A preliminary study of the impacts of alien *Acacia* infestation (*A.saligna*) on the relative rates of nitrogen and phosphorus cycling in Lowland Fynbos, southwestern Cape, South Africa.

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October 1988

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1. Abstract

This study was carried out on Sand Plain Lowland fynbos at Pella from April to September 1988. Environmental factors, nitrogen and phosphorus pool sizes and mineralization processes were investigated in the surface soils (1-10cm) of 7-8 year old fynbos vegetation and an adjacent Acacia saligna (Labill.) Wendl. infestation. While there was no significant difference in soil temperature between fynbos and acacia sites, soil moisture and organic matter content was significantly higher in the acacia soils. This favoured decomposition so that soil nutrient analyses showed enrichment of the soils (higher N and P) by the acacia infestation.

Soil N and P mineralization was assayed using in situ incubations. Due to their higher soil total N concentrations, acacia soils showed greater inorganic N concentrations. In both acacia and fynbos soils ammonium was the dominant N form. This was ascribed to the high soil moisture content, while the low temperatures appeared to be the factor most strongly influencing ammonium accumulation. The low nitrate accumulations even in the field incubations indicated that the nitrification process was inhibited, probably by the high soil moisture content and low temperatures.

The variable patterns of inorganic P accumulation were ascribed mainly to fluctuations between microbial mineralization and immobilization.

Contrary to the hypothesis that the higher soil organic matter and greater concentrations of total N and P in acacia soils would result in higher mineralization rates, there was no significant difference in the rates of N and P mineralization between fynbos and acacia soils. Thus it was concluded that the higher decomposition rates in acacia soils was not associated with greater mineralization rates during the wet season (period of study).

2. Introduction

The extent and effects of the wide range of exotic plant invaders that have established in the fynbos biome have received much attention since the early decades of this centuary. In spite of attempts to contain the spread of alien plants since the 1940's (Macdonald et al 1985), it is reported that 24% of the whole biome is infested by woody alien species (Macdonald 1984). An assessment of the extent of infestation in Lowland Fynbos indicates that a major problem occurs in this vegetation type - 68% of the remaining natural vegetation is infested, mainly by Australian Acacia species (Macdonald et al 1985).

The need for control of these species in Lowland Fynbos is therefore urgent. However, information on all aspects of their control is inadequate (Macdonald et al 1985). The area inwhich this study was carried out is severely infested with Acacia saligna (Labill.) Wendl. Macdonald et al (1985) propose that its control should not be undertaken without the use of chemicals in combination with other techniques. This would further modify the chemical balance of a system already altered by the acacia infestations. Milton (1980) suggests that Acacia species make the environment less suitable for fynbos species (adapted to nutrient-poor soils) by enriching the soils. Thus before alien control practices are initiated, it is necessary to investigate the impacts of the invasives on the soil nutrient processes. If an infestation were successfully eliminated but it had altered the soil environment to the extent that re-establishment of

fynbos species is prevented, the effect of clearing (eg. wind and water erosion) might be more detrimental to the system than the infestation.

Raison (1980) proposes that the impacts of disturbance (eg. alien infestation) on the functioning of an ecosystem may be evaluated by detailed studies of the nutrient processes of the system. The relative capacity of ecosystems to endure disturbance can be described in terms of their resistance (to displacement from the undisturbed state) and resilience (recoverability). Resistance is related more to the size of the nutrient pools and resilience to rates of nutrient turnover. Alteration of either of these parameters is likely to be important in the nutrient-limited fynbos environment and was thus investigated in this study.

The soil nutrients investigated in this study were nitrogen and phosphorus, the elements most severely limiting plant growth in the southwestern Cape and southwestern Australia (Groves 1983). Since both the indigenous fynbos vegetation and the Australian Acacia species are coastal shrub forms adapted to low nutrient environments, it might seem unexpected that acacia infestations should alter the nutrient status of the fynbos systems. However, the adaptive strategies adopted by each is different and this could be important when comparing nutrient cycling.

Mitchell et al (1987) describe the range of mechanisms exhibited by fynbos species to overcome nutrient limitation. One such mechanism significant to this study is the internal cycling of nutrients - from work on litterfall and decomposition processes

in coastal fynbos vegetation. Mitchell et al (1986) found that sclerophyllous litter has a low N and P content, due possibly to internal recycling prior to abscission. It was also found that annual litter production at Pella is extremely low when compared with other mediterranean-type ecosystems and the decomposition of this litter is relatively slow (the time for 95% of the steady state litter to accumulate or to decay (T95%) is 16-19 years). Overall, there is a reduced return of nutrients to the soil.

Stock (1988) describes the ability of Acacia spp., indigenous to similar low nutrient soils in Western Australia, to symbiotically fix atmospheric N (due to the activity of the symbiotic Rhizobium / Bradyrhizobium bacteria in nodules), a strategy relatively unimportant in the south western Cape. According to Hoffman & Mitchell (1986) the success of A.saligna in the fynbos biome can be attributed in part to its extensive root system, abundant root nodules and the presence of mycorrhiza which are able to take up and accumulate P. These mechanisms for enhancing nutrient uptake could account for the finding that the N and P content of foliage of Australian acacias is two to four times as great as that of fynbos plants (A.B. Low unpubl., cited by Milton 1981). This enables acacias to maintain fast growth rates, large biomass, and produce more litter than fynbos plants (Milton 1981). Milton (1981) found that the average annual litterfall of exotic acacias is three times as great as that for mediterranean scrub and this litter has a rapid decomposition rate (T95%=7-9yr, compared to 16-19yr for fynbos). The result is enrichment of the soil - N is added to the soil by the litter (Milton 1981); the P

content of the acacia litter exceeded that of litter from indigenous vegetation (Witkowski & Mitchell 1987).

Limited research has been done on the effect of alien infestation on the nutrient pool sizes of fynbos soils, and to date no work has yet been done on the relative rates of nutrient cycling in alien and indigenous communities (Macdonald & Richardson 1986, Versfeld & van Wilgen 1986, Mitchell et al 1987 and Stock 1988).

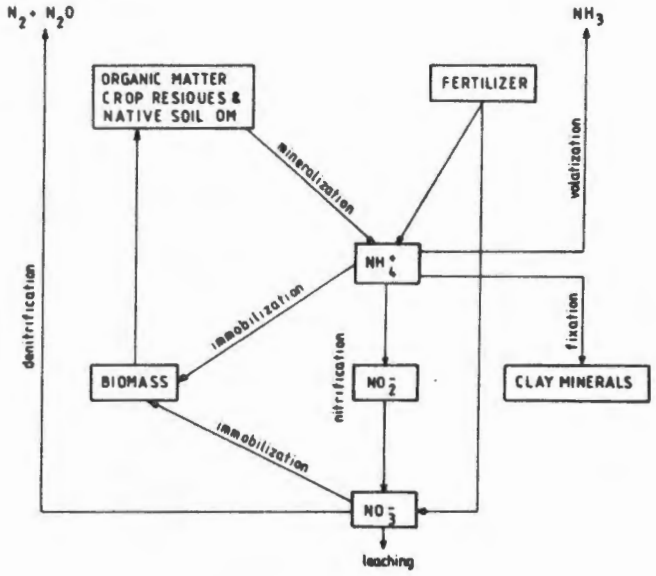

Figure 1 General outline of the nitrogen cycle (van Veen et al 1981).

A general outline of the N cycle is given in Figure 1. The lack of accumulation of either nitrate or ammonium in significant quantities in the fynbos (Stock & Lewis 1986) is ascribed to a balance between inorganic inputs to the soil from mineralization and atmosphere and losses from plant uptake, leaching, microbial immobilization and denitrification. This delicate balance,

together with the adaptations of the indigenous plants for efficient use and conservation of N results in a "tight" N cycle, indicative of an undisturbed natural ecosystem (Stock 1985). However, a disturbance (probably human activities) followed by invasion by an exotic weed would disrupt this tight cycle by increasing/decreasing one or more of the inputs and/or outputs. In the case of acacia invasions, it seems that the major alteration is an increased input of organic matter (litter) with a higher nutrient content. This would imply high potential rates of mineralization and nitrification.

From a study of N mineralization in fynbos soils, Stock et al (1988) concluded that increased mineralization and nitrificaton appeared to be associated with increased soil total-N content. Also, Alexander (1977) states that "the rate of production of inorganic N is closely correlated with the total-N content of the soil." Thus we may hypothesize that the acacia infested soils with its higher total N levels would show both a greater amount and rate of mineralization than the fynbos soils. This will be investigated in this study, together with the environmental factors which also play a part in the mineralization process.

According to Stock et al (1988), the most important environmental factors controlling the mineralization process in fynbos soils are temperature and moisture. When considering the soil microclimate, these two factors are in turn influenced by the vegetation structure. Since acacia stands are generally denser than fynbos (Versfeld & van Wilgen 1986), they should alter the

soil microclimate and therefore affect the rate of mineralization processes. The different microfloral populations responsible for various stages of N mineralization responds differently to temperature and moisture regimes (Alexander 1977). Therefore, the different soil microclimates created by acacia and fynbos should affect different stages of the mineralization process and so influence the rate of nutrient cycling.

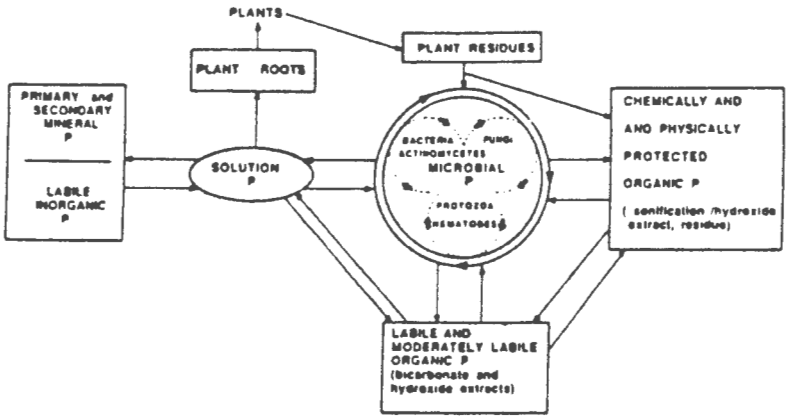

Figure 2 Schematic illustration of the phosphorus cycle (Stewart & Tiessen 1987).

Mineralization rates of P were also investigated. Phosphorus has a local or sedimentary type biochemical cycle as opposed to the gaseous one of N (Alexander 1977). Figure 2 presents a simplified P cycle. While soil micro-organisms are responsible for the mineralization of organic phosphates, the rate of mineralization will depend upon the activity of phosphatase enzymes. These in turn will be largely influenced by moisture and suitable temperatures during autumn, winter and spring when soils are moist (Rundel et al 1983).

According to Alexander (1977), phosphate release is most rapid under conditions favouring ammonification. Thus there should be a

correlation between the rates of N and P conversion to inorganic forms. Further, the rate of P mineralization is also directly correlated with the quantity of substrate (Alexander 1977). Therefore it seems that the P mineralization process is also influenced by the microclimate and input of organic P from leaf litter and so warrants comparison in acacia and indigenous communities, especially as P can often act as a factor limiting effective N fixation in legume/rhizobium interactions (Cole & Heil 1981).

3. Study Area

The study sites were located on the Burgherspost Farm, about 500m south of the Fynbos Biome Research site at Pella (33° 31´S: 18° 32´E; altitude 160-220m; 62km north of Cape Town, South Africa). Since the rainfall occurs predominantly in the winter season (76% of the 599mm mean annual rainfall occurs in the April - September period (Jarman & Mustart 1988)), the climate is typically Mediterranean (Csa), characterized by dry summers and wet winters (Schultz 1947, cited by Stock & Lewis 1986).

The vegetation of the Pella region has been described as Sand Plain Lowland Fynbos to distinguish it from other forms of coastal fynbos (Moll et al 1984). It is dominated by evergreen sclerophyllous shrubs with ericoid and restioid elements in the understorey. The study area consisted of 7-8yr old Leucospermum parile (Salis.ex J.Knight)Sweet / Thamnochortus punctatus Pill. shrubland, with an adjacent infestation of well-established (7-8yr) Acacia saligna. While the acacia site had been infested with A.saligna since the fire in 1980, Brownlie (1982) records continuous infestation of this area since 1960.

The average height of the indigenous fynbos vegetation was about 1-1.5m, while the A.saligna stand was more than 3-4m high. The greater canopy cover and litter production in acacias (Milton 1981) accounts for the thick layer of litter (mainly phyllodes as well as pods and twigs) that totally covered the ground beneath the acacia thickets to a depth of about 5cm. In contrast, the sparse vegetation cover and small amount of litter (consisting of

fine restioid culms and narrow leaves) in the fynbos site left much exposed soil.

The soil type was the Clovelly form (shallow orthic A over a yellow-brown apedal B) classified according to MacVicar et al (1977, cited by Mitchell et al 1984). The B horizon is comprised essentially of fine (0.02-0.2mm) to medium (0.2-0.5mm) sand (Brown & Mitchell 1986). This sandy soil with only a trace of a clay fraction (Brown & Mitchell 1986), results in well-drained, acidic, low-nutrient soils (Stock & Lewis 1986). The pH and concentrations of total N and total P are given in Table 1. While the "fynbos" soils showed low concentrations of these elements, the "acacia" soils had significantly higher levels of N and P. The greater litter production of acacia thickets would account for the higher organic content and moisture retention of the acacia soils.

Table 1 Total nitrogen, total phosphorus, pH and organic matter (Means ± 1 S.E.M.) at the soil surface (0-10cm) of the fynbos and acacia sites.

Site	Soil Total N ($\mu g\ g^{-1}$)	Soil Total P ($\mu g\ g^{-1}$)	Soil pH	Soil Organic Matter (%)
Fynbos	193 ±13.6	35.9 ±0.33	4.7 ±0.04	1.21 ±0.03
Acacia	422 ±73.5	56.7 ±3.5	4.9 ±0.12	1.96 ±0.06
t	3.04	5.9	1.84	12.12
d.f.	14	14	14	18
P	<0.01	<0.001	N.S.	<0.001

4. Materials and Methods

4.1 Soil collection and incubation

Soil samples were collected and incubated monthly for the investigation of the rate of soil nutrient (N and P) cycling over the wet season (April-September) when maximum release of nutrients occurs (Brown et al 1984; Stock & Lewis 1986). Three random plots were established within both the fynbos vegetation and a dense 2ha acacia stand. At each plot, three sample sites were demarcated. Soil samples were taken to a depth of 10cm where biological activity and nutrient concentrations are greatest (Stock 1985). Presumably this region would also be most susceptible to environmental or microclimatic changes.

The experiment began on 14 April 1988 (towards the end of the dry summer period) when three soil samples (about 57cm each) were taken at each plot and returned to the laboratory for analysis. This represents the initial or fresh soil samples. Incubation samples were set up simultaneously at each site by extracting soil undisturbed cores in plastic cylinders (4cm diameter, 9cm length). Each soil filled cylinder was enclosed by two polyethylene bags (100 x 150mm), secured with an elastic band and buried in the soil at the depth from where they were removed. The incubated cores were maintained at the initial field moisture content, since the polyethylene bags are waterproof yet allow gaseous exchange.

After 28 days of field incubation, the cores were collected for analysis, together with another set of fresh samples. A new set of cores were set up for incubation. This procedure was carried out until August 1988. The experiment ended in September 1988 when only the incubated cores were collected from the field.

4.2 Soil Temperature

Soil thermometers were placed in the field (4 each in the fynbos and acacia stands) to monitor the soil temperatures at 10cm depth over the incubation periods. The temperatures were recorded daily.

4.3 Soil Moisture

The moisture content of the fresh and incubated soils was determined each month as the mass lost by a 4g sample dried in a forced-draught oven at 105 °C for 24 hours (Stock & Lewis 1986).

4.4 Soil Organic Matter

The oven-dried soil was used to determine the organic matter content which was calculated as the mass lost-on-ignition during 16 hours in a furnace at 450 °C (Mitchell et al 1984).

4.5 Soil pH

pH was determined on the final sample set by mixing 20g fresh soil in 50cm^3 0.01M CaCl for 30minutes. The pH values of the soil solutions were obtained using the Radiometer PH M29 pH meter.

4.6 Soil Nutrient Analyses

At each sampling date, soil samples collected in the field (18 fresh + 18 incubated) were returned to the laboratory on the same day for immediate nutrient extraction to avoid changes which occur in stored samples (Stock 1983). Each sample was first sieved through a 2mm mesh.

4.6.1 Nitrogen analysis

Inorganic N extraction

From each field-moist sample, 10g soil was added to 40ml 1M KCl and shaken for one hour. The filtrate (filtered through Whatman No 1 filter paper) was used for ammonium, nitrate and nitrite analysis. Inorganic N analyses were carried out each month on the fresh and incubated samples.

Ammonium determination

Ammonium was determined by a manual Indo-phenol blue procedure described by Stock (1983). To 2ml of sample extract or standard the following reagents were sequentially added: 1.6ml 10% (w/v) sodium potassium tartrate solution, 0.2ml 0.16% (w/v) sodium nitroprusside solution, 0.4ml sodium phenate reagent and 0.2ml sodium hypochlorite with 5% available Cl^-. The reagents were mixed, made up to 10ml with distilled water and incubated for 20 minutes in a waterbath at 40°C. After cooling, the absorbance was read within 10 minutes at 625nm with a Bausch and Lomb Spectronic 21 spectrophotometer. Because of the 10 minute time limit for

taking readings, not more than 18 samples were run simultaneously. Each run included five standards prepared from 0.1M ammonium chloride solution and 1M KCl in the range 0.5 to 2.5 μg N ml^{-1}, two 1M KCl blanks and two Whatman No 1 filtered 1M KCl blanks (to analyse the solutions for ammonium which may be present in the filter paper) (Stock 1983). These blanks and standards were used to construct a standard curve from which ammonium concentrations were calculated.

Nitrate and nitrite determinations

These were also carried out according to Stock (1983) whereby nitrate is reduced to nitrite by the copper-cadmium method. Nitrite was determined by the Griess-Ilosvay method.

For copperized cadmium reduction, 0.1ml 1M magnesium chloride, 2g prepared Cu/Cd and 1.9ml 0.4M ammonium chloride buffer (pH 9.6) were added to 3ml KCl soil extracts. This mixture was shaken for precisely 10 minutes afterwhich a 1ml aliquot was removed for nitrite determination by the Griess-Ilosvay method. Two 1M KCl blanks and 5 standards (0.1M potassium nitrate prepared in the range 0.2 to 2.0 μg N ml^{-1}) were run simultaneously.

Griess-Ilosvay nitrite determinations involved adding 1ml 1% (w/v) sulphanilamide in 1.5N HCl and 1ml 0.01% (w/v) N-(1-napthyl)ethylene HCl solution to 1ml KCl soil extracts or Cu/Cd reduced solution. After 10 minutes of colour development, absorbances were read at 540nm on the L & B Spec 21. Five nitrite standards (using sodium nitrite) were prepared in the range 0.1 to 1.0 μg N ml^{-1}.

Soil Total N

Total N was determined on the final sample set by micro-Kjeldahl digestion. To 1g of air-dried soil in 25cm Kjeldahl digestion tubes, 1ml distilled water, 3ml N-free concentrated hydrogen sulphate containing 34g l^{-1} salicylic acid, a selenium-catalyst tablet and 0.2g (spatula tip) sodium thoisulphate were added. After digestion on an aluminium-block digester (carried out by initially leaving the tubes overnight at 150 °C, increasing the temperature from 220 to 300 °C at one hour intervals and after digest cleared, digested at 350 °C for 2 hours) the digest was made up to 50ml with distilled water. The ammonium content was determined by a phenyl-hypochlorite method (Smith 1980).

Phenyl-hypochlorite determination was carried out by adding 25ml 0.12% (w/v) EDTA, 2ml reagent A (equal parts of 0.5% (w/v) sodium nitroprusside and 10% (w/v) phenol in 95% ethanol) and 5ml reagent B (4 parts alkaline phosphate buffer to 1 part 1.5% sodium hypochlorite) to 1ml digestion solution. The solution was made up to 50ml, left for 60 minutes and read at 635nm. Two blanks and 5 ammonium sulphate standards in the range 0.1 to 0.8 μg N g^{-1} were read simultaneously.

4.6.2 Phosphorus analysis

The inorganic P content of the soil samples was determined each month by the Anion Exchange Resin Extraction procedure described by Sibbesen (1977). Fresh soil samples (20g) were tumbled in sealed jars on the Schnapel mixer with 100ml distilled water and

a resin bag (300micron mesh polyester bags containing 8g anion exchange resins, activated by stirring in 0.5M sodium chloride) for 16 hours. The phosphate absorbed by the resin of each bag was extracted with 75ml 0.4N HCl by shaking/tumbling for 1 hour. A 10ml aliquot of the filtered eluate was then assayed for P by adding 8ml of Murphy & Riley's (1962) solution (prepared each time by adding 250ml 5N hydrogen sulphate, 2.64g ascorbic acid, 150ml water, 75ml ammonium molybdate and 25ml potassium antimony tartrate). The solution was made up to 50ml with distilled water and read at 882nm on the B & L Spec 21 after 40 minutes of colour development. Resin-extractable (plant available) phosphorus concentrations were determined using a standard curve in the range 0 to 8 μg P ml^{-1}.

Soil total P was determined on the final sample set by the method of Hesse (1971). Two grams of air-dried soil was heated at 240 °C (in a muffle furnace) for 90 minutes, transferred to thick walled boiling tubes and 10ml concentrated HCl added. The tubes were then heated at 110 °C for 30 minutes. After cooling and adding 20ml distilled water, the tubes were heated at 90 °C for 30 minutes. The solution was filtered through Whatman No 1 and made up to 100ml. A 4ml aliquot was assayed for P using the Murphy & Riley (1962) method. Total P concentrations were determined using a standard curve in the range 0 to 0.4 μg P ml^{-1}.

4.7 Statistical Analyses

Student's t-test was used to test for significant differences between means. A stepwise multiple linear regression was carried out on total accumulated inorganic N, ammomium and nitrate concentrations to determine the significance of environmental factors as determinants of the observed variance in each.

5. Results

5.1 Soil temperature, moisture and organic content

The mean monthly temperature, moisture and organic matter content of the fynbos and acacia soils during the period of study are presented in Figures 3, 4 and 5. Over the study period, fynbos and acacia soil temperatures showed <5 °C variation, the lowest temperatures being recorded during June-July. Even though there was no significant difference between fynbos and acacia temperatures the acacia soils tended to be about 1°C higher than that of the fynbos (Figure 3). Fynbos and acacia soils showed similar variations in moisture content over the study period, both with large increases over the June to August period (Figure 4). The soil moisture content under the acacia stand was significantly higher than that of fynbos soils ($t=2.46$; $P<0.05$). Relative to the constant low organic content of fynbos soils, acacia soils were found to contain a higher % organic matter. The acacia organic matter content was also more variable through the study period with lowest values recorded in May and August (Figure 5).

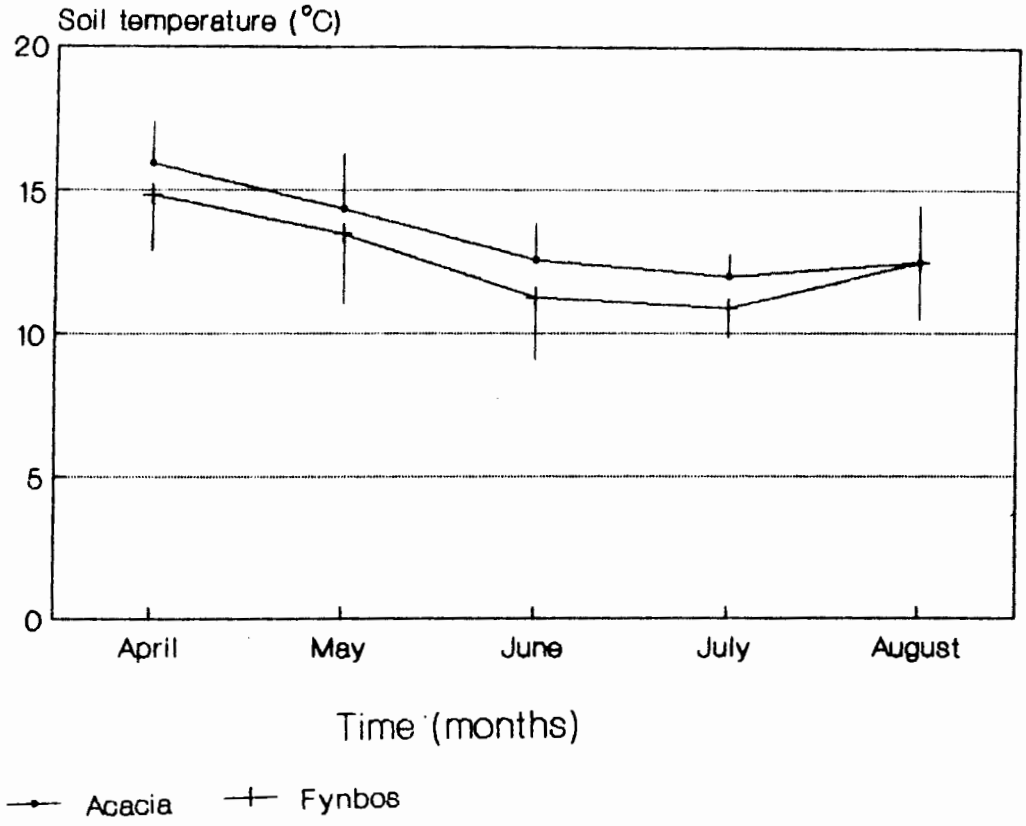

Figure 3 Monthly variations in the temperature of the surface soil (1-10cm) from the fynbos and acacia sites (vertical bars represent 1 S.E.M.).

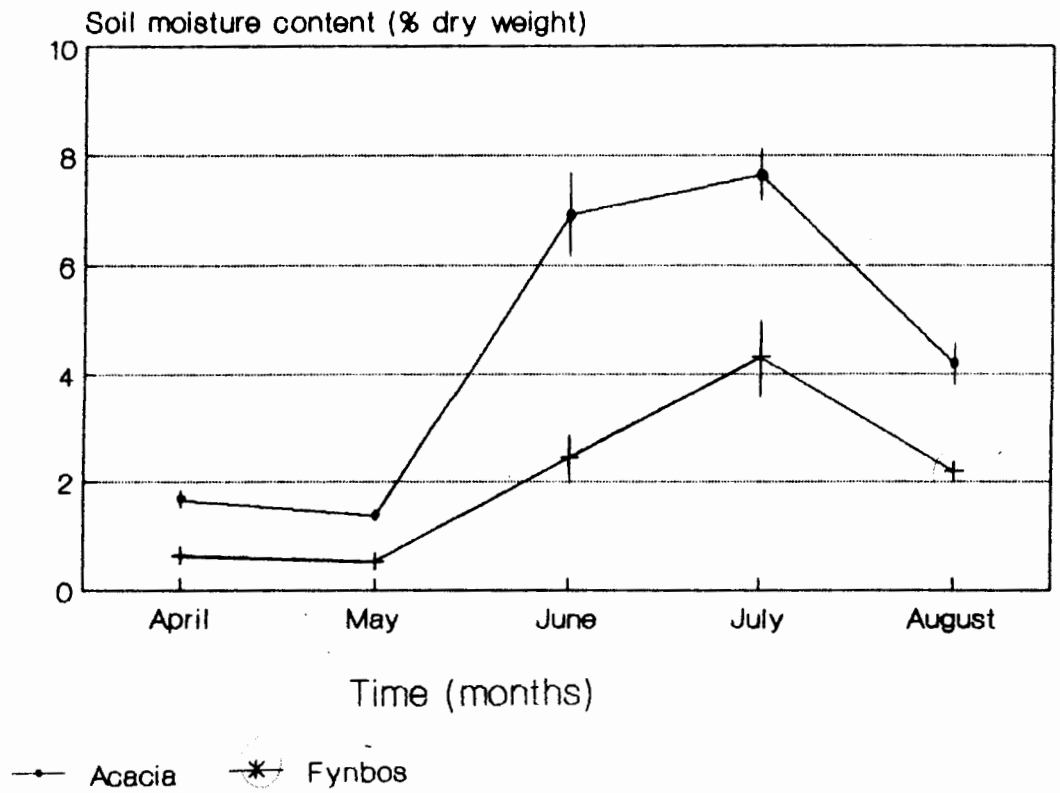

Figure 4 Monthly variations in the moisture content of the surface soil (0-10cm) from the fynbos and acacia sites (vertical bars represent 1 S.E.M.).

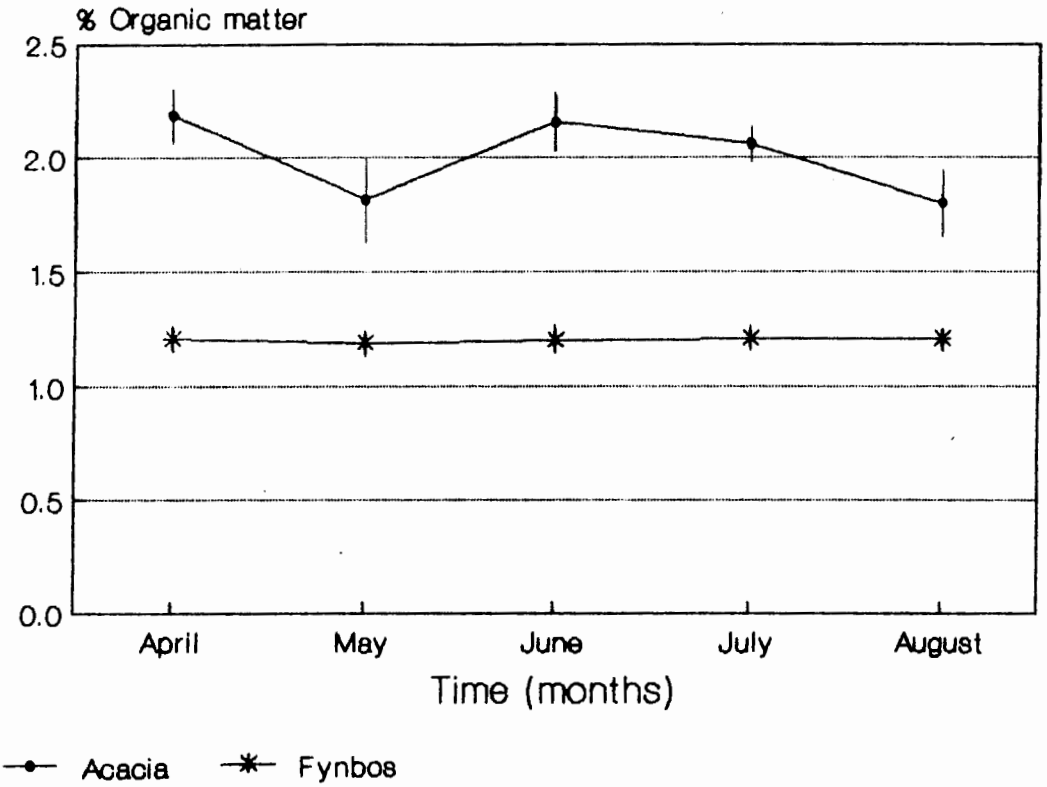

Figure 5 Monthly variations in the organic content of the surface soil (1-10cm) from the fynbos and acácia sites (vertical bars represent 1 S.E.M.).

5.2 Soil Nitrogen

Due to a practical error in setting up the incubations for the first month (April), the cores became waterlogged. Thus the physical and microbial conditions of these cores were not representative of the typical situation and so are presented separately in Figure 6. April's fynbos and acacia incubated cores contained unusually high concentrations of inorganic N (more than double the corresponding concentrations in Figure 7). An accumulation of ammonium accounted for these high values.

Overall, inorganic N concentrations were greater in acacia soils. Ammonium always made up a greater proportion of the inorganic N concentration than nitrate (Figure 7). (All samples were analysed for nitrite but this N form was either absent or found only in trace amounts; presumably any nitrite present would be included in the nitrate fraction determined by the Griess-Ilosvay method after Cu/Cd reduction).

The inorganic N concentration of the fresh samples from the fynbos sites decreased steadily from May to July with an increase in August. The incubated samples showed a contrasting trend with an increasing inorganic N concentration from May to August. The incubated acacia samples showed a similar pattern. Fresh acacia samples showed no pattern over the study period (Figure 7).

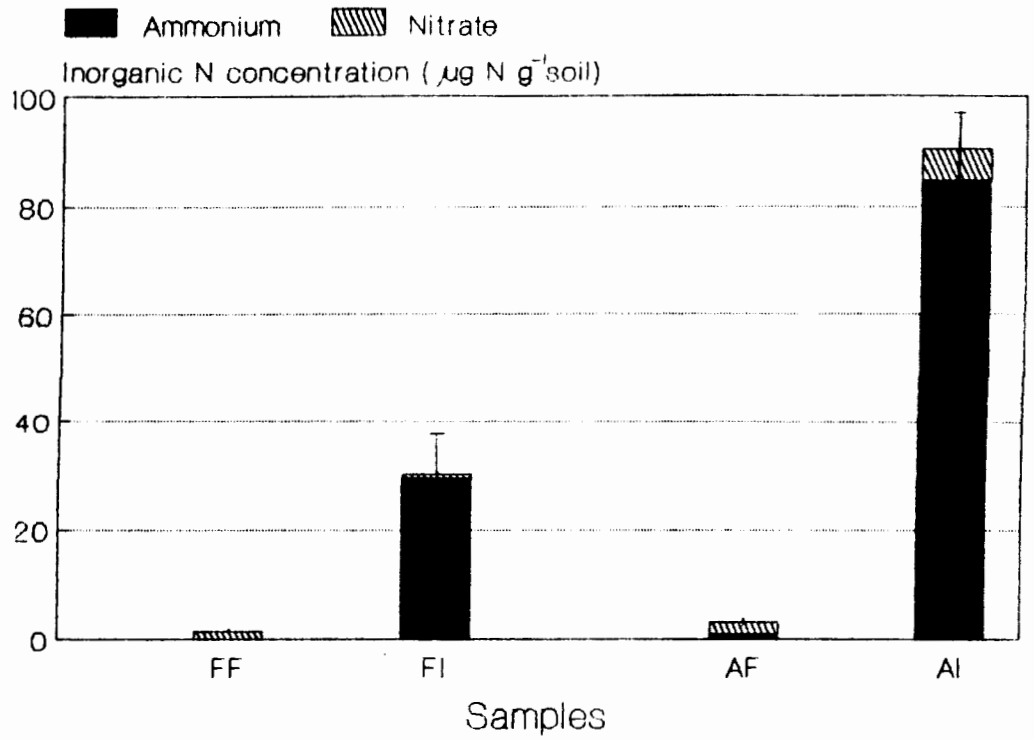

Figure 6 Mean inorganic nitrogen concentrations of fynbos fresh (FF), fynbos incubated (FI), acacia fresh (AF) and acacia incubated (AI) samples from the April incubation period (vertical bars represent 1 S.E.M.).

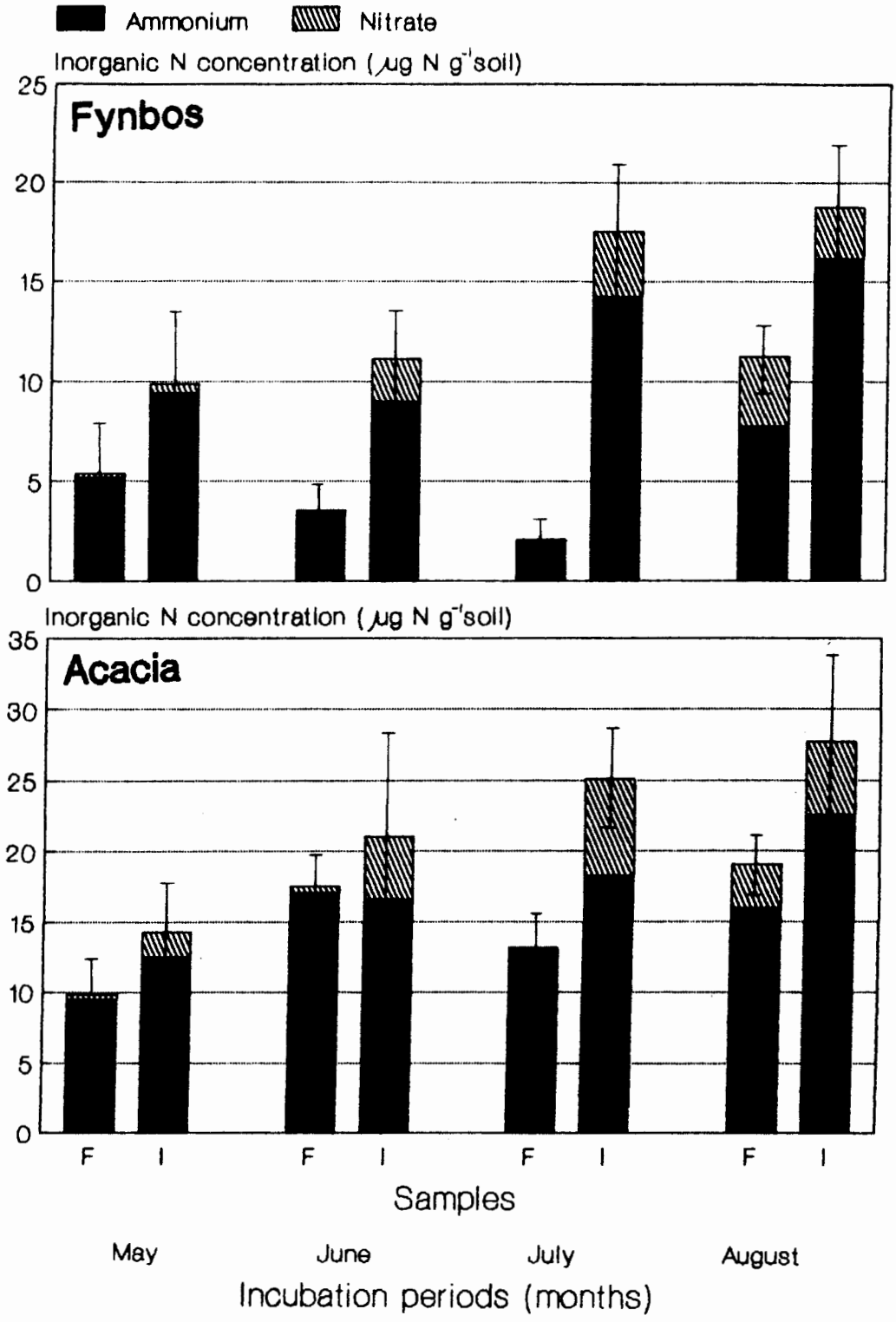

Figure 7 Mean inorganic nitrogen concentrations of the fresh (F) and incubated (I) soil samples for each incubation period (vertical bars represent 1 S.E.M.).

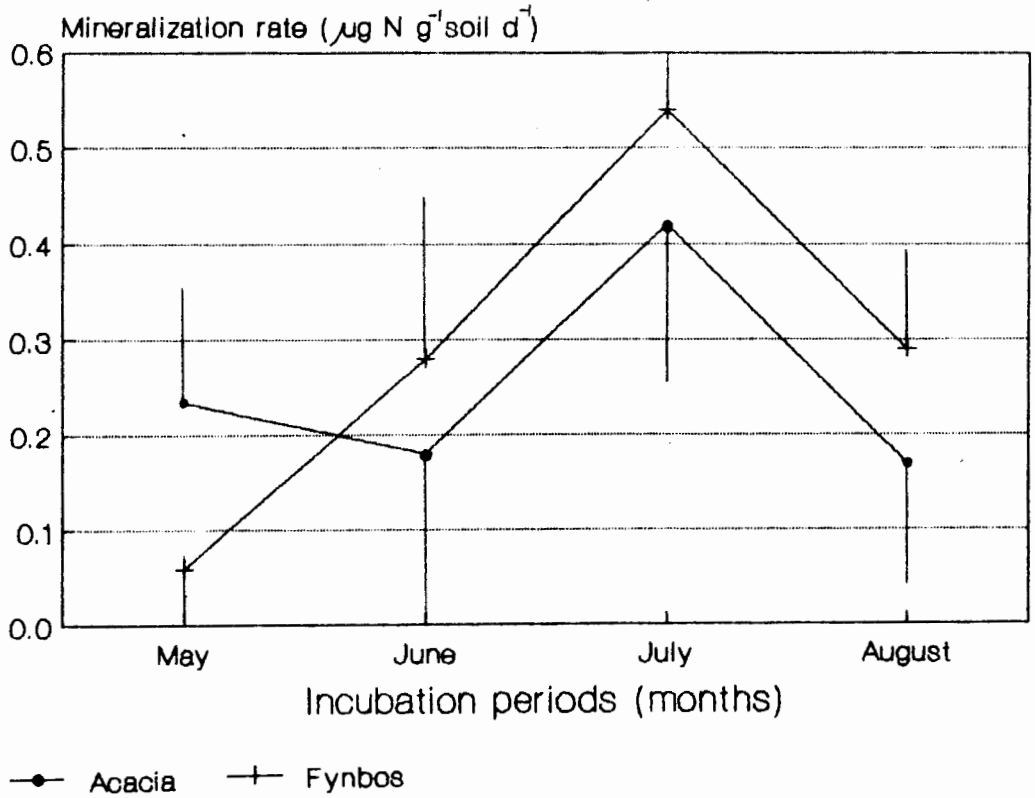

Figure 8 The mean nitrogen mineralization rates in acacia and fynbos soils during each incubation period (vertical bars represent 1 S.E.M.).

5.3 Nitrogen Mineralization

The difference in nutrient concentration between fresh and incubated samples for each month represented the amount mineralized. Overall there was an increase in total inorganic N (ammonium and nitrate) except in the acacia soils during June when there was a decrease in ammonium concentration (Figure 7). The net accumulation of mineralized N over each incubation period (28 days) was calculated as a mineralization rate ($\mu g\ N\ g^{-1} soil\ d^{-1}$) and the monthly variations presented in Figure 8. The mineralization rates in fynbos soils increased from May, reached a maximum in July and decreased again during August. The acacia soils showed a more random pattern decreasing in June but also reaching a maximum in July. A t-test (Two-sample analysis) applied to the mineralization rates calculated for each month showed that there was no significant difference in N mineralization rates between fynbos and acacia sites.

To determine which factor (soil temperature, moisture or organic matter) was most significant in determining the observed variation in the accumulation of mineralized N, a "stepwise multiple linear regression" was carried out. The results are presented in Table 2. The soil organic matter content accounted for 77% of the variation in total inorganic N concentrations and moisture alone accounted for 66%. The final model selected by the system included organic matter, moisture content and temperature which in combination determined 85%. However, the system excluded organic matter as a significant determinant of ammonium

accumulation; here temperature determined 71% of variance. Nitrate accumulation was determined most significantly by the organic matter content - 78%.

Table 2 Results of the "stepwise selection multiple regression" to determine the relative significance of environmental factors on the concentrations ($\mu g\ N\ g^{-1}$ soil) of total inorganic nitrogen, ammonium and nitrate accumulation.

Independent variable	Dependent variables in model	Coeffecient of determination (r^2)	d.f.	P
Total inorganic nitrogen	Organic	0.77	54	<0.001
	Moisture	0.66	54	<0.001
	Organic + moisture	0.82	53	<0.001
	* Organic + moisture + temperature	0.85	52	<0.001
Ammonium	Temperature	0.71	54	<0.001
	* Temperature + moisture	0.78	53	<0.001
Nitrate	Organic	0.78	54	<0.001
	Organic + moisture	0.80	53	<0.001
	* Organic + moisture + temperature	0.82	52	<0.001

Footnote: * indicates final model chosen by the system

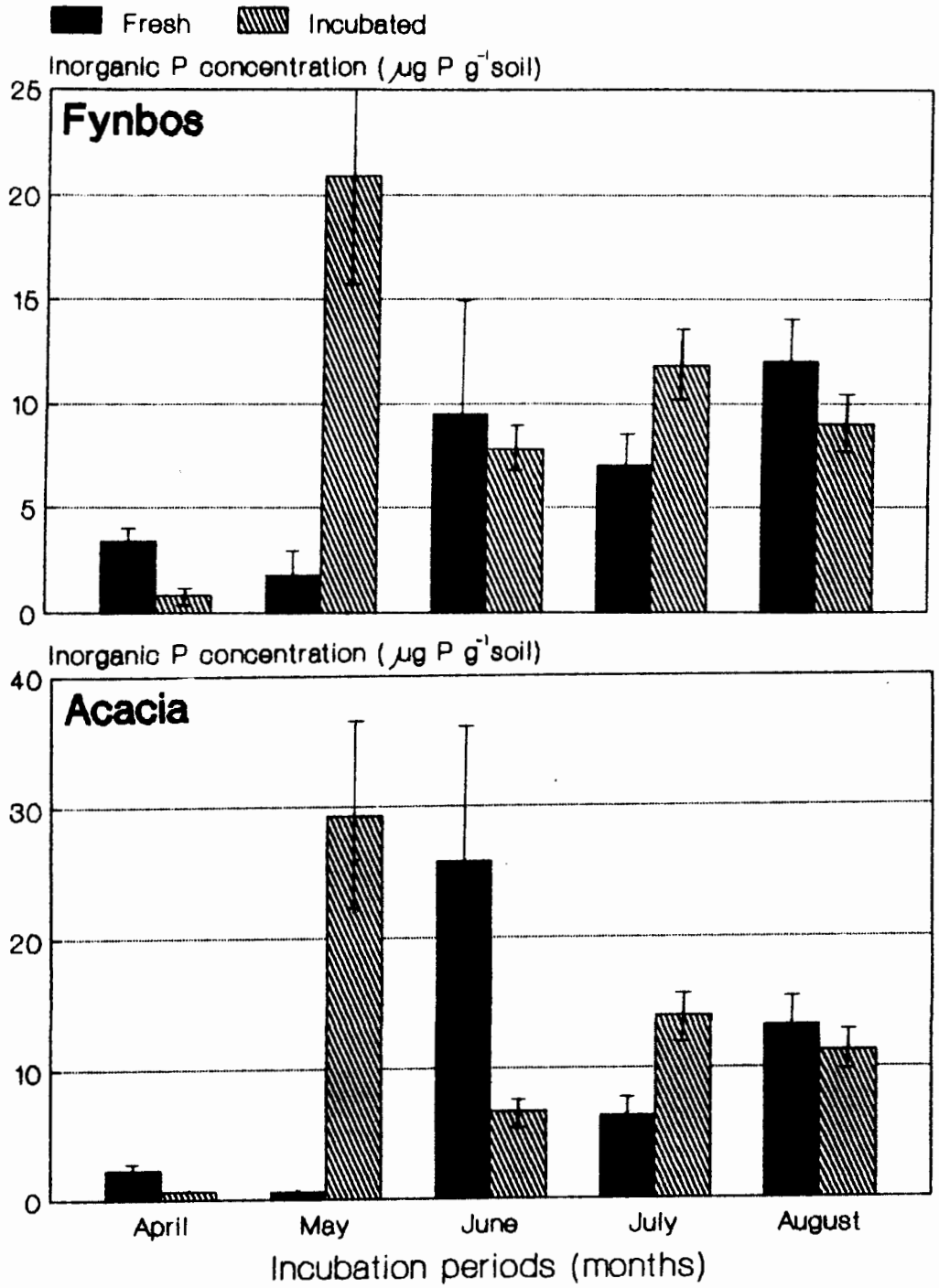

Figure 9 Mean inorganic phosphorus concentrations of the fresh and incubated samples for each incubated period (vertical bars represent 1 S.E.M.).

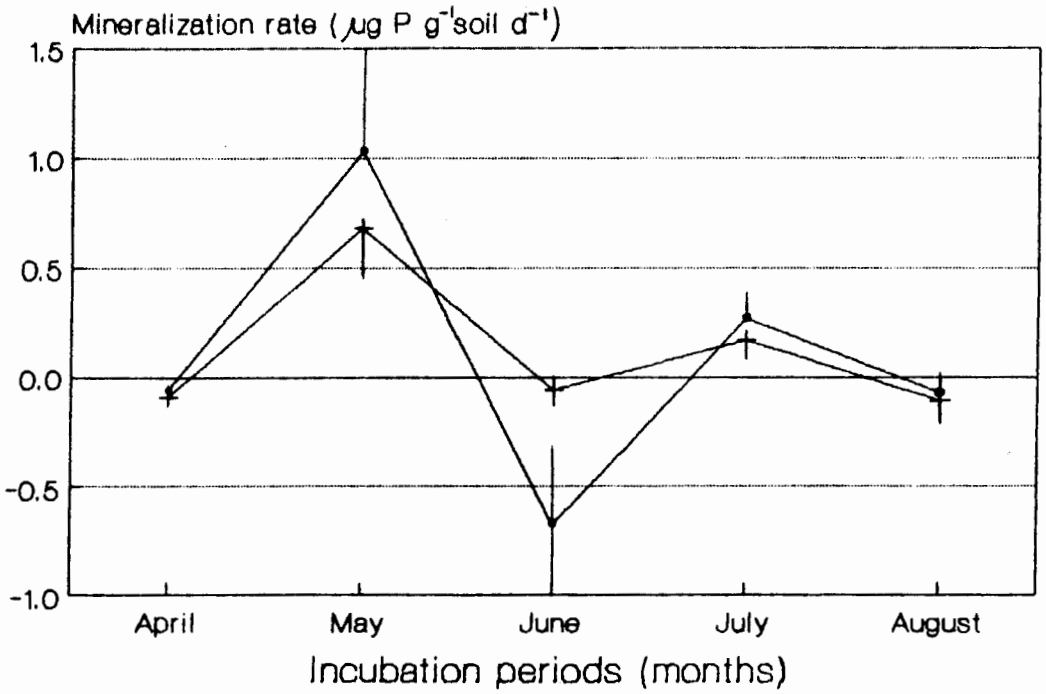

Figure 10 The mean phosphorus mineralization rates of acacia and fynbos soils during each incubation period (vertical bars represent 1 S.E.M.).

5.4 Soil Phosphorus

Errors in laboratory procedure during determinations of inorganic P accounted for the low P concentrations in April incubated and May fresh samples as well as the extremely high concentrations in May incubated and June fresh (Figure 9). Overall, inorganic P concentrations were greater in acacia soils. Considering the fresh samples from April, July and August, there was an increase in inorganic P concentration in both fynbos and acacia soils. Disregarding the May peak, the net accumulation of mineralized P was greatest in July (Figure 9).

5.5 Phosphorus mineralization

Figure 10 presents P mineralization rates. Due to the inaccuracies of April to June determinations, only July and August are valid. In fynbos and acacia July showed a small positive mineralization rate (ie inorganic P was accumulated). However, during August there was a loss of inorganic P indicated by the negative mineralization rate.

6. Discussion

6.1 Soil temperature, moisture and organic matter content

The observed variations in soil temperature and moisture (Figures 3 and 4) would be expected in a region with a mediterranean climate where the cooler winter months (June to August) receives the highest rainfall (Brown & Mitchell 1986). The fact that the edaphic environment is generally more constant than the atmospheric situation ("the soil serves as a buffer to the drastic changes that occur above ground" (Alexander 1977)) is shown by the <5 °C drop in soil temperature over the study period (Figure 3) compared to the >10°C seasonal variation in air temperature recorded at Pella by Brown & Mitchell (1986). The slightly higher soil temperature under the acacia thicket could be explained by its dense canopy cover and litter layer. Since the soil surface is covered, evapotranspiration would be limited and so temperature loss from the soil reduced. The more exposed soil surfaces of fynbos sites would be more susceptible to evapotranspiration. Also the poor water retaining ability of the sandy, freely draining soils (Stock 1985) would result in more rapid reductions in soil temperatures as rainfall increased.

The annual mass of acacia litterfall per unit area being 3-4 times greater than in fynbos communities (Milton 1981) would account for the greater organic content of acacia soils (Figure 3). Due to the long-lived evergreen leaves of fynbos vegetation at Pella, annual litter production is low (Mitchell et al 1986), resulting in the low organic content of the soils (Figure 3).

This difference in organic content would influence the water retaining ability (moisture content) of the respective soils. While the relatively high organic content of acacia soils would absorb water, fynbos soils are well-drained. The porosity of fynbos soils would be facilitated rather than reduced by the litter accumulation considering that the major component of the sparse litter is ericoid elements (Mitchell et al 1986).

6.2 Soil Nitrogen

Compared to the moisture contents of the soils represented in Figure 4, the mean moisture contents of 15 and 11% determined for April's fynbos and acacia incubated cores respectively were substantially higher even than the fresh samples taken during the wettest months (June to August). These unnaturally high moisture contents would evpectedly alter the mineralization and nitrification processes.

Considering the extremely high ammonium concentrations evolved over the April incubation period (Figure 6) it seems that the increasing moisture content favoured decomposition and mineralization (Schaefer 1973). Thus the greater organic content of acacia soils would account for the greater ammonium accumulation relative to fynbos soils. Also, an accumulation of ammonium would indicate an inhibition of nitrification. However, as the moisture content increased further and assuming that anaerobic conditions can be predicted simply from high soil water content, denitrification may have occurred.

Soil denitrification occurs under anaerobic conditions and refers to the processed involved in the reduction of nitrate, with the formation of N_2O and N_2 gases (Marion 1987; Figure 1). The process is carried out by taxonomically and biochemically diverse groups of aerobic bacteria which in response to a lack of oxygen are able to synthesize a series of reductases which enable them to carry out respiration using nitrate and nitrite instead of O (Knowles 1981). This would explain the loss of nitrate from the fynbos incubated cores. However, ammonium accumulation seemed to be the dominant process in this situation. Figure 11 shows an alternative process involved in denitrification whereby nitrite is converted to ammonium. Even though this path of nitrate reduction requires more energy (Marion 1987), denitrifying bacteria require ammonium for growth (Alexander 1977). The apparent different rates of denitrification between fynbos and acacia would be related to the different organic matter contents - the greater ammonium accumulation in acacia incubated cores may be explained by the higher organic content which provides energy for nitrate reduction to ammonium as well as the carbon substrates needed for amino acid synthesis in the bacteria cells (Alexander 1977; Marion 1987).

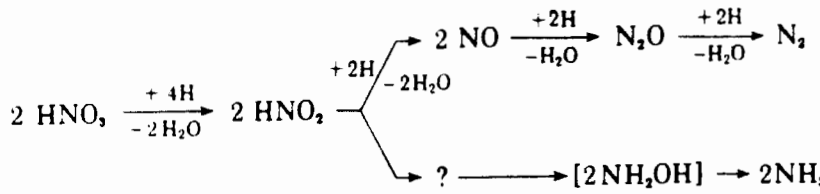

Figure 11 Biochemical pathway of nitrate reduction and denitrification (Alexander 1977).

To return to soil N processes under "normal" conditions (Figure 7) the greater inorganic N concentrations in acacia soils can be ascribed to the greater amount of soil total N (Table 1) which agrees with the results of Stock et al (1988) where increased mineralization and nitrification appeared to be associated with the quantity of soil total N. Another characteristic of the inorganic N in this study was the greater proportion of ammonium relative to nitrate (Figure 7), which Stock (1985) ascribes to the dominance of environmental factors favouring the ammonification rather than nitrification process. A factor regarded to be of major significance in determining the presence of nitrifying bacteria and therefore nitrification is pH. Little nitrification usually occurs in acid soils (particularly pH<5) (Alexander 1977). Therefore the low pH of both fynbos and acacia soils would account for their low levels of nitrate.

Another factor which would be responsible for the low concentrations of nitrate in fresh samples is the leaching of this water soluble ion. Cationic ammonium is less prone to leaching than anionic nitrate (Mitchell et al 1987). This would also attribute to the slightly higher nitrate concentrations determined in acacia soils where greater water retention reduces leaching of soluble nutrients.

6.3 Nitrogen Mineralization

Even when the monthly inorganic N concentrations of the fresh fynbos samples decreased steadily, the concentrations in all the incubated cores increased from May to August (Figure 7). Also,

the mineralization rates of both fynbos and acacia reached a peak over this period (Figure 8). Thus it seems that some environmental conditions during this period must have favoured the mineralization processes.

Relating the accumulation of mineralized N to the environmental factors (Table 2; fynbos and acacia mineralized N levels were tested together since no significant difference was found between them), it seems that the soil organic content was most significant in determining N mineralization. However, as previously stated, Stock (1988) associates mineralization primarily with the quantity of soil total N (this factor could not be included in the stepwise regression analysis since it was not determined for every sample; however, the study of the organic matter content closely approximates total N). Alexander (1977) relates these factors in stating that the mineralization rate is clearly dependent on the N content of the organic matter and its accessibility to the micro-organisms involved. Even after decomposition and the release of amino acids from the litter, 20-50% remains in a bound state (as organic matter eg protein). The release of this organic N (ie mineralization) is very slow as shown by Mitchell et al (1986) for fynbos and Specht (1981) for Australian Banksia heathland. Release is further reduced in systems with high levels of phenolic compounds (as in fynbos) (Read & Mitchell 1983). This would explain the low mineralization rates determined for fynbos and acacia systems as well as the dominating correlation between mineralization and organic matter (which presumably includes a soil N fraction).

Even though ammonification involves the conversion of organic N to ammonium, it does not seem to be dependent on the soil organic matter content (Table 2). Perhaps factors not included in the stepwise regression such as pH and soil phenolic levels result in substantial differences between total soil organic matter content and the organic N components available for ammonification. The micro-organisms responsible for ammonification are considered to be less sensitive to environmental conditions than those carrying out nitrification (Stock 1985). Thus even though the optimal conditions for ammonification are high soil water content (50-75% of their total water holding capacity) and high soil temperatures (40-60 °C) (Alexander 1977), ammonification still occurs at the below optimal conditions found at the study sites. Instead of high rainfall and temperatures co-occurring (as in summer rainfall areas), the winter rainfall of the south western Cape results in moisture levels being most suitable when temperatures are low. During the study period (rainy season) water was not a limiting factor and was therefore shown to be only of secondary significance in determinating ammonification. Instead the influence of temperature was revealed to be the dominating factor (Table 2). The low soil temperatures (Figure 3) would reduce the maximum ammonification potential relative to moisture availability.

Nitrification processes in contrast are highly sensitive to lower water potentials, temperatures and low pH values (Stock 1985). As mentioned previously, the low pH values of soils supporting

fynbos vegetation are considered to be of major significance in reducing nitrification processes. Another factor that was shown to be of importance in affecting nitrification is soil moisture content; it had a greater influence than temperature on nitrate accumulation (Table 2). Presumably the relatively high soil moisture contents during the study period (the rainy season) suppressed nitrification to negligible rates, since nitrate accumulation in the field depends on a progressive drying period after rain. This provides favourable conditions of aeration and temperature for rapid bacterial nitrification. Thus nitrate accumulates and the lack of heavy rains reduces losses by leaching (Schaefer 1974). This would also explain why Stock et al (1988) found nitrate to be the dominant N form in soils which were collected during the dry summer months while in this study ammonium occurred in much higher concentrations than nitrate (Figure 7). The factors determining nitrate accumulation as well as the respective correlation coefficients are very similar to those of total N (Table 2). Thus while nitrification is greatly reduced by unfavourable environmental conditions, the limited amount that does occur is primarily controlled by the organic content and presumably its total N, made available to nitrifiers by ammonification.

In spite of the strong influence of soil organic content on the accumulation of inorganic N (Table 2), the significant difference in organic content between fynbos and acacia soils (Table 1) as well as the higher N content of acacia litter did not result in significant differences in mineralization rates (Figure 8).

However, assuming that the higher concentrations of ammonium relative to nitrate indicates that ammonification is the dominant process, then temperature would be the controlling factor in N cycling. No significant difference in soil temperature between fynbos and acacia was found (Table 1; Figure 3). This could account for the lack of a significant difference between fynbos and acacia mineralization rates (Figure 8). If mineralization rates in fynbos and acacia are similar then some other process in the N cycle must account for the difference in total N levels determined for these systems. A possible explanation is given after a brief discussion of soil P and its mineralization.

6.4 Soil Phosphorus and Mineralization

Even though the total P concentrations in acacia soils is significantly higher than that of the fynbos, there is very little difference in the respective inorganic P concentrations (considering July and August; Figure 9). This indicates that in spite of a large reservior of organic bound P, conditions favouring microbial activity are needed for the conversion of organic P to inorganic forms (Alexander 1977). There was no difference between mineralization rates and thus it seems that acacia infestation does not change the soil environment sufficiently to alter the mineralization process. As with N mineralization processes, P cycling is reportedly also controlled by soil pH, temperature, moisture and the P organic component (Tate 1984; Stewart & Tiessen 1987). The affect of these factors on the microbial population responsible for P mineralization in

turn may control the balance between mineralization and immobilization (Tate 1984).

While mineralization seems to have been the dominant process during the July incubation period, immobilization would account for the negative mineralization during August (Figure 10). The only factor that showed any substantial change over this period was soil moisture levels (Figure 4). Tate (1984) reports on studies where mineralization increased with cool temperatures. If the high moisture content and low temperatures favoured microbial growth during July, then the increased population would account for the increase in the mineralization rate of P (Figure 10). Also the concentration of inorganic P in both fynbos and acacia fresh soils increased over this period (Figure 9). However, during August there was an immobilization of inorganic P. This could be due to the increased microfloral population needing more P than is being released by decomposition of the organic matter which is common in P-poor environments. The net effect is immobilization of the inorganic fraction (Alexander 1977). However, as the microbial population decreases, a return of P to the soil solution occurs (Stewart & Tiessen 1987). Thus with soil micro-organisms comprising an important source and sink for P as well as being the agents of transformation (Tate 1984), fluctuations between mineralization and immobilization take place, particularly in nutrient poor environments (Alexander 1977).

Another factor responsible for inorganic P immobilization is the adsorption of P to metal ions. Mitchell et al (1984) found that 67% of the inorganic P in Clovelly soils at Pella are iron-bound while 5% is Ca-bound. Thus it seems that a combination of soil microbial activity and chemical properties may have accounted for the observed fluctuations in inorganic P concentration and mineralization rates.

6.5 Soil Enrichment

So far this study has supported the proposal that acacia infestation results in increases in the soil N and P pool sizes. The process of enrichment seems to be associated with the different strategies adopted by fynbos shrubs and exotic acacias to cope with nutrient limitation.

While there are fynbos species that reveal adaptations to overcome nutrient limitations by improved nutrient uptake eg. ericaceous mycorrhizal fungi, finely divided proteoid roots (Lamont 1983), the effectiveness of these adaptations will eventually be limited by the low absolute nutrient concentrations in nutrient stressed environments. Thus the more widespread characteristics of sclerophyllous shrubs in low nutrient fynbos habitats is low plant nutrient (N and P) content, low growth rates and low response to nutrient addition (Mitchell et al 1987). Thus it appears that these plants are physiologically adapted to tolerate nutrient stress. Not only are the carbon : nutrient ratios of attached sclerophyllous leaves high (high fibre and phenolic content relative to low nutrient levels) (Read

& Mitchell 1983) but due to recycling of nutrients prior to abscission, this ratio is further increased in leaf litter (Mitchell et al 1986). Mitchell et al (1986) found the C:N ratios of leaf litter of proteoid, ericoid and restioid elements of similar L.parile/T.punctatus vegetation at Pella to be 90, 90 and 116:1 respectively. Since microbial mineralization does not normally occur until the C:N ratio drops below 30:1 (Schlesinger & Hasey 1981) the high C:N ratio increases the time needed for decomposition, thus reducing the decomposition rate (T95%=16-19yr, Mitchell et al (1986)).

Acacias may be considered as nutrient stress avoiders, since mechanims such as nodules and mycorrhizae enhance nutrient uptake so that these plants have a N and P content 2-4 times greater than the fynbos (Milton 1981). However, as mentioned before, the effectiveness of enhanced nutrient uptake from severely nutrient stressed soils is limited. However, symbiotic bacteria such as Rhizobium located in root nodules of Acacia species exploit alternative forms of N. They symbiotically fix atmospheric and free soil N (Lamont 1983). This N supply may be adjusted by P supply, since nodulation and N fixation are stimulated by increased phosphate (Cole & Heil 1981). Thus mycorrhizae, which enhance the uptake and accumulation of phosphates (Lamont 1983) form an important association with nodulated legumes such as Australian Acacia species and thereby link N and P processes.

The effectiveness of the enhanced uptake of P by acacias may be relative to the southwestern Cape soils where the available soil phosphate is greater than the corresponding Australian soils

(Mitchell et al 1986). Since P has been suggested as the major element limiting growth of acacias in southwestern Australia (Beadle 1966), the higher P levels of the southwestern Cape soils may account for the success of acacias in this region.

The result of these strategies for enhanced N and P uptake by acacias is the higher concentrations of these elements in acacia foliage (Mitchell et al 1987). Presumably the carbon : nutrient ratios of acacia litter are higher than in fynbos, resulting in the rapid decomposition rates (T95%=7-8yr).

Therefore it seems that the different strategies adopted by fynbos and acacia to cope with nutrient limitation results in the formation of litter at different rates and with different nutrient levels. The more rapid rates of litter production and decomposition in acacias would presumably increase the rate of return of nutrients to the soil and thus account for the enrichment of the soil. Factors affecting nutrient accumulation in the soils would also influence soil enrichment. The highly soluble anionic nitrate ion is prone to leaching (Mitchell et al 1987). Also organic P in solution is more mobile than inorganic P (Witkowski & Mitchell 1987). Thus it would be expected that the accumulation of nitrate and organic P is greater in acacia soils where the greater organic matter content as well as the extensive root and litter mass at the soil surface reduce leaching. The accumulation of these soluble compounds would be limited in the freely draining fynbos soils, particularly during the heavy rains of winter.

6.6 Mineralization Rates

The greater release of nutrients from decomposition and their accumulation in acacia infested soils (greater total N and P) relative to fynbos soils led to the hypothesis that these soils would show greater rates of mineralization. However, the results from this study (Figures 8 & 10) indicate that there was no significant difference in either N or P mineralization rates between acacia and fynbos soils. Thus the apparent different soil microclimates created by acacia and fynbos vegetation did not seem to have altered the soil microbial processes associated with mineralization even though infestation by A.saligna has been recorded at the study site since 1960 (Brownlie 1982).

Thus the greater decomposition rates calculated for acacia litter by Milton (1980) relative to that for lowland fynbos as presented by Mitchell et al (1986) cannot be accounted for by greater rates in the mineralization phase of decomposition. Perhaps the initial phase of decomposition, namely the release of organic nutrients from litter, occurs at greater rates in acacia soils. This seems likely when considering that decomposition only proceeds once the litter is covered by the following years leaf fall, thus reducing exposure to the atmosphere (Specht 1981). The high rates of annual leaf fall in acacias would rapidly cover the previous years litter, while the fynbos litter would be left exposed for a long time. Also the greater moisture content of acacia would favour this early phase of decomposition (Schaefer 1974).

Considering Raison's (1980) proposed evaluation of the capacity of an ecosystem to endure disturbance, it may be concluded that since the acacia infestation resulted in substantial increases in the size of the nutrient pools, the fynbos system at the study site is not resistant to disturbance by acacia invasion. However, in spite of the long history of invasion (Brownlie 1982), the soils of this area are still resilient, since the rates of nutrient turnover appeared to be relatively unaltered. Thus attempted elimination or reduction of the A.saligna infestation would be worthwhile, particularly since the fynbos seems likely to re-establishment.

This study was restricted to a five month period. However, more extensive research currently being undertaken is investigating N and P cycling over 18 months, and will thus detect any seasonal fluctuations in mineralization rates.

Acknowledgements

I would like to thank W.D. Stock for his advice, assistance and comments on earlier drafts. I am grateful to Andrew Baker for assistance in the field and the laboratory. The recording of daily temperatures by Johan Pickard is appreciated. This work was done while I held a CSIR Honours bursary.

References

ALEXANDER, M. 1977. Introduction to Soil Microbiology (2nd ed.). John Wiley & Sons, New York.

BEADLE, N.C.W. 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation with reference to xeromorphy and sclerophylly. Ecology 47: 992-1007.

BROWN, G. & MITCHELL, D.T. 1986. Influence of fire in the soil phosphorus status in sand plain lowland fynbos, south-western Cape. S. Afr. J. Bot. 52: 67-72.

BROWN, G., MITCHELL, D.T. & STOCK, W.D. 1984. Atmospheric deposition of phosphorus in a Coastal Fynbos ecosystem of the south-western Cape, South Africa. J. Ecol. 72: 547-551.

BROWNLIE, S.F. 1982. The effects of recent landuse on a fynbos site. M.Sc. Thesis, University of Cape Town.

COLE, C.V. & HEIL, R.D. 1981. Phosphorus effects on terrestrial nitrogen cycling. In: Terrestrial Nitrogen Cycles, eds Clark, F.E. & Rosswall, T. Ecol. Bull., Stockholm. pp. 363-374.

GROVES, R.H. 1983. Nutrient cycling in Australian heath and South African fynbos. In: Mediterranean-type Ecosystems. The role of Nutrients, eds Kruger, F.J., Mitchell, D.T. & Jarvis, J.U.M. Vol.43 Ecological Studies. Springer, Berlin. pp 179-191.

HESSE, D.R. 1971. A textbook of Soil Chemical Analysis. Murray, London.

HOFFMAN, M.T. & MITCHELL, D.T. 1986. The root morphology of some legume spp. in the south-western Cape and the relationship of vesicular-arbuscular mycorrhizas with dry mass and phosphorus content of Acacia saligna seedlings. S. Afr. J. Bot. 52: 316-320.

JARMAN, M.L. 1988. A description of the fynbos biome project intensive study site at Pella. Report of terrestrial ecosystems. Occasional Report 33.

KNOWLES, R. 1981. Denitrification. In: Terrestrial Nitrogen Cycles, eds Clark, F.E. & Rosswall, T. Ecol. Bull., Stockholm. pp 363-374.

LAMONT, B.B. 1983. Strategies for maximizing nutrient uptake in two mediterranean ecosystems of low nutrient status. In: Mediterranean-type Ecosystems. The Role of Nutrients, eds Kruger, F.J., Mitchell, D.T. & Jarvis, J.U.M. Vol. 43 Ecological Studies. Springer, Berlin. pp. 179-191.

MACDONALD, I.A.W. 1984. Is the fynbos biome especially susceptible to invasion by alien plants - a re-analysis of available data. S. Afr. J. Sci. 80(8): 369-376.

MACDONALD, I.A.W., JARMAN, M.L. & BEESTON, P. 1985. Management of invasive alien plants in the Fynbos Biome. S. Afr. Nat. Sci. Prog. Report 111. CSIR, Pretoria.

MACDONALD, I.A.W. & RICHARDSON, D.M. 1986. Alien species in terrestrial ecosystems of the fynbos biome. In: The Ecology and Management of Biological Invasives of South Africa eds Macdonald, I.A.M., Kruger, F.J. & Ferrar, A.A. Oxford University press, Cape Town.

MARION, G.M. 1987. Use of nitrogen-15 to assess terrestrial nitrogen cycling processes. In: Plant Response to Stress, eds Tenhunen, J.D., Catarino, F.M., Lange, O.L. & Oechel, W.C. Springer-Verlag, Berlin.

MILTON, S.J. 1980. Studies on Australian Acacias in the south-western Cape, South Africa. M.Sc. Thesis. University of Cape Town.

MILTON, S.J. 1981. Litterfall of the Exotic Acacias in the south western Cape. J. S. Afr. Bot. 47(2): 147-155.

MITCHELL, D.T., BROWN, G. & JONGENS-ROBERTS, S.M. 1984. Variation in forms of phosphorus in the sandy soils of coastal fynbos, south-western Cape. J. Ecol. 72: 575-584.

MITCHELL, D.T., COLEY, P.G.F., WEBB, S. & ALLSOPP, N. 1986. Litterfall and decomposition processes in the coastal Fynbos vegetation, south-western Cape, South Africa. J. Ecol. 74: 977-993.

MITCHELL, D.T., STOCK, W.D. & JONGENS-ROBERTS, S.M. 1987. Nitrogen and Phosphorus cycling in the Fynbos biome. Report of terrestrial ecosystems. Occasional Report 18.

MOLL, E.J., CAMPBELL, B.M., COWLING, R.M., BOSSI, L., JARMAN, M.L. & BOUCHER,C. 1984. A description of major vegetation categories in and adjacent to the fynbos biome. Nat. Prog. Environ. Sci. Report 83, S. Afr. CSIR, Pretoria.

MURPHY, J. & RILEY, J.P. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta. 27: 31-36.

RAISON, R.J. 1980. A review of the role of fire in nutrient cycling in Australian native forests, and of methodology for studying the fire-nutrient interaction. Austr. J. Ecol. 5: 15-21.

READ, D.J. & MITCHELL, D.T. 1983. Decomposition and mineralization processes in mediterranean-type ecosystems and in heathlands of similar structure. In: Mediterranean-type Ecosystems. The Role of Nutrients, eds Kruger, F.J., Mitchell, D.T. & Jarvis, J.U.M. Vol. 43 Ecological Studies. Springer, Berlin. pp. 208-232.

RUNDEL, P.W., BATE, G.C., LOW, A.B. MILLER, P.C. PATSY MILLER & MITCHELL, D.T. 1983. Nutrient cycling processes. In: Mineral nutrients in mediterranean ecosystems, ed Day, J.A. S. Afr. Nat. Sci. Prog. Report 71.

SCHAEFER, R. 1973. Microbial Activity under Seasonal Conditions of Drought in Mediterranean Climates. In: Mediterranean-type Ecosystems: Origin and Structure, eds DiCastri, F. & Mooney, H.A. Springer, Berlin. pp. 191-198.

SIBBESEN, E. 1977. A simple ion-exchange resin procedure for extracting plant-available elements from the soil. Plant and Soil 46: 665-669.

SMITH, V.R. 1980. A phenol-hypochlorite determination of ammonium-nitrogen in kjeldahl digests of plant tissue. Comm. Soil Sci. Plant Anal. 11: 709-722.

SPECHT, R.L. 1981. Nutrient release from decomposing leaf litter of Banksia ornata, Dark Island heathland, South Australia. Austr. J. Ecol. 6: 59-63.

STEWART, J.W.B. & TIESSEN, H. 1987. Dynamics of soil organic phosphorus. Biogeochemistry 4: 41-60.

STOCK, W.D. 1983. An evaluation of some manual colorimetric methods for the determination of inorganic nitrogen in soil extracts. Comm. Soil Sci. Plant Anal. 14(10): 925-936.

STOCK, W.D. 1985. An investigation of nitrogen cycling processes in a Coastal Fynbos Ecosystem in the south western Cape Province, South Africa. Ph.D. Thesis, University of Cape Town.

STOCK, W.D. 1988. The Role of Indigenous Acacias in nutrient cycling in south western Australia. In press.

STOCK, W.D. & LEWIS, O.A.M. 1986. Soil nitrogen and the role of fire as a mineralizing agent in a South African Coastal Fynbos Ecosystem. J. Ecol. 74: 317-328.

STOCK, W.D., LEWIS, O.A.M. & ALLSOPP, N. 1988. Soil Nitrogen Mineralization in a Coastal Fynbos Succession. In: Plant and Soil 106: 295-298.

TATE, K.R. 1984. The biological transformation of P in soil. Plant and Soil 76: 245-256.

VAN VEEN, J.A., MCGILL, W.B., HUNT, H.W., FRISSEL, M.J. & COLE, C.V. 1981. Simulation models of the Terrestrial Nitrogen cycle. In: Terrestrial Nitrogen Cycles, eds Clark, F.E. & Rosswall, T. Ecol. Bull., Stockholm. pp. 363-374.

VERSFELD, D.B. & VAN WILGEN, B.W. 1986. Impacts of woody aliens on ecosystem properties. In: The Ecology and Management of Biological Invasives of South Africa, eds Macdonald, I.A.W., Kruger, F.J. & Ferrar, A.A. Oxford University press, Cape Town.

WITKOWSKI, E.T.F. & MITCHELL, D.T. 1987. Variations in soil phosphorus in the fynbos biome, South Africa. J. Ecol. 75: 1159-1171.