed together with the Analysis of Covariance, to show differences between species.

The means of the data collected and standard errors were calculated and graphically represented. Lastly, nitrogen and phosphorus results were regressed against percentage organic

matter. All statistics were performed on the computer package "Statgraphics" (Statgraphic-statistical graphic system by Statistical Graphics Corp. 1988).

## RESULTS

The results of the Two-Way ANOVA are set out in Table 1. There is no significant difference between under canopy samples and adjacent open areas, with respect to percentage organic matter, nitrogen content and percentage open ground. However, pH, phosphorus and equitability showed significant differences. The ANOVA among species revealed highly significant differences, with pH being the only exception. The interaction between species under the canopy and in adjacent open areas revealed no significant differences, except for percentage organic matter.

Table 1: Two-Way ANOVA on the results of soil pH, % organic matter, phosphorus and nitrogen content, equitability and % open ground, with respect to under canopy and open areas, and among species.

	TREATMENT	D.F.	F-ratio	Sig. Level
pH	Under_Open	1	15.701	0.0001
	Spp.	4	2.118	n.s.
	Un_Op x Spp.	4	0.912	n.s.
Phosphorus	Under_Open	1	6.471	0.0127
	Spp.	4	3.374	0.0128
	Un_Op x Spp.	4	1.708	n.s.
% Organic Mat.	Under_Open	1	2.854	n.s.
	Spp.	4	6.795	0.0001
	Un_Op x Spp.	4	2.612	0.0405
Nitrogen	Under_Open	1	2.463	n.s.
	Spp.	4	4.942	0.0012
	Un_Op x Spp.	4	1.708	n.s.
Equitability	Under_Open	1	4.740	0.0325
	Spp.	4	20.049	<0.0001
	Un_Op x Spp.	4	0.573	n.s.
% Open Ground	Under_Open	1	3.618	n.s.
	Spp.	4	3.879	0.0063
	Un_Op x Spp.	4	1.173	n.s.

n.s. - not significant; D.F. - Degrees of Freedom  
 $p < 0.05$ ; Un\_Op - Under canopy and Open areas

Table 2 represent the results of Analysis of Covariance of the soil analysis and vegetation cover data. The results thereof will be mentioned in conjunction with the following figures.

Table 2: Analysis of Covariance of soil pH, % organic matter, phosphorus and nitrogen content, equitability and % open ground. Covariate - Open areas;  $p < 0.05$ ; n.s. - not significant; D.F. - Degrees of Freedom.

	TREATMENT	D.F.	F-ratio	Sig. Level
pH	OPEN AREA	1	8.833	0.0048
	UNDER CANOPY	4	1.775	0.1510
Phosphorus	OPEN AREA	1	2.379	0.1302
	UNDER CANOPY	4	4.132	0.0063
% Organic mat.	OPEN AREA	1	19.040	0.0001
	UNDER CANOPY	4	4.309	0.0050
Nitrogen	OPEN AREA	1	7.963	0.0074
	UNDER CANOPY	4	3.265	0.0208
Equitability	OPEN AREA	1	44.089	<0.0001
	UNDER CANOPY	4	5.894	0.0009
% Open Ground	OPEN AREA	1	2.803	0.1023
	UNDER CANOPY	4	3.174	0.0241

Figures 2 - 7 illustrate the relationship between under canopy and adjacent open areas; as well as the differences among species. The letters above the under canopy bars indicate the results of the multiple range test for homogeneous groups among the under canopy samples of the various species (95 % Confidence limits). Vertical lines in bars indicate standard error values.

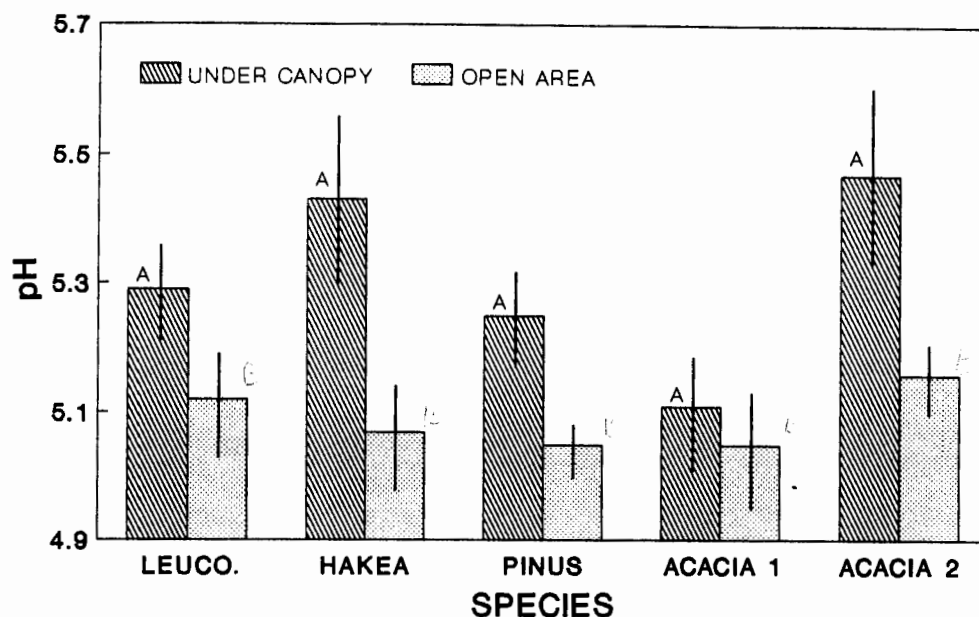


Fig.2 : Mean soil pH values from under-canopy and adjacent-open areas for the five study species.

With respect to pH, there appears to be no significant difference between open areas among the five species (Fig. 2), this was confirmed by a One-Way ANOVA. There is however, a significant difference between under canopy and open areas (Table 1, Fig. 2). No significant difference was found among species (Table 2), which were also found to be homogeneous.

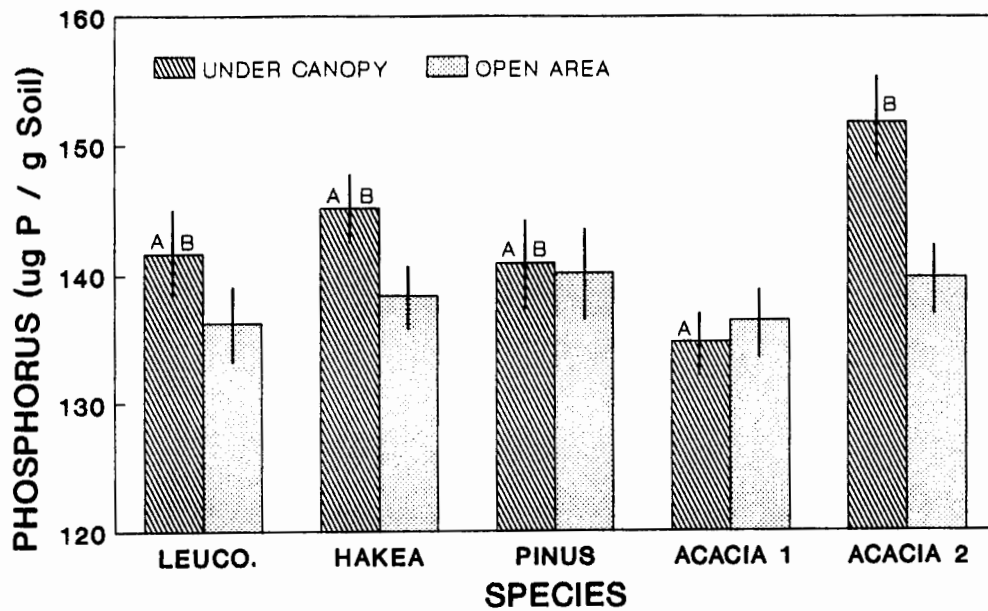


Fig.3 : Mean soil phosphorus (total) content from under-canopy and adjacent-open areas for the five study species.

Phosphorus (Fig.3) showed a significant difference between species under the canopy, however, the covariate was not significant. A One-Way ANOVA was therefore performed on the open areas, and it was found that there was no significant difference between phosphorus in the open areas. A One-Way ANOVA on the under-canopy samples gave a significant difference, with *Acacia cyclops* and *A.saligna* showing the greatest differences between each other (Fig.3).

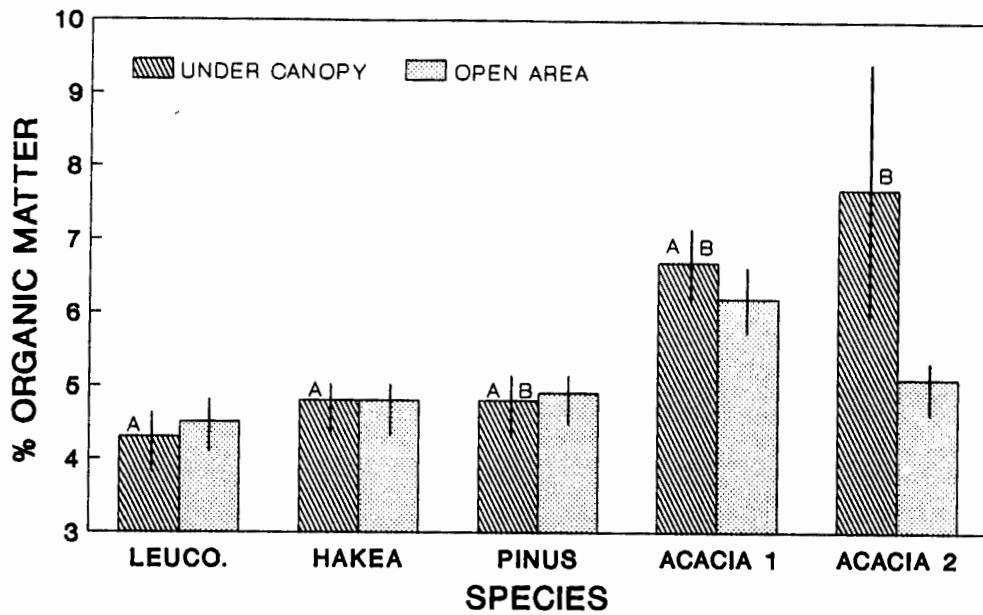


Fig.4 : Mean soil % organic matter from under-canopy and adjacent-open areas for the five study species.

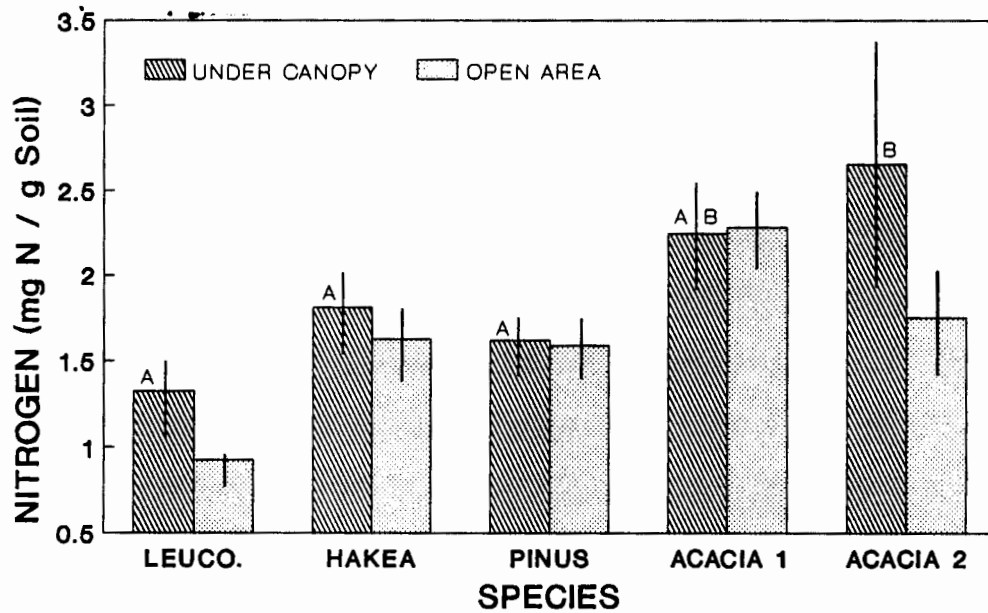


Fig.5 : Mean soil nitrogen content from under-canopy and adjacent-open areas for the five study species.

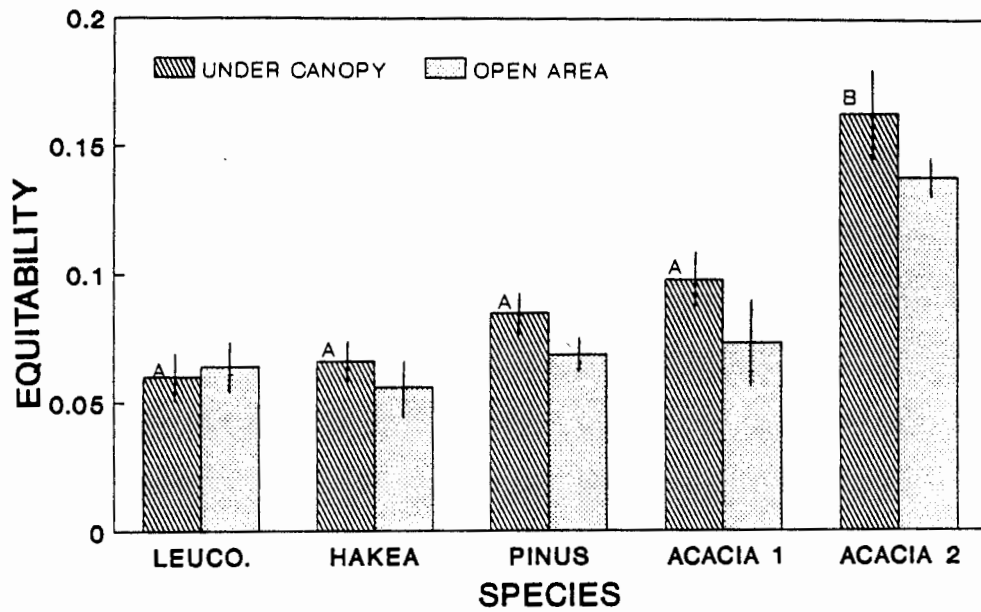


Fig.6 : Equitability results of vegetation survey, from under-canopy and adjacent-open areas for the five study species.

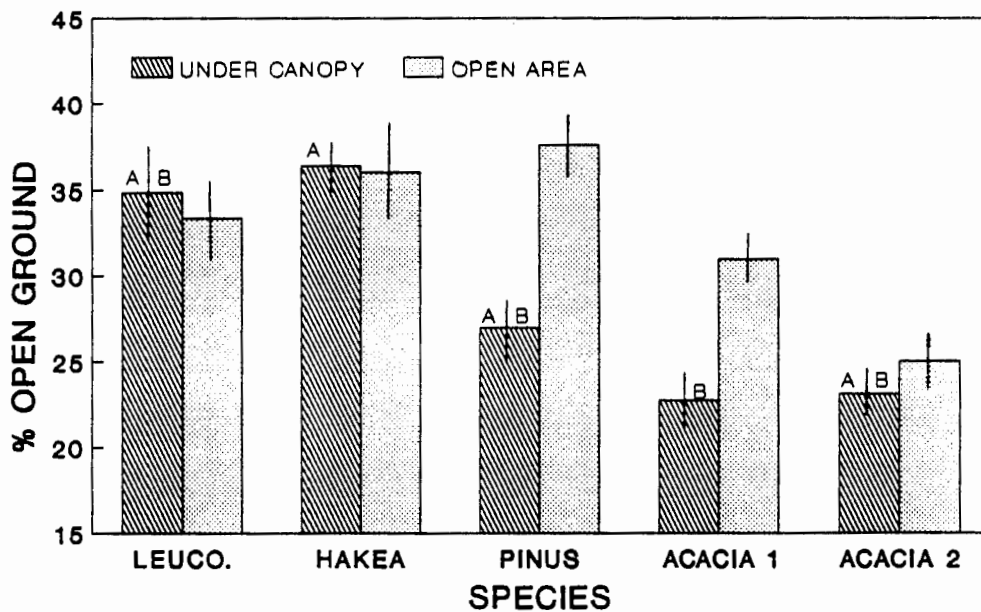


Fig.7 : % Unvegetated ground (i.e. % Open Ground) from under-canopy and adjacent-open areas for the five study species.



Percentage organic matter under the canopies of the various treatments were found to be significantly different (Table 2). Results of the multiple range test revealed significant differences between *Leucospermum* & *Hakea* and *Acacia saligna* (Fig.4). There appears to be a close following of organic matter in the open areas with organic matter in the under areas, *Acacia saligna* being the exception (Fig.4). Also, *Acacia cyclops* appears to have more organic matter on average than *Leucospermum*, *Hakea* or *Pinus*, despite the difference not being significant.

It would appear from Fig.5 that the alien species enrich the soil with nitrogen, more than the indigenous *Leucospermum*. There is a significant difference between species in the under canopy areas (Table2). The Multiple range test showed similarity between all species except *Acacia saligna*, which was significantly different (Fig.5), while *Acacia cyclops* appears to be intermediate.

Nitrogen regressed against percentage organic matter was found to be highly significant ( $r^2 = 0.69$ ;  $p < .0000$ ). However, phosphorus regressed against percentage organic matter showed no significant correlation.

#### Vegetation

There appears to be a slight increase in equitability under *Pinus* and *Acacia cyclops*, and a large increase in *Acacia saligna* (Fig.6). However, only *Acacia saligna* was significantly different from the other species (Fig.6, Table2).

The proportion of unvegetated ground were greatest under the canopies of *Leucospermum* and *Hakea* (Fig.7). There was a significant difference among species in under canopy areas, however the covariate was not significant. The multiple range test indicated that only *Hakea* and *Acacia cyclops* were significantly different. However, it would appear that the *Acacia* spp. have much less open space under the canopies, on average, than the other species.

It can also be noted that there appears to be similar trends among percentage organic matter, nitrogen content of soil and equitability (Fig.4-6) ; and a reverse trend with respect to unvegetated ground beneath the canopies of the various species (Fig.7).

## Discussion

### **The Effect of Alien Vegetation on Various Edaphic Factors**

The results would seem to indicate that the invasive alien species are having some effect on the soil dynamics of fynbos, in a relatively short period of time. This could have a profound effect on the future survival and ecology of fynbos.

The slight variation in soil pH between under and open samples, i.e. under-canopy samples having a higher pH, could be a function of fire and organic matter. Brown and Mitchell (1986) found that soil pH in fynbos was elevated shortly after fire, but soon returned to its normal state.

The alien vegetation appears to have some effect on soil organic matter and nitrogen content. The results indicate that organic matter is closely linked to the nitrogen content of soil. Therefore, those plants with more organic matter under their canopy generally have more nitrogen. There appears to be little difference between the soil percentage organic matter / nitrogen concentration under the indigenous *Leucospermum* and the alien species, *Pinus pinaster* and *Hakea gibbosa*. However, the *Acacia* spp. had on average approximately 1.5 - 2 times more organic matter below its canopies (Fig.4) and significantly more nitrogen (*A.saligna*) (Fig.5) than the other species studied. The reason for this is probably two-fold: firstly, *A.cyclops* and *A.saligna* have been reported to possess nitrogen-fixing symbioses (Roux & Warren 1963, Nakos 1977, Haxen 1978); and secondly, they are able

to grow taller and faster than indigenous fynbos, thereby giving rise to a greater biomass production (Milton 1980, 1981, Milton & Siegfried 1981, Versveld 1981, van Wilgen & le Maitre 1981, van Wilgen 1982). Consequently, the higher levels of organic matter below these *Acacia* canopies results in concomitant increase in soil nitrogen. *Acacia*'s would therefore act as fertilizers of the environment they inhabit (Shea & Kitt 1976, Hansen & Pate 1987).

According to Agren & Bosatta (1987) the long-term productivity of terrestrial ecosystems is closely related to the quality and quantity of soil organic matter. Fynbos has been noted for its low biomass (Kruger 1977), therefore low quantity organic matter; as well as a low quality litter (Read & Mitchell 1983). Thus the increase in organic matter and nitrogen levels below *Acacia* spp. may adversely affect fynbos.

Experiments have shown that fertilisation (with N & P) of nutrient poor environments can cause a complete change in the species and growth form composition of the area (Specht 1963; Connor & Wilson 1968; Heddle & Specht 1975; Specht et al. 1977; McMaster et al. 1982). In lowland fynbos, Witkowski (1989) and Witkowski & Mitchell (1989) found that nitrogen addition resulted in a significant increase in the growth of only the restioid, graminoid and annual species. Increases in growth have been observed in the proteoid (*Leucospermum parile*) and the ericoid shrub (*Phyllica cephalantha*) to an increase in nitrogen (Witkowski 1988), however, some members of the indigenous Proteaceae have

been found to be unable to utilize high levels of nitrogen (Lewis & Stock 1978). It would therefore appear that nitrogen limits certain groups of plants within the fynbos. However, despite the increase in various plant groups there seems to be little change in plant mortality patterns. Thus fynbos would appear to be resilient to nutrient input perturbation (Witkowski 1989). Witkowski (1989) predicts that greater levels of nitrogen (i.e.  $5 \text{ gN.m}^{-2}$ ) may result in long-term changes in species composition within the fynbos.

Hansen et al. (1987) found that nitrogen fixation is greatly improved under conditions of increased water and phosphorus, producing  $4\text{-}35 \text{ kgN.ha}^{-1}\text{.yr}^{-1}$  under fertilized conditions. Phosphorus levels in Australia are however, very low (Hedde & Specht 1975; Groves & Keraitis 1976) and would appear to lower the amount of nitrogen fixed (maximum input  $0.88 \text{ kgN.ha}^{-1}\text{.yr}^{-1}$  a year post-fire)(Hansen et al. 1987). Also, *Acacia* spp. in their native habitat added the greatest quantity of nitrogen within two years after a fire, thereafter nitrogen input was minimal and declining. Therefore, under low phosphorus levels nitrogen input into the soil will be negligible. Fynbos soils, which are equally low in phosphorus (Kruger et al. 1983, Mitchell et al. 1984), would similarly reduce nitrogen fixation. As a result nitrogen input into the soil would be small, having little effect on fynbos vegetation structure (Witkowski 1989a). Strandveld, on the other hand, shows substantially higher phosphorus levels than other fynbos communities (Witkowski & Mitchell 1987), and it

is likely that the effects of *Acacia* spp. on total nitrogen in soil will have an effect on fynbos community structure and composition in these areas.

According to Hutchinson (1957), phosphorus is likely to be the most ecologically important nutrient, being able to act as a determinant of vegetation structure and function when limiting (Bieleski 1976, Smith 1980, Groves 1983, Kruger et al. 1983). It has been found in Australia that not only is phosphorus present in low concentrations (Specht and Rayson 1957), but the plants respond to increased phosphorus (Groves 1965, Heddle & Specht 1975). Conversely, despite fynbos' relatively low phosphorus levels, phosphorus fertilization of fynbos seems to have little impact on species growth or mortality (Witkowski 1989). It would therefore seem that phosphorus is not limiting to the same extent as other elements. The significant increase in phosphorus found under *Acacia saligna* canopies is likely to have little effect on altering fynbos. The other four species studied were not significantly different from one another or between open and under-canopy areas (Table 1).

#### **The Effect of Aliens on Post-Fire Vegetation**

The equitability data (Fig.6 ) shows that a number of non-dominant species occupy 65% of the ground below the canopy of *Leucospermum conocarpodendron* (Fig.7). These two values would seem to indicate a high species diversity for these areas. *Hakea* showed a similar trend to *Leucospermum*, and would therefore

appear to have little effect on the immediate post-burn vegetation, when it occurs in low densities. However, as density increases *Hakea* has been found to have an effect on indigenous Proteaceae (Breytenbach 1986). This species therefore has the potential to alter the fynbos physical environment, if allowed to persist and establish dense stands.

*Pinus*, on the other hand, has less open ground beneath its canopies, indicating greater abundance of plants and a greater equitability, therefore a slight increase in dominant species. The latter however is not significantly different from *Hakea* or *Leucospermum*. *Pinus* has been reported to decrease species diversity on plantations (Richardson & van Wilgen 1986). Thus this plant does pose a threat to the fynbos community; even in such low densities it appears to cause a decrease in diversity.

The invasive aliens that have caused most variation thus far, namely the two *Acacia* spp., also appear to have the greatest effect on species diversity and relative abundance of vegetation (Fig. 6 & 7). Both these species show increased abundance under their canopies (Fig.7) which appears to be a function of the organic matter / nitrogen content of the soil. However, the response of the indigenous vegetation to these increases are different. *Acacia cyclops* appears to have a non-significant increase in equitability, indicating a relatively unchanged species diversity under the canopy. Nevertheless, certain species did appear to be more dominant than others in these areas (pers. obs.). *Acacia cyclops* has also been found to possess

substances which delay germination of certain indigenous species (Jones et al. 1963), however no such pattern of inhibition was observed. *Acacia saligna* on the other hand has fewer dominant species below its canopy (Fig.6 - indication). It was noted that the species below *Acacia saligna* showed greater vigour than below the other species studied here. Also, the dominant species beneath its canopy was of *Acacia saligna* seedlings. It would therefore appear that this species forms a major threat to fynbos, in that not only does it affect the soil chemistry of the area it also appears to modify it in favour of its conspecifics.

#### Conclusion

It would appear that *Hakea gibbosa* and *Pinus pinaster* are having little effect on the physical environment of fynbos, when in low densities. The *Acacia* spp. (in particular *A.saligna*) seem to alter the soil status to a certain extent. However, fynbos would appear to be resilient to the effects of nutrient enrichment (in terms of, change in species and growth form composition), and thus probably be able to re-establish in areas where *Acacia* spp. have been removed. The latter may however not be true for Strandveld areas which exhibit high phosphorus levels (relative to Australia as well as other fynbos areas) and therefore probably greater nitrogen-fixation by these legumes. The effect of extreme nitrogen enrichment on fynbos has not been studied as yet, therefore predictions of vegetation change cannot be made.

With respect to alien impact on the immediate post-fire fynbos



vegetation, *Acacia* spp. would seem to have the greatest effect of lowering species diversity, and increasing the abundance of weedy species (in particular its conspecifics). The acacias would therefore appear to alter the composition of early pioneers in the pyric succession of fynbos. However, the effect they may have on the later successional species is not known as yet. It is nevertheless important that these *Acacia* spp. be removed, since they not only affect soil nitrogen levels but also species diversity of post-fire fynbos communities.

### Acknowledgements

I would firstly like to thank my supervisor, Dr W. Bond, for his assistance and encouragement in this project. Secondly, I would like to thank Miss A.Proudfoot, Mr V.Tichardt, Mr M.Gammon for their help with the data collection; and Ms N.Allsopp, Ms K.Wienand, Dr W.Stock and Dr E.Witkowski for their assistance with soil analysis, reference material and ideas.

## References

- Agren, G.I. & Bosatta, E. 1987 . Theoretical analysis of the long-term dynamics of carbon and nitrogen in soils. *Ecology* 68: 1181-1189.
- Barrow, N.J. 1977 . Phosphorus uptake and utilization by tree seedlings. *Aust.J.Bot.* 25: 571-584.
- Bieleski, R.L. 1976 . The passage from soil to plant. In: Blair, G.J. (ed.) *The Efficiency of Phosphorus Utilization . Reviews in Rural Science* ,3. University of New England Press, Armidale, New South Wales.
- Breytenbach, G.J. 1986 . Impacts of alien organisms on the terrestrial communities with emphasis on the communities of the south western Cape. In: MacDonald, I.A.W., Kruger, F.J. & Ferrar, A.A. (eds.) *The ecology and management of biological invasions in southern Africa*. Oxford University Press, Cape Town. pp.229-238.
- Brown, G. & Mitchell, D.T. 1986 . Influence of fire on the soil phosphorus status in sand plain lowland fynbos, south-western Cape. *S.Afr.J.Bot.* 52: 67-72.
- Connor, D.J. & Wilson, G.L. 1968. Response of a coastal Queensland heath community to fertilizer application. *Aust.J.Bot.* 16: 117-123.
- Groves, R.H. 1965 . Growth of heath vegetation .II. The seasonal growth of a heath on ground water podzol at Wilson's Promontory, Victoria. *Aust.J.Bot.* 15: 161-173.
- Groves, R.H. 1983 . Nutrient cycling in Australian heath and South African fynbos. In: Kruger, F.J., Mitchell, D.T. & Jarvis, J.U.M. (eds.) *The role of Nutrients*. Vol. 43 *Ecological Studies*, Springer, Berlin, pp. 179-191.
- Groves, R.H. & Keraitis, K. 1976 . Survival and Growth of seedlings of three Sclerophyll species at high levels of Phosphorus and Nitrogen. *Aust. J. Bot.* 24: 681-690.
- Hall, A.V. 1978 . Endangered species in a rising tide of human population growth. *Trans. Royal Soc. S. Afr.* 43: 37-49.
- Hansen, A.P. & Pate, J.S. 1987 . Comparative growth and symbiotic performance of seedlings of *Acacia* spp. in defined Pot Culture or as Natural Understorey components of a Eucalypt forest ecosystem in S.W. Australia. *J.Exp.Bot.* 38: 13-25.
- Hansen, A.P., Pate, J.S., Hansen, A. & Bell, D.T. 1987 . Nitrogen economy of post-fire stands of shrub legumes in Jarrah (*Eucalyptus marginata* Donn ex Sm.) Forest of S.W. Australia. *J.Exp.Bot.* 38: 26-41.
- Hedde, E.M. & Specht, R.L. 1975 . Dark Island Heath (Ninety-mile plain, South Australia). VIII. The effect of fertilizers on composition and growth, 195-60. *Aust.J.Bot.* 23: 151-64.
- Hutchinson, G.E. 1957 . *A treatise in Limnology, Geography, Physics and Chemistry*, Vol.1, John Wiley, New York.
- Jackson, M.L. 1958 . *Soil chemical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.
- Jones, R.M., Roux, E.R. & Warren, J.M. 1963 . The production of Toxic substances by *Acacia cyclops* and *A.cyanophylla* and their possible ecological significance. *S.Afr.J.Sc.* 59:295-296.
- Kruger, F.J. 1977 . A preliminary account of aerial plant biomass

- in fynbos communities of the Mediterranean-type climate zone of the Cape Province. *Bothalia* 12: 301-307.
- Kruger, F.J., Mitchell, D.T. & Jarvis, J.U.M. (eds.) 1983 . Mediterranean-type Ecosystems. The Role of Nutrients. Ecological Studies Series Vol. 43. Springer, Berlin. Low, A.B. 1980 . Preliminary observations on specialized root morphologies in plants of the western Cape. *S.Afr.J.Sci.* 76: 513-516.
- Langkamp, P.J. & Dalling, M.J. 1982 . Nutrient cycling in stands of *Acacia holosericea* A.Cunn.ex G. Don. II. Phosphorus and endomycorrhizal associations. *Aust. J. Bot.* 30: 107-119.
- Lewis, O.A.M. & Stock, W.D. 1978 . A preliminary study of the nitrogen nutritional status of members of the South African Proteaceae. *J.S.Afr.Bot.* 44: 143-151.
- Low, A.B. 1980 . Preliminary observations on specialized root morphologies in plants of the Western Cape. *S.Afr.J.Sc.* 76: 513-516.
- MacDonald, I.A.W. & Jarman, M.L. 1984 . Invasive alien organisms in the terrestrial ecosystems of the fynbos biome, South Africa. *S.Afr.Nat.Sc.Prog.Report* No. 85, Pretoria.
- MacDonald, I.A.W. & Richardson, D.M. 1986 . Alien species in terrestrial ecosystems of the fynbos biome. In: MacDonald, I.A.W., Kruger, F.J. & Ferrar, A.A. (eds.) *The Ecology and Management of Biological Invasions in Southern Africa*. Oxford University Press, Cape Town.
- Marais, L.M. & Kotze, J.M. 1977 . Notes on Ectotrophic Mycorrhizae of *Pinus patula* in South Africa. *S.Afr. Forestry J.* 100: 61-64.
- McMaster, G.S., Jow, W.M. & Kummerow, J. 1982 . Response of *Adenostoma fasciculatum* and *Ceanothus greggii* chaparral to nutrient additions. *J.Ecol.* 70: 745-756.
- Milton, S.J. 1980 . Studies on Australian acacias in the southwestern Cape: South Africa. MSc Thesis, University of Cape Town.
- Milton, S.J. 1981 . Litterfall of the exotic acacias in the southwestern Cape. *J. S. Afr. Bot.* 47: 147-155.
- Milton, S.J. & Siegfried, W.R. 1981 . Above-ground biomass of Australian acacias in the southern Cape, South Africa. *J. S. Afr. Bot.* 47: 701-716.
- Mitchell, D.T., Brown, G. & Jongens-Roberts, S.M. 1984 . Variations of forms of phosphorus in the sandy soils of coastal fynbos, south-western Cape. *J.Ecol.* 72:575-584.
- Murphy, J. & Riley, J.P. 1962 . A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27: 31-36.
- Nakos, A. 1977 . Acetylene reduction by nodules of *Acacia cyanophylla*. *Soil Biol. Biochem.* 9: 131-133.
- Read, D.J. & Mitchell, D.T. 1983 . Decomposition and Mineralization processes in Mediterranean-type ecosystems and in heathlands of similar structure. In: Kruger, F.J., Mitchell, D.T. & Jarvis, J.U.M. (eds.) *Mediterranean-type ecosystems: the role of nutrients*. Springer-Verlag, Berlin.

- Richardson, D.M. & Van Wilgen, B.W. 1986 . Changes in the composition of fynbos vegetation following thirty years of afforestation with pines at Jonkershoek, Stellenbosch. S. Afr. Forestry Research Inst., Jonkershoek Forestry Research Centre Report 85/10. pp. 24.
- Roux, E.R. & Warren, J.L. 1963 . Studies in the Autecology of Australian acacias in South Africa. 2 . Symbiotic nitrogen fixation in *Acacia Cyclops* A. Cunn. S.Afr.J.Sc. 59: 294-295.
- Shea, S.R. & Kitt, R.J. 1976 . The capacity of jarrah forest native legumes to fix nitrogen. Research paper No. 21, Forests Department of Western Australia. pp. 2-4.
- Smith, R.L. 1980 . Ecology and Field Biology, 3rd ed. Harper & Row, New York.
- Specht, R.L. 1963 . Dark Island Heath (Ninety-Mile Plain, South Australia). VII. The effect of fertilizers on comp[osition and growth, 1950-60. Aust.J.Bot. 11: 67-94..
- Specht, R.L. 1981 . Nutrient release from decomposing litter of *Banksia ornata* . Dark Island Heathland, south Australia. Aust. J. Ecol. 6: 59-63.
- Specht, R.L., Connor, D.J. & Clifford, H.T. 1977 . The heath-savanna problem: The effects of fertilizers on sand-heath vegetation of North Stradbroke Island, Queensland. Aust.J.Ecol. 2:179-186.
- Specht, R.L. & Rayson. 1957 . Dark Island Heath (Ninety-mile plain, S. Australia). VII: The effect of fertilizers on composition and growth, 1950-60. Aust.J.Bot. 11: 67-94.
- Stirton, C.(ed.) 1978 . Plant invaders: Beautiful but Dangerous. Cape Dept. of Nature and Environmental Conservation.
- Stock, W.D. 1985 . An investigation of nitrogen cycling processes in a coastal fynbos ecosystem in the south western Cape Province, South Africa. Unpublished Phd thesis, University of Cape Town.
- Van Wilgen, B.W. & le Maitre, D.C. 1981 . Preliminary estimates of the nutrient levels in Fynbos vegetation and the role of fire in nutrient cycling. S.Afr. Forestry J. 119: 24-28.
- Vitousek, P.M. 1986 . Biological invasions and ecosystem properties: Can Species make a Difference ? In: Mooney, H.A. & Drake, J.A. (eds.) Ecology of Biological Invasions of North America and Hawaii. Ecol. Studies 58: 163-178.
- Witkowski, E.T.F. 1988 . Respose of a sand-plain lowland fynbos ecosystem to nutrient additions. Ph.D. thesis. University Cape Town.
- Witkowski, E.T.F. 1989 . Response to nutrient additions by the plant growth forms of sand-plain lowland fynbos, South Africa. Vegetatio 79:89-97.
- Witkowski, E.T.F. & Mitchell, D.T. 1987 . Variations in soil phosphorus in the fynbos biome, South Africa. J.Ecol. 75: 1159-1171.

## APPENDIX 1

### KJELDAHL DIGESTS OF SOIL MATERIAL

#### 1. Digestion Preparation

(Use long thick boiling tubes rinse with deionized water & dry)

- Weigh out approximately 1 g of 2 mm sieved soil
- Add 1 ml distilled water;
  - 3 ml  $H_2SO_4$  (Chemically pure) with Salicylic acid ( $34 \text{ g.l}^{-1}$  of  $H_2SO_4$ );
  - A spatula tip of Na-Thiosulphate;
  - 1 Kjeldahl tablet (Selenium catalyst).

#### Blanks & Standards

- At the same time digest 3 blanks (distilled water) of 1 ml volume & 1 ml of 5 standards  $(NH_4)_2SO_4$ .
- These concentrations ammonium sulphate replace the 1 ml distilled water above:  
 $0.1 ; 0.2 ; 0.4 ; 0.6 \text{ \& } 0.8 \text{ mg N ml}^{-1}$ .

#### 2. Digestion

- (a) Put in digestion block at  $0^\circ C$ .
- (b) Set to  $150^\circ C$  & leave overnight.
- (c) Next, set to :
  - $220^\circ C$  for 1 hour;
  - $250^\circ C$  for 1 hour;
  - $280^\circ C$  for 1 hour;
  - $300^\circ C$  for 1 hour;
  - $350^\circ C$  for 2 hours.
- (d) Switch off the block & leave overnight to cool.
- (e) Next, set block to  $150^\circ C$  for approx. 30 minutes until digest dissolves.

- (f) Take tubes out of the blocks & allow to cool for 5 - 10 minutes, add 5 - 10 ml of distilled water & swirl tubes.
- (g) Decant very carefully into wide-necked 50 ml flasks using the test tube shaker to swirl the mixture. Make up the last bit to 50 ml with distilled water. Stopper tubes.

## **PHENOL - HYPOCHLORITE DETERMINATION**

### **1. Reagents**

1. EDTA (0.12 % W/V)
2. 0.5 % (W/V) Sodium nitroprusside (make each time)
3. 10 % (W/V) Phenol in 95 % Ethanol
4. Alkaline - phosphate buffer  
(6.93 g  $\text{Na}_2\text{HPO}_4 \text{ l}^{-1}$  & 20.65 g  $\text{NaOH l}^{-1}$ )
5. 1.5 % Sodium hypochlorite  
(Use fresh dilution of stock solution 1 : 3.9628 water)  
(dilution 1 : 6 ie. 12.5 cc up to 75 ml)

**Reagent A** = Mix equal parts of 2 & 3

**Reagent B** = Mix four parts of 4 with one part of 5

### **2. Procedure**

(In 50 ml flasks or thin-walled tubes)

- (a) Take 1 ml of digestion solution (Shake flask or container thoroughly before removal of aliquot so that it is properly mixed).
- (b) Add 25 ml EDTA.
- (c) Add 2 ml reagent A.
- (d) Mix properly.
- (e) Add 5 ml reagent B.

(f) Make up to volume ie. add 17 ml distilled water.

(g) Leave for 60 minutes and read at 635 nm off a spectrophotometer.

## APPENDIX 2

### **TOTAL PHOSPHORUS IN SOIL**

(Based on Hesse : A textbook of soil chemical analysis - pp 296)

- Heat 2 g soil (2 mm sieved & air dried) in closed crucible in a muffle furnace at 240°C for 90 - 120 minutes.
- Allow sample to cool to approx. 100°C before removing.
- Transfer sample to a 50 ml digestion flask; rinse crucible with 5 ml concentrated HCl & transfer to digestion flask.
- Add a further 5 ml HCl.
- Digest for 30 minutes in a boiling water-bath.
- Add 20 ml distilled water & leave in the water-bath for another 30 minutes.
- Filter diluted digest into 100 ml volumetric flasks - rinse with distilled water (4 aliquots of 5 ml).
- Make up volume to 50 ml & mix well.
- Take 4 ml diluted digest & transfer to 50 ml volumetric flask
  - dilute to 40 ml with distilled water;
  - add 8 ml Murphy & Riley (1962) mixed reagent;
  - make up to 50 ml volume with distilled water & shake well.
- Read at 882 nm, after 30 minutes, on a spectrophotometer.