RESPONSE OF A SAND-PLAIN LOWLAND FYNBOS ECOSYSTEM TO NUTRIENT ADDITIONS

BY

EDWARD TADEUSZ FERNANDO WITKOWSKI

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University of Cape Town

Department of Botany

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ABSTRACT

The effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) on various components of the soils and vegetation of a sand-plain lowland fynbos ecosystem at Pella, south-western Cape Province, South Africa were studied, namely:

1) Soil nutrient dynamics.
2) Phenology, shoot growth, reproductive output and nutrient acquisition in a proteoid (Leucospermum parile) and an ericoid (Phylica cephalantha) evergreen shrub.
3) Dry mass, phosphorus and nitrogen allocations to the various above and below ground organs of pre-reproductive and reproductive male plants of Thamnochortus punctatus (Restionaceae).
4) Litter production and nutrient return.
5) Above-ground phytomass, nitrogen and phosphorus contents of the representative plant growth forms in response to non-factorial addition of N, P and M.
6) Foliage projective cover of the representative growth forms of sand-plain lowland fynbos.

Five g N m^{-2} as NH_4NO_3 and 0.5 g P m^{-2} as $Ca_3(PO_4)_2$ were the amounts and forms of nitrogen and phosphorus added, being the approximate return after a wildfire at the study site in November 1980. All other nutrients were based on a Long

Ashton nutrient solution in proportion to the N and P applications. In addition, a pot experiment determining the effects of a range of concentrations of N, P and M on the distribution of dry mass, phosphorus and nitrogen in Protea repens (L.) L. (Proteaceae) seedlings was also studied.

Soil concentrations of ammonium and nitrate in the N amended plots declined by 80 % within one month after fertilizer addition, whereas phosphorus concentrations remained elevated throughout the two year monitoring period. Soil K concentrations were elevated for approximately six months, while those of Ca and Mg rapidly returned to control levels. No significant differences in soil pH were found between treatments. Leaching of nitrate and K down the soil profile to a depth of 1 m was found, whereas ammonium, and to a lesser extent phosphorus, appeared to be immobilized by the soil micro-organisms. Nutrient additions had no discernible effects on the timing of the various phenophases of the mid-late successional dominant, L. parile, or the early successional dominant, P. cephalantha. Small increases in shoot growth in response to nitrogen application were found during the first growing season, while P addition tended to result in a decline in both species during both growing seasons. Inflorescence production increased in P. cephalantha and decreased in L. parile in response to nitrogen addition during the first season. Shoot nitrogen contents increased by 66 % and 55 %

in L. parile and P. cephalantha respectively, during the first season, whereas shoot phosphorus contents increased slightly. During the second season, stored nitrogen in N amended L. parile shrubs resulted in a 44 % increase in inflorescence production compared with the control. In P. cephalantha, either the hotter and drier conditions during the second year, or the depletion of plant nutrient reserves due to the large fruit crop produced during the first year, resulted in an approximately 50 % reduction in shoot growth and an even greater decrease in inflorescence production. Plasticity in nutrient storage was found, rather than large increases in shoot growth, although reproductive effort is also a relatively plastic character in both species.

In pre-reproductive T. punctatus, N application increased shoot dry mass and nitrogen uptake. However in reproductively mature male plants, N addition decreased the allocations of dry mass and nitrogen to culms and inflorescences (mature characters) and increased these to vegetative branches (juvenile character). The addition of P tended to increase resource allocations to the inflorescences, while that of M resulted in increased resource allocations to the below-ground organs. Tissue nutrient concentrations, reproductive effort and root to shoot partitioning of resources were all plastic characters in T. punctatus.

Litter production was positively correlated with wind-run and absolute maximum monthly temperature, and tended to increase in response to the additions of N and M. Phosphorus return increased with P addition during the first year, whereas it increased in response to N and M during the second year. Nitrogen return in response to N addition only increased during a period of moisture stress in the vegetation. Nitrogen addition resulted in increased foliage projective cover (FPC) of the graminoid, annual and restioid growth forms, whereas no significant differences in ericoid or proteoid shrubs were found between treatments.

Protea repens seedlings exhibited increased dry mass and nitrogen and phosphorus acquisition in response to increasing application level of P. Increasing application level of N, and to a lesser extent M, resulted in plant mortality and reduced growth. The ratio of available nitrogen to available phosphorus was approximately one order of magnitude higher in the pot incubated soils than in the field and total mineral nitrogen concentrations were also increased. This explains the positive growth response to P in the pot experiment compared with N at the field site.

These results are discussed in terms of the nutrient-poor soils and mediterranean climate of the fynbos biome and compared with the response of other mediterranean-type ecosystems to nutrient additions.

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PREFACE

The combination of both the nutrient-poor soils and mediterranean climate of the fynbos biome begs the question of how the indigenous plant species are adapted to these conditions. A series of intensive investigations, under the auspices of the CSIR's Fynbos Biome Project, are studying the adaptations of these plants to the nutrient-poor soils and the mediterranean climate of the south-western Cape. Studies on nitrogen and phosphorus cycling, litter production and decomposition, mycorrhizas and symbiotic nitrogen fixation have or are currently being undertaken. Presently an emphasis has been placed on the responses of fynbos ecosystems to disturbance (Cowling et al. 1987). Responses of these communities and their component species provide insights into their adaptations to environmental stress and disturbance. In this study, the responses of the various growth forms to factorial application of nutrients indicates which nutrients, if any, are limiting in terms of vegetative and reproductive growth. In addition, nutrient acquisition and allocation patterns were also studied. This work was stimulated by the often dramatic responses to fertilizer addition in the edaphically similar Australian heathlands. No prior knowledge of which nutrient elements limit plant growth in this nutrient-poor ecosystem was available, but from studies undertaken elsewhere, it was apparent that nitrogen and phosphorus were the two most likely and thus these were studied

specifically. The effects of all the other essential nutrients were determined by applying these as a mixture. The main approach to the study was a field factorial fertilizer experiment in conjunction with some pot experiments. On the basis of other studies, four main aspects were selected for investigation:

1) Nutrient dynamics of fertilized soils.

2) Growth responses, both vegetative and reproductive, nutrient acquisition and allocation in the three main growth forms (ericoid, proteoid and restioid).

3) Litter production and nutrient return to the soil.

4) Changes in species and growth form composition.

Lowland Fynbos was the vegetation category chosen for this study for two main reasons, namely:

A) The precarious conservation status of this vegetation type, particularly along the Cape west coast. It is threatened by agricultural development, infestations of alien vegetation and urbanization. Accidental inputs of fertilizers from adjacent agro-ecosystems is a strong possibility in these island-like patches of lowland fynbos.

B) Most of the previous ecophysiological investigations were carried out in lowland fynbos.

This thesis is structured into twelve chapters. The general introduction comprises a brief review of some of the literature and states the aims and objectives of the study. The four main aspects listed above are dealt with in papers which constitute the following eight chapters. Of necessity, some repetition is found between papers to ensure that each forms an entity and differences in style and emphasis are a result of the requirements of the journals for which the papers were written. A general discussion summarizes the main findings and presents a synthesis of ideas, as well as future avenues of research. A published paper on variations in soil phosphorus in the fynbos biome is presented in Appendix 1 and is included because it provides further background information to the study. This paper highlights differences in total and available, organic and inorganic forms of phosphorus in the soils of the major vegetation categories of the fynbos biome. In the paper a detailed study of the phosphorus composition along a 2 km transect from the west coast inland through indigenous strandveld, as well as strandveld and coastal fynbos vegetation invaded by introduced Australian Acacia species, is presented.

CONTENTS

Shaw 1985

CHAPTER 1

GENERAL INTRODUCTION

The sclerophyllous heathlands and shrublands of the mediterranean climate zone of the south-western Cape Province, South Africa forms part of the Cape Floral Kingdom (Takhtajan 1969; Good 1974) which corresponds geographically with the Fynbos Biome. It is the smallest of the six floral kingdoms of the world, covering only 0.04 % of the earth's surface (Hall 1978) and contains some 8550 species of vascular plants, of which 73 % are endemic (Goldblatt 1978). Of the 957 genera, 198 are endemic and seven families, namely the Bruniaceae, Penaeaceae, Grubbiaceae, Roridulaceae, Retziaceae, Stilbaceae and Geissolomataceae are endemic (Goldblatt 1978). The extent of this unique flora has been drastically reduced from an original area of 67 000 km^2 to 40 000 km^2 (Jarman 1982; Moll & Bossi 1984) as a result of increases in agriculture, forestry and urbanization. In addition, factors such as alien plant invaders, artificially increased fire frequencies and nutrient pollution are adversely impacting the flora. The high degree of endemism and relatively small distribution ranges of many plant species has resulted in 1244 species being classified as endangered, vulnerable or rare (Hall & Veldhuis 1985). Already 47 % of lowland fynbos (sensu Moll et al. 1984) has been lost, and in particular, only 15 % of the vegetation of the western coastal forelands is in a reasonably natural state (Boucher 1983) and thus has the highest conservation priority rating (Hilton-Taylor 1988). Besides its scientific, recreational and aesthetic value,

the fynbos biome is an important source of water and flowers for the cut-flower industry.

Heathlands are found in a broad range of climatic zones, stretching from the tundra and cool temperate regions of the northern hemisphere, to the warm and seasonally dry heaths in the mediterranean climate regions of South Africa and Australia. Despite these variations in climate and geography, heaths are generally characterized by their evergreen, sclerophyllous vegetation restricted mainly to acidic soils of a low nutrient status (Specht 1979).

Nutrient cycling studies in heathlands have concentrated on nitrogen and phosphorus because of their high level of interaction in plant nutrition and their importance in the control of nutrient cycling processes (Groves 1983). In south Australia, levels of soil organic matter, nitrogen and phosphorus are comparable to those found in the fynbos (Read & Mitchell 1983). The amounts of mineral nitrogen and phosphorus which enter heathland ecosystems are low and the major reserves of these elements is in the soil organic matter (Groves 1983; Read & Mitchell 1983). The sclerophyllous vegetation of heathlands can contain high levels of lignin and phenolics which render the litter resistant to microbial degradation. Microbial activity is further inhibited by the high C : N and C : P ratios of the fallen leaves. In Australia and South Africa, the

mediterranean-type climate causes seasonal moisture stress which may reduce leaching of minerals from fallen litter, retard microbial decomposition and promote seasonal peaks in mineralization activities. In general, mineralization rates of phosphorus and nitrogen in heathland ecosystems are low (Read & Mitchell 1983; Harley & Smith 1983; Stock et al. 1988).

The advent of the Fynbos Biome Project (FRD, CSIR, Pretoria) stimulated many ecophysiological investigations into fynbos vegetation, particularly nutrient cycling. It has been suggested that in both South African and Australian mediterranean ecosystems, the nutrient elements nitrogen and phosphorus are in particularly low supply (Wild 1958; Specht 1979; Read & Mitchell 1983). Nutrients were thus identified as being of crucial importance in the structure and functioning of the fynbos vegetation (Cowling & Campbell 1980; Campbell 1983; Kruger et al. 1983). In addition, divergence in vegetation structure of the Australian and South African mediterranean regions, compared with the other mediterranean regions of the world, has been attributed to the nutrient-poor soils of the former (Cody & Mooney 1978; Specht 1979; Cowling & Campbell 1980; Kruger et al. 1983). It has been shown that the Californian chaparral, which has a mediterranean climate, is moisture and nutrient limited (Hellmers et al. 1955), with low levels of soil nitrogen found to be one of the major nutrient limitations (Jenny et

al. 1950; Vlamis et al. 1958; Christensen & Muller 1975). Substantial plant growth responses to phosphorus addition have shown the importance of this element in the Australian environment, where increased adult mortality and decreased seedling vigour was found for many of the characteristic species of the region (Specht 1963; Groves 1965; Heddle & Specht 1975; Specht et al. 1977). In the chaparral, the importance of nitrogen and phosphorus is equivocal, as it has been shown that nitrogen and phosphorus addition to soils resulted in varied growth responses (Hellmers et al. 1955; Schultz et al. 1958; McMaster et al. 1982; Gray & Schlesinger 1983).

"The overall and ultimate objective of the (Fynbos Biome) project .... to provide sound scientific knowledge of the structure and functioning of constituent ecosystems as a basis for the conservation and management of the fynbos biome." (Kruger 1978), forms the background to this thesis. In this study, both academic (theoretical) and management orientated research were combined. Studies of fertilizer effects on species and growth form composition, residence times of particular nutrients in the soils, nutrient losses from fertilized vegetation and flower production of Leucospermum parile shrubs were studied and can be readily incorporated into management plans.

Perturbation studies have been classified into two types (Bender et al. 1984). Firstly, PULSE experiments, in which a perturbation is imposed which alters the density of a subset of species, and the community is then allowed to respond. Alternately, PUSH experiments which require the long term maintenance of a new distribution density for the subset of species chosen, while the responses of the other species are monitored. This study is akin to a PULSE experiment, although species densities were changed in response to nutrient additions (manipulation of the environment) and not direct manipulation.

In this study the fate and passage of applied nutrients were studied to obtain an understanding of the effects of nutrient additions at the ecosystem level. The hypothesis tested was that the vegetative growth and reproductive output, of species representing the dominant ericoid, restioid and proteoid growth forms of the fynbos, are limited by soil nutrient concentrations. It has been hypothesized that plants adapted to nutrient-poor soils have inherently slow growth rates which do not increase when nutrient availability is increased (Clarkson 1967). Often increased nutrient levels are actually toxic to the plant as well as causing changes in species composition because of competition with nutrient demanding species (Heddle & Specht 1975). In addition, these plants are able to absorb and accumulate nutrients during periods of greater mineral

availability and subsequently use them to maintain growth during periods of reduced nutrient availability. Thus it was predicted that during periods of increased nutrient availability, the ericoid, restioid and proteoid species of the fynbos should accumulate nutrients in their tissues and display only small increases in vegetative growth and reproductive output. To test these hypotheses this project was set up to study the effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) on sand-plain lowland fynbos vegetation at Pella, south-western Cape. The study included the following aspects:

1) The nutrient dynamics of fertilized soils over a two year period. The effects of nutrient additions on soil pH and organic matter content were also determined. These results aid in the interpretation of the responses of the various plant growth forms to nutrient additions during the two seasons studied (Chapter 2).

2) The growth response of two shrub species, Leucospermum parile (proteoid) and Phylica cephalántha (ericoid) to nutrient additions in terms of shoot and canopy growth, reproductive effort (P. cephalantha only) and nutrient acquisition and allocation patterns (Chapter 3).

3) The response of a shallow-rooted, dioecious restioid species, Thamnochortus punctatus, to nutrient additions during the pre-reproductive and reproductively mature (male plants) phases of its life-history. The allocation patterns of dry mass, nitrogen and phosphorus to the various above- and below-ground parts were studied (Chapter 4).

4) Litter production and nutrient return over a three year period and changes in the contribution of the major plant growth form categories (ericoid, restioid, proteoid and miscellaneous), to total litter production over a two year period. In addition, ground litter dry mass and nutrient contents two years after fertilizer addition were also investigated (Chapter 5).

5) Responses to non-factorial addition of N, P and M by the representative plant growth forms of sand-plain lowland fynbos vegetation, in terms of above-ground dry mass, nitrogen and phosphorus contents (Chapter 6).

6) Changes in the foliage projective cover of the representative plant growth forms of sand-plain lowland fynbos, in response to factorial fertilizer addition during two growing seasons (Chapter 7).

7) The effects of nutrient additions on inflorescence and seed production of the proteoid shrub, L. parile. Seed

size variation and maternal control of reproduction were also studied (Chapter 8).

8) The responses of Protea repens (Proteaceae) seedlings to applications of increasing concentrations of N, P and M. In addition, a comparison of field and pot soils in terms of the availability of nitrogen and phosphorus, was also undertaken (Chapter 9).

The form of phosphorus applied in this study was similar to that used in other fertilizer experiments in the mediterranean-type ecosystems of the Australian heathlands and the Californian chaparral (Specht 1963; McMaster et al. 1982). Calcium phosphate ($Ca_3(PO_4)_2$; chemically pure) was used instead of superphosphate because chemical impurities in the latter (Specht 1963) would have confounded the interpretation of responses to phosphorus addition, as micronutrient deficiency symptoms have been observed in fynbos plants growing in some degraded sites (Schütte 1960). Nitrogen was applied as NH_4NO_3 because Protea repens seedlings were found to be capable of taking up ammonium and nitrate from growth media (Stock & Lewis 1984). Nutrients were applied during the season when root growth reaches a peak (late-winter to early-spring; Jongens-Roberts & Mitchell 1986; Stock et al. 1987) to facilitate plant uptake and vegetational responses.

CHAPTER 2

RESPONSE OF A LOWLAND FYNBOS ECOSYSTEM, SOUTH AFRICA, TO NUTRIENT ADDITIONS. I. NUTRIENT DYNAMICS IN FERTILIZED SOILS

(To be submitted to Acta Oecologica - Oecologia Plantarum)

SUMMARY

The effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P), and a mixture of all essential nutrients excluding N and P (M) on soil nutrient concentrations in 4-6 year old sand-plain lowland fynbos vegetation at Pella, south-western Cape, South Africa was studied. Five g nitrogen m^{-2} as NH_4NO_3 and 0.5 g phosphorus m^{-2} as $Ca_3(PO_4)_2$ were the amounts and forms of N and P added, which were the approximate amounts returned to the soil after a fire at Pella in November 1980. Nitrate, ammonium and total nitrogen, resin-extractable, Bray No.2 and total phosphorus, exchangeable Ca, Mg and K concentrations, organic matter and pH were monitored in open patches between shrubs and in the rhizosphere of Phylica cephalantha over a two year period (1984-86) in these nutrient-poor, acidic and sandy soils.

Soil ammonium and nitrate concentrations in N-fertilized plots decreased by approximately 80 % within one month after application, although remaining significantly higher than in non-fertilized plots for one year. Phosphorus concentrations remained significantly higher in P-fertilized plots throughout the study period whereas exchangeable potassium concentrations were elevated for at least 6 months in M-fertilized plots. The nutrient applications resulted in slight increases of total nitrogen and phosphorus

concentrations but no significant differences in soil pH. The fate of the nutrients added was similar in open patches between shrubs and in the rhizosphere of P. cephalantha. Leaching of nitrate and potassium was demonstrated, while added phosphorus remained in the surface soil layer (0-10 cm depth). Ammonium and, to a lesser extent, phosphorus appear to be immobilized.

INTRODUCTION

The role of nutrients in the structure and function of mediterranean-type ecosystems has been reviewed (Kruger et al. 1983) and it has been postulated that growth and reproduction of fynbos vegetation may be nutrient limited. The fynbos biome is the richest and smallest of the world's six floral kingdoms, covering only 0.04 % of the earth's surface (Hall 1978) and is highly threatened by urbanization, agricultural development, artificially increased fire frequencies, invasive alien vegetation and nutrient pollution. Soil nutrient concentrations, particularly nitrogen and phosphorus are very low (Mitchell et al. 1984; Stock & Lewis 1986b; Witkowski & Mitchell 1987) and the soils are more similar to those of the Australian heaths than the other mediterranean-type ecosystems.

The dynamics of soil nutrients applied to stands of natural vegetation has not been monitored in most studies of the

effects of fertilizer addition. In studies of agro-ecosystems, monitoring the fate of applied nutrients has facilitated the interpretation of the plant responses to the nutrient applications (eg. Turner & Lambert 1986; Bergstrom & Brink 1986). Seldom has it been possible to detect single nutrient elements or specific environmental factors which impose a clear-cut limit on an ecosystem. Instead, complex interactions occur and these are often related to either short or prolonged duration effects on the component species of an ecosystem (Pomeroy 1970; Chapin & Shaver 1985; Shaver et al. 1986).

The objectives of this study were to examine the effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) on total and available (resin-extractable and Bray No. 2) phosphorus, ammonium, nitrate and total nitrogen, available Ca, Mg and K concentrations, organic matter and pH in the soil of 4-6 year-old lowland fynbos vegetation at Pella over two growing seasons. These were monitored in open patches between shrubs and in the rhizosphere of a dominant shrub species, Phylica cephalantha Sonder. Soil nutrient dynamics are a function of soil processes such as mineralization, immobilization and leaching and changes in these processes induced by nutrient additions need to be understood prior to evaluating changes in vegetation dynamics.

STUDY AREA

The CSIR fynbos biome intensive study site at Pella on the Burgherspost Farm 62 km north of Cape Town south-western Cape, South Africa (33°31' S, 18°32' E; 15 km inland from the west coast; altitude 160-220 m; 269 ha) was used as the study area. The climate is mediterranean (Köppen's Csa and Csb) which is characterized by hot dry summers and wet winters (Schulz 1947). The 49 year mean annual rainfall for the Burgherspost Farm was 522 mm. Mean annual temperature is 17.3° C and frost is virtually absent.

The soils are well drained aeolian acidic sands of approximately 2 m in depth and classified as the Geelhout series of Clovelly (orthic A horizon overlying a yellow/brown apedal B) according to the South African soil classification system (MacVicar et al. 1977). They are low in both phosphorus and nitrogen and display seasonal variations of these nutrients at the surface (Mitchell et al. 1984; Stock & Lewis 1986b) where the highest concentrations are found. The inorganic phosphorus fractions consist predominantly of Fe-bound phosphorus and approximately 70 % of the total phosphorus is organically bound (Witkowski & Mitchell 1987). Atmospheric input of phosphorus and nitrogen is low but may be significant for plant growth (Brown et al. 1984; Stock & Lewis 1986a). The rate of decomposition of plant material and nutrient

turnover was found to be very slow due to the poor quality of the litter (Mitchell et al. 1986).

The vegetation is broadly classified as sand-plain lowland fynbos (Moll et al. 1984) and consists predominantly of low evergreen sclerophyllous shrubs and hemicryptophytes of the Restionaceae. An area of approximately 1 ha in the centre of a 26 ha patch of Clovelly soil was chosen at Pella for this study. It was positioned on a gentle 5^{o} easterly slope in homogeneous four-year old post-fire vegetation which is classified as Leucospermum parile - Thamnochortus punctatus mid-high open shrubland of Phylica cephalantha fynbos (Boucher & Shepherd 1987).

METHODS

Fertilizer addition

A complete factorial fertilizer addition of nitrogen (N), phosphorus (P), and a mixture of all essential nutrients excluding N and P (M) were randomly applied to thirty-two 10x5 m sized plots arranged in a grid pattern (8x4) at Pella and separated by 5 m wide strips. All possible combinations of these make up eight additions, namely: nitrogen (N), phosphorus (P), all essential nutrients excluding N and P (M), nitrogen and phosphorus (NP), all essential nutrients excluding P (NM), all essential nutrients excluding N (PM), all essential nutrients (NPM)

and unfertilized control (C). An additional four plots, positioned at the corners of the grid were assigned as four further unfertilized controls. Nutrients were added at low concentrations to the plots during 15-17 September 1984, towards the end of the rainy season. Nitrogen was added as NH_4NO_3 (5 g N m^{-2}) and P as $Ca_3(PO_4)_2$ (0.5 g P m^{-2}), these being the approximate amounts returned to the soil and surface ash after a fire at Pella in November 1980 (Brown & Mitchell 1986; Stock & Lewis 1986b). All other nutrients added were based on a Long Ashton nutrient solution (Hewitt & Smith 1975) in proportion to the N and P inputs (Table 2.1). All nutrients were dissolved in deionized water and applied to the plots using watering cans. Control plots were also watered with the same volume (25 l) of deionized water.

Soil sampling

Soil samples were collected in open patches between shrubs from each of the 36 plots on the following dates: 26 September 1984, 8 October 1984, 24 October 1984, 20 November 1984, 17 December 1984, 12 February 1985, 20 May 1985, 20 September 1985, 5 December 1985 and 17 September 1986 and from the rhizosphere of P. cephalantha at the same dates except 8 October 1984 and 20 September 1985. Intervals between monitoring periods were shorter at the beginning of the study because nutrient changes were likely to be rapid during this period. The rhizosphere of P. cephalantha was

Table 2.1. Chemicals used as nutrient sources and application levels onto four year old post-fire sand-plain lowland fynbos vegetation at Pella, South Africa. *, the amount of $CaCl_2$ added was adjusted if $Ca_3(PO_4)_2$ was also added so that total Ca application would remain 1.95 g m^{-2}. [1], Sulphur sources.

Nutrient	Chemical Sources	Application Level ($g\ m^{-2}$)
N	NH_4NO_3	5
P	$Ca_3(PO_4)_2$*	0.5
K	K_2SO_4[1]	1.9
Mg	$MgSO_4$[1]	0.44
Ca	$CaCl_2$*	1.95
Na	NaCl	0.38
Fe	Fe Citrate $5H_2O$	0.069
Mn	$MnSO_4\ 4H_2O$[1]	0.007
B	H_3BO_3	0.006
Zn	$ZnSO_4\ 7H_2O$[1]	0.0009
Cu	$CuSO_4\ 5H_2O$[1]	0.0007
S	[1]Sulphur sources	0.59

chosen in preference to that of other shrubs because this species regenerates by resprouting after fire and thus has a well defined rhizosphere. At each collection time in each plot, four soil cores (100 mm depth and 67 mm diameter) were taken from open patches and bulked and a single soil core was removed from the rhizosphere of P. cephalantha. Soil cores were also collected from open patches and from the rhizospheres of L. parile, Metalasia adunca Less. and P. cephalantha 10 months after fertilizer addition (8 July 1985) from the N, P, M and C amended plots. In September 1985 and 1986 (one and two years after fertilizer addition respectively), six 1 m deep soil cores were taken with a brass corer of internal diameter 70 mm, from open patches in the control and NPM treated plots. Soil samples at 0-10 cm, 20-30 cm, 45-55 cm and 95-105 cm depths were taken from each core and these depth categories are referred to as 0, 25, 50 and 100 cm depth respectively. Surface soil samples were always taken between 9 and 11 am in case of diurnal changes in the form and concentration of soil nitrogen.

Soil analyses

Each sample was sieved through a 2 mm mesh and thoroughly mixed. Resin-extractable and Bray No. 2 phosphorus, nitrate, ammonium, pH and water content were determined on fresh soil. Total nitrogen and phosphorus and exchangeable Ca, Mg and K and organic matter were determined on air-dried soil. On arrival at the laboratory, nitrate and ammonium

were immediately extracted from 10 g soil with 1 M KCl. Nitrate was determined by a copper-cadmium reduction technique (Bate & Heelas 1975) and measured colorimetrically by the Griess-Ilovsay method as described by Stock (1983). Nitrite levels were found to be negligible in the soils at Pella (Stock & Lewis 1986b) and thus the results were not corrected for its presence. Ammonium was determined colorimetrically by a phenol-hypochlorite procedure modified from Allen et al. (1974) as described by Stock (1983). Total nitrogen was determined by Kjeldahl digestion of 1 g soil using a selenium catalyst. Salicylic acid and sodium thiosulphate were added to convert all nitrate and nitrite to ammonium which was determined colorimetrically (Smith 1980). Both Bray No. 2 and resin extractable phosphorus are measures of plant-available phosphorus. Total, Bray No. 2 and resin-extractable phosphorus were extracted from 2, 8 and 20 g of soil respectively using methods described by Hesse (1971), Bray and Kurtz (1945) and Sibbesen (1977), respectively. The phosphate concentration in the extracts was determined colorimetrically (Murphy & Riley 1962). Soil pH, moisture content, organic matter and texture were determined using the same methods as those of Mitchell et al. (1984) and Witkowski & Mitchell (1987). Exchangeable Ca, Mg and K were extracted from 10 g soil with 1 M ammonium acetate (pH 7) and determined by atomic absorption spectrophotometry (Anon 1980). Organic carbon, cation exchange capacity, total cations and resistance of soil

paste were determined on five soil cores collected in December 1983 and analyzed using methods described by Anon (1980).

Statistical analyses

Comparisons of soil nutrient levels between fertilized and non-fertilized plots were determined by t-tests at each sampling interval. Other comparisons were analyzed by two-way and three-way analysis of variance (SAS GLM procedure; SAS Institute 1985). The effects of factorial addition of P and M on soil mineral nitrogen (ammonium and nitrate) concentrations was analyzed by two-way analysis of variance with repeated measures (SAS GLM procedure; SAS Institute 1985). The effects of factorial addition of N and M on available phosphorus (resin-extractable and Bray No. 2) concentrations were analyzed in the same way. Nitrate and ammonium concentrations were log transformed and all percentage values were arcsin transformed prior to statistical analyses. All analyses of variance met the assumptions of normality and homogeneity of variance (Zar 1984).

RESULTS

Climate

Seasonal temperature and rainfall variations from March 1984 to September 1986 at the study site displayed typical

mediterranean climatic conditions (Fig. 2.1). Highest temperatures were recorded during November 1985 (42^{o} C). The longest period of low rainfall since records have been kept at the site (February 1981) was the 20 week period from November 1985 to March 1986 when only 15.5 mm of rainfall was recorded (Jarman & Mustart 1987). Annual rainfall during the 1984-85 season (June 1984-85) was 577 mm compared with 451 mm that fell during the 1985-86 season. Only 91 mm fell during the dry season (October to April) of 1985-86 compared with 293 mm during that of 1984-85.

Soil nutrient levels at the surface

The soil consists predominantly of medium textured sand, was low in organic carbon and total cations and has a low cation exchange capacity (Table 2.2). In the plots amended with nitrogen, there was a marked decrease of soil nitrate and ammonium concentrations with time at the surface, both in the open and the rhizosphere of P. cephalantha (Fig. 2.2). Approximately 80 % of the soil nitrate and ammonium concentrations were lost from the 0-10 cm depth (leached, taken up by plant roots or immobilized by soil micro-organisms) within one month after fertilizer application (Fig. 2.2). Between fertilizer application and the first soil sampling (September 17-26) only 3.3 mm of rain fell, but from September 26 to October 10, when the second soil analysis was performed, 81 mm of rain had fallen, 70 mm on the 6th October alone, indicating that leaching may have

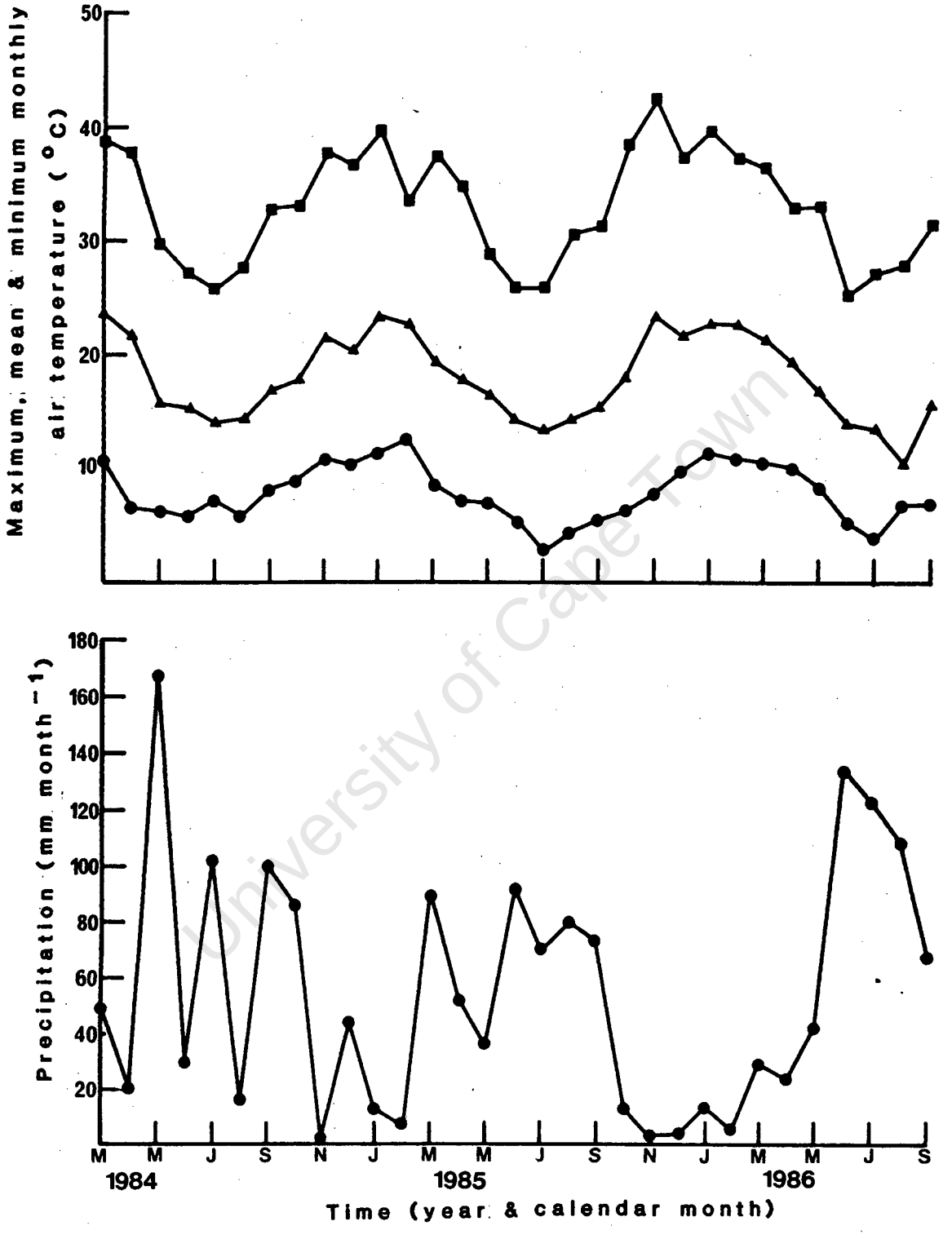

Fig. 2.1. Seasonal variations in air temperatures and rainfall at Pella, South Africa.

Table 2.2. Physical and chemical characteristics (Mean ± S.E.) of Clovelly soil at Pella, South Africa. All values are for 0-10 cm soil depth unless otherwise indicated. Numbers in parentheses are arcsin transformations ± S.E. Significance by means of one-way analysis of variance: * $P<0.05$, ** $P<0.01$.

Bulk Density (kg l^{-1})	1.4±0.03
Organic Carbon (%)	0.7(4.8±0.16)
Cation Exchange Capacity (milliequivalents %)	0.62(4.49±0.25)
Total Cations (%)	0.70(4.80±0.13)
Resistance of Soil Paste (Ohms)	8260±382

Soil Texture:

Soil Depth (cm)	0-10	20-30	45-55	95-105	F
Coarse Sand (%) (0.5-2.0 mm)	1.5 (6.9±0.6)	1.7 (7.6±0.1)	1.8 (7.6±0.4)	1.4 (6.9±0.2)	0.88
Medium Sand (%) (0.2-0.5 mm)	54.6 (47.7±3.4)	70.2 (57.0±1.6)	79.8 (63.4±1.4)	82.0 (65.0±1.9)	8.55**
Fine Sand (%) (0.02-0.2 mm)	41.8 (40.2±3.3)	26.3 (30.7±1.7)	17.3 (24.5±1.4)	14.8 (22.4±2.1)	8.79**
Silt + Clay (%) (<0.02 mm)	2.0 (8.2±0.2)	1.8 (7.7±0.3)	1.1 (6.1±0.3)	1.7 (7.6±0.2)	7.06*

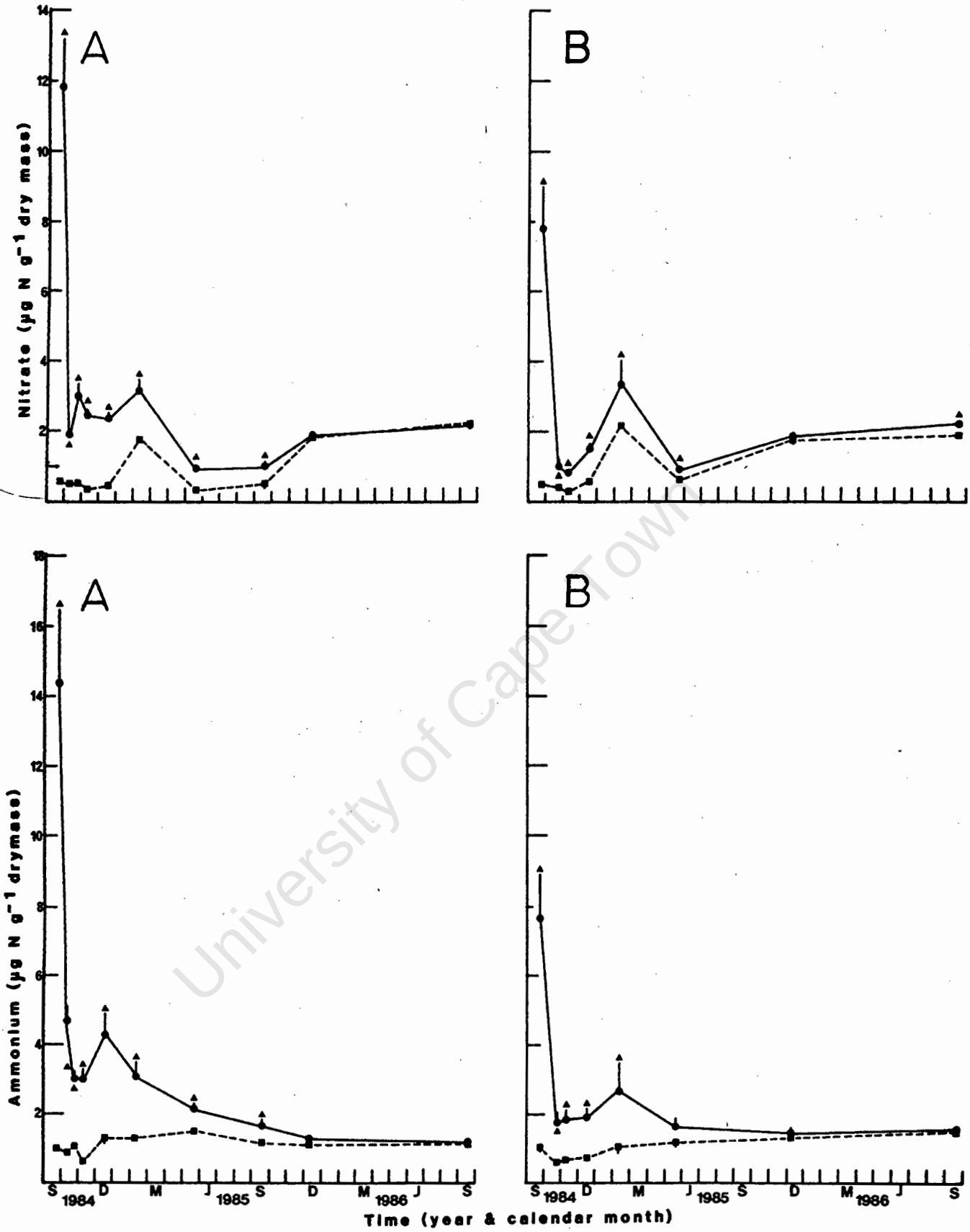

Fig. 2.2. Variations in soil nitrate and ammonium concentrations at the surface (0-10 cm depth) between nitrogen and non-nitrogen amended plots in (A) the open, and (B) the rhizosphere of Phylica cephalantha, for a period of 2-years after fertilizer addition at Pella, South Africa. Symbols: (●—●), nitrogen amended; (■--■), non-nitrogen amended; ▲, significant differences by t-tests, $P<0.05$; vertical bars represent 1 S.E.

been considerable. However, significant differences ($P<0.05$) between N-fertilized and non N-fertilized plots were found for at least one year (Fig. 2.2). The decrease of nitrate was more rapid than ammonium. In the N-fertilized plots, the rhizosphere of P. cephalantha exhibited significantly lower concentrations of nitrate and ammonium than in the open, 10 days after fertilizer addition ($t=2.11$, $P<0.05$, $d.f.=30$; $t=2.63$, $P<0.05$, $d.f.=30$, respectively), which may be the result of plant uptake. Seasonal peaks in nitrate and ammonium concentrations were found in summer (December-March) in all treatments. Total nitrogen concentration was only slightly increased by the fertilizer application and no significant differences were found between N-fertilized and non N-fertilized plots one month after fertilizer addition (Fig 2.3).

Total soil phosphorus levels were only slightly elevated with P addition but remained higher throughout the two year study period (Fig. 2.3). Both resin-extractable and Bray No. 2 phosphorus in the P-fertilized plots remained significantly higher ($P<0.05$) than the non P-fertilized plots in the open and the rhizosphere of P. cephalantha throughout the study period (Fig. 2.4). Both declined at the end of the study period following the wetter than average winter period (May to September 1986; 475 mm). Exchangeable Ca, Mg and K declined from September 1984 to May 1985 (Fig. 2.5). Higher K concentrations were found in

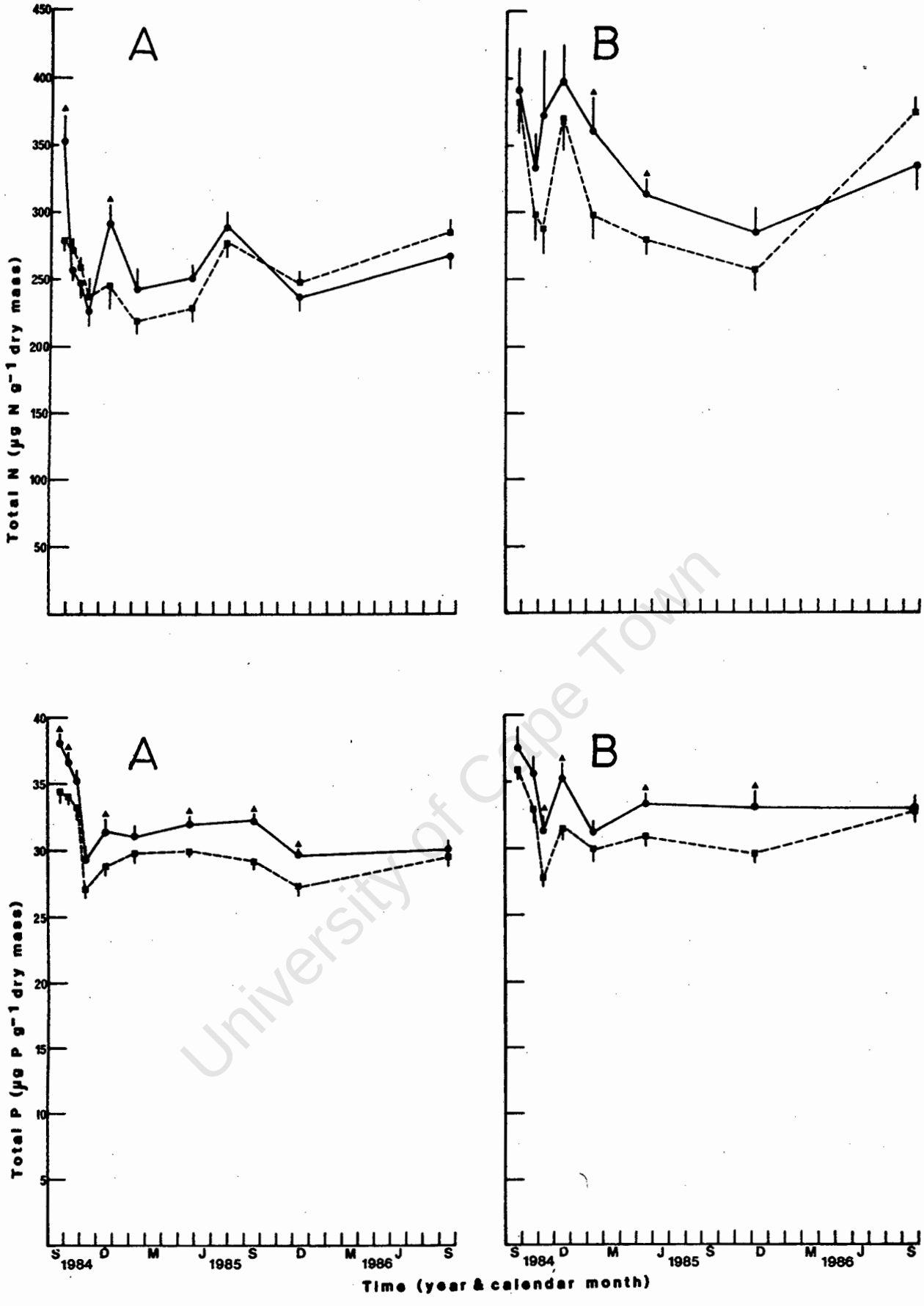

Fig. 2.3. Variations in soil total nitrogen and phosphorus concentrations at the surface (0-10 cm depth) between nitrogen and non-nitrogen and phosphorus and non-phosphorus amended plots respectively, in (A) the open, and (B) the rhizosphere of Phylica cephalantha, for a period of 2-years after fertilizer addition at Pella, South Africa. Symbols: (●—●), nitrogen amended; (■--■), non-nitrogen amended; (●—●), phosphorus amended; (■--■), non-phosphorus amended; ▲, significant differences by t-tests, $P<0.05$; vertical bars represent 1 S.E.

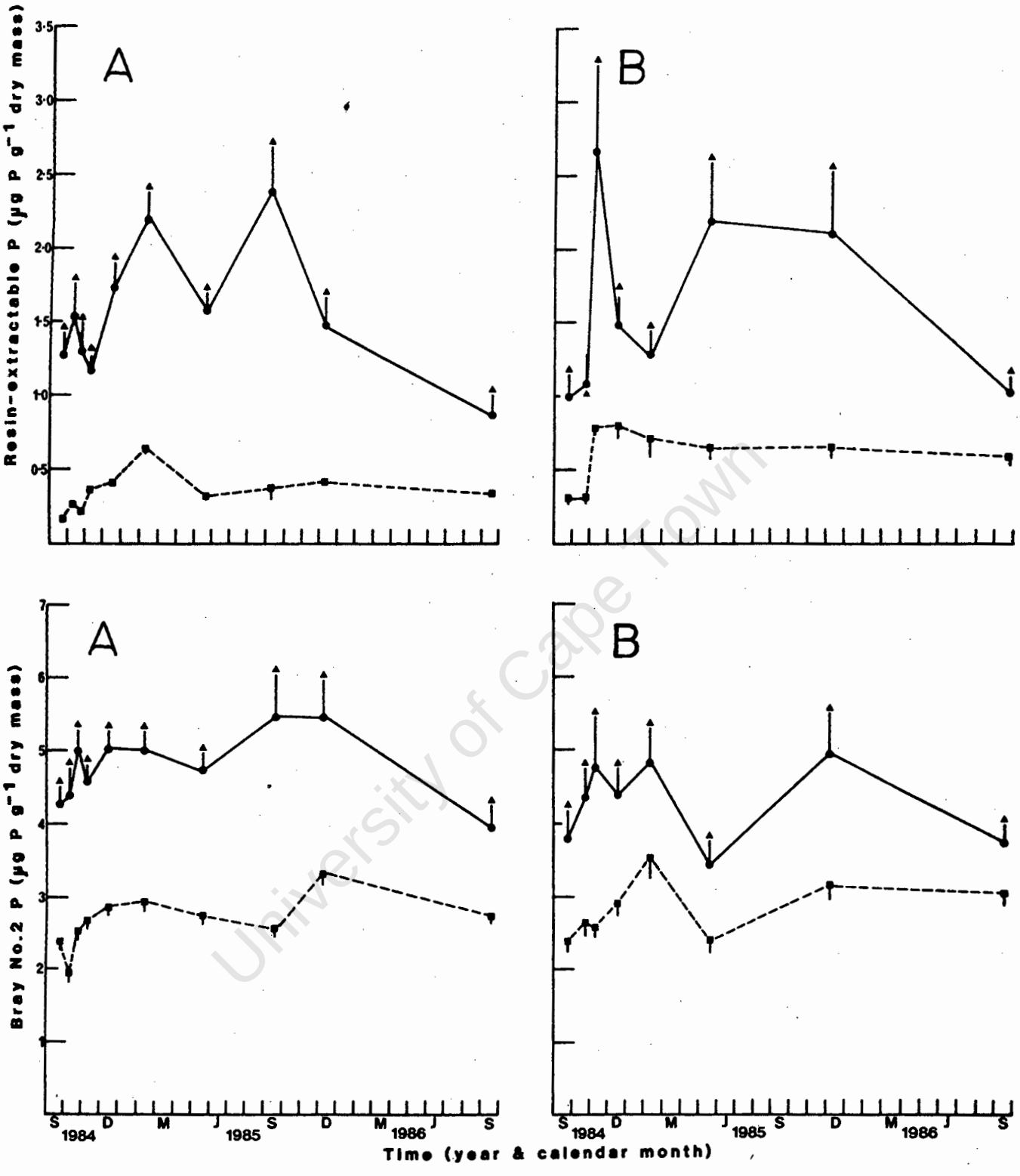

Fig. 2.4. Variations in soil resin-extractable and Bray No.2 phosphorus concentrations at the surface (0-10 cm depth) between phosphorus and non-phosphorus amended plots in (A) the open, and (B) the rhizosphere of Phylica cephalantha, for a period of 2-years after fertilizer addition at Pella, South Africa. Symbols: (●—●), phosphorus amended; (■--■), non-phosphorus amended; ▲, significant differences by t-tests, $P<0.05$; vertical bars represent 1 S.E.

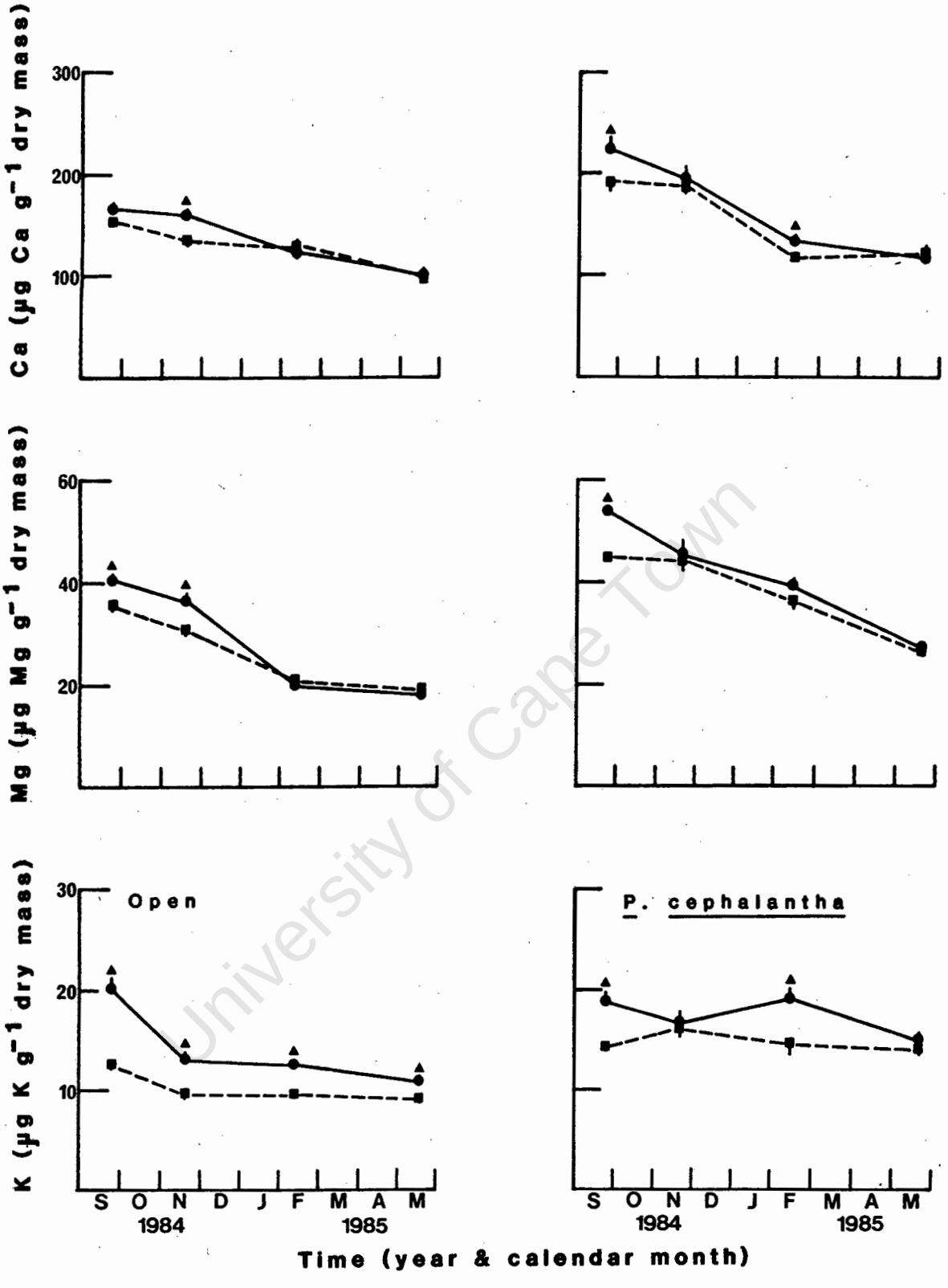

Fig. 2.5. Variations in soil calcium, magnesium and potassium concentrations at the surface (0-10 cm depth) between plots amended with a mixture of all essential nutrients excluding N and P (M) and those not amended with these nutrients, in the open, and the rhizosphere of Phylica cephalantha, for a 6 month period after fertilizer addition at Pella, South Africa. Symbols: (●—●), M amended; (■---■), non-M amended; ▲, significant differences by t-tests, $P<0.05$; vertical bars represent 1 S.E.

M-fertilized plots, for at least 6 months in the open, compared with non M-fertilized plots (Fig. 2.5).

A significant increase in soil organic matter content was found with the interaction of N and P in October 1984, November 1984 and September 1986 ($P<0.05$) in the open, and with N addition in October 1984 and February 1985 in the rhizosphere of *P. cephalantha*. Soil organic matter content varied seasonally in the control plots, ranging from 0.76 to 1.06 % in the open and from 1.38 to 1.81 % in the rhizosphere of *P. cephalantha*. Highest values occurred from February to May 1985 in the open ($F_{8,315}=21.12$, $P<0.001$ for all plots; and $F_{8,63}=4.8$, $P<0.001$ for the unfertilized control plots) and in December 1984 in the rhizosphere of *P. cephalantha* ($F_{7,280}=5.1$, $P<0.001$ for all plots; and $F_{7,56}=4.46$, $P<0.001$ for the unfertilized control plots). No significant differences in pH were found between treatments, but pH varied seasonally at the surface in the open ($F_{6,245}=32.81$, $P<0.001$ for all plots; and $F_{6,49}=4.55$, $P<0.001$ for the unfertilized control plots) and in the rhizosphere of *P. cephalantha* ($F_{5,210}=13.66$, $P<0.001$ for all plots; and $F_{5,42}=3.15$, $P<0.05$ for unfertilized control plots). Soils were more acidic during the rainy winter months probably as a result of leaching. Total nitrogen and phosphorus, organic matter, pH and exchangeable Ca, Mg and K concentrations in unfertilized plots were higher in

the rhizosphere of P. cephalantha than in the open throughout the two year study period.

The soil nutrient concentrations in the rhizospheres of L. parile, P. cephalantha and M. adunca and the in open, for four of the nutrient additions (N, P, M and C) 10 months after fertilizer addition, were analyzed using two-way analysis of variance (Tables 2.3 & 2.4). Significant differences in nitrate and ammonium concentrations were found with nitrogen addition, but only increases in the open were found (Table 2.3). However, there were significant differences in ammonium and not in nitrate concentrations between species and the open. Resin-extractable and Bray No. 2 phosphorus increased with P addition, but no significant differences were found between the rhizospheres of all species and the open. Significant differences in total phosphorus and nitrogen, soil organic matter and pH were found between the rhizospheres of all species and the open but not between treatments (Tables 2.3 & 2.4).

Statistical analyses showed that P addition resulted in lower soil ammonium concentrations in the open and M addition in lower ammonium and nitrate concentrations in the rhizosphere of P. cephalantha (Table 2.5). The addition of M also resulted in increased Bray No. 2 phosphorus concentrations in the rhizosphere of P. cephalantha (Table 2.6).

Table 2.3. Soil nutrient concentrations (μg g^{-1} dry mass), pH (Mean ± S.E.) and organic matter (%) in the rhizosphere of three species (Metalasia adunca, Leucospermum parile and Phylica cephalantha) and the open (0-10 cm depth), in the unfertilized control (C), phosphorus (P), nitrogen (N) and mixture of all essential nutrients excluding N and P (M) treated plots, 10 months after fertilizer addition at Pella, South Africa. Figures in parentheses are arcsin transformations ± S.E.

	Treatments			
Nutrient	C	P	N	M
Resin-extractable-P				
Open	0.35±0.05	1.28±0.29	0.31±0.05	0.31±0.03
M. adunca	0.48±0.15	1.01±0.4	0.43±0.02	0.25±0.02
L. parile	0.22±0.03	1.39±0.5	0.29±0.07	0.25±0.02
P. cephalantha	0.67±0.07	1.43±0.14	0.73±0.12	0.53±0.08
Bray No.2-P				
Open	2.61±0.14	4.05±0.5	2.86±0.08	2.73±0.4
M. adunca	2.80±0.6	4.15±0.4	3.20±0.3	2.73±0.5
L. parile	2.52±0.4	4.25±1.3	2.60±0.3	2.43±0.09
P. cephalantha	2.62±0.4	3.05±0.2	2.59±0.4	2.10±0.6
Total-P				
Open	28.9±0.9	29.7±0.7	30.3±1.3	30.0±1.1
M. adunca	30.4±2.0	32.3±1.3	33.1±1.2	33.8±3.7
L. parile	28.6±1.0	29.2±1.7	29.4±1.5	29.7±1.1
P.cephalantha	30.2±1.7	32.0±0.9	32.6±1.3	30.1±2.0
Nitrate				
Open	0.27±0.05	0.29±0.04	0.83±0.30	0.42±0.03
M. adunca	1.03±0.31	0.51±0.04	0.79±0.19	0.38±0.05
L. parile	0.66±0.23	0.45±0.12	0.59±0.02	0.66±0.16
P. cephalantha	0.64±0.09	0.60±0.14	0.72±0.05	0.53±0.09
Ammonium				
Open	1.73±0.23	1.33±0.08	2.88±0.52	1.72±0.04
M. adunca	1.64±0.13	1.37±0.19	1.40±0.15	1.26±0.10
L. parile	1.86±0.35	1.41±0.10	1.70±0.15	1.91±0.26
P. cephalantha	1.27±0.16	0.80±0.12	1.55±0.48	0.95±0.18
Total-N				
Open	242±23	202±8	263±38	216±6
M. adunca	342±58	282±37	301±35	316±79
L. parile	295±40	220±36	233±23	303±34
P. cephalantha	272±15	243±15	333±28	282±18
Organic Matter				
Open	1.37 (6.7±0.4)	1.14 (6.1±0.2)	1.27 (6.5±0.3)	1.23 (6.3±0.3)
M. adunca	1.01 (5.6±0.7)	0.96 (5.5±0.6)	0.96 (5.6±0.3)	1.13 (5.9±0.7)
L. parile	0.94 (5.6±0.5)	0.93 (5.5±0.3)	0.88 (5.3±0.4)	0.98 (5.7±0.2)
P. cephalantha	1.30 (6.5±0.3)	1.25 (6.4±0.2)	1.39 (6.8±0.4)	1.25 (6.5±0.2)
pH				
Open	4.61±0.07	4.61±0.08	4.51±0.07	4.64±0.04
M. adunca	4.98±0.09	5.03±0.09	4.91±0.04	4.93±0.09
L. parile	4.78±0.05	4.90±0.09	4.78±0.05	4.70±0.09
P. cephalantha	4.66±0.03	4.71±0.03	4.69±0.07	4.71±0.07

Table 2.4. Variations by two-way analysis of variance of soil nutrient concentrations, organic matter and pH at the surface (0-10 cm depth) between the rhizosphere of three species and the open in the control, nitrogen (N), phosphorus (P) and mixture of all essential nutrient excluding N and P (M) additions, 10 months after fertilizer addition at Pella, South Africa. Values are F values. * P<0.05, ** P<0.01, *** P<0.001. Species and treatment d.f. =3,48, Species x treatment d.f. =9,48.

	Source		
Nutrient	Species	Treatment	Species x Treatment
Nitrate-N	1.64	2.84*	1.54
Ammonium-N	7.75***	5.11**	1.88
Total-N	3.11*	1.94	0.63
Resin-extractable-P	2.41	21.90***	0.43
Bray No.2-P	1.19	6.00**	0.25
Total-P	5.61*	2.28	0.71
Organic Matter	6.50***	0.25	0.20
pH	38.34***	0.79	0.35

Table 2.5. Variations by two-way analysis of variance with repeated measures of the effects of factorial addition of phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) on soil (0-10 cm depth) ammonium and nitrate concentrations in open patches between shrubs and in the rhizosphere of Phylica cephalantha at Pella, South Africa. Values are F values. * P<0.05, ** P<0.01, *** P<0.001.

		Nitrogen Form			
		Ammonium		Nitrate	
Source	d.f.	Open	P.cephalantha	Open	P.cephalantha
P	1,16	9.42**	3.25	0.26	0.00
M	1,16	0.21	5.31*	0.65	7.07*
P x M	1,16	0.14	5.88*	0.68	0.55
Time	7,112	9.12***	11.32***	161.79***	151.59***
Time x P	7,112	0.47	0.66	0.98	0.77
Time x M	7,112	1.43	1.56	0.94	0.48
Time x P x M	7,112	0.45	0.64	1.16	2.61*

Table 2.6. Variations by two-way analysis of variance with repeated measures of the effects of factorial addition of nitrogen (N) and a mixture of all essential nutrients excluding N and P (M) on soil (0-10 cm depth) available phosphorus (resin-extractable and Bray No. 2) concentrations in open patches between shrubs and in the rhizosphere of Phylica cephalantha at Pella, South Africa. Values are F values. * P<0.05, ** P<0.01 *** P<0.001.

		Method of Available Phosphorus Determination			
		Resin-extractable-P		Bray No.2-P	
Source	d.f.	Open	P. cephalantha	Open	P.cephalantha
N	1,16	1.05	0.55	0.20	0.37
M	1,16	0.31	1.49	2.37	6.13*
N x M	1,16	0.87	3.74	0.00	1.42
Time	7,112	30.36***	8.06***	10.60***	5.25***
Time x N	7,112	0.72	0.35	0.88	0.95
Time x M	7,112	0.80	1.15	1.52	0.90
Time x N x M	7,112	0.75	0.90	0.50	0.54

Nutrient levels down to one meter depth

Soil nitrate concentration was found to be higher in the NPM-fertilized plots at all four soil depths measured (0, 25, 50 and 100 cm) one-year after fertilizer addition compared with the control (Fig. 2.6 & Table 2.7). Two years after fertilizer addition, higher nitrate concentrations in the NPM treated plots were found only at the 100 cm depth (Fig. 2.6). Soil ammonium and total nitrogen concentrations showed significant differences with depth but not between treatments (Table 2.7). Resin-extractable and Bray No. 2 phosphorus concentrations were significantly different between treatments and depths for both years (Fig. 2.7 & Table 2.7). However, the phosphorus added remained predominantly at the surface, and was significantly lower in the second year (t=3.11, $d.f.$=10, P<0.01; t=2.00, $d.f.$=10, P<0.05 respectively). Total phosphorus concentration varied significantly with depth but not between treatments (Fig. 2.7 & Table 2.7). Exchangeable Ca, Mg and K concentrations decreased significantly with depth in both years (Fig. 2.8 & Table 2.7). Significant differences between treatments were found for Ca and K one-year after fertilizer addition (Table 2.7). Soil organic matter was higher in the fertilized plots (NPM) than the control, but this was only significantly different during the first year (Fig. 2.9. & Table 2.7). Soil pH was not significantly different between treatments, but increased with depth (Fig. 2.9 & Table 2.7). All nutrients studied had higher

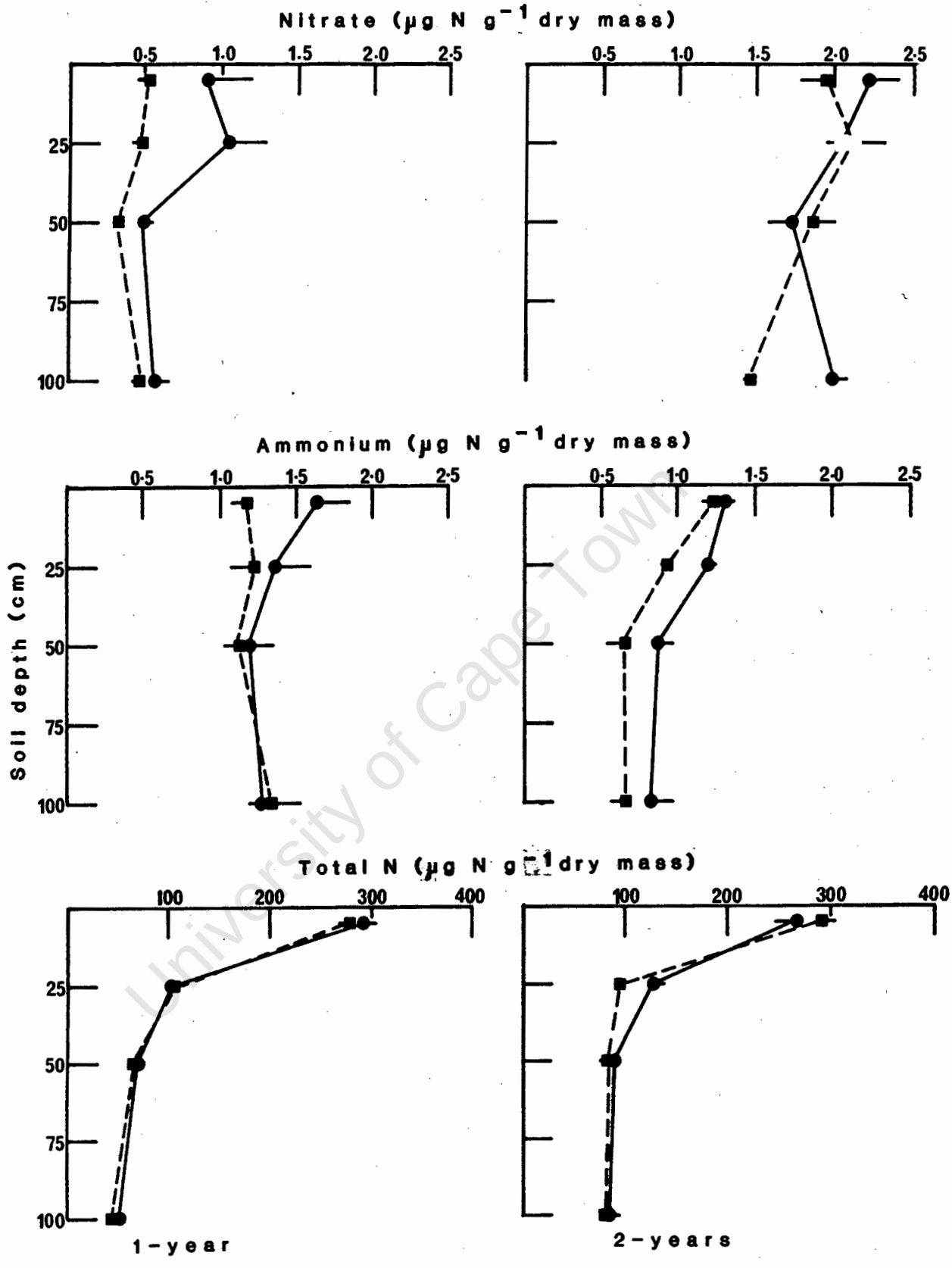

Fig. 2.6. Variations in soil nitrate, ammonium and total nitrogen concentrations with depth, 1- and 2-years after fertilizer addition (ie. September 1985 and 1986 respectively), in the complete nutrient fertilized (NPM) and control plots, in open patches between shrubs at Pella, South Africa. Symbols: (●—●), NPM amended; (■--■), control; horizontal bars represent 1 S.E.

Table 2.7. Variations by two-way analysis of variance of soil nutrient concentrations, organic matter and pH, at four depths (0, 25, 50 and 100 cm) between the complete fertilizer treatment (NPM) and the control, one and two years after fertilizer addition at Pella, South Africa. Values are F values. Treatment d.f. =1,40 and depth and treatment x depth d.f. =3,40. * P<0.05, ** P<0.01, *** P<0.001.

	Source					
	One Year			Two Year		
Nutrient	Treatment	Depth	Treatment x Depth	Treatment	Depth	Treatment x Depth
Nitrate-N	7.08*	2.00	0.93	2.16	3.12*	2.45
Ammonium-N	1.21	0.75	0.90	5.45	12.54***	0.28
Total-N	0.69	195.00***	0.52	0.28	124.00***	1.85
Resin-extractable-P	15.02***	23.10***	15.02***	9.53**	12.76***	4.42**
Bray No.2-P	8.83**	28.77***	8.51***	5.36*	56.25***	4.54**
Total-P	3.89	31.74***	1.00	3.77	123.00***	0.17
Ca	4.69*	30.54***	1.12	0.05	40.88***	0.85
Mg	2.55	16.49***	0.61	1.31	11.18***	2.15
K	12.80***	13.30***	2.00	0.04	31.44***	0.44
Organic Matter	7.79**	51.49***	0.88	1.90	44.01***	0.07
pH	0.09	25.22***	2.10	0.04	18.83***	0.55

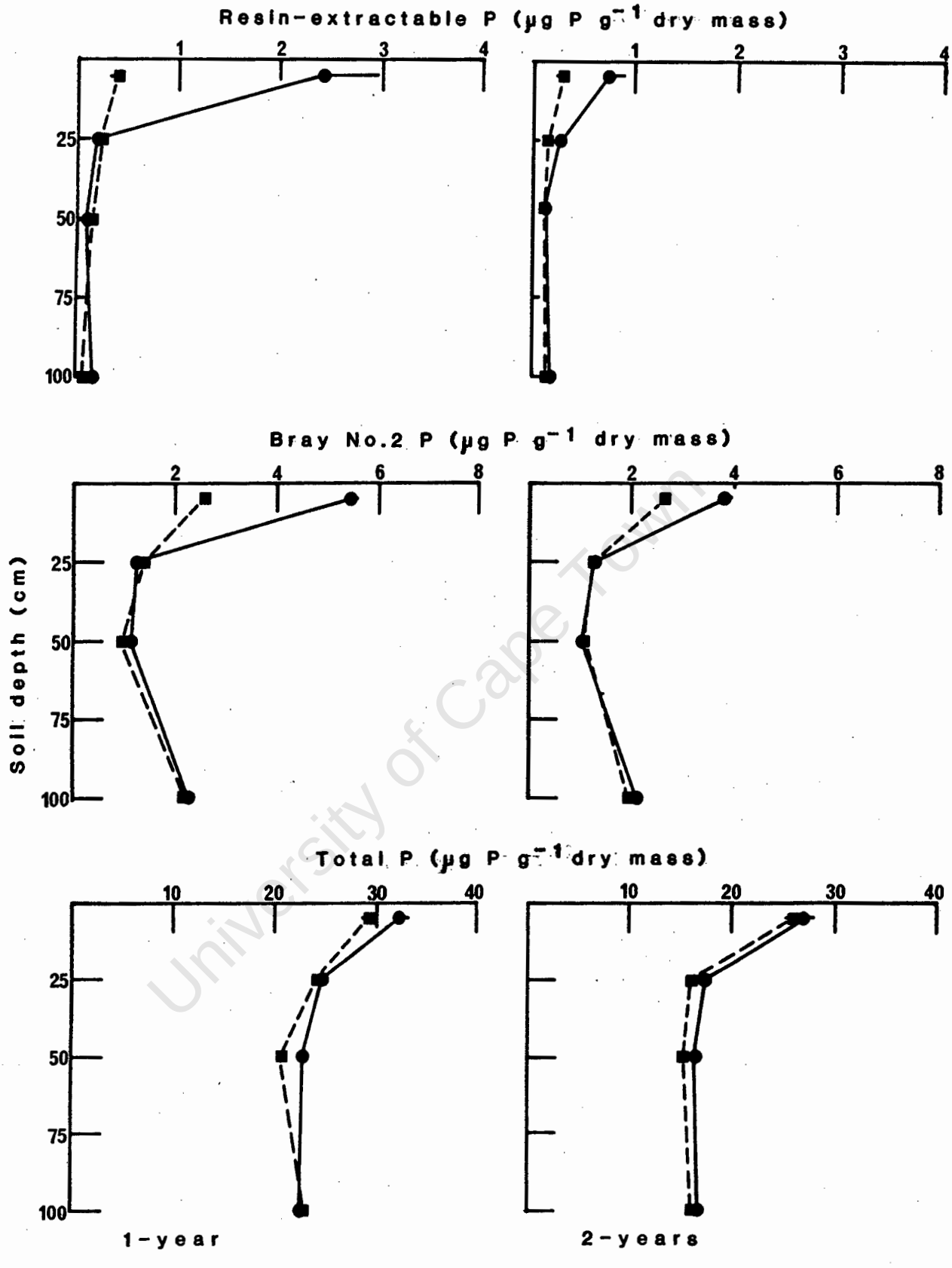

Fig. 2.7. Variations in soil resin-extractable, Bray No.2 and total phosphorus concentrations with depth, 1- and 2-years after fertilizer addition (ie. September 1985 and 1986 respectively), in the complete nutrient fertilized (NPM) and control plots, in open patches between shrubs at Pella, South Africa. Symbols: (●—●), NPM fertilized; (■--■), control; horizontal bars represent 1 S.E.

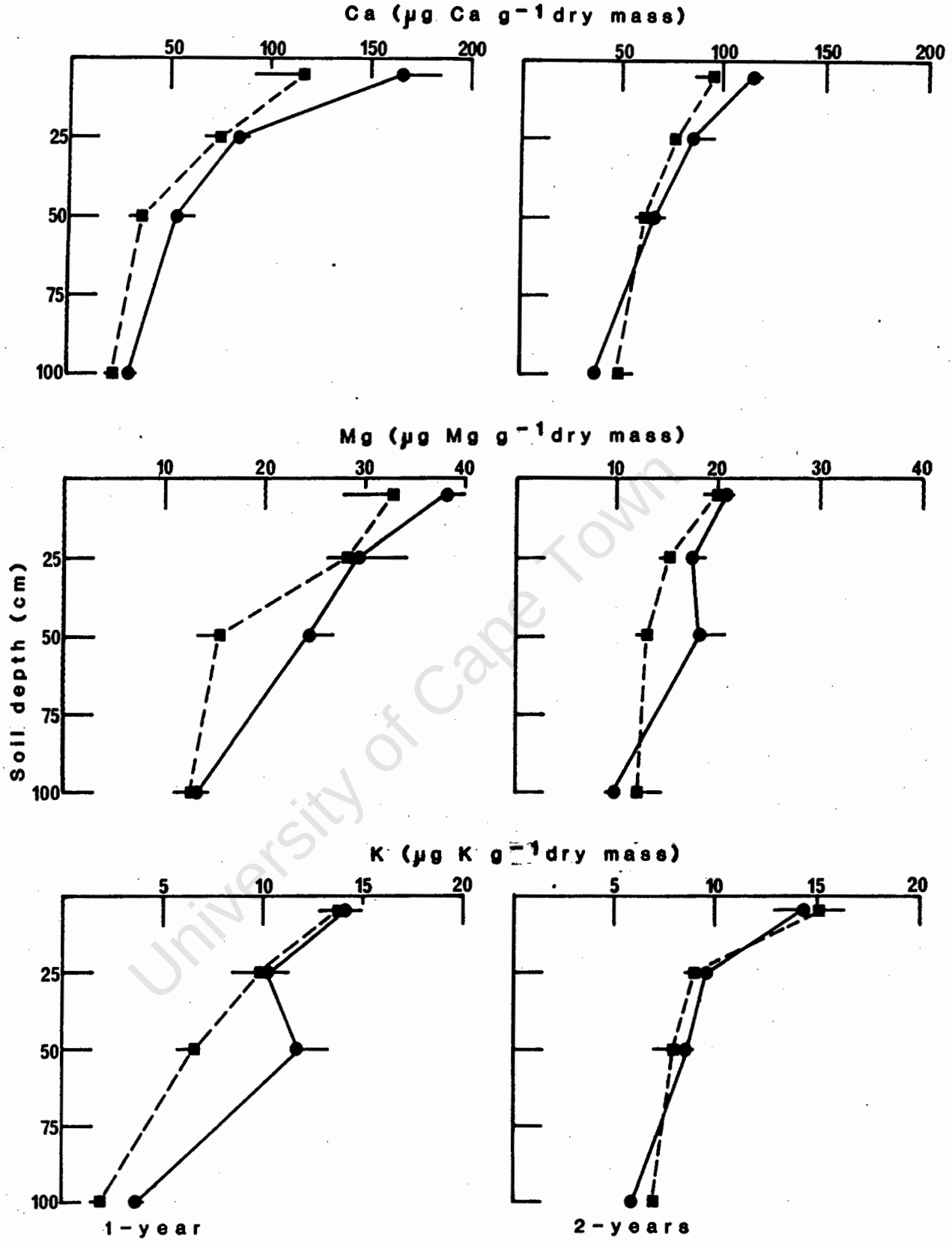

Fig. 2.8. Variations in soil calcium, magnesium and potassium concentrations with depth, 1- and 2-years after fertilizer addition (ie. September 1985 and 1986 respectively), in the complete nutrient fertilized (NPM) and control plots, in open patches between shrubs at Pella, South Africa. Symbols: (●—●), NPM fertilized; (■--■), control; horizontal bars represent 1 S.E.

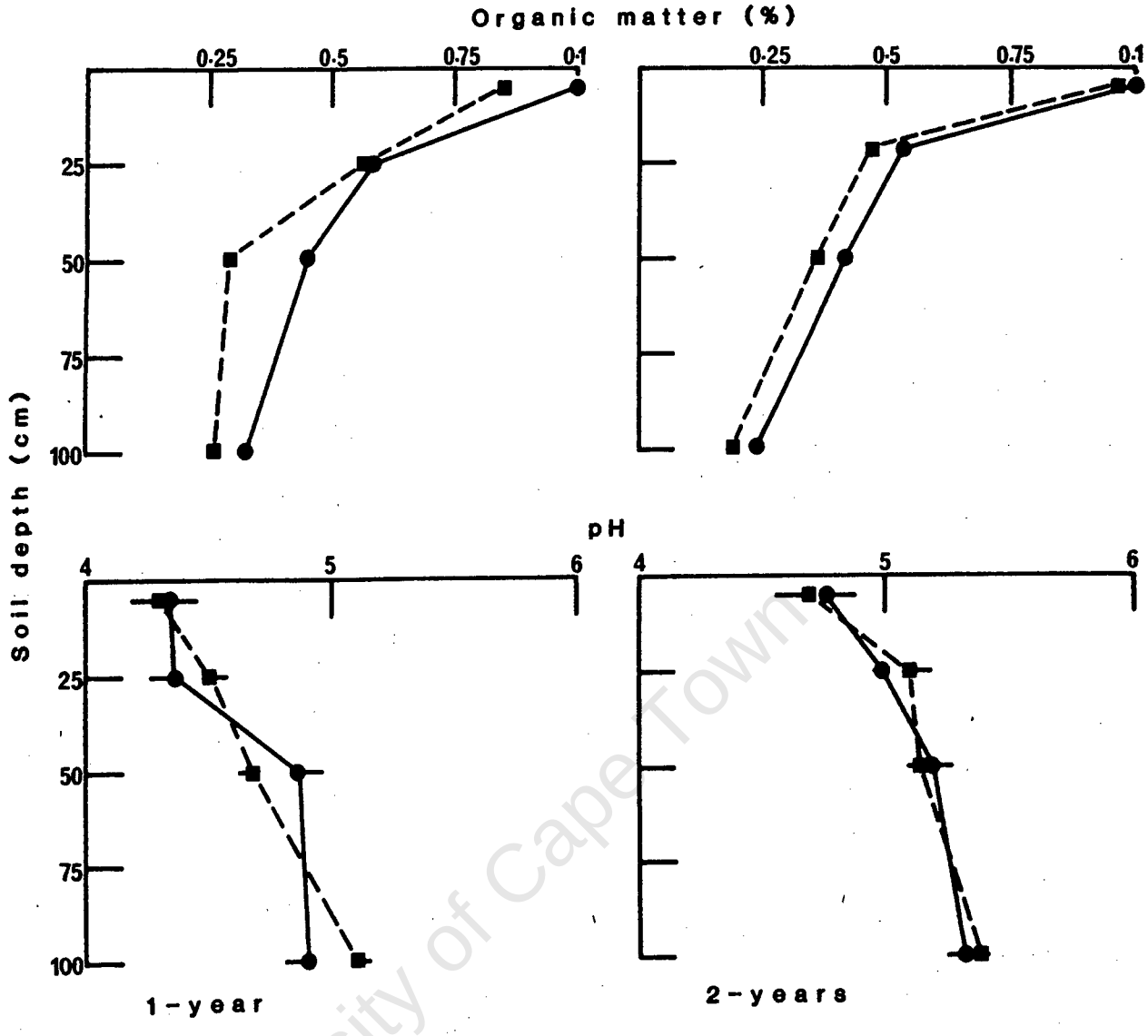

Fig. 2.9. Variations in soil organic matter content and pH with depth, 1- and 2-years after fertilizer addition (ie. September 1985 and 1986 respectively), in the complete nutrient fertilized (NPM) and control plots, in open patches between shrubs at Pella, South Africa. Symbols: (●—●), NPM fertilized; (■--■), control; horizontal bars represent 1 S.E.

concentrations at the soil surface. For the unfertilized control plots, similar patterns of soil phosphorus and nitrogen concentrations with season and depth were found by Mitchell et al. (1984) and Stock & Lewis (1986b) respectively.

DISCUSSION

Depletion or conversion of plant available nitrogen added to the soil, whether in the nitrate or ammonium form, was rapid after fertilizer addition as soil concentrations dropped by 80 % within one month, although remaining significantly higher for one year. Plant available nitrogen concentrations in the rhizosphere of P. cephalantha were depleted more rapidly than in the open and this may be due to plant uptake. Fynbos plants have been shown to take up both nitrate and ammonium to satisfy their low nitrogen requirements (Stock & Lewis 1984), although ammonium is the dominant mineral form of nitrogen in these soils (Stock & Lewis 1986b).

The loss of added nitrate and potassium from the soil surface is probably attributable to leaching as their concentrations increased at lower soil depths (Figs 2.6 & 2.8 respectively). The low cation exchange capacity, organic carbon, silt and clay content, of these soils, limits their ability to prevent leaching of mobile ions such

as nitrate and potassium. Leaching of nitrate down the soil profile was shown to occur during the wet winter, approximately 8 months after a fire at Pella (Stock & Lewis 1986b). The decrease in ammonium concentrations is probably the result of immobilization by soil micro-organisms or plant uptake. Some of the added nitrate may also have been immobilized. Summer peaks of ammonium and nitrate indicate reduced uptake by plants or reduced leaching of these ions when soil moisture status is low. Root growth and nutrient uptake appear to occur predominantly during the moist winter to early spring period (Jongens-Roberts & Mitchell 1986; Stock et al. 1987).

Although fire releases large amounts of available nitrogen, and mineralization rates are enhanced, more nitrogen is made available by decomposition between fires, suggesting that decomposition is the most important process rendering nitrogen available in mediterranean-type ecosystems (Marion 1982). Nitrogen mineralization studies in the soils at Pella (Stock et al. 1988) showed no evidence of increasing allelopathic inhibition of nitrification with successional development, as most of the nitrogen accumulating in in situ incubation bags was in the form of nitrate. Further, the ratio of ammonium to nitrate remained constant throughout all the seral stages of the vegetation. In addition, in situ production of mineral nitrogen appeared to be related to temperature, total nitrogen and moisture content of the

soil; all of which vary through successional stages due to the changing structure of the vegetation (Stock et al. 1988). The fynbos areas of the western Cape with winter temperature means of 10 - 12^{o} C (Kruger 1979) are unlikely to experience low temperature inhibition of microbial activity, while the characteristic seasonality of rainfall in this mediterranean climate suggests that soil moisture during summer may be a limiting factor (Read & Mitchell 1983). Nitrogen mineralization was found to be more sensitive to moisture than to temperature fluctuations in the mediterranean Californian chaparral (Schaefer 1973; Mooney & Rundel 1979; Marion 1982).

Soil phosphorus concentrations, both total and available, remained significantly higher in the P-fertilized plots than those not amended with P throughout the study period, both in the open and the rhizosphere of P. cephalantha. Phosphorus is a relatively immobile element in the soil (Bieleski 1976) and little movement of this element down the soil profile was found (Fig. 2.7). However, phosphorus concentrations at the surface in the P amended plots declined by approximately 50 % after two years, probably as the result of plant uptake, chemical conversion to unavailable forms and immobilization by soil micro-organisms. In Australian heaths, Heddle & Specht (1975) found soil phosphorus concentrations were still elevated 22 years after heavy fertilizer additions totaling

13.4 g P m^{-2}. Because added phosphorus has a long residence time in the soil, compared with added nitrogen, long term changes in the community composition are more likely with the addition of this element. This has been confirmed for Australian heathlands (Specht 1963: Heddle & Specht 1975). In addition, phosphorus addition may result in increased nitrogen fixation by both free-living soil micro-organisms and nitrogen fixing legumes as nitrogen fixation is often phosphorus limited (Postgate 1978). Nitrogen fixation by bacteria and actinomycetes has been found to be a major source of nitrogen input in other mediterranean regions such as the Californian chaparral (DeBano & Dunn 1982).

Significant increases in soil organic matter with the interaction of N and P addition in the open and N addition in the rhizosphere of P. cephalantha may be the result of increased microbial activity. Immobilization of N and P in nutrient-poor soils by soil micro-organisms is a well established phenomenon (Enwezor 1976). A consequence of this is that organic material produced in nutrient-poor sites decomposes and releases nutrients more slowly than that produced in nutrient-rich sites, because of high carbon to mineral nutrient ratios, as well as the presence of high concentrations of phenolics and lignin (Chapin et al. 1986). Similar results have been found in the fynbos biome (Mitchell et al. 1986). The lack of response in tussock

tundra, Alaska, to low levels of fertilizer addition was attributed to immobilization of the added nutrients by the soil organic matter (Shaver & Chapin 1980). The factorial addition of P and M resulted in a significant reduction in soil ammonium concentrations, but only M addition resulted in decreased nitrate concentrations. These effects may be ascribed to interactions between the nutrients which affect the decomposition process.

In conclusion, immobilization of ammonium and to a lesser extent, phosphorus, and leaching of nitrate and potassium occurred in response to the addition of these nutrients to the nutrient-poor, acidic and sandy soils of lowland fynbos. Few differences in added nutrient element dynamics were found when comparing open patches between shrubs and the rhizosphere of P. cephalantha. This study confirms that added phosphorus is held in the soil system and if added in large enough quantities, will probably result in long term changes in nutrient cycling and species composition to more ephemeral nutrient demanding herbaceous and graminoid species. This has been found with P addition in nutrient-poor Australian heathlands (Specht 1963; Connor & Wilson 1968; Heddle & Specht 1975; Specht et al. 1977), and with increased soil nitrogen as a result of acid rain in Calluna heath (Heil & Diemont 1983; Heil & Bruggink 1987).

CHAPTER 3

RESPONSE OF A LOWLAND FYNBOS ECOSYSTEM, SOUTH AFRICA, TO NUTRIENT ADDITIONS. II. SHOOT GROWTH AND NUTRIENT CONTENTS OF A PROTEOID (*LEUCOSPERMUM PARILE*) AND AN ERICOID (*PHYLICA CEPHALANTHA*) EVERGREEN SHRUB

(To be submitted to Acta Oecologica - Oecologia Plantarum)

SUMMARY

The effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P), and a mixture of all essential nutrients excluding N and P (M) on shoot extension and phenology, shoot dry mass, nitrogen and phosphorus contents and canopy growth in Leucospermum parile and Phylica cephalantha growing in sand-plain lowland fynbos at Pella, south-western Cape Province South Africa, were studied from 1984 to 1986. Five g nitrogen m^{-2} as NH_4NO_3 and 0.5 g phosphorus m^{-2} as $Ca_3(PO_4)_2$ were the amounts and forms of N and P added, which approximated amounts returned to the soil after a fire at Pella in November 1980.

Increases in shoot extension and dry mass in response to N addition were found in both species during the first season (1984-85) after fertilizer addition, although not the second (1985-86), during which soil nitrogen concentrations in the N fertilized plots were no longer elevated. Phosphorus addition either did not affect or reduced shoot growth. The effects of M addition were more variable and often interacted with N or P addition. Increases in shoot nitrogen contents and concentrations of both species, in response to N addition were found during the first but not the second season. Although tissue phosphorus concentrations tended to increase with P addition in P. cephalantha, only one-year old twigs harvested at the end of

the 1985-86 season showed a significant increase. Irrespective of whether P was added, shoot phosphorus concentrations were significantly reduced with N addition in L. parile during both seasons, whereas N addition resulted in increased shoot phosphorus contents in P. cephalantha.

No significant differences in leaf specific mass of L. parile were found between nutrient treatments, whereas mean leaf area increased with N fertilization and branching with the addition of N plus M. Nutrient additions had no effect on the date of commencement of shoot extension in either species. Phylica cephalantha appears to have alternating years of high and low reproductive effort, which was not influenced by the addition of nutrients. Vegetative growth was delayed and reduced in the growing season after a year of high reproductive output. However, shoot extension and dry mass production in L. parile were not significantly different between growing seasons. These indigenous fynbos evergreen shrub species do not exhibit plasticity in morphological growth in response to unpredictable increases in nutrient availability, but reversible physiological changes such as nutrient storage.

INTRODUCTION

Nutrient limitations of plant growth have been demonstrated in ecosystems with nutrient-poor soils, such as tundra

(Shaver & Chapin 1980; Lechowicz & Shaver 1982; Chapin & Shaver 1985; Shaver et al. 1986; Henry et al. 1986), heathlands (Connor & Wilson 1968; Specht et al. 1977; Heil & Diemont 1983), bogs (Simms 1987), and in mediterranean regions such as the Californian chaparral (McMaster et al. 1982) and the Australian heathlands (Specht 1963; Heddle & Specht 1975). The fynbos biome has a mediterranean climate and is edaphically more similar to the Australian heathlands than the other mediterranean-type ecosystems (Mitchell et al. 1984; Witkowski & Mitchell 1987). Phosphorus and to a lesser extent nitrogen limit the growth of sclerophyllous shrubs on nutrient-poor soils in southern Australia (Specht & Rayson 1957). In the heaths of south-eastern Australia, there was a growth response by the vegetation when phosphorus was added, which was further enhanced by the addition of nitrogen (Specht 1963). Addition of nitrogen, Cu or Zn (without simultaneous addition of phosphorus) provoked no response, although these elements were deficient for the growth of introduced herbaceous plants (Riceman 1948). Short-lived understorey species showed the greatest response to added nutrients, while long-lived, deep rooting overstorey species such as Banksia ornata (Proteaceae) showed only a small growth response. Phosphorus addition also decreased shrub life-span and seedling survival and it has been postulated that nutrient stress delays reproduction (Goodman & Perkins 1968a,b). In the Californian chaparral, the major response, of the shrub species studied, was to

nitrogen and combined nitrogen and phosphorus (McMaster et al. 1982). Similar studies have not been undertaken in the fynbos biome.

The objectives of this study were to examine the effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) on shoot extension, phenology, shoot dry mass, nitrogen and phosphorus contents and allocation patterns and canopy growth, in a proteoid (Leucospermum parile (Salisb. ex J. Knight) Sweet) and an ericoid (Phylica cephalantha Sonder) shrub species, in 4-6 year-old sand-plain lowland fynbos vegetation at Pella south-western Cape, South Africa. The responses of the two species are compared and related to soil nutrient dynamics and climatic variation between the two growing seasons studied (reported in Chapter 2). These results are compared with similar studies from other mediterranean-type ecosystems.

STUDY AREA

The study area was the CSIR fynbos biome intensive study site at Pella on the Burgherspost Farm 62 km north of Cape Town, south-western Cape, South Africa ($33^{o}31'$ S, $18^{o}32'$ E; 15 km inland from the west coast; altitude 160-220 m; 269 ha). The climate and soils have been previously described (Chapter 2). Pella is an area of sand-plain lowland fynbos

(Moll et al. 1984), consisting of low evergreen sclerophyllous vegetation growing on acidic sands of aeolian origin. The site was burnt by a moderately intense wildfire in November 1980.

An area of approximately 1 ha in the centre of a 26 ha patch of Clovelly soil was chosen at Pella during 1983 for this study. It was positioned on a gentle 5^{o} easterly slope in homogeneous four-year old post-fire vegetation which is classified as Leucospermum parile-Thamnochortus punctatus mid-high open shrubland of Phylica cephalantha fynbos (Boucher & Shepherd 1987). The vegetation is typically dominated by three growth forms: the proteoid, tall sclerophyllous shrubs with broad isobilateral leaves; ericoid containing low evergreen leptophyllous shrubs and restioid elements comprising wiry aphyllous hemicryptophytes of the Restionaceae and Cyperaceae (Taylor 1978). The ericoid element was the dominant physiognomic type. The most common ericoid species were P. cephalantha and P. stipularis L. (Rhamnaceae) which are both multi-stemmed shrubs resprouting from rootstocks after fire and dominate throughout sand-plain lowland fynbos (Boucher 1983). Other common ericoid species are Metalasia adunca Less. (Asteraceae) and Griesbachia plumosa Klotzsch (Ericaceae), both seed regenerators. The proteoid elements are predominantly seed regenerating and dominated by L. parile. The restionaceae are dominated by Thamnochortus punctatus

Pill., Cannomois parviflora (Thunb.) Pill. and Staberoha distachya (Rottb.) Kunth.

Leucospermum parile is a sclerophyllous reseeding mid-late successional dominant growing up to 1.3 m in height and is endemic in the Malmesbury area of the south-western Cape where Pella is situated. Phylica cephalantha is a shorter leptophyllous early successional dominant with small curled isobilateral leaves. Phylica cephalantha resprouts within one month after fire and is thus thought to be capable of utilizing the flush of available nitrogen and phosphorus which occurs for approximately 4-9 months after fire (Stock & Lewis 1986b; Brown & Mitchell 1986). Growth of this species is relatively fast for the first 2 to 3 years, after which it slows down. Seeds of L. parile germinate during the winter after fire, by which time the soil nutrient levels have returned to pre-fire levels. Both species reach reproductive maturity approximately three years after fire (secondary juvenile period for P. cephalantha).

METHODS

Fertilizer addition

A complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) were randomly assigned to 10x5 m sized plots as described in Chapter 2. Nutrients were added at

low concentrations to the plots during 15-17 September 1984, towards the end of the rainy season. Five g nitrogen m^{-2} as NH_4NO_3 and 0.5 g phosphorus m^{-2} as $Ca_3(PO_4)_2$ were added, these being the approximate amounts returned to the soil and surface ash after a fire at Pella in November 1980 (Brown & Mitchell 1986, Stock & Lewis 1986b). All other nutrients added were based on a Long Ashton nutrient solution (Hewitt & Smith 1975) in proportion to the N and P inputs. The plots were divided into destructive and non-destructive sampling halves, both 5x5 m in size.

Plant growth and sample collection

In the spring of 1984-85 and 1985-86, ten shoots of a L. parile and P. cephalantha shrub were randomly tagged in the destructive sampling half of each plot. Only flowering shrubs of L. parile were selected. Shoot extension was measured at monthly intervals until the end of the growing season (May to June), whereupon all tagged shoots were harvested. Leaves and flowers were immediately removed from the shoots to prevent the possibility of nutrient transfer between plant parts. The number of branches on L. parile and flowers on P. cephalantha shoots were counted. From the 1984-85 season harvest, leaf mass per unit area of L. parile was obtained by measuring the area of two fully expanded leaves per shoot and weighing after oven-drying at 80°C for 48 h. At the end of the 1985-86 season, shoot

material which had grown during the previous 1984-85 season was also harvested from both species.

The canopy areas and volumes of tagged shrubs of both species were determined in November 1984 and 1985. Individuals of both species in the non-destructive half of the plot were sampled during September 1984 (pre-fertilizer addition), September 1985 and 1986. Canopy volume was determined by measuring the major and minor axes of each 20 cm height segment from the ground upwards. Each segment was treated as an ellipse and the volume calculated using the following formula:

$$\sum[(\text{major axis} \times \text{minor axis})/4 \times \pi \times \text{depth of segment}].$$

The rooting depth and spread of P. cephalantha was determined by excavation whereas that of L. parile has been described previously (Moll & Sommerville 1984; Jongens-Roberts & Mitchell 1986).

Plant analyses

All plant material was oven-dried at 80° C for 48 h, weighed and ground to 40 mesh in a Wiley mill and analyzed for nitrogen and phosphorus in triplicate. Leaves of L. parile collected in 1984-85 were also analyzed for total Ca, Mg and K. Nitrogen was determined on 0.1 g plant material by Kjeldahl digestion and measured colorimetrically (Smith 1980). Total phosphorus was determined on 0.1 g plant

material by the methods of Jackson (1958) and Murphy and Riley (1962). Calcium, Mg and K were determined on 1 g of plant material ashed in a muffle furnace for 5 h at 500° C, dissolved in HF/HCl/HNO_3 (1:8:4) and concentrations of each element were determined on a Varian No. 6 atomic absorption spectrophotometer.

Statistical analyses

Comparisons of shoot extension and dry mass were made between treatments by three-way analysis of variance with nesting, whereas three-way analysis of variance was used for other comparisons (SAS GLM procedure; SAS Institute 1985). In L. parile, comparisons of branch number per shoot between the control and each fertilizer treatment combination were performed on proportional cumulative frequencies by the Kolmogorov-Smirnov statistic (Zar 1984). Changes in shrub canopy area and canopy volume, in response to fertilizer additions in the non-destructive half of the plots, were analyzed by three-way analysis of covariance using the pre-fertilizer values as covariates (SAS GLM procedure; SAS Institute 1985). All percentage values were arcsin transformed prior to statistical analyses. Where data did not satisfy the assumptions of normality and homogeneity of variance for analysis of variance (Zar 1984), they were transformed to average normal deviates of ranked values (Fisher & Yates 1967) and then analyzed by analysis of variance (Green 1979).

RESULTS

Phenology and shoot extension

Shoot growth of L. parile commenced in late September- early October and continued until April, although it commenced later during the second season (from mid-late October; Fig. 3.1). During the 1984-85 growing season, an increase in shoot extension with N addition was found ($P<0.001$), whereas phosphorus addition effects, as analyzed by a three-way ANOVA showed statistically reduced shoot extension in 1985-86. In addition, significant interactions between P and both the N and M treatments were found in 1985-86 ($P<0.001$; Appendix 2). There was no correlation between mean shoot extension and plant canopy volume for control L. parile plants during 1984-85 ($r=0.25$, $d.f.=6$, $P>0.05$), and thus differences in mean shoot extension are not a function of shrub size but of fertilizer additions. Increased branching in L. parile only occurred in N plus M amended plants during the 1985-86 growing season (Table 3.1).

Shoot growth of P. cephalantha occurs from late September until the beginning of February (Fig. 3.2), which is at least two months less than that of L. parile. Nitrogen addition resulted in the largest growth increment during 1984-85 ($P<0.001$), whereas a reduction in shoot extension in response to the interaction of the P and M treatments was found during 1985-86 ($P<0.001$; Appendix 2). Shoot growth was also delayed for P. cephalantha in 1985-86, it commenced

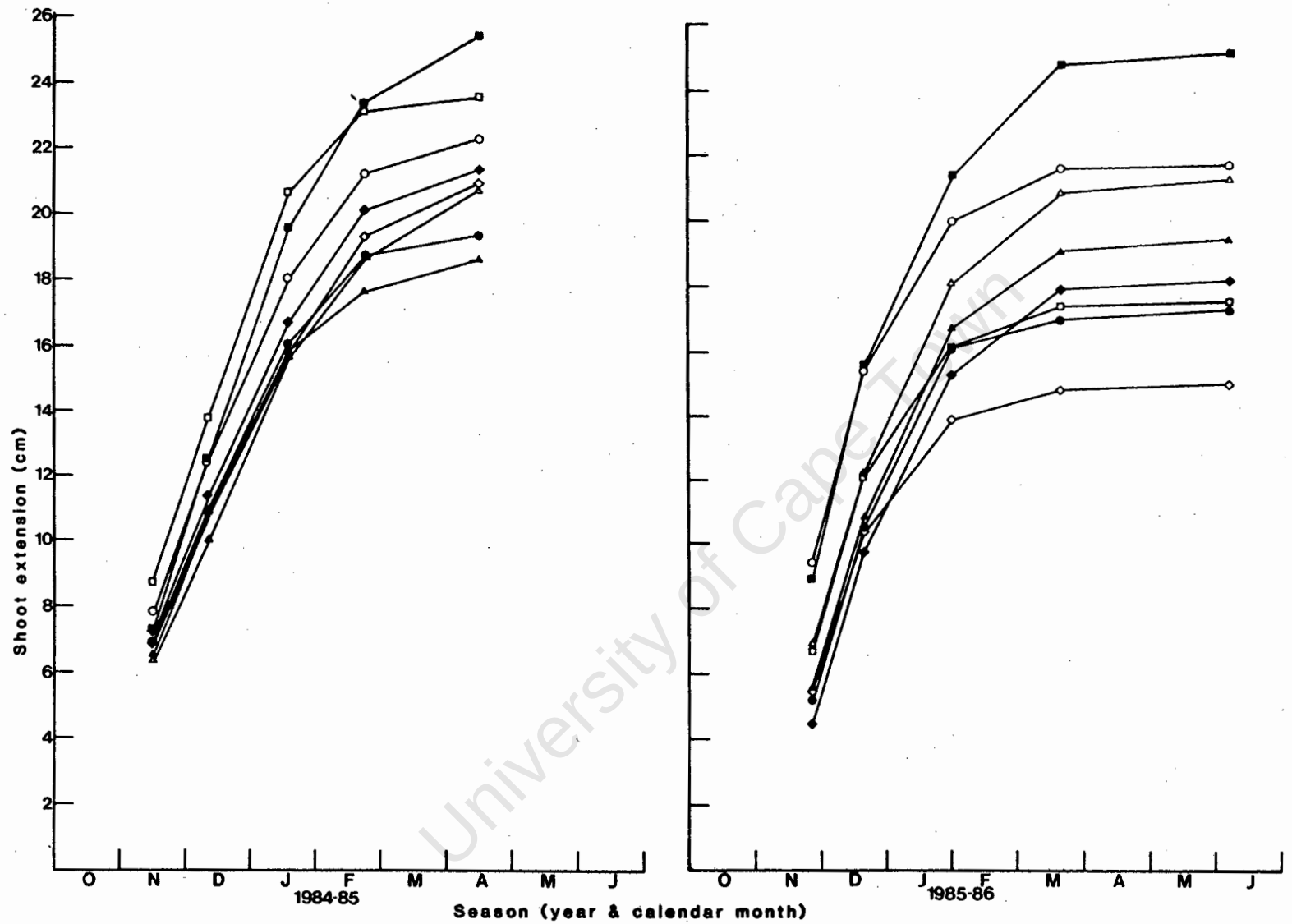

Fig. 3.1. Shoot extension of Leucospermum parile during the 1984-85 and 1985-86 growing seasons as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Symbols: ●, unfertilized control; O, N; ▲, P; △, M; □, NP; ■, NM; ◆, PM; and ◇, NPM.

Table 3.1. Branching (mean) during the 1984-85 and 1985-86 growing seasons and leaf specific mass and leaf area (mean ± 1 S.E.) during 1984-85 of Leucospermum parile as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P), and a mixture of all essential nutrients excluding N and P (M) at Pella, South Africa. Significance levels of Kolmogorov Smirnov statistic of cumulative frequency distributions between the control and each fertilizer treatment: *, $P<0.05$, **, $P<0.01$. C denotes unfertilized control.

Treatment	C	N	P	M	NP	NM	PM	NPM
Branching (% shoots)								
1984-85	15.0	5.0	12.5	27.5	26.3	20.0	22.5	27.5
1985-86	17.0	32.5	30.0	25.0	17.5	45.0	17.5	2.5
Mean number branches per shoot								
1984-85	0.39	0.13	0.20	0.45	0.55	0.33**	0.55	0.60
1985-86	0.40	0.78	0.65	0.68	0.55	1.43	0.40	0.05
Leaf specific mass 1984-85 ($g\ dm^{-2}$)	1.60 ±0.05	1.58 ±0.05	1.60 ±0.06	1.53 ±0.06	1.61 ±0.06	1.61 ±0.06	1.63 ±0.09	1.51 ±0.07
Leaf area 1984-85 ($cm^2\ leaf^{-1}$)	1.99 ±0.07	2.53 ±0.17	1.97 ±0.21	2.13 ±0.14	2.19 ±0.21	2.05 ±0.10	1.87 ±0.14	1.96 ±0.13

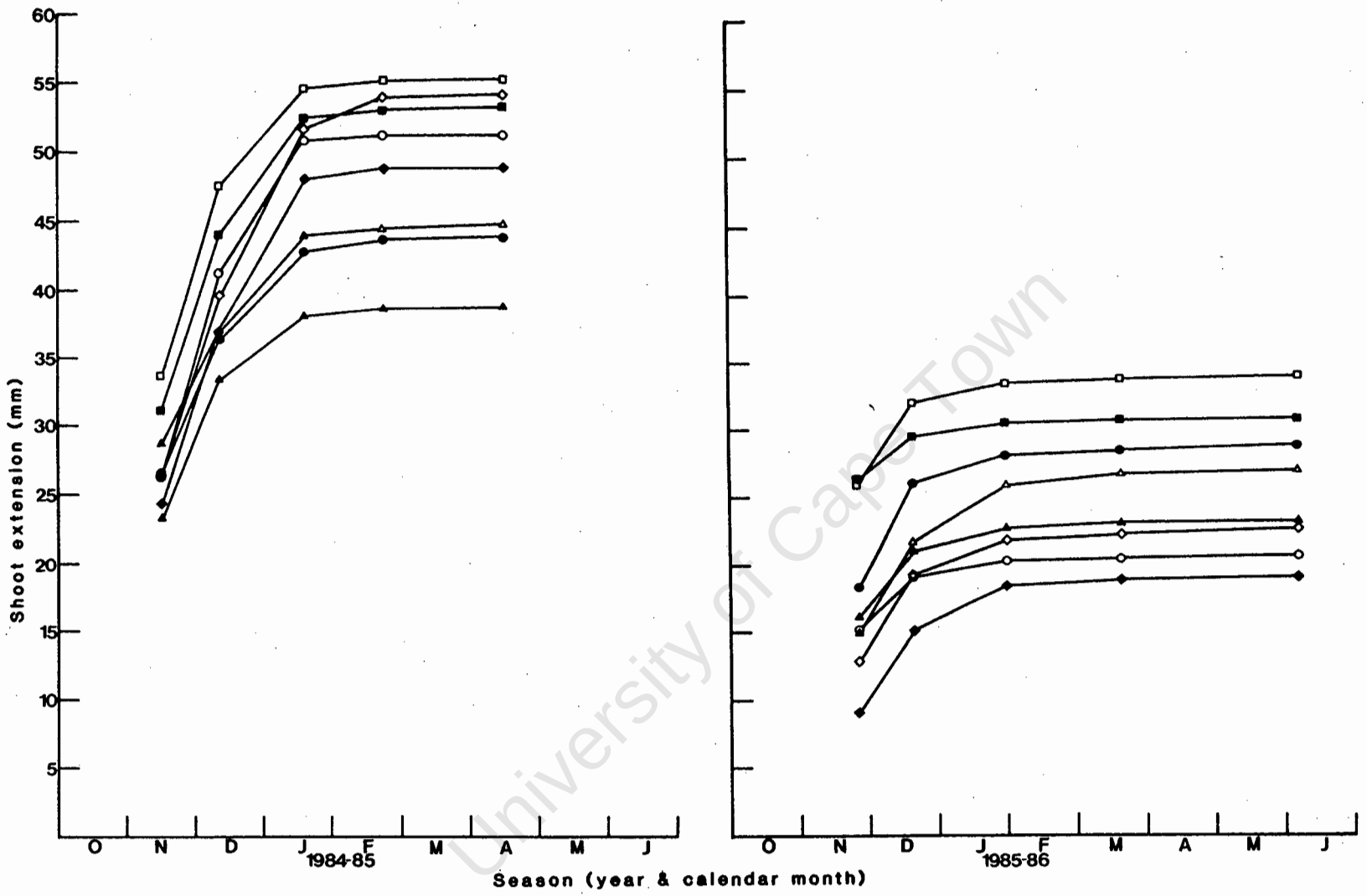

Fig. 3.2. Shoot extension of Phylica cephalantha during the 1984-85 and 1985-86 growing seasons as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Symbols: ●, unfertilized control; ○, N; ▲, P; △, M; □, NP; ■, NM; ◆, PM; and ◇, NPM.

during early-mid October. Shoot extension of control plants was reduced from a mean of 43 mm during 1984-85 to only 29 mm during 1985-86 (t=2.85, $d.f.$=6, P<0.01; Fig 3.2). There was a weak correlation between mean shoot extension and shrub canopy volume for control P. cephalantha plants in 1984-85 (r=0.65, $d.f.$=6, P<0.05), but the canopy volumes of tagged shrubs were not significantly different between treatments (P>0.05). From 0 % (NP & NM) to 33 % (NPM) of tagged buds remained dormant during the 1985-86 growing season compared with none during the previous season (Table 3.2). Phylica cephalantha produces up to 10 flowers at the end of each shoot towards the end of the growing season. There was a weak correlation between shoot extension and number of flowers per shoot for control shrubs during 1984-85 (r=0.67, $d.f.$=6, P<0.05) In 1984-85, the number of flowers per shoot increased with N addition (P<0.05) whereas during 1985-86, flower production was reduced irrespective of fertilizer treatments (Table 3.2).

Rooting depth

The tap root of P. cephalantha extends to a depth of 1.3 m and laterals extend horizontally at a depth of approximately 0.3 m to a distance of over 2 m. Numerous surface feeder roots extend from the top of the tap root. Leucospermum parile roots to a depth of 2 m and also has extensive laterals and proteoid roots in the upper soil layers (Jongens-Roberts & Mitchell 1986).

Table 3.2. Percentage of dormant buds, mean number of inflorescences per shoot, and percentage allocation of shoot dry mass, nitrogen and phosphorus to inflorescences in Phylica cephalantha shrubs harvested in May-June 1985 and 1986 as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) at Pella, South Africa. C denotes unfertilized control.

Treatment	C	N	P	M	NP	NM	PM	NPM
Dormant buds per plant (%)								
1984-85	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1985-86	2.6	30.0	2.7	13.9	0.0	0.0	5.1	33.3
Mean number flowers per shoot								
1984-85	2.26	2.29	1.71	1.45	2.63	2.16	1.93	3.06
1985-86	1.11	0.54	0.84	1.13	1.43	0.30	0.84	0.70
Allocation of shoot Dry mass to inflorescences (%)								
1984-85	13.2	12.5	12.3	10.7	10.3	10.7	11.1	18.2
1985-86	10.1	14.7	5.8	19.4	4.9	0.7	9.5	17.7
Allocation of shoot phosphorus to inflorescences (%)								
1984-85	21.1	20.8	19.3	18.6	20.6	17.5	16.6	30.1
1985-86	16.3	19.5	9.5	31.4	9.6	1.3	16.5	29.9
Allocation of shoot nitrogen to inflorescences (%)								
1984-85	17.2	15.2	17.6	13.3	11.3	10.6	11.6	21.6
1985-86	11.5	15.9	6.2	24.1	4.7	0.8	11.7	20.6

Shoot dry mass

During 1984-85, leaf, twig and total shoot dry mass of *L. parile* increased with nitrogen addition ($P<0.01$), whereas in 1985-86, these were reduced with P and the interaction of P and M addition ($P<0.001$, Appendix 2; Fig. 3.3). Total shoot dry mass was similar in both growing seasons and no significant differences were found between control plants ($t=-1.17$, $d.f.=6$, $P>0.05$). There were no significant differences in leaf specific mass between treatments in 1984-85, although mean area per leaf increased with nitrogen addition ($P<0.05$, Table 3.1).

In 1984-85, N addition resulted in increases in leaf ($P<0.001$), stem, total shoot ($P<0.01$) and flower ($P<0.05$, Appendix 2) dry mass of *P. cephalantha* (Fig. 3.4). The proportion of shoot dry mass allocated to inflorescences was determined as a measure of reproductive effort. It varied from 10 % to 18 % but was not significantly different between treatments (Table 3.2). In 1985-86, shoot dry mass of *P. cephalantha* was only approximately half that of the previous growing season and inflorescence dry mass was even further reduced (Fig. 3.4). Several interactions were found between treatments (Appendix 2). Reproductive effort was reduced and more variable between treatments during 1985-86, with a coefficient of variation (CV) of 58 % for the control plants, compared to only 25 % during 1984-85 (Table 3.2).

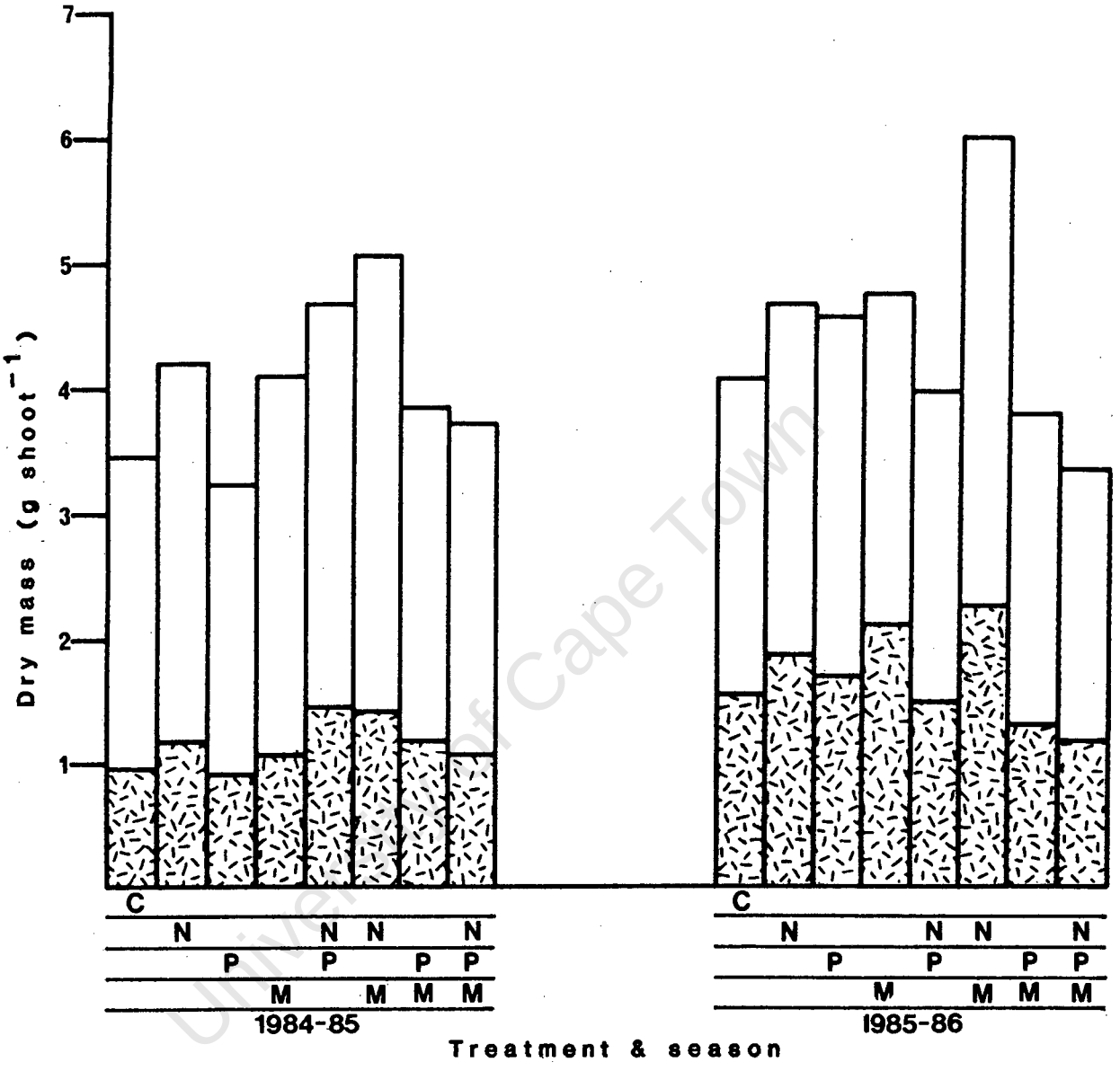

Fig. 3.3. Shoot mass of Leucospermum parile at the end of the 1984-85 and 1985-86 growing seasons as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Shading: □, leaf; ▨, twig. C denotes unfertilized control.

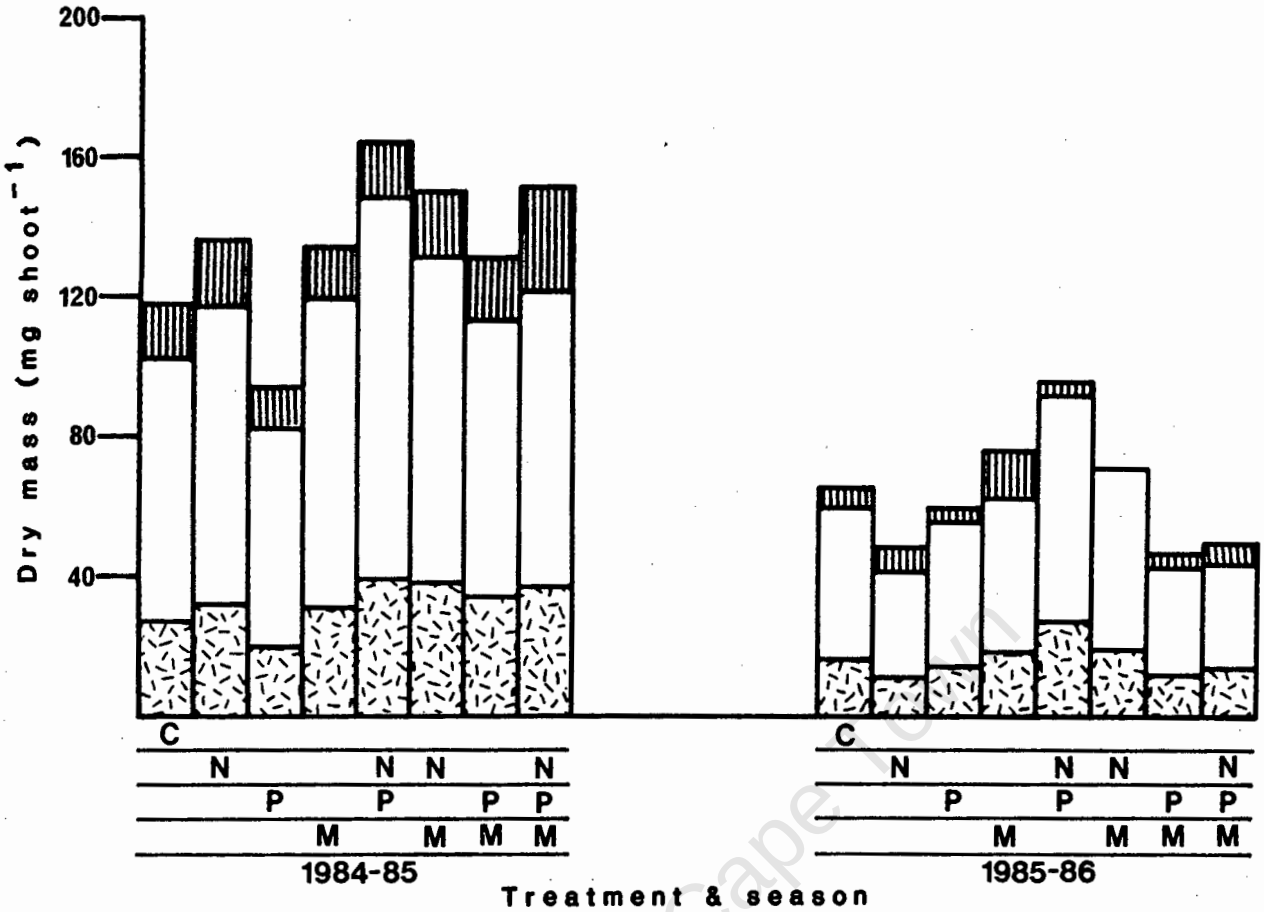

Fig. 3.4. Shoot mass of Phylica cephalantha at the end of the 1984-85 and 1985-86 growing seasons as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Shading: ☐, leaf; ▨, twig; ▥, inflorescence. C denotes unfertilized control.

Shoot phosphorus content

No significant differences in leaf, twig and total shoot phosphorus contents of *L. parile* were found between treatments during either growing season (Fig. 3.5). However, leaf and twig phosphorus concentrations were reduced by N addition in both seasons ($P<0.01$), as were one-year old twigs harvested in 1985-86 ($P<0.001$; Table 3.3). Leaf and twig phosphorus concentrations were reduced with N addition irrespective of whether P was added or not.

In 1984-85, *P. cephalantha* leaf phosphorus content increased with N addition ($P<0.05$) and that of twig, inflorescence and total shoot tended to be higher, whereas during 1985-86, that of total shoot, twig ($P<0.05$) and leaf ($P<0.01$) were reduced with the interaction of the P and M treatments (Fig. 3.6). Inflorescence phosphorus content and phosphorus allocation to inflorescences were not significantly different between treatments during either season (Table 3.2). Phosphorus allocation to inflorescences was more variable during 1985-86 with a CV of 54 % in the control plants compared with only 26 % during 1984-85 (Table 3.2). In 1984-85, *P. cephalantha* twig phosphorus concentration increased ($P<0.05$) with the interaction of N, P and M addition, while that of inflorescence was reduced with the addition of N ($P<0.01$; Table 3.4). In 1985-86, no significant difference in phosphorus concentration was found in the current season's shoots, whereas an increase in the

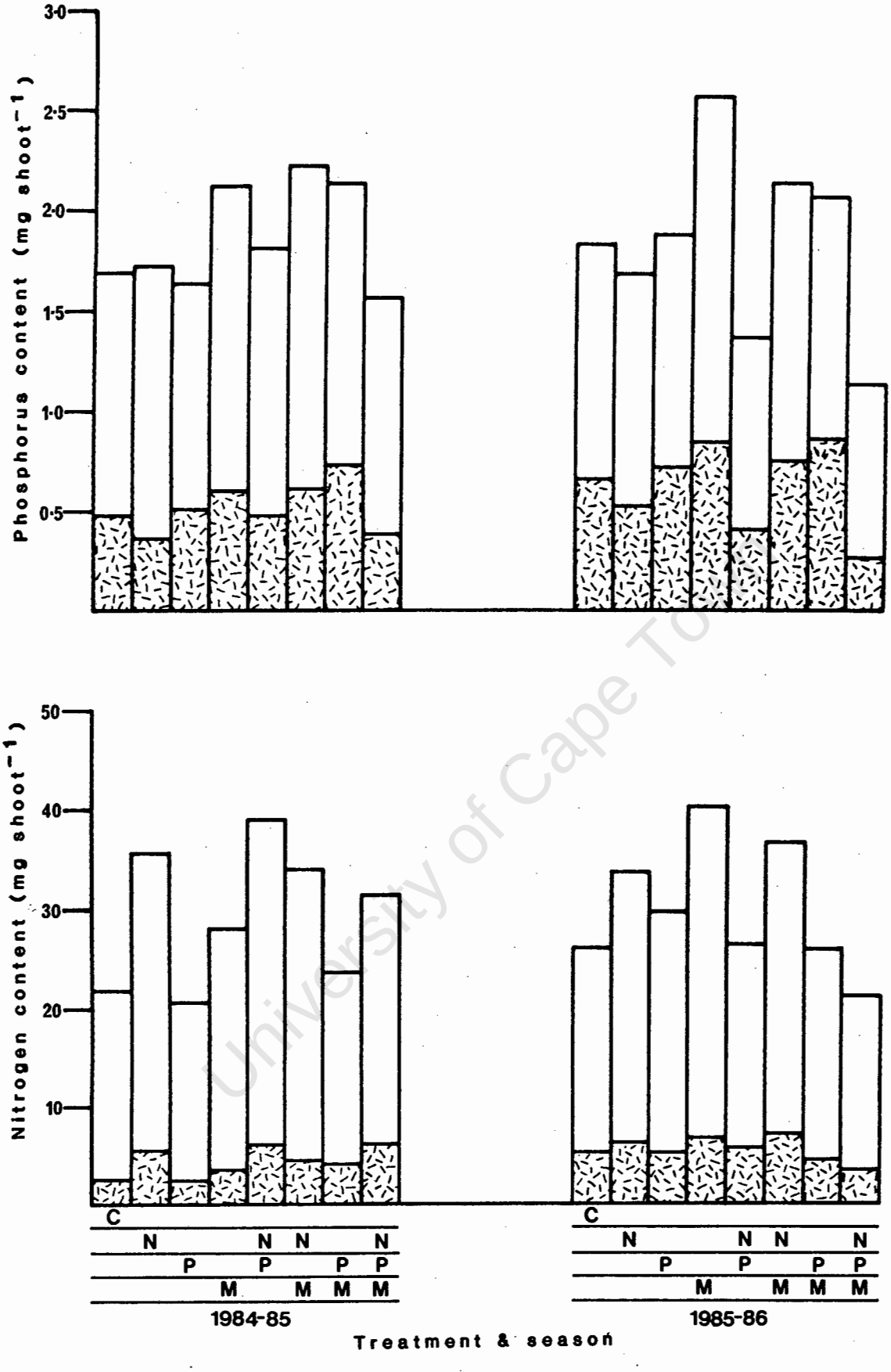

Fig. 3.5. Shoot phosphorus and nitrogen contents of Leucospermum parile at the end of the 1984-85 and 1985-86 growing seasons as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Shading: ☐, leaf; ▨, twig. C denotes unfertilized control.

Table 3.3. Tissue phosphorus (μg P g^{-1} dry mass) and nitrogen (mg N g^{-1} dry mass) concentrations (Mean ± 1 S.E.) of current shoots in May-June 1985 and 1986 and 1-year old leaves and twigs in 1986 and calcium, magnesium and potassium (mg g^{-1} dry mass) leaf concentrations in 1985 of Leucospermum parile as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) at Pella, South Africa. C denotes unfertilized control.

Tissue	Treatments							
	C	N	P	M	NP	NM	PM	NPM
Phosphorus								
1985								
Leaf	473 ±23	452 ±35	488 ±39	502 ±28	419 ±14	439 ±7	531 ±16	445 ±24
Twig	471 ±61	312 ±14	561 ±72	601 ±157	318 ±27	394 ±100	620 ±94	357 ±37
1986								
Leaf	437 ±24	409 ±28	400 ±29	451 ±48	388 ±41	378 ±39	488 ±47	388 ±8
Twig	436 ±44	289 ±49	409 ±59	382 ±58	266 ±40	322 ±71	697 ±185	239 ±35
1-year leaf	408 ±21	424 ±40	390 ±34	388 ±10	367 ±9	341 ±28	461 ±44	371 ±19
1-year twig	340 ±32	234 ±21	349 ±84	336 ±56	248 ±44	243 ±22	437 ±51	244 ±39
Nitrogen								
1985								
Leaf	7.52 ±.63	9.91 ±.47	7.69 ±1.3	7.94 ±.66	9.79 ±.84	8.02 ±.88	7.28 ±.55	9.46 ±1.0
Twig	2.68 ±.22	4.65 ±.22	2.59 ±.48	3.30 ±.26	3.95 ±.44	3.03 ±.41	3.48 ±.14	5.78 ±.50
1986								
Leaf	7.86 ±.23	9.56 ±.70	8.41 ±1.1	8.87 ±.46	8.40 ±.35	7.90 ±.47	8.57 ±.59	7.94 ±.49
Twig	3.72 ±.47	3.30 ±.48	3.04 ±.07	3.35 ±.26	3.84 ±.51	3.13 ±.12	3.45 ±.25	3.31 ±.39
1-year leaf	6.34 ±.36	7.22 ±.54	6.11 ±.36	6.99 ±.26	6.91 ±.40	5.77 ±.28	6.39 ±.32	6.49 ±.32
1-year twig	2.59 ±.16	2.91 ±.14	2.86 ±.36	2.88 ±.18	2.84 ±.29	2.41 ±.15	2.75 ±.22	3.00 ±.27
Cations 1985								
Leaf-Ca	3.93 ±.30	4.14 ±.15	4.19 ±.79	4.78 ±.62	3.78 ±.28	4.14 ±.52	4.76 ±.47	4.33 ±.24
Leaf-Mg	3.29 ±.17	4.00 ±.28	3.73 ±.13	4.27 ±.12	3.26 ±.34	3.55 ±.38	3.46 ±.31	3.90 ±.27
Leaf-K	1.77 ±.07	2.04 ±.05	1.67 ±.17	1.98 ±.23	1.70 ±.05	2.21 ±.10	1.92 ±.01	2.12 ±.18

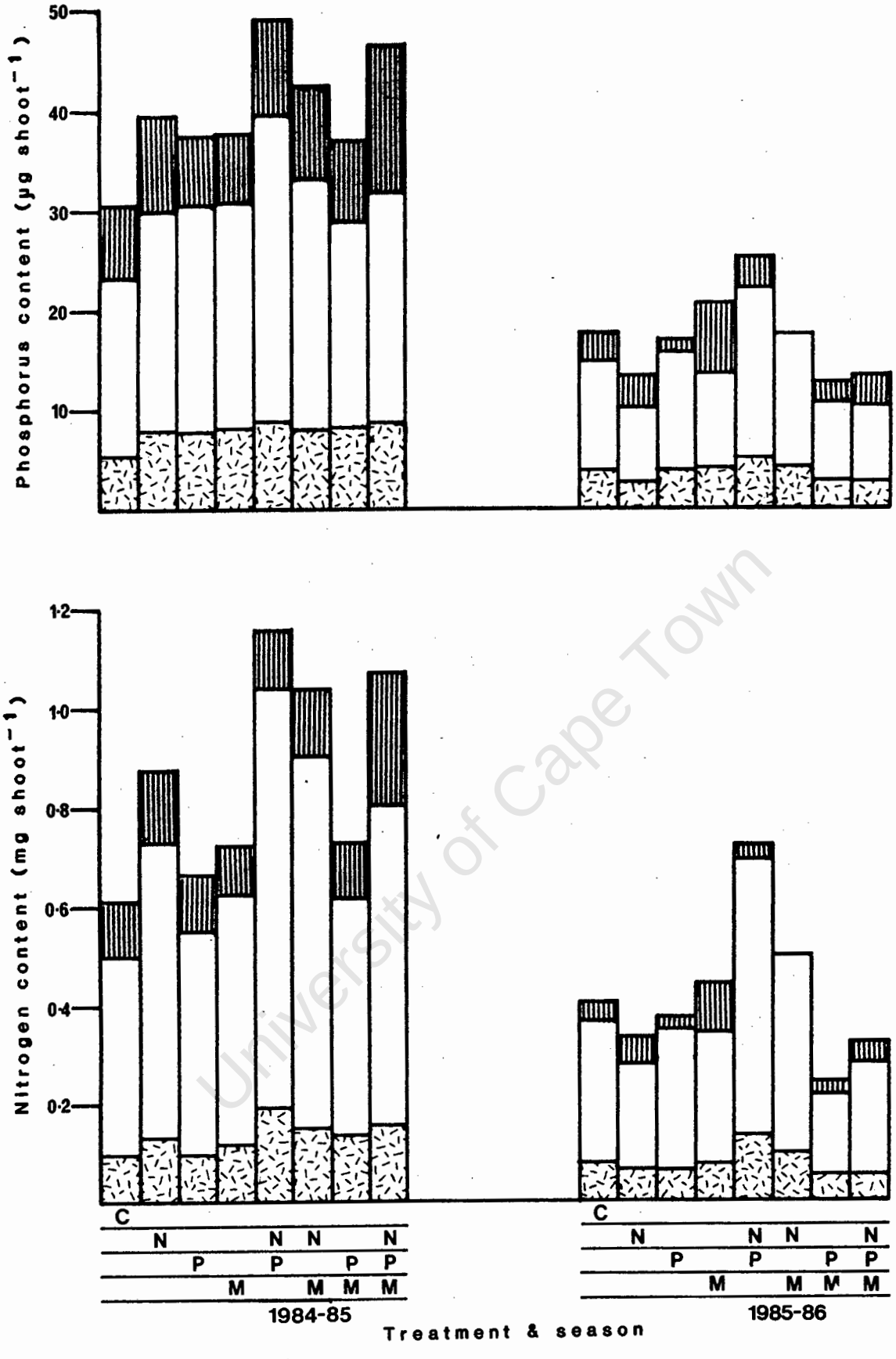

Fig. 3.6. Shoot phosphorus and nitrogen contents of Phylica cephalantha at the end of the 1984-85 and 1985-86 growing seasons as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Shading: □, leaf; ▨, twig; ▥, inflorescence. C denotes unfertilized control.

Table 3.4. Tissue phosphorus (μg P g^{-1} dry mass) and nitrogen (mg N g^{-1} dry mass) concentrations (Mean ± 1 S.E.) of current shoots in May-June 1985 and 1986 and 1-year old leaves and twigs in 1986, of Phylica cephalantha as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) at Pella, South Africa. C denotes unfertilized control.

Tissue	Treatments							
	C	N	P	M	NP	NM	PM	NPM
Phosphorus								
1985								
Leaf	267 ±8	257 ±5	283 ±10	255 ±21	284 ±6	268 ±9	267 ±21	278 ±18
Twig	229 ±19	250 ±5	300 ±38	264 ±32	220 ±17	218 ±9	235 ±24	242 ±25
Inflorescence	459 ±20	484 ±40	484 ±15	478 ±29	611 ±64	470 ±42	421 ±15	535 ±20
1986								
Leaf	255 ±9	257 ±25	287 ±27	239 ±28	266 ±10	262 ±7	255 ±17	246 ±24
Twig	244 ±12	231 ±26	273 ±23	258 ±61	231 ±24	229 ±16	250 ±17	229 ±24
Inflorescence	487 ±22	475 ±21	466 ±13	510 ±32	526 ±17	480 ±41	505 ±18	517 ±40
1-year leaf	249 ±8	238 ±11	248 ±12	217 ±24	264 ±16	249 ±7	246 ±12	239 ±23
1-year twig	217 ±7	228 ±9	248 ±24	200 ±11	200 ±11	181 ±5	222 ±14	207 ±9
Nitrogen								
1985								
Leaf	5.99 ±.53	7.01 ±.21	5.66 ±.28	5.74 ±.44	7.80 ±.26	7.97 ±.59	5.78 ±.65	7.65 ±.46
Twig	4.07 ±.14	4.10 ±.14	3.66 ±.10	3.79 ±.31	4.66 ±.38	4.06 ±.26	3.96 ±.31	4.17 ±.33
Inflorescence	7.39 ±.43	7.83 ±.36	7.53 ±.86	6.25 ±.71	7.72 ±.36	6.45 ±.66	5.60 ±.82	8.01 ±.93
1986								
Leaf	6.46 ±.64	7.06 ±.62	6.91 ±.37	6.05 ±.49	8.59 ±.36	7.63 ±.81	5.56 ±.43	7.00 ±.93
Twig	4.77 ±.39	5.19 ±.56	4.57 ±.61	4.12 ±.34	5.25 ±.31	4.97 ±.26	4.38 ±.23	3.75 ±.23
Inflorescence	6.57 ±.31	7.86 ±.36	6.84 ±.47	7.11 ±.29	7.04 ±.21	7.57 ±.29	7.14 ±.33	7.05 ±.51
1-year leaf	5.98 ±.14	6.58 ±.08	6.20 ±.27	6.07 ±.49	6.84 ±.37	6.34 ±.64	4.37 ±.61	6.08 ±.51
1-year twig	4.74 ±.33	4.61 ±.23	4.32 ±.27	4.60 ±.18	4.88 ±.34	4.75 ±.22	4.31 ±.28	4.83 ±.27

one-year old twigs with P addition ($P<0.05$) and a reduction with M addition ($P<0.05$) were found (Table 3.4).

Shoot nitrogen content

In 1984-85, leaf, twig and total shoot nitrogen contents of L. parile increased in response to N addition ($P<0.01$, Fig. 3.5), an average increase of 60 % and 113 % for leaf and twig respectively, compared with the control. However, in 1985-86, leaf nitrogen content was reduced with P addition ($P<0.05$). In 1984-85, leaf ($P<0.01$) and twig ($P<0.001$) nitrogen concentrations increased with N addition, whereas no differences in current or one-year old shoots were found between treatments during 1985-86 (Table 3.3).

In 1984-85, leaf, total shoot ($P<0.01$) and twig ($P<0.05$) nitrogen contents of P. cephalantha increased with N fertilization (Fig. 3.6) and inflorescence nitrogen content also tended to be higher. In 1985-86, total shoot, twig ($P<0.05$) and leaf ($P<0.01$) nitrogen content decreased with the interaction of P and M addition (Fig. 3.6). No significant differences in inflorescence nitrogen content and nitrogen allocation to inflorescences were found between treatments during either growing season (Table 3.2). Nitrogen allocation to inflorescences was more variable in the second, compared with the first season; ie. CV for control plants of 63 % and 23 % respectively. In the 1984-85 growing season, P. cephalantha leaf nitrogen concentration increased in response to N addition ($P<0.001$),

whereas that of inflorescence was reduced by M addition ($P<0.05$; Table 3.4). In 1985-86, current leaf and inflorescence nitrogen concentrations were increased with N fertilization and twigs with M addition ($P<0.05$), whereas that of one-year old leaves were increased with N addition ($P<0.001$) and reduced with M addition ($P<0.05$; Table 3.4).

Shoot Ca, Mg and K contents of Leucospermum parile

In the 1984-85 season, leaf Mg content increased with M addition ($P<0.05$) and leaf K with N addition ($P<0.05$), while leaf Ca and K contents tended to increase with M addition (Fig. 3.7). Leaf Mg concentration varied significantly with the interaction of the N, P and M treatments ($P<0.01$) and leaf K concentration increased with M ($P<0.01$) and N addition ($P<0.05$; Table 3.3).

Canopy area and volume

In all plots from 1984 to 1986, total canopy area and volume per plot of L. parile increased, whereas that of P. cephalantha decreased slightly during the drier 1985-86 growing season (Table 3.5). Pre-fertilizer addition variation in the canopy area of L. parile was greater than that of P. cephalantha (Table 3.5). This is because L. parile regenerates from seeds, which mostly fall below the canopy of the parent plant resulting in a clumped distribution of this species in the first few years after fire. Density-dependent competition between these seedlings results in mortality which was noted as a mean

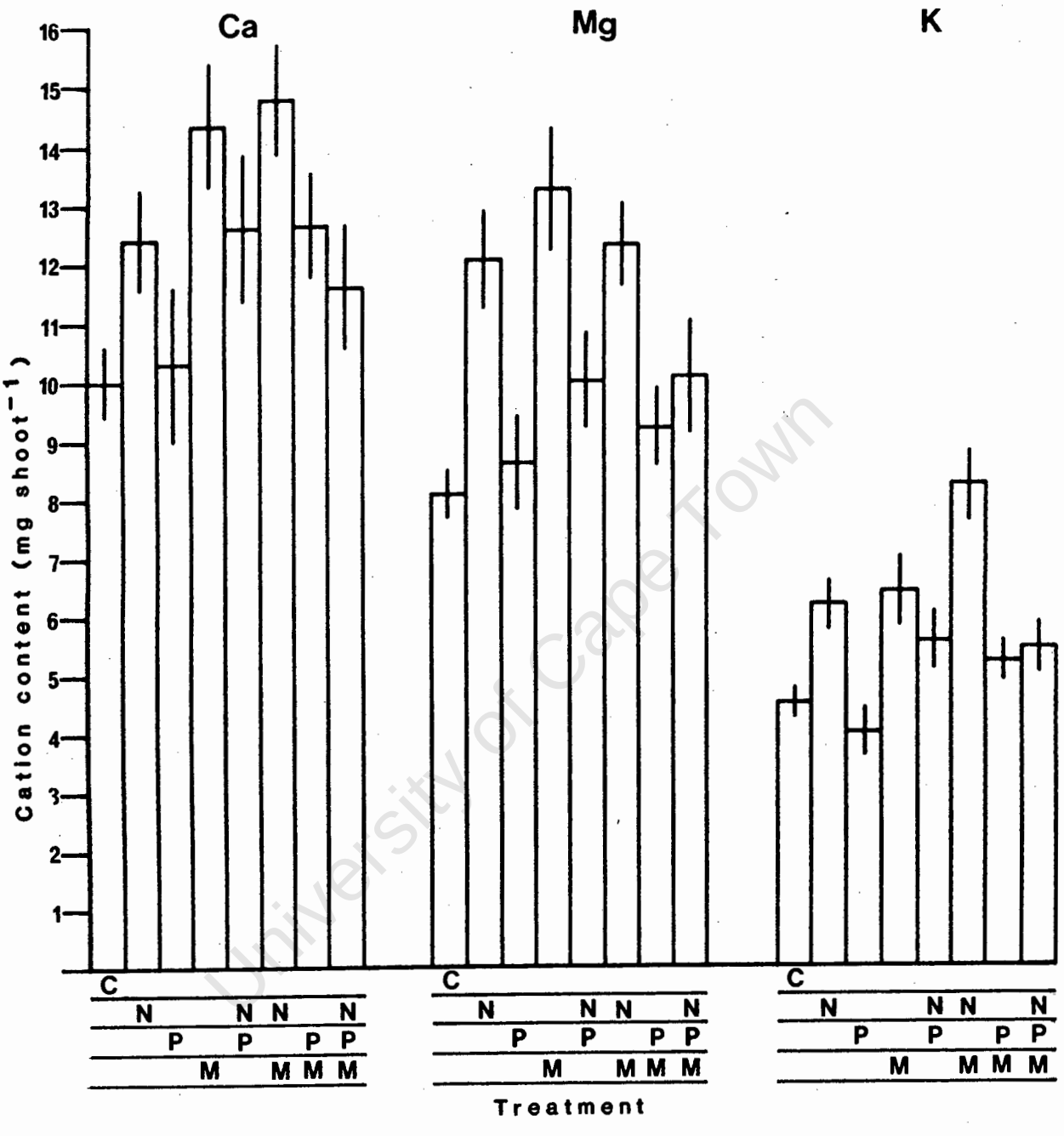

Fig. 3.7. Leaf calcium, magnesium and potassium contents of Leucospermum parile at the end of the 1984-85 growing season as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. C denotes unfertilized control.

Table 3.5. Total canopy area (m^2) and canopy volume (m^3) and number of individual shrubs (Mean ± 1 S.E.) of Leucospermum parile and Phylica cephalantha in 5x5 m subplots in September 1984 (pre-fertilization) and September 1985 and 1986, one and two years after application of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) at Pella, South Africa. C denotes unfertilized control.

Species		Treatment							
		C	N	P	M	NP	NM	PM	NPM
L. parile									
Canopy area:	84	0.83 ±0.46	0.28 ±0.16	1.12 ±1.00	0.35 ±0.21	0.90 ±0.22	1.21 ±0.93	0.95 ±0.46	0.78 ±0.50
	85	1.69 ±0.64	0.75 ±0.28	2.38 ±1.88	1.17 ±0.55	2.35 ±0.59	2.56 ±1.87	2.79 ±1.00	1.47 ±0.90
	86	2.72 ±0.79	1.27 ±0.39	2.82 ±2.00	2.08 ±0.90	2.97 ±0.66	2.89 ±1.74	4.03 ±0.79	2.43 ±1.42
Canopy volume:	84	0.41 ±0.29	0.12 ±0.08	0.45 ±0.42	0.09 ±0.05	0.46 ±0.17	0.59 ±0.51	0.38 ±0.21	0.31 ±0.23
	85	1.05 ±0.56	0.19 ±0.07	1.30 ±1.12	0.47 ±0.19	1.45 ±0.43	1.75 ±1.43	1.42 ±0.56	1.12 ±0.87
	86	1.77 ±0.62	0.87 ±0.31	1.81 ±1.38	1.15 ±0.42	2.26 ±0.47	1.88 ±1.29	2.43 ±0.48	1.57 ±1.07
Shrub number:	84	4.8 ±1.1	1.8 ±0.5	5.0 ±2.2	7.5 ±5.2	3.0 ±0.6	4.5 ±1.3	7.0 ±1.9	4.3 ±0.9
	85	3.9 ±0.7	1.5 ±0.3	5.0 ±2.2	5.8 ±3.1	3.0 ±0.6	4.5 ±1.3	6.5 ±1.8	3.5 ±1.2
	86	3.6 ±0.8	1.5 ±0.3	3.5 ±1.9	5.3 ±2.9	2.3 ±0.5	4.0 ±1.5	6.3 ±1.8	2.8 ±1.4
P. cephalantha									
Canopy area:	84	3.83 ±0.57	3.54 ±0.56	4.00 ±0.46	4.30 ±1.28	4.13 ±0.57	6.36 ±0.34	3.86 ±0.45	3.46 ±0.47
	85	3.69 ±0.46	3.54 ±0.74	4.11 ±0.72	3.85 ±1.27	3.75 ±0.34	5.89 ±0.37	3.71 ±0.44	2.98 ±0.34
	86	3.12 ±0.52	2.87 ±0.41	3.28 ±0.36	3.46 ±1.25	3.07 ±0.51	5.17 ±0.63	3.74 ±0.55	2.97 ±0.33
Canopy volume:	84	1.77 ±0.31	1.71 ±0.39	1.78 ±0.24	2.03 ±0.65	1.59 ±0.30	3.09 ±0.15	1.88 ±0.31	1.62 ±0.30
	85	1.70 ±0.22	1.66 ±0.45	1.77 ±0.18	1.83 ±0.69	1.76 ±0.15	2.96 ±0.14	1.85 ±0.28	1.43 ±0.26
	86	1.39 ±0.25	1.22 ±0.39	1.37 ±0.17	1.59 ±0.62	1.36 ±0.25	2.35 ±0.23	1.60 ±0.28	1.21 ±0.21
Shrub number:	84	14.4 ±2.4	15.8 ±2.5	17.8 ±2.8	12.0 ±2.4	14.5 ±3.3	18.0 ±1.5	13.8 ±2.8	11.5 ±0.9
	85	13.5 ±2.2	18.8 ±3.1	19.8 ±4.8	13.0 ±4.1	13.5 ±2.4	18.5 ±1.3	12.8 ±5.0	12.8 ±1.6
	86	12.9 ±1.6	12.5 ±1.4	16.3 ±3.9	10.8 ±2.7	12.3 ±1.6	17.3 ±2.3	13.5 ±2.1	11.5 ±1.3

reduction in shrubs per plot of 11 % and 13 % during the first and second growing seasons respectively. No significant differences in total canopy area and volume per plot of either species were found between treatments.

DISCUSSION

The consistent growth response of both species to N fertilization in the first (1984-85) but not the second (1985-86) season, during which soil inorganic nitrogen concentrations in the N fertilized plots were no longer elevated (Chapter 2), indicates that nitrogen may often limit vegetative growth in evergreen shrub species of sand-plain lowland fynbos. These small growth increases corresponded with increased tissue concentrations and contents of nitrogen during 1984-85. Phosphorus addition however tended to result in reduced growth of both species during both seasons. Concentrations of available phosphorus remained significantly higher in the soils of the P fertilized plots throughout the study period (Chapter 2). The tendency for phosphorus addition to reduce growth is probably the result of a nutrient imbalance. The effects of M addition were more variable and often interacted with N or P addition.

This growth response to nitrogen is different to the general response to phosphorus in the edaphically similar Australian

heathlands (eg. Heddle & Specht 1975). Two hypotheses are proposed which may explain this difference. Firstly, the soil nitrogen pools may have been depleted by the artificially short (4-6 year) burning frequency at Pella (Boucher & Shepherd 1987), resulting in loss of nitrogen due to volatilization and thus a greater response by the vegetation to nitrogen addition. There is evidence from other mediterranean-type ecosystems that short-term burning frequencies can lead to site degradation (Marion 1982). Volatilization of N from a fynbos fire has been estimated as 20.4 - 158.5 kg ha^{-1} (Stock 1985). Nitrogen input by fixation in indigenous legumes and free-living soil micro-organisms in the fynbos biome have not been studied and indigenous legumes are a minor component of the vegetation (Hoffman et al. 1987), while atmospheric input of nitrogen is significant (1.99 kg ha^{-1} $year^{-1}$; Stock & Lewis 1986a). Secondly, it is hypothesized that on acid soils, growth responses to phosphorus may be greater in moister fynbos ecosystems, while responses to nitrogen may be greater in drier areas, such as Pella, because of differences in soil N : P ratios in moist and dry fynbos ecosystems. A strong positive correlation has been found between soil total nitrogen concentration and annual rainfall in the montane regions of the fynbos biome (Campbell 1983). Most of these mountains consist of Table Mountain sandstone which supports a soil with very low total and available phosphorus concentrations (Witkowski & Mitchell 1987) and thus the soil

N : P ratio increases with increasing rainfall. Tilman (1982) argues that species specialize not on particular resources but on ratios of resources and thus the soil N : P ratio may be more important than the absolute amounts of N and P. The largest responses to nitrogen fertilization in a nutrient-poor tundra ecosystem were found in the driest community rather than in the more mesic and wet-mesic communities (Henry et al. 1986). Similarly pine plantations in moist mountain catchments in the Cape have shown greater growth responses to P rather than N addition (Schönau 1983).

Leaves and twigs were found to be sites of nutrient storage in L. parile, whereas in P. cephalantha only the leaves performed this function. In a seasonal study, Jongens-Roberts & Mitchell (1986) found that leaves were the major sites of phosphorus storage in L. parile. Stems were found to be major sites of nutrient accumulation in the Australian Proteaceae species Banksia ornata and B. marginata (Groves et al. 1986). Storage or luxury consumption of nutrients is related to an asynchronous organ growth pattern (Mooney et al. 1977). Root growth of L. parile and thus nutrient uptake occurs predominantly during the wet winter - early spring period (Jongens-Roberts & Mitchell 1986), while shoot growth occurs in spring and summer when temperatures and photosynthetically active radiation are high. A similar

pattern of growth was found for the fynbos restioid species Thamnochortus punctatus (Stock et al. 1987).

In L. parile, no significant difference in leaf specific mass was found between treatments. Leaf specific mass has been used as a measure of sclerophylly and varies with water supply (Miller 1983), phosphorus (Mooney 1983) and nitrogen content (Gulmon & Chu 1981). It is positively correlated with leaf duration and the longest leaf durations generally occur on plants occupying the most nutrient-poor habitats (Mooney 1983). Leaf specific mass of L. parile has been shown to increase with leaf age (Jongens-Roberts & Mitchell 1986) and the lack of change in leaf specific mass in this investigation may be due to the low levels of nutrients applied.

An approximately 50 % reduction in shoot dry mass increments in P. cephalantha and a delay in the commencement of shoot growth was found in the second, compared with the first growing season, irrespective of fertilizer treatments. Dormant shoots were found in P. cephalantha but not L. parile and flower production was also reduced in P. cephalantha. This could be the result of two possibilities. Firstly, the hotter and drier weather during the summer of 1985-86 may have resulted in increased moisture stress in P. cephalantha. Secondly the production of a large fruit crop during the previous season may have depleted the nutrient reserves of this species, resulting in

delayed and reduced shoot production. Alternating years of high and low reproduction, and negative relationships between reproductive output and subsequent vegetative growth are well-known phenomena in many iteroparous species (Harper 1977; Samson & Werk 1986). In addition, fruit production of P. cephalantha shrubs during November 1985 and 1987 was observed to be much greater than that during November 1984 and 1986 (personal observation).

The nutrient treatments had no effect on the date of commencement of shoot extension for either species and this may be controlled either by the environment or by endogenous rhythms within the plant (Pierce 1984). The addition of N plus M resulted in increased branching in L. parile during 1985-86. In other mediterranean regions such as the Californian chaparral, addition of N plus P stimulated new shoot production in Adenostoma fasciculatum shrubs (McMaster et al. 1982), and it has previously been shown that N application can overcome apical dominance in several species (McIntyre 1977).

A deeper rooting system probably allows L. parile to maintain active shoot growth until April, compared with January-February for P. cephalantha, and this may also confer a greater ability to withstand seasonal drought. Fertilizer nutrient uptake may have been allocated to below ground growth or below ground storage in the resprouting P. cephalantha to replenish root reserves depleted by the rapid

above-ground growth after fire. As the vegetation ages, the probability of a wildfire increases, and replenishment of root reserves is essential for rapid post-fire growth. Phylica cephalantha may have shown a greater growth response if fertilized at a younger post-fire age, because early successional species grow rapidly and exhibited a greater growth response to nutrient additions when young (Chapin et al. 1986).

The growth response of these indigenous fynbos species to nutrient additions, both in terms of shoot and canopy growth, was relatively small and was similar to that of slow growing evergreen shrubs from other nutrient-poor ecosystems (Specht 1963; McMaster et al. 1982; Chapin 1980; Chapin et al. 1986; Grime et al. 1986). Fynbos shrubs are well adapted to low nutrient availability and appear to exhibit a low degree of plasticity in vegetative growth. Under conditions when nutrients become more available, these plants may readily exploit these nutrients and store them without changing their allocation patterns (Bloom et al. 1985).

In this study, the evergreen shrub species responded to nitrogen fertilization by small increases in vegetative growth and storage of nitrogen. Phosphorus, however resulted in either no growth response or a tendency to reduce vegetative growth. Although the results of

fertilization during the two year period of this study exhibit the greater influence of nitrogen addition, over a longer time period, phosphorus addition will probably result in more significant changes in nutrient cycling and species composition because of the longer residence time of phosphorus in these soils compared with nitrogen (Chapter 2).

CHAPTER 4

RESPONSE OF A LOWLAND FYNBOS ECOSYSTEM, SOUTH AFRICA, TO NUTRIENT ADDITIONS. III. ALLOCATION OF DRY MASS, PHOSPHORUS AND NITROGEN IN THE ENDEMIC PLANT *THAMNOCHORTUS PUNCTATUS* PILL. (RESTIONACEAE)

(To be submitted to Oecologia)

SUMMARY

The effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) on dry mass, phosphorus and nitrogen contents and allocation patterns in pre-reproductive and reproductively mature male Thamnochortus punctatus Pill. (Restionaceae) plants growing in 4-6 year-old post-fire sand-plain lowland fynbos vegetation was studied. In pre-reproductive plants, increased nitrogen concentrations and contents in all plant parts and increased allocations of dry mass and phosphorus to shoots were found with N addition. An increase in the allocation of dry mass to the rhizome and roots in response to M addition may be indicative of a nutrient imbalance. In reproductively mature male plants, N addition resulted in increased allocations of dry mass, nitrogen and phosphorus to vegetative branches (juvenile character) and decreased allocations of dry mass and nitrogen to culms and inflorescences (mature characters), indicating delayed reproductive output. Phosphorus addition resulted in increased phosphorus concentrations in all tissues except inflorescences in the reproductive plants, and the sole addition of P tended to increase the allocations of dry mass and nitrogen to inflorescences. In T. punctatus, phenotypic plasticity in response to nutrient additions, appears to be related to its sequential seasonal organ growth pattern and nutrient storage, rather than large

increases in plant size. It is concluded that vegetative growth of T. punctatus in these nutrient-poor fynbos soils is limited by soil nitrogen concentrations. Nitrogen addition resulted in increased above-ground vegetative growth and a reduction in the allocation of resources to the inflorescences. Phosphorus addition appears to result in increased resource allocation to the inflorescences and M addition to the below-ground parts.

INTRODUCTION

The soils of the fynbos biome have been shown to be low in phosphorus (Mitchell et al. 1984; Witkowski & Mitchell 1987) and nitrogen (Stock & Lewis 1986b) and are more similar to those of Australian heaths than other mediterranean-type ecosystems. In south-eastern Australian heaths, the vegetation responded to P addition with markedly increased vegetative growth, and for some species, increased flowering (Specht 1963). Additions of nitrogen, Cu or Zn provoked no response, these elements being deficient for the growth of introduced herbaceous plants (Riceman 1948). Short-lived understorey species showed the greatest response to added nutrients, while long lived, deep rooting, overstorey species such as Banksia ornata (Proteaceae) showed only a small growth response. In the Californian chaparral however, the shrub species studied responded to nitrogen and

combined nitrogen and phosphorus addition (McMaster et al. 1982).

The Restionaceae consist of 290 species in the fynbos biome (Bond & Goldblatt 1984), they are wiry aphyllous hemicryptophytes with photosynthetic culms and occupy the niche normally filled by graminoids in adjacent biomes (Linder 1984) and make up a large proportion of the understorey vegetation (Specht et al. 1983). Restionaceae have shallow fibrous root systems, often confined to the 0-15 cm soil depth (Linder 1984; Moll & Sommerville 1985; Higgins et al. 1987). They appear to be non-mycorrhizal but characteristic root clusters known as capillaroid roots may be present (Lamont 1982). Thamnochortus punctatus Pill., a dominant restioid species of sand-plain lowland fynbos, has a caespitose funnel shaped habit, reaches reproductive age after three years and is dioecious. It is usually water stressed in summer and autumn (Miller et al. 1983; Moll & Sommerville 1985), and its shape and the persistence of standing dead culms in the older plants has been postulated to act as a mechanism to trap mist (Moll & Romoff 1983). The seasonal allocation patterns of dry mass and nitrogen have been studied in reproductively mature male T. punctatus plants (Stock et al. 1987).

This paper describes the effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a

mixture of all essential nutrients excluding N and P (M) on dry mass, nitrogen and phosphorus contents and allocation patterns in the various above- and below-ground organs of pre-reproductive and reproductively mature male T. punctatus, in 4-6 year-old post-fire sand-plain lowland fynbos at Pella, South Africa.

STUDY AREA

The study site was the CSIR Fynbos Biome intensive study site at Pella, on the Burgherspost Farm, 62 km North of Cape Town (33° 31' S, 18° 32' E; altitude 160-220 m; area 269 ha) on the coastal forelands of the south western Cape Province, South Africa. The climate is mediterranean (Csa and Csb), characterized by dry summers and wet winters (Schulz 1947). The 49 year mean annual rainfall is 522 mm, the mean annual temperature is 17.3° C and frost is virtually absent (Jarman & Mustard 1987). The soils are well drained acidic aeolian sands of approximately 2 m in depth, of the Clovelly soil form (orthic A horizon overlying a yellow-brown apedal B), Geelhout series, according to the South African binomial classification (MacVicar et al. 1977). The vegetation is broadly classified as sand-plain lowland fynbos (Moll et al. 1984) and is described as Thamnochortus punctatus - Leucospermum parile mid-high open shrubland of Phylica cephalantha fynbos (Boucher & Shepherd 1987). The site was burnt by a moderately intense wildfire in November 1980.

Regeneration of T. punctatus from seeds occurred during the following winter (1981), and a second cohort in the winter of 1982.

METHODS

Thirty-two 10x5 m plots, separated by 5 m wide strips, were positioned in a grid pattern (8x4) on a gentle 5^{o} easterly slope in homogeneous undisturbed four-year-old post-fire vegetation in the centre of a 26 ha patch of Clovelly soil. Each plot was randomly assigned one of eight nutrient treatment combinations, namely: nitrogen (N), phosphorus (P), all essential nutrients excluding N and P (M), nitrogen plus phosphorus (NP), all essential nutrients excluding phosphorus (NM), all essential nutrients excluding nitrogen (PM), all essential nutrients (NPM) and unfertilized control (C). An additional four plots positioned at the corners of the grid were used as further unfertilized controls. Thus each treatment combination was replicated four times except the control which was replicated eight times. Five g N m^{-2} as NH_4NO_3 and 0.5 g P m^{-2} as $Ca_3(PO_4)_2$, these being the approximate amounts returned to the soil and surface ash after a fire at Pella in November 1980 (Brown & Mitchell 1986; Stock & Lewis 1986b), were added in liquid form during 15-17 September 1984, towards the end of the rainy season. All other nutrients were based on a Long Ashton nutrient solution (Hewitt & Smith 1975) in proportion to the N and P

additions. A detailed description of the nutrients used and methods of application is given in Chapter 2.

In March 1985, one pre-reproductive unsexed plant of age 2-3 years was harvested from each plot. These plants were part of the second cohort of seedlings which germinated approximately 20 months after the fire, and were chosen because a greater proportion of their life-span had been influenced by the fertilizer addition compared with the first cohort. In March 1986, when inflorescence growth had peaked (during anthesis), reproductively mature 4-5 year-old male plants were harvested. The latter portion of the growing season was selected as previous studies on herbs indicated that this was the period of minimal above ground nutrient change (Grigal & Ohmann 1980; Stock et al. 1987). The plant's roots were harvested by digging around the root system to a depth of 30 cm and the whole soil monolith was removed and washed from the root system. Only roots attached to the rhizome were harvested as part of the plant. In the field, the pre-reproductive plants were divided into roots, rhizome and shoots (which only consisted of vegetative branches at this stage; terminology from Stock et al. 1987), to obviate translocation of nutrients between plant parts after harvesting. The shoots of the reproductive plants were divided into culms, vegetative branches and inflorescences. Plant material was oven-dried at 80^{o} C for 48 h, ground to 40 mesh and nitrogen and

phosphorus analyzed in triplicate. Total nitrogen was determined by Kjeldahl digestion of 0.1 g of plant material, using a selenium catalyst, salicylic acid and sodium thiosulphate to convert nitrate and nitrite to ammonium which was determined colorimetrically (Smith 1980). Total phosphorus was determined by digesting 0.1 g of plant material by the method of Jackson (1958), and the phosphate concentration was measured colorimetrically (Murphy & Riley 1962).

These data were analyzed by three-way analysis of variance (SAS GLM procedure; SAS Institute 1985). In the reproductive plants, allocations of dry mass, nitrogen and phosphorus were determined for above-ground plus rhizome plant parts as some root material may have been lost during harvesting. All percentage allocation data were arcsin transformed prior to statistical analysis (Zar 1984).

RESULTS

Dry mass production and allocation pattern

No significant differences in total dry mass were found between treatments for either age of plant ($P>0.05$; Fig. 4.1), probably due to mean treatment combination coefficients of variation of approximately 50% for both ages. Apart from the possibility of uneven nutrient addition, and the proximity of competing plants, the

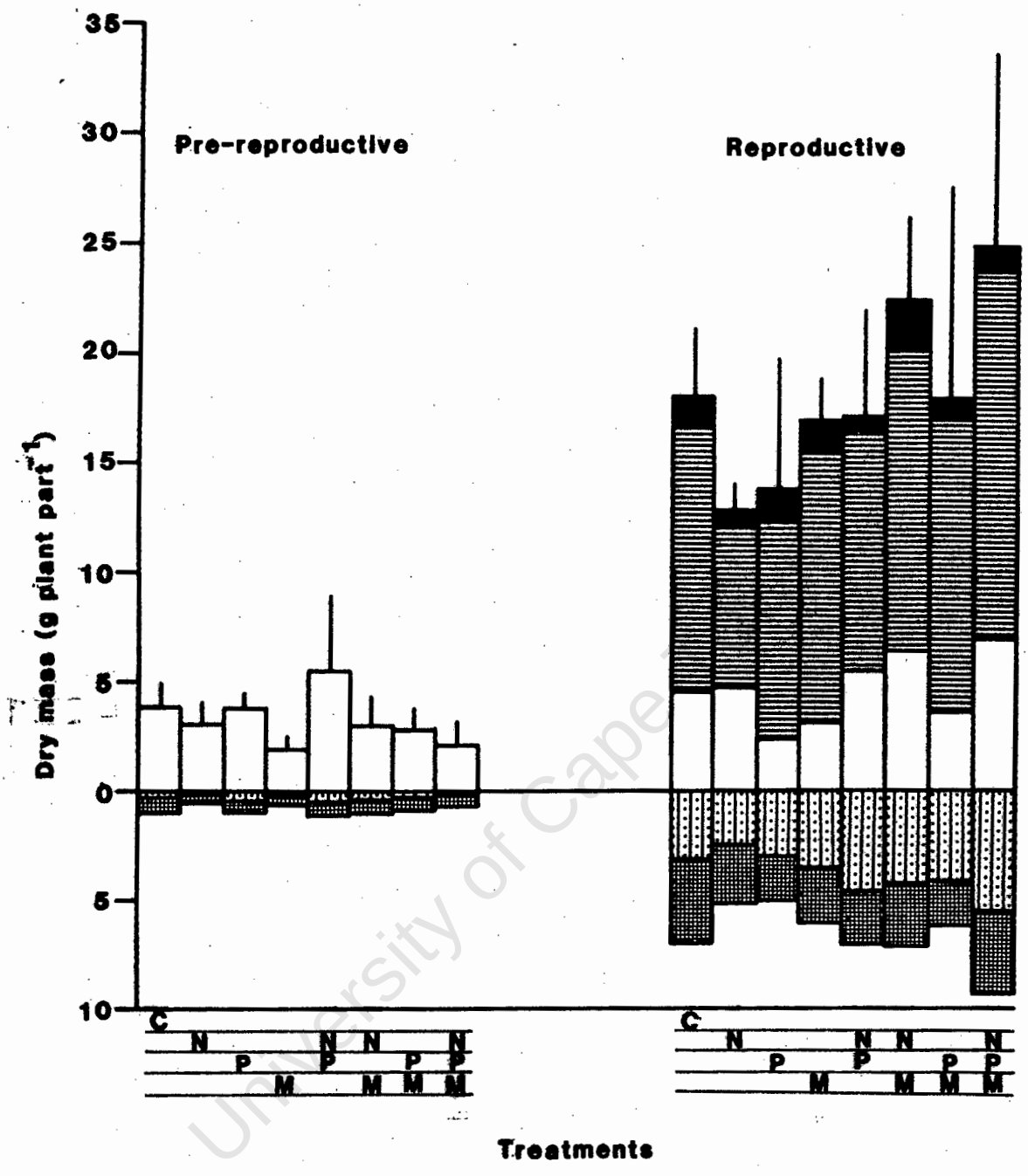

Fig. 4.1. Dry mass (g; Mean) of inflorescences ( ), vegetative branches ( ), culms ( ), rhizome ( ) and roots ( ) in pre-reproductive and reproductive Thamnochortus punctatus plants amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Pre-reproductive plants were unsexed, 2-3 year-old and harvested in March 1985, and reproductive plants were 4-5 year-old males harvested in March 1986. Vertical bars represent S.E. of total plant dry mass. C, denotes unfertilized control.

variance in plant mass is also a function of the rate of growth, the duration of growth and the size per plant at the start of the period (Benjamin & Hardwick 1986). Highest total plant dry mass was recorded for the NP amended pre-reproductive plants and NPM and NM amended reproductive plants. There were significant differences in rhizome and root dry mass with the interaction of P and M addition in pre-reproductive plants whereas increased vegetative branch dry mass was found in reproductive plants amended with N ($P<0.05$; Fig. 4.1).

In pre-reproductive plants, an increased allocation of dry mass to shoots with N addition was found ($P<0.05$), whereas a reduction in allocation to shoots and an increase to the rhizome ($P<0.05$) were found with M addition (Table 4.1). In the reproductive plants, an increased allocation of dry mass to vegetative branches ($P<0.01$) and a decrease to culms and inflorescences ($P<0.05$) were found in response to N addition. Reproductive effort (allocation of dry mass to inflorescences) tended to be highest in plants amended with the sole addition of P (8.1 %). Nitrogen addition resulted in the lowest reproductive effort, with mean values for the four treatment combinations containing N ranging from 3.1 % to 4.2 %.

Table 4.1. Percentage dry mass allocation to plant parts and root/shoot (below- to above-ground) ratios (Mean) of Thamnochortus punctatus amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P), and a mixture of all essential nutrients excluding N and P (M), applied on 15-17 September 1984 at Pells, South Africa. Pre-reproductive plants were 2-3 year-old and harvested in 1985, and reproductive plants were 4-5 year-old males harvested in 1986. C, denotes unfertilized control.

Plant Parts	Treatment							
	C	N	P	M	NP	NM	PM	NPM
Pre-reproductive								
Shoots	77.8	83.0	75.7	72.8	80.4	75.2	76.6	78.5
Rhizome	9.5	6.1	9.5	11.3	7.6	11.1	10.0	8.9
Roots	12.7	10.9	14.7	15.9	12.1	13.7	14.4	12.5
Root/shoot ratio	0.29	0.21	0.32	0.37	0.24	0.33	0.33	0.28
Reproductive								
Inflorescences	6.6	4.2	8.1	6.0	3.3	4.2	4.1	3.1
Branches	21.2	30.2	16.1	14.6	24.8	24.4	15.5	29.8
Culms	56.7	49.5	59.8	60.9	51.1	54.9	61.7	49.2
Rhizome	15.5	16.2	16.1	18.4	20.8	16.5	18.7	17.9
Root/shoot ratio	0.42	0.36	0.46	0.41	0.41	0.38	0.41	0.35

Phosphorus uptake and allocation pattern

A significant increase in the phosphorus content of shoots was found with the interaction of all three treatments ($N^{*}P^{*}M$, $P<0.05$; Fig. 4.2) in the pre-reproductive plants. In the reproductive plants, an increase in rhizome phosphorus content was found with P addition ($P<0.05$). Allocation of phosphorus was increased to the shoots ($P<0.01$) and reduced to the rhizome and roots ($P<0.05$) of N amended pre-reproductive plants (Table 4.2). An increase in phosphorus allocation to vegetative branches ($P<0.01$) and a decrease to inflorescences ($P<0.05$) with N addition and an increase to the rhizome with P addition ($P<0.05$) were found in reproductive plants. Allocation of phosphorus to inflorescences tended to be highest in the control plants (20 %) and lowest in the four treatment combinations containing N, with means ranging from 6.2 % to 11.6 %.

No significant differences in phosphorus concentration were found in the plant parts of pre-reproductive *T. punctatus* (Table 4.3). Culms and roots ($P<0.01$), vegetative branches ($P<0.05$) and the rhizome ($P<0.001$), although not inflorescences, exhibited increased phosphorus concentrations in the P amended reproductive plants. Phosphorus concentrations in the culms, rhizome and roots of P amended plants were increased by 35 %, 58 % and 54 % respectively, compared with the control.

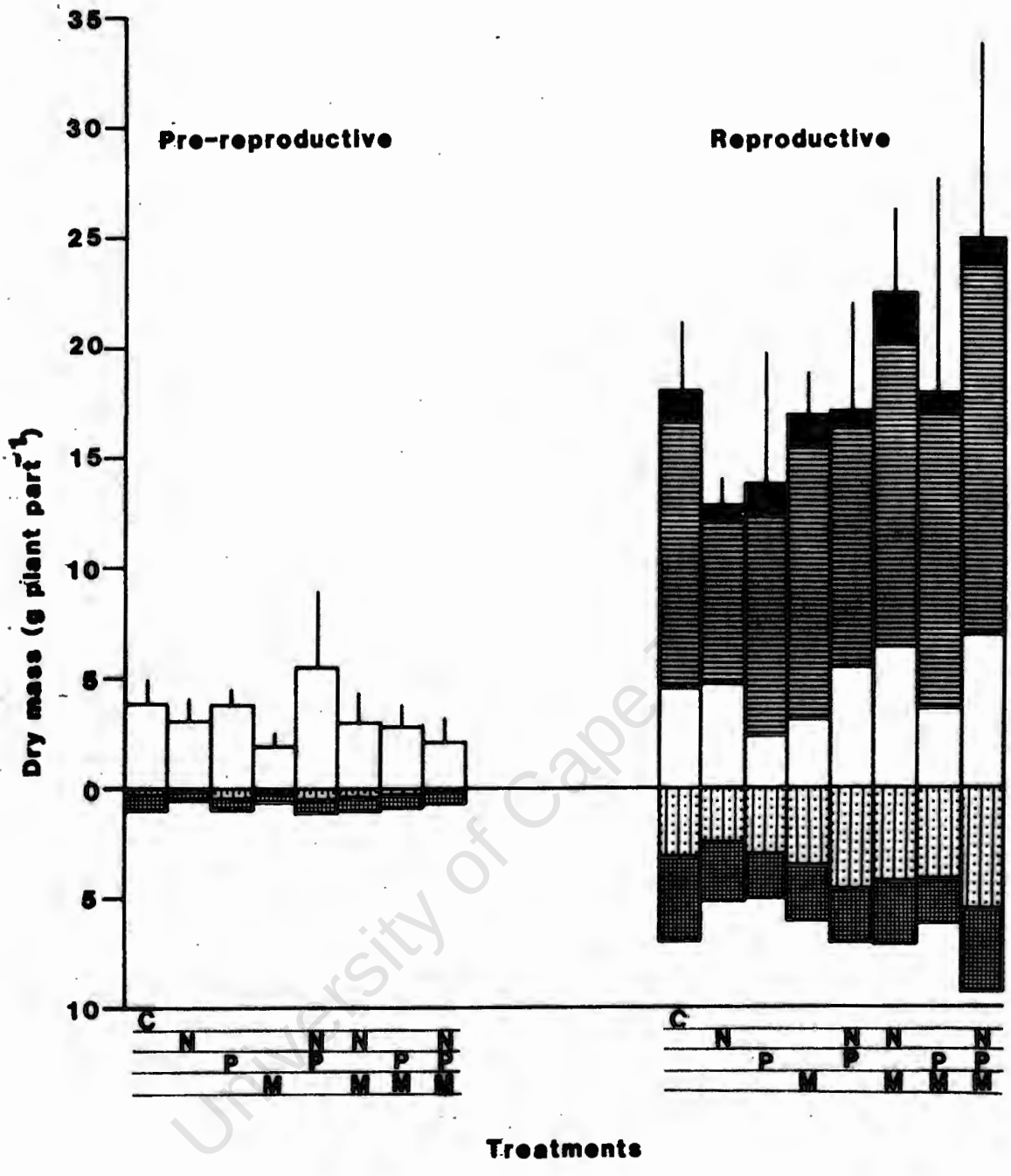

Fig. 4.1. Dry mass (g; Mean) of inflorescences ( ), vegetative branches ( ), culms ( ), rhizome ( ) and roots ( ) in pre-reproductive and reproductive Thamnochortus punctatus plants amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Pre-reproductive plants were unsexed, 2-3 year-old and harvested in March 1985, and reproductive plants were 4-5 year-old males harvested in March 1986. Vertical bars represent S.E. of total plant dry mass. C, denotes unfertilized control.

Table 4.2. Percentage phosphorus and nitrogen allocation to plant parts and root/shoot (below- to above-ground) phosphorus and nitrogen ratios (Mean) of Thamnochortus Punctatus amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P), and a mixture of all essential nutrients excluding N and P (M), applied on 15-17 September 1984 at Pella, South Africa. Pre-reproductive plants were 2-3 year-old and harvested in 1985, and reproductive plants were 4-5 year-old males harvested in 1986. C, denotes unfertilized control.

	Treatment							
Plant Parts								
Phosphorus	C	N	P	M	NP	NM	PM	NPM
Pre-reproductive								
Shoots	81.3	82.8	78.2	75.6	86.8	84.2	80.4	84.8
Rhizome	7.4	6.1	9.9	10.0	4.4	6.3	8.4	6.0
Roots	11.4	11.0	11.9	14.4	8.8	9.5	11.2	9.2
Root/shoot ratio	0.24	0.22	0.30	0.32	0.15	0.19	0.25	0.18
Reproductive								
Inflorescences	19.7	11.3	18.0	14.6	6.2	11.6	10.3	7.4
Branches	16.9	29.2	11.1	11.3	21.9	22.2	13.9	26.2
Culms	52.0	47.4	54.7	60.2	52.5	53.5	56.4	51.2
Rhizome	11.5	12.0	16.3	14.0	19.3	12.7	19.3	15.3
Root/shoot ratio	0.32	0.33	0.36	0.33	0.39	0.28	0.40	0.36
Nitrogen								
Pre-reproductive								
Shoots	90.3	91.2	91.6	85.8	88.9	86.6	88.6	90.6
Rhizome	4.7	3.5	2.4	5.7	3.3	4.6	4.6	4.3
Roots	5.0	5.3	6.0	8.6	7.7	8.8	6.8	5.1
Root/shoot ratio	0.11	0.10	0.09	0.17	0.12	0.16	0.13	0.10
Reproductive								
Inflorescences	9.7	5.9	12.9	8.5	4.4	6.3	6.1	3.7
Branches	26.0	42.8	18.4	19.5	36.2	33.1	18.8	39.8
Culms	55.8	43.2	58.9	61.1	49.2	52.5	64.8	47.0
Rhizome	8.5	8.1	9.7	10.9	10.2	8.1	10.3	9.5
Root/shoot ratio	0.23	0.22	0.21	0.22	0.20	0.18	0.20	0.23

Table 4.3. Phosphorus and nitrogen concentrations (μg g^{-1} and mg g^{-1} dry mass respectively; Mean ± S.E.) of plant parts of Thamnochortus punctatus amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Pre-reproductive plants were 2-3 year-old and harvested in 1985, and reproductive plants were 4-5 year-old males harvested in 1986. C, denotes unfertilized control.

Plant Parts	Treatment							
	C	N	P	M	NP	NM	PM	NPM
Phosphorus								
Pre-reproductive								
Shoots	219±20	207±22	198±22	189±19	243±28	244±9	265±45	318±70
Rhizome	167±20	154±10	185±64	159±13	130±13	125±11	220±53	205±43
Roots	192±29	162±9	155±17	165±12	163±2	155±25	212±23	213±38
Reproductive								
Inflorescences	547±46	462±31	629±87	502±74	517±42	473±86	541±45	533±64
Branches	147±13	175±10	182±36	138±42	250±58	165±25	212±55	217±43
Culms	184±23	173±10	262±16	175±25	286±48	181±15	210±26	238±25
Rhizome	154±24	139±34	286±17	135±22	264±53	139±21	236±61	190±30
Roots	162±16	160±25	274±40	184±16	273±63	161±16	242±30	208±34
Nitrogen								
Pre-reproductive								
Shoots	9.02 ±0.79	12.90 ±1.70	8.07 ±0.81	8.38 ±0.44	11.24 ±1.15	9.95 ±1.19	7.44 ±0.22	13.32 ±1.02
Rhizome	3.88 ±0.30	7.02 ±0.26	2.80 ±0.24	3.59 ±0.62	4.57 ±0.44	3.51 ±0.77	2.92 ±0.23	5.73 ±0.42
Roots	2.95 ±0.17	6.05 ±0.82	2.73 ±0.24	3.77 ±0.43	6.45 ±0.34	5.55 ±0.40	3.32 ±0.19	4.55 ±0.75
Reproductive								
Inflorescences	9.40 ±0.52	8.70 ±0.44	8.86 ±1.40	8.97 ±0.98	8.6 ±1.15	9.83 ±0.44	9.05 ±1.05	7.94 ±1.24
Branches	7.32 ±0.75	8.77 ±0.42	6.34 ±0.88	7.48 ±1.05	9.83 ±1.14	9.26 ±0.76	7.57 ±0.58	9.78 ±1.06
Culms	6.07 ±0.33	5.33 ±0.12	5.42 ±0.68	5.47 ±0.33	6.49 ±0.71	6.28 ±0.27	6.37 ±0.70	6.54 ±0.43
Rhizome	3.36 ±0.26	3.07 ±0.12	3.27 ±0.33	3.16 ±0.21	3.28 ±0.29	3.20 ±0.13	3.34 ±0.36	3.62 ±0.28
Roots	3.92 ±0.21	3.85 ±0.38	3.41 ±0.31	3.55 ±0.38	4.26 ±0.43	4.33 ±0.26	3.60 ±0.65	4.37 ±0.38

Nitrogen uptake and allocation pattern

Significant increases in the nitrogen content of shoots, the rhizome ($P<0.05$), roots ($P<0.01$) and of the total plant ($P<0.05$) were found in pre-reproductive plants and in the vegetative branches ($P<0.01$) of reproductive *T. punctatus* in response to N addition (Fig. 4.3). A decrease in nitrogen allocation to shoots and an increase to roots ($P<0.05$) were found in M amended pre-reproductive plants, although this was nullified when both P and M were added (ie. a significant interaction between P and M addition, $P<0.05$; Table 4.2). An increase in nitrogen allocation to the rhizome with M addition ($P<0.05$) and a decrease with P addition ($P<0.05$) were also found. In reproductive plants, nitrogen allocations to inflorescences and culms were reduced ($P<0.01$) and allocation to vegetative branches ($P<0.001$) increased in response to N addition (Table 4.2). Nitrogen allocation to inflorescences tended to be highest in plants treated with the sole addition of P (12.9 %). Nitrogen addition resulted in the lowest nitrogen allocation to inflorescences, with means for the four treatment combinations containing nitrogen ranging from 3.7 % to 6.3 %, compared with 9.7 % for the control.

In pre-reproductive plants, all plant parts exhibited significantly increased tissue nitrogen concentrations ($P<0.001$) with N addition, while a decrease in rhizome nitrogen concentration with P addition was also found

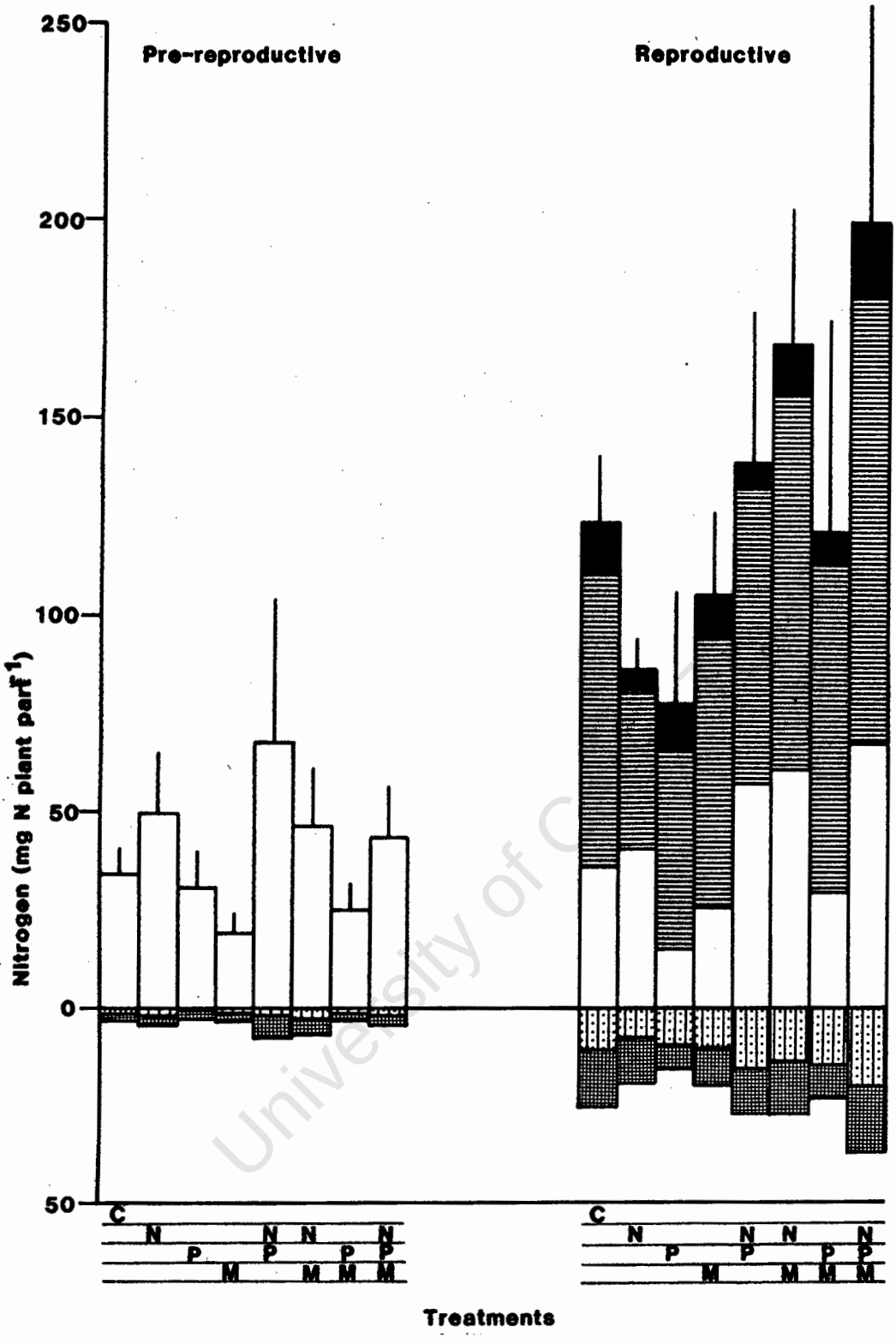

Fig. 4.3. Nitrogen content (mg N; Mean) of inflorescences (■), vegetative branches (□), culms (▤), rhizome (▦) and roots (▩) in pre-reproductive and reproductive Thamnochortus punctatus plants amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Pre-reproductive plants were unsexed, 2-3 year-old and harvested in March 1985, and reproductive plants were 4-5 year-old males harvested in March 1986. Vertical bars represent S.E. of total plant nitrogen content. C, denotes unfertilized control.

($P<0.01$; Table 4.3). Significant interactions were found in vegetative branches ($P^{*}M$; $P<0.05$), the rhizome ($N^{*}P$, $P^{*}M$ and $N^{*}P^{*}M$; $P<0.05$) and roots ($N^{*}M$; $P<0.05$). In reproductive plants, an increase in nitrogen concentration was only found in the vegetative branches of N amended plants ($P<0.01$). Nitrogen concentrations increased with N addition in the shoots, rhizome and roots of pre-reproductive plants by 31 %, 34 % and 92 % respectively, and in the vegetative branches of reproductive plants by 29 % compared to the control.

DISCUSSION

In perennial, evergreen plants growing in nutrient-poor soils, Mooney et al. (1977) suggested that an asynchronous growth pattern enables a plant to perform better because of an ability to re-utilize existing plant nutrient capital for sequential development of all organs. Thamnochortus punctatus displays a sequential seasonal organ growth pattern, with root growth occurring predominantly in winter, culm growth in spring to early summer, followed by inflorescence development in late summer (Stock et al. 1987). Water and thus nutrient uptake is halted in autumn because of water stress resulting from reduced soil moisture content (Moll & Sommerville 1985) and by the shedding of the absorptive root cortex during summer (Stock et al. 1987). Maximum activity of specialized root uptake mechanisms,

except those attached to some deep rooted plants appears to be restricted to winter-spring (Lamont 1982). This growth pattern in T. punctatus is possible because of the ability of these plants to reallocate scarce nutrients from senescing and possibly also seasonally dormant organs from one season to the next (Stock et al. 1987).

After fertilizer addition in September 1984, 2-3 year-old pre-reproductive T. punctatus exhibited increased nitrogen concentrations and contents in all plant parts in response to N addition. This together with significantly increased allocations of dry mass and phosphorus to shoots and a reduction to the rhizome in N amended plants may have enabled them to increase their photosynthetic capacity. A reduction in dry mass allocation to shoots and an increase to the rhizome in pre-reproductive plants, in response to M addition, may be indicative of a nutrient imbalance or an induced nitrogen deficiency, resulting in increased below-ground growth. No phenotypic nutrient deficiency symptoms were observed and increased below-ground growth is probably an adaptation to increase nitrogen acquisition from the soil.

The increased allocation of resources to vegetative branches (juvenile character) and decreased allocations to culms and inflorescences (mature characters) in reproductively mature plants, in response to N addition, indicates a slowing down

of the life-cycle of the plant. Plants amended with the sole addition of P tended to exhibit the highest reproductive effort and allocation of nitrogen to reproduction. McMaster et al. (1982) also found that N addition resulted in increased vegetative growth in the chaparral shrub Adenostoma fasciculatum, while P addition resulted in increased reproduction. In the Australian heaths, P addition speeded up the life-cycle of certain species by lowering the age of reproduction and senescence (Specht 1963; Heddle & Specht 1975).

The root to shoot ratio of a plant at any point in time is simultaneously subject to genetic, ontogenetic and environmental control (Hunt & Burnett 1973; Hunt & Nicholls 1987). The partitioning of resources between below- and above-ground plant parts is jointly controlled by the absolute amounts of below- and above-ground environmental stress, by the below- to above-ground environmental stress ratio, and by the growth potential of the species itself (Hunt & Nicholls 1987). The decrease in below- to above-ground ratios of dry mass and nitrogen in pre-reproductive plants, in response to N addition compared with the other treatments, indicates a reduction in (below-ground) nutrient stress as a result of nitrogen addition. No significant differences in the below- to above-ground ratios of dry mass, phosphorus or nitrogen were found in the reproductively mature plants. However, soil nitrate and

ammonium concentrations had returned to control levels during the rainy season of the year prior to harvesting (July 1985), although soil phosphorus concentrations remained elevated throughout the study period (Chapter 2). Similar results were found by Hunt et al. (1975) for cranberry (Vaccinium macrocarpon Ait.).

Phenotypic plasticity in T. punctatus, in response to a nutrient flush, appears to be related to its sequential seasonal organ growth pattern (Stock et al. 1987) and nutrient storage, rather than greatly increasing plant size. Plants growing in nutrient-poor soils from numerous parts of the world have been described as "slow-growing and conservative" (Chapin 1980) and respond to nutrient additions by nutrient storage and changes in resource allocation patterns (Bloom et al. 1985; Grime et al. 1986).

In conclusion, T. punctatus plants growing in Clovelly soil at Pella are limited by soil nitrogen concentrations. This species however, has adapted to the low soil N levels by its sequential seasonal organ growth pattern. It responds to nutrient flushes by changes in resource allocation to the various above- and below-ground plant parts and by nutrient storage (luxury consumption) and can thus be classified as a nutrient stress tolerant species (sensu Grime 1977). Nitrogen addition results in increased above-ground vegetative growth and a reduction in allocation of resources

to reproduction. Phosphorus addition appears to result in increased resource allocation to the inflorescences and M addition to the below-ground parts.

CHAPTER 5

RESPONSE OF A LOWLAND FYNBOS ECOSYSTEM, SOUTH AFRICA, TO NUTRIENT ADDITIONS. IV. LITTER PRODUCTION AND NUTRIENT RETURN

(To be submitted to the South African Journal of Botany)

SUMMARY

Litter production and nitrogen and phosphorus return were determined at bimonthly intervals for three years in 10x5 m plots amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M), in a 4-7 year-old post-fire sand-plain lowland fynbos ecosystem, South Africa. Litter production increased with vegetation age, was highly seasonal and peaked from late spring to mid-summer (November to January). It was positively correlated with wind run and absolute monthly maximum temperature. No significant differences in annual litter production and N return were found between treatments for the first two years after fertilizer addition, although both tended to increase during the second year in response to N and M addition. Phosphorus return increased significantly with P, and to a lesser extent N addition, during the first year, but increased with N and M, and decreased with P addition, during the second year. Nutrient applications did not result in changes in the timing of the peak litter production period or the growth form composition of litter. An increase in the proportion of proteoid and a decrease in ericoid and miscellaneous litter occurred during the study period. Litter layer dry mass, nitrogen and phosphorus contents increased in response to N and M addition, while P addition resulted in increased phosphorus contents. The November 1985 litter collection period coincided with an

unusually dry and hot period and resulted in increased litter production with the interaction of N and M addition. This is interpreted as a response to moisture stress which was exacerbated by the increased shoot growth in response to fertilizer addition.

INTRODUCTION

The vegetation structure and growth form composition of the Cape fynbos was found to be divergent to the northern hemisphere and Chilean matorral mediterranean-type ecosystems, and this has been attributed to the more nutrient-poor soils of the Cape (Cody & Mooney 1978; Cowling & Campbell 1980). The evergreen sclerophyllous shrubs, characteristic of the nutrient-poor mediterranean regions, produce a low quality litter in terms of both organic and inorganic constituents (Read & Mitchell 1983). Reabsorption of nitrogen and phosphorus prior to leaf abscission and re-allocation of these nutrients is a mechanism to cope with low soil nutrient levels (Chapin 1980), and results in a low quality litter. Decomposition of litter and turnover times in lowland and mountain fynbos vegetation has been shown to be very slow (Mitchell *et al.* 1986; Mitchell & Coley 1987). Turnover time for the leaf litter of the sclerophyllous shrub, *Protea repens* (Proteaceae), was more rapid in a higher nutrient status mountain fynbos community than a lowland fynbos community

(Mitchell & Coley 1987). The effects of nutrient additions on litter production and nutrient return has been little studied in mediterranean-type ecosystems. Increased growth of a proteoid (Leucospermum parile), an ericoid (Phylica cephalantha) and a restioid (Thamnochortus punctatus) species (the three dominant growth forms) were found in response to N addition in a nutrient-poor sand-plain lowland fynbos ecosystem (Chapters 3 & 4). Nutrients taken up by the plant, in response to fertilizer addition, may be stored, utilized for increased vegetative growth and reproductive output, or result in litter with increased nutrient contents.

The effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) on litter production and nitrogen, phosphorus, Ca, Mg and K return to the soil, were studied in a nutrient-poor sand-plain lowland fynbos ecosystem at Pella, South Africa. In addition, the effects of nutrient additions on the growth form composition of litter and the litter layer were determined. In chaparral, litterfall makes up over 90 % of the annual dry mass and nitrogen and phosphorus return to the soil, the rest occurring as branch mortality, throughfall and stemflow (Gray 1983). Similarly, litterfall was responsible for nearly all the nitrogen and phosphorus return of Corsican pine trees (Miller et al. 1976), while the nitrogen and

phosphorus contents of throughfall and stemflow in a woodland recently established on heathland was found to be the same or less than in precipitation (Alcock & Morton 1985). Throughfall and stemflow are probably even less important in the fynbos because of the lower foliar nitrogen and phosphorus concentrations and higher leaf specific mass (more sclerophyllous nature) of fynbos sclerophylls (Mooney 1983). In addition, branch mortality is low in vegetation of this age (4-7 years) and therefore only litterfall was monitored.

STUDY AREA

The study site was the Fynbos Biome intensive study site at Pella (33^{o} 31' S; 18^{o} 32' E; area 269 ha; altitude 160-220 m), located on the Burgherspost Farm in the Malmesbury district of the Cape Province, South Africa. It has a true mediterranean, warm temperate climate designated CSa according to Köppen's system (Schultz 1947). Mean annual rainfall (1928-1976) is 522 mm and mean annual temperature is 17.3^{o} C. Strong, predominantly south-easterly winds occur in summer and north-westerlies in winter, with mean wind speeds of 22.4 and 17.4 km h^{-1} respectively (Jarman & Mustart 1987). The vegetation is dominated by the three typical fynbos growth forms, namely: ericoid, which are low evergreen leptophyllous shrubs; proteoid, which are taller evergreen sclerophyllous shrubs with broad isobilateral

leaves; and restioid, aphyllous hemicryptophytes of the Cyperaceae and Restionaceae (Taylor 1978), which together make up over 95 % of the biomass of mature stands of vegetation. The fire-prone vegetation at Pella reaches maximum cover and species richness five years after fire (Hoffman et al. 1987). The vegetation was previously burnt by a moderate wildfire in November 1980 and was approximately four years of age at the beginning of the study. Most of the species become reproductively mature after 3 years, flower during winter and spring, while shoot extension occurs during spring and summer (Sommerville 1983). The soil type was classified as a Clovelly form Geelhout series, according to the South African classification system (MacVicar et al. 1977). The soils consist predominantly of medium textured, acidic aeolian sands of a low phosphorus and nitrogen status (Mitchell et al. 1984; Stock & Lewis 1986b).

METHODS

A fertilizer study was initiated on four-year old sand-plain lowland fynbos vegetation at Pella south-western Cape, South Africa during 15-17 September 1984. Thirty-two 10x5 m plots separated by 5 m wide strips were positioned on a gentle 5^{o} easterly slope, in homogeneous undisturbed vegetation, in the centre of a 26 ha patch of Clovelly soil. Each plot was randomly assigned one of eight fertilizer

additions, namely: nitrogen (N), phosphorus (P), a mixture of all essential nutrients excluding N and P (M), nitrogen and phosphorus (NP), all essential nutrients excluding phosphorus (NM), all essential nutrients excluding nitrogen (PM), all essential nutrients (NPM) and unfertilized control (C). An additional four plots positioned at the corners of the grid were used as further unfertilized controls. Five g N m^{-2} as NH_4NO_3 and 0.5 g P m^{-2} as $Ca_3(PO_4)_2$ were added, these being the approximate amounts returned to the soil and surface ash after a wildfire at Pella in November 1980 (Brown & Mitchell 1986; Stock & Lewis 1986b). All other nutrients were based on a Long Ashton nutrient solution (Hewitt & Smith 1975) in proportion to the N and P additions (Chapter 2).

Random litter was collected at bimonthly intervals from litter traps of area 0.125 m^2 placed centrally in each plot. The shallow (4 cm depth), flat-bottomed traps were made of fine polyester mesh (0.5 mm) glued to the edge of a circular frame of galvanized hoop-iron. The trap diameter of 0.4 m was approximately the distance between shrubs. Traps were placed onto plots two days after fertilizer addition, and litter collected for 26 month, after which part of the study site was consumed by another wildfire (end of November 1986). Litter was collected from the ten remaining unburnt plots for a further 12 months. Litter collected during the peak production periods of November 1984 and 1986 was sorted

into the growth form categories of ericoid, restioid, proteoid and miscellaneous. The litter layer was collected from 18 of the original 36 plots as the remainder were destroyed before they could be collected in the November 1986 wildfire. Sampling was by means of four 30x30 cm quadrats placed systematically across the plot. Litter samples were dried at 70° C for 72 h and litter layer samples for 1 week. Animal excrement, fras and sand were removed prior to weighing and then all samples were ground to 40 mesh in a Wiley mill for nutrient analyses.

Phosphorus and nitrogen were determined for all samples. Phosphorus was determined on 0.1 g plant material by the methods of Jackson (1958) and Murphy & Riley (1962). Total nitrogen was determined on 0.1 g plant material by standard Kjeldahl procedures using a selenium catalyst, salicylic acid and sodium thiosulphate to convert nitrate and nitrite to ammonium, which was determined colorimetrically (Smith 1980). Litter layer samples and those collected at peak (November) and lowest litter production periods (July) were also analyzed for Ca, Mg and K. These cations were determined on 1 g material ashed in a muffle furnace at 550° C for 5 h, dissolved in $HF/HCl/HNO_3$ (1:8:4) and concentrations of each determined on a Varian No. 6 atomic absorption spectrophotometer.

Litter production and its phosphorus, nitrogen, Ca, Mg and K contents were analyzed by three-way analysis of variance with repeated measures (SAS GLM procedure, SAS Institute 1985). Annual litter production and N and P return were analyzed by three-way analysis of variance. Five-way analysis of variance was used to analyze changes in litter growth form composition in response to the fertilizer treatments after two years. As a result of the wildfire, the litter layer was not sampled in all plots, and the samples collected were thus analyzed by one-way analysis of variance. Litter dry mass and nutrient contents were log transformed and all percentage values were arcsin transformed prior to statistical analyses. The correlation of mean unfertilized control plot litter production with various climatic variables were determined separately for the first and second years after fertilizer addition. Daily values for these measures were summed or averaged for the exact period over which litter was collected for each collection interval.

RESULTS

Climatic conditions

During the 1984-87 period, seasonal variations in air temperature (maximum, mean and minimum), rainfall, pan evaporation, relative humidity and wind run at Pella were typical of a mediterranean-type climate (Fig. 5.1).

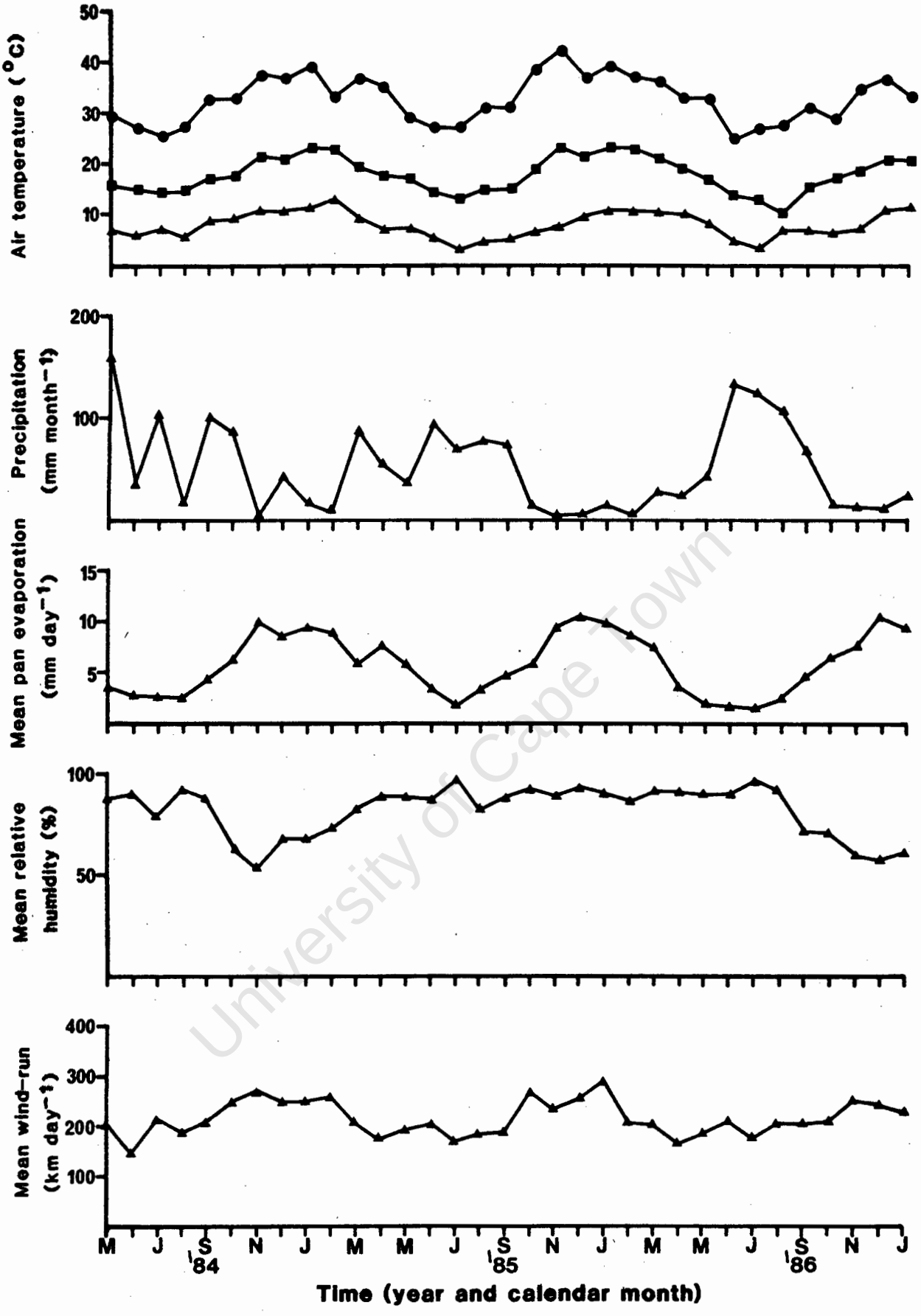

Fig. 5.1. Seasonal variation in air temperature (●, maximum; ■, mean; ▲, minimum), relative humidity, precipitation, pan evaporation and wind-run at Pella, South Africa.

However, the 20 week period from November 1985 to March 1986 was exceptional in being the longest period of low rainfall since records have been kept at the site in 1980 (Jarman & Mustart 1987).

Litter production

Litter production increased with vegetation age, was highly seasonal and peaked during the late spring to mid-summer period (November to January; Table 5.1; Fig. 5.2). Analyzing the data by three-way analysis of variance with repeated measures showed no significant differences between treatments ($P>0.05$). From November 1985 to January 1986, litter production peaked and was approximately one order of magnitude higher than in the corresponding period of the previous year. The unfertilized control plots and those amended with only P exhibited smaller peaks than the other additions (Fig. 5.2). An increase in litter production with the interaction of N and M addition ($P<0.05$) was found for the peak production period of November 1985. No significant differences in total annual litter production were found in either year, although tending to increase in response to N and M addition during the second year (Table 5.1). Litter production in control plots showed little correlation with the environmental factors measured during the first year, but was highly positively correlated with wind run and absolute maximum monthly temperature during the second ($r=0.93$, $P<0.01$; $r=0.72$, $P<0.05$; respectively).

Table 5.1. Annual litter production (g m^{-2} $year^{-1}$; September to September) and its N and P content (mg m^{-2} $year^{-1}$) in plots amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P), and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 in a nutrient-poor fynbos ecosystem at Pella, South Africa. Values are means ± S.E. C denotes control; [1], data from only 10 unburnt plots.

	Treatments							
	C	N	P	M	NP	NM	PM	NPM
Dry mass								
1984-85	31 ±6	34 ±8	35 ±6	32 ±3	70 ±29	53 ±8	57 ±13	43 ±3
1985-86	69 ±8	143 ±23	85 ±14	161 ±33	177 ±42	279 ±139	155 ±10	138 ±40
1986-87[1]	109 ±25	-	199 ±27	236 ±42	-	69	-	482
Phosphorus								
1984-85	9 ±2	11 ±3	13 ±3	13 ±1	66 ±26	15 ±3	22 ±5	22 ±2
1985-86	27 ±5	34 ±5	28 ±4	50 ±10	80 ±17	133 ±74	78 ±8	160 ±40
1986-87[1]	25 ±6	-	34 ±8	55 ±10	-	10	-	107
Nitrogen								
1984-85	317 ±75	345 ±81	301 ±56	387 ±39	826 ±332	479 ±74	510 ±120	494 ±39
1985-86	699 ±61	1489 ±360	687 ±97	1187 ±237	1150 ±235	1626 ±698	1298 ±88	1375 ±365
1986-87[1]	638 ±163	-	684 ±60	1012 ±50	-	250	-	1630

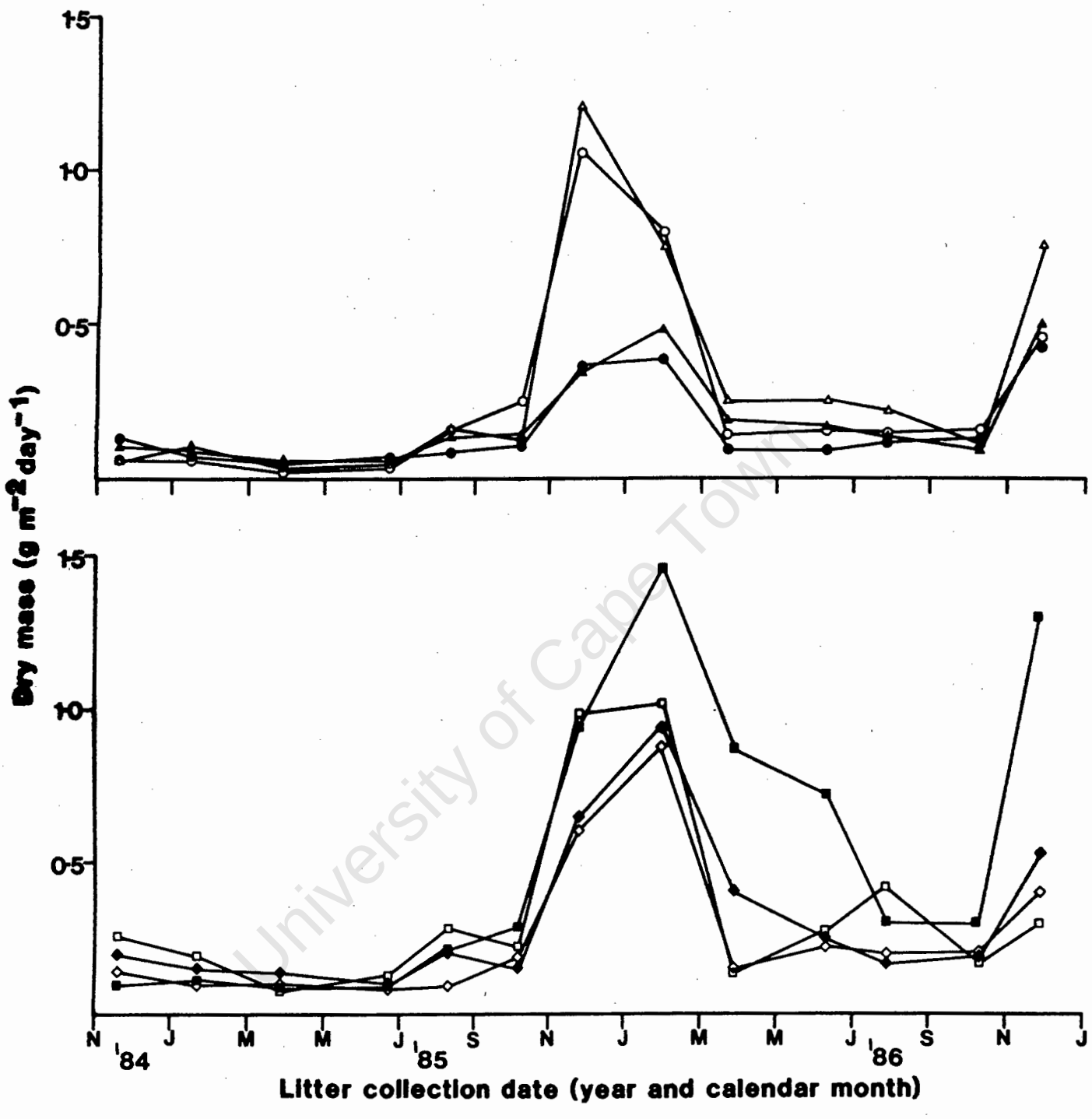

Fig. 5.2. Seasonal variation in litter production in plots amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Symbols, above: ○—○, N addition; ▲—▲, P addition; △—△, M addition; ●—●, control; below: □—□, N plus P addition; ■—■, N plus M addition; ◆—◆, P plus M addition; ◇—◇, N plus P plus M addition.

Phosphorus return

Phosphorus return varied seasonally and also peaked during the late spring to mid-summer (November to January) period (Fig. 5.3). Three-way analysis of variance with repeated measures showed a significant increase in phosphorus return with P, M ($P<0.01$) and N ($P<0.05$) addition. During the peak litter release period (November 1985), phosphorus return increased in response to N ($P<0.01$) and M ($P<0.001$), whereas it decreased in response to P ($P<0.001$), with an interaction between N and P addition ($P<0.05$). An increase in annual phosphorus return in response to P ($P<0.001$), and to a lesser extent N ($P<0.05$), and an interaction between N and M addition ($P<0.05$) were found in the first year after fertilizer addition, whereas it increased with M ($P<0.001$) and N ($P<0.01$), and decreased with P addition ($P<0.05$) during the second year (Table 5.1).

Nitrogen return

Nitrogen return showed a similar seasonal pattern to phosphorus (Fig. 5.4). Three-way analysis of variance with repeated measures showed no significant differences in nitrogen return between treatments. The NP, PM and NPM treatment combinations resulted in the highest nitrogen return during the first year (Fig. 5.4). Nitrogen return peaked in November 1985, although the unfertilized control and P amended plots tended to have lower peaks than the other treatments. An increase in nitrogen return in November 1985 in response to N, and an interaction between N

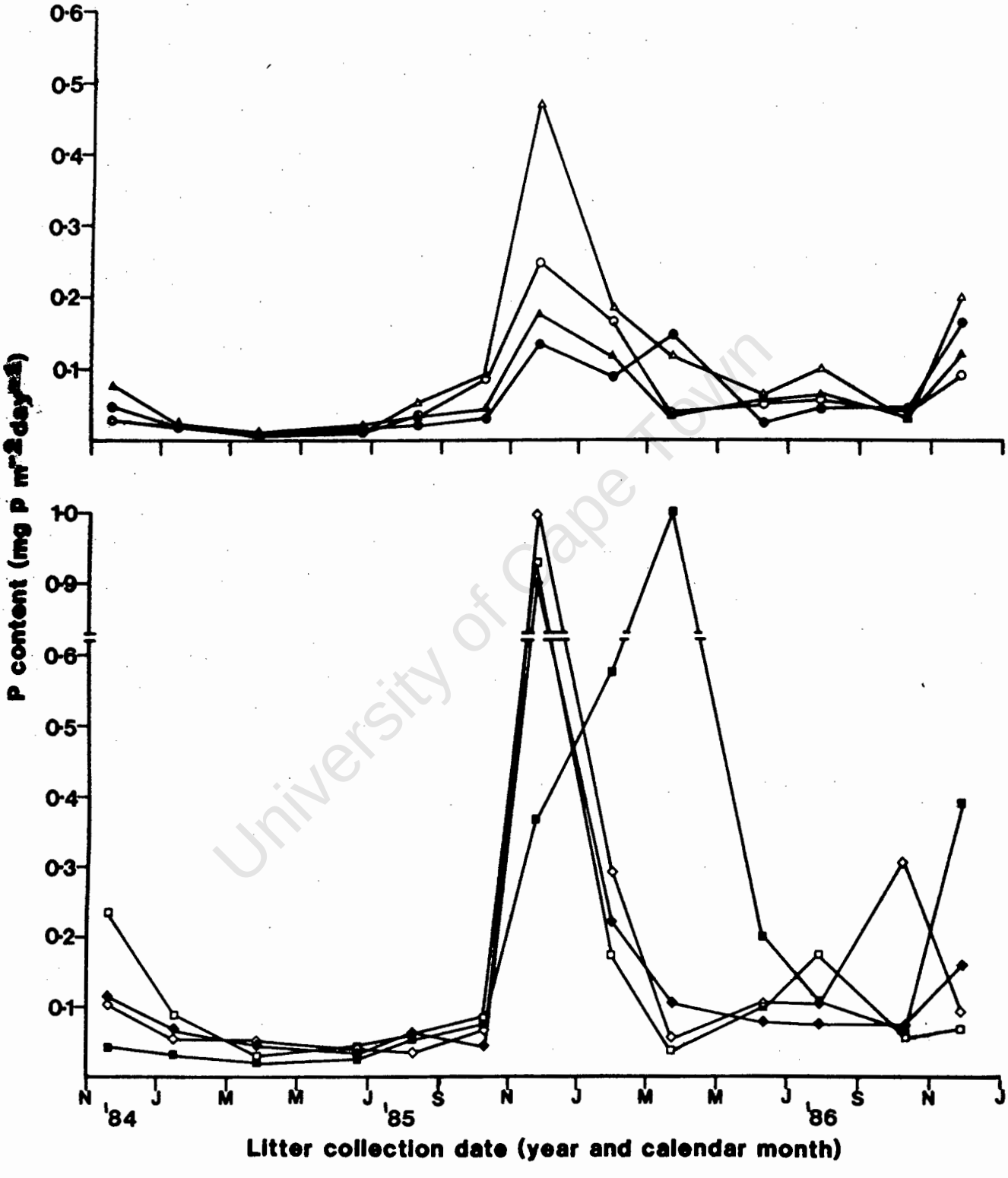

Fig. 5.3. Seasonal variation in phosphorus content of litter produced in plots amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Symbols as for Fig. 5.2.

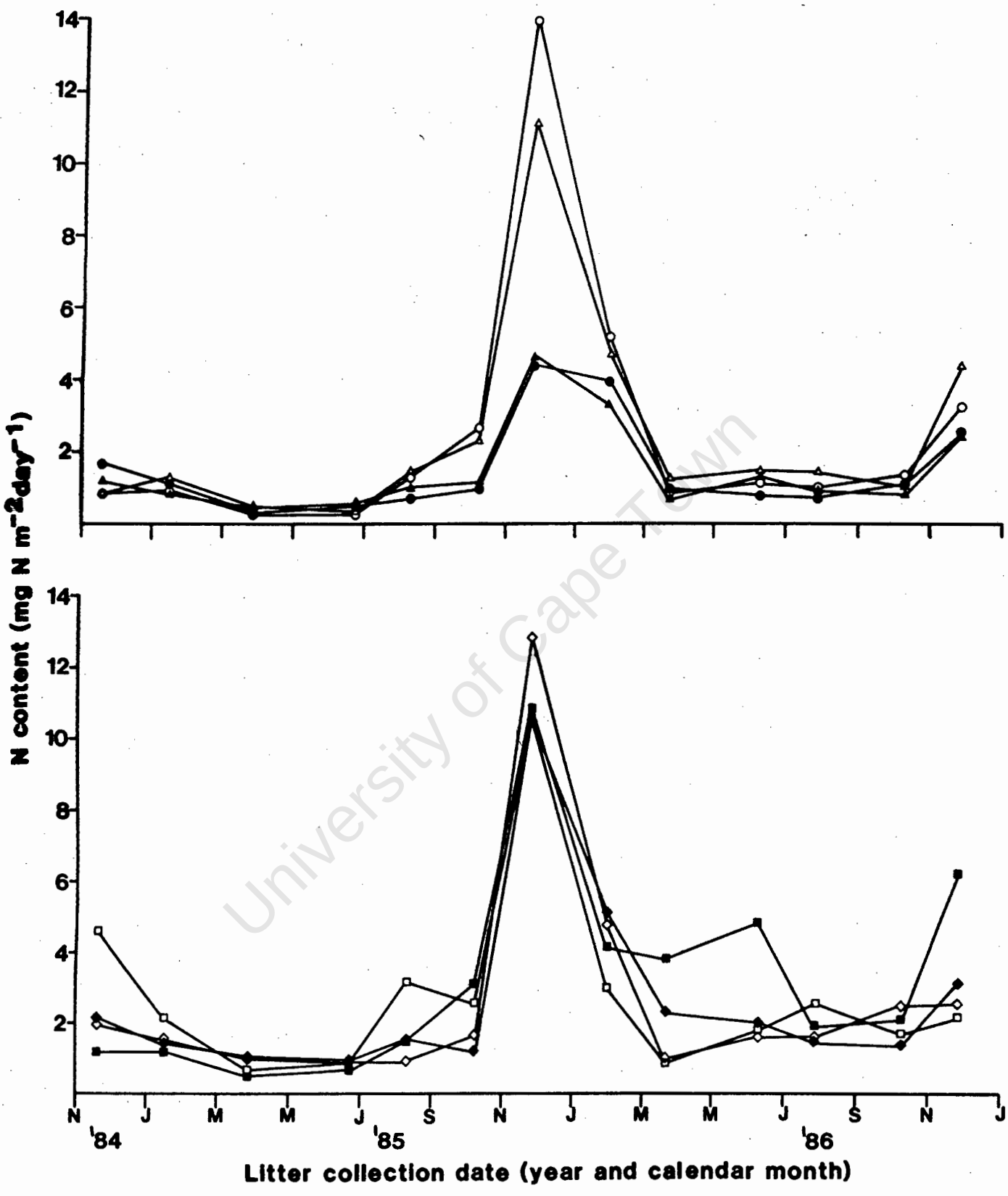

Fig. 5.4. Seasonal variation in nitrogen content of litter produced in plots amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. Symbols as for Fig. 5.2.

and M addition ($P<0.05$) were found. No significant differences in annual nitrogen return were found between treatments in either year, although it tended to increase with N and M addition during the second year (Table 5.1).

Calcium, magnesium and potassium return

Three-way analysis of variance with repeated measures showed increased Ca and Mg contents of litter with the interaction of N and M addition ($P<0.05$; Table 5.2), whereas no significant differences in K content were found. Phosphorus, nitrogen, Ca, Mg and K return increased with vegetation age (Tables 5.1 & 5.2).

Litter growth form composition

Growth form composition of the litter was dominated by the ericoid element at the start of the study (November 1984), ranging from 60 to 90 % of the total input (Table 5.3). In most plots there was a decrease in the proportion of ericoid and miscellaneous categories with a concomitant increase in the proteoid component of the litter in November 1986 compared with November 1984. Significant differences were found between growth forms ($F_{3,192}=85.61$, $P<0.001$) and an interaction between growth form and collection time ($F_{3,192}=4.71$, $P<0.01$), but no differences in response to the fertilizer treatments. These results reflect the successional changes in the vegetation during this period, with the proteoid shrubs increasing in dominance as the vegetation aged (Table 5.3).

Table 5.2. Calcium, magnesium and potassium contents of litter (mg m^{-2}; mean ±S.E.) collected from plots amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. C denotes control.

	Treatments							
	C	N	P	M	NP	NM	PM	NPM
Calcium								
November 84	29.12 ±11.22	18.38 ±6.79	27.08 ±10.97	15.74 ±2.74	75.12 ±26.16	37.22 ±15.10	66.88 ±21.70	41.90 ±8.40
July 85	11.45 ±2.26	21.64 ±7.67	24.78 ±4.70	28.83 ±5.27	98.71 ±39.80	41.53 ±13.87	45.70 ±12.87	22.43 ±3.72
November 85	77.84 ±10.36	257.42 ±77.85	68.97 ±13.81	211.89 ±56.97	264.36 ±71.34	284.00 ±36.89	215.15 ±49.26	255.74 ±70.88
July 86	24.19 ±4.34	32.73 ±3.02	40.78 ±3.46	79.32 ±21.74	88.52 ±36.81	82.73 ±37.10	45.99 ±7.51	47.22 ±14.59
November 86	70.36 ±18.40	60.72 ±3.52	81.12 ±23.89	150.49 ±41.94	68.71 ±20.25	153.39 ±107.46	187.59 ±15.05	71.30 ±26.87
Magnesium								
November 84	15.27 ±5.88	6.55 ±2.42	9.72 ±3.94	6.51 ±1.13	28.09 ±9.78	8.07 ±3.27	17.76 ±5.76	17.92 ±3.59
July 85	5.35 ±1.06	7.99 ±2.83	10.53 ±2.00	12.05 ±2.20	20.51 ±8.27	11.18 ±3.73	13.38 ±3.77	8.42 ±1.40
November 85	40.42 ±5.61	113.14 ±34.22	32.82 ±6.57	164.87 ±44.33	116.26 ±31.38	100.94 ±13.11	75.95 ±17.39	76.96 ±21.33
July 86	7.31 ±1.32	9.71 ±0.90	10.05 ±0.85	20.40 ±5.59	33.71 ±14.02	27.06 ±12.13	12.36 ±2.02	16.67 ±5.15
November 86	27.11 ±7.07	45.10 ±2.61	47.86 ±14.09	80.22 ±22.36	24.51 ±7.22	104.12 ±72.94	64.86 ±5.20	40.79 ±15.37
Potassium								
November 84	6.41 ±2.47	3.69 ±1.36	7.01 ±2.84	3.27 ±0.57	26.51 ±9.23	4.69 ±1.90	15.38 ±4.99	11.95 ±2.40
July 85	1.72 ±0.34	3.07 ±1.09	2.31 ±0.44	4.42 ±0.81	7.98 ±3.22	5.54 ±1.85	4.69 ±1.32	3.37 ±0.56
November 85	51.25 ±6.14	154.66 ±46.77	49.31 ±9.88	247.60 ±66.57	139.41 ±37.62	146.82 ±19.07	69.60 ±15.93	106.86 ±29.62
July 86	4.75 ±0.84	3.75 ±0.35	5.10 ±0.43	6.65 ±1.82	11.53 ±4.79	7.51 ±3.37	5.30 ±0.87	5.19 ±1.60
November 86	44.95 ±11.73	33.23 ±1.93	83.05 ±24.46	137.12 ±38.22	16.00 ±4.72	147.79 ±103.53	69.14 ±5.55	71.30 ±26.87

Table 5.3. Percentage growth form composition of litter dry mass produced during the peak production period (mid September to mid November) of 1984 and 1986 in plots amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. C denotes control.

Growth Form	Year	Treatments								Mean
		C	N	P	M	NP	NM	PM	NPM	
Ericoid	84	75.6	74.1	70.9	71.6	79.1	70.0	75.5	45.7	70.9
	86	44.9	86.2	34.5	43.6	57.6	11.7	63.7	45.2	48.1
Restioid	84	12.5	13.5	9.1	15.4	12.7	8.2	5.4	15.0	11.6
	86	8.6	13.1	7.7	3.1	29.9	2.5	1.6	10.8	9.5
Proteoid	84	0.0	0.0	9.1	5.5	0.0	5.6	0.0	12.7	3.7
	86	45.6	0.0	54.8	50.0	7.9	83.7	26.3	40.1	39.3
Miscellaneous	84	11.8	12.4	10.9	7.5	8.3	16.0	19.1	26.5	13.8
	86	0.8	0.8	3.0	3.3	4.6	2.2	8.8	4.0	3.1

Litter layer

Significant differences in litter layer dry mass, phosphorus, nitrogen, Ca and Mg contents, although not K and the ratio of N/P, were found between nutrient treatment combinations (Table 5.4). Apart from the sole addition of P, all additions displayed higher dry mass and nutrient contents than the control. The NM, NP and NPM additions resulted in from 2-3 times more dry mass and still greater nutrient contents than the control. Significant differences in litter layer phosphorus and nitrogen ($F_{4,10}$=5.82 and 5.17, respectively, P<0.05), although not Ca, Mg and K ($F_{4,10}$=1.90, 2.06 and 0.25, respectively, P>0.05) concentrations, were found between nutrient treatment combinations (Table 5.4). Litter layer phosphorus concentrations were highest in the NPM and P and lowest in the N and control plots, whereas nitrogen concentrations were elevated by the addition of NP, NM and NPM.

DISCUSSION

Annual litter production in unfertilized control plots increased with post-fire vegetation age and was similar to values determined by Mitchell et al. (1986) from 5-7 year-old vegetation at Pella. Litter production, which consists predominantly of leaf material, is low when compared with other mediterranean regions such as Australian

Table 5.4. Litter layer dry mass (g m^{-2}), its P, N, Ca, Mg and K contents (mg m^{-2}; mean ±S.E.) and N/P ratio in plots amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. C, denotes control; n, number of plots sampled; [1], not included in one-way analysis of variance because remainder of treated plots destroyed by a wildfire; ***, significance of one-way analysis of variance at $P<0.001$; NS, not significant ($P>0.05$).

Treatment	Mass	P	N	Ca	Mg	K	N/P	n
C	132 ±17	19 ±4	666 ±80	267 ±5	118 ±19	107 ±23	37 ±3	5
N[1]	176	21	913	594	132	44	44	1
P	108 ±3	25 ±1	606 ±1	409 ±1	104 ±2	80 ±15	24 ±1	2
M	192 ±27	32 ±5	1220 ±113	982 ±274	216 ±11	148 ±63	39 ±3	3
NP	356 ±52	70 ±6	2421 ±84	1788 ±209	427 ±16	296 ±75	35 ±2	3
NM[1]	381	80	2746	2388	378	229	34	1
PM[1]	186	30	1059	637	134	91	35	1
NPM	257 ±19	61 ±8	1905 ±102	1451 ±422	278 ±20	150 ±2	32 ±6	2
F	11.4	19.7	57.4	12.8	54.0	3.0	2.6	
d.f.	4,10	4,10	4,10	4,10	4,10	4,10	4,10	
P	***	***	***	***	***	NS	NS	

coastal scrub heath, (Maggs & Pearson 1977), Californian sclerophyllous scrub, (Mooney et al. 1977), Californian coastal sage scrub (Gray & Schlesinger 1981) and Chilean sclerophyllous scrub (Mooney et al. 1977; 409, 355, 194 and 245 g m^{-2} respectively). However, annual litter production at Pella during the 1985-86 and 1986-87 seasons, in plots amended with nutrient additions which included N or M, were similar to those of the other mediterranean regions. During the 1985-86 season, mean annual litter production, in response to N addition, was from 2 to 4 times higher than in the control plots. Phosphorus addition had no significant effect on litter production. Similarly, an increase in needlefall and N and K return and a decrease in phosphorus, Ca and Mg return with N fertilizer applied over three years was found in Corsican pine (Miller et al. 1976).

Litter production from sclerophyllous shrubs and trees follows a simple harmonic function (Ashton 1975, Maggs & Pearson 1977, Lee & Correll 1978, and in this study). Vegetation of mediterranean-type ecosystems have similar seasonality of litter production, which appears to be moisture dependent (Kummerow 1983) and litterfall is probably the best synchronized phenophase in plants of mediterranean-climate areas. Nutrient additions did not result in any change in the timing of the peak release period, which occurred between November and January (late spring to mid-summer). Litter production was low during

the first year and did not correlate with the measured climatic variables, probably because of the relatively young age of the vegetation, but was highly correlated with wind run and absolute maximum monthly temperature during the second year.

The increased litter production with the interaction of N and M addition during the peak production period of November 1985, which was an unusually dry and hot period, is interpreted as a response to increased plant moisture stress due to increased shoot growth in response to fertilizer addition. This supports Kummerow's (1982) hypothesis of reduced drought tolerance of sclerophylls in response to nutrient additions as a result of decreased root to shoot ratios in fertilized plants. Litter release peaks occur with the onset of moisture stress at the end of spring and during summer (Moll & Sommerville 1985). Deep rooting proteoid shrubs such as L. parile tend to maintain high stem xylem pressures potentials throughout the summer drought period and show little moisture stress. Shallow-rooted restioid elements, such as T. punctatus, have low xylem pressure potentials and transpiration is greatly reduced during this period (Moll & Sommerville 1985). Ericoid elements tend to have rooting depths intermediate between those of restioid and proteoid plants (Higgins et al. 1987). Leaf abscission appears to be a response to leaf age (senescence) and seasonal moisture stress. During the very

dry period between November 1985 and March 1986, 1-2 year-old leaves were released from certain individual N amended L. parile and P. cephalantha shrubs. Normally only leaves of at least two years of age and older are released. Nutritional controls on evergreen leaf senescence have been suggested by Turner & Olson (1976), Reader (1980) and Chapin (1980). Shaver (1981; 1983) has shown that leaf longevity of the evergreen tundra shrub, Ledum palustre spp decumbens, decreased with NPK fertilization. Shaver (1981) also found a negative correlation between leaf longevity of L. palustre and soil nitrogen and phosphorus concentrations from a range of sites.

Relative to the other nutrient treatments, phosphorus return in litter increased in response to P addition during the first year, whereas nitrogen return, in response to N addition, only increased during a period of moisture stress in the vegetation. Litter phosphorus, nitrogen, Ca and Mg contents were highest during the November to January period, largely as a result of seed dispersal of the dominant ericoid (P. cephalantha) and proteoid (L. parile) shrubs. No significant differences in K return were found between treatments, but K is highly mobile and can be rapidly leached from foliage prior to, or soon after, leaf abscission (Gray 1983; Schlesinger 1985).

The litter layer dry mass of sand-plain lowland fynbos increases with post-fire age at a slower rate than in mountain fynbos vegetation (Van Wilgen 1982), due to lower primary production and because mole-rats, more prevalent on the deep aeolian sands of sand-plain lowland fynbos, tend to bury litter during their burrowing activities (Davies & Jarvis 1986). Immobilization of added N and P in the litter layer was demonstrated in this study, which is consistent with the findings of Mitchell *et al.* (1986) and Mitchell & Coley (1987), of increased nitrogen and phosphorus contents of decomposing leaf litter during the first two years of decomposition. Nitrogen and phosphorus were also immobilized in the litter layer of *Ceanothus megacarpus* chaparral, which showed no net release of these nutrients during a 3 year period (Schlesinger 1985). Litter acquires nutrients from atmospheric precipitation, throughfall from the canopies of shrubs, animal fras, soil contaminants and nutrients imported by fungal hyphae (eg. Schlesinger 1985). If the low nutrient content of litter is the factor which limits the rate of decomposition and not lignin or other organic constituents, nutrient additions may increase the rate of decomposition and nutrient turnover in this ecosystem.

Drought-tolerant plants (*sensu* Grime 1977) show many of the morphological and physiological characteristics found in nutrient-stress-tolerating plants (Stock 1987), such as slow

growth rates, perennial evergreen habit, increased leaf longevity, sclerophylly and a root system with both deep and shallow roots. The restricted incidence of succulence in the fynbos biome and the edaphically similar western Australian kwongan vegetation, supports the hypothesis that these floras have specialized "xeromorphic" anatomical features as the by-product of physiological adaptations to low nutrient availability, rather than as a response to drought stress (Stock 1987). In conclusion, increased annual litterfall in response to the addition of N and M shows the nutritional control of leaf senescence, whereas increased litterfall during the unusually hot and dry November 1985 period also shows the relationship between litterfall and plant moisture stress in this nutrient-poor mediterranean ecosystem.

CHAPTER 6

THE EFFECTS OF NUTRIENT ADDITIONS ON ABOVE-GROUND PHYTOMASS AND ITS PHOSPHORUS AND NITROGEN CONTENTS OF SAND-PLAIN LOWLAND FYNBOS.

(Submitted to the South African Journal of Botany in June 1988)

SUMMARY

The effects of 0.5 g phosphorus m^{-2} ($Ca_3(PO_4)_2$), 5 g nitrogen m^{-2} (NH_4NO_3) and a mixture of all essential nutrients excluding N and P (M) on above-ground phytomass (biomass plus necromass) and nitrogen and phosphorus contents of the representative plant growth forms of sand-plain lowland fynbos vegetation at Pella, south western Cape were studied. One year after fertilizer addition, a significant difference in the biomass of annuals was found between treatments, with increases in response to the three fertilizer treatments. The biomass of graminoids and the tufted perennial Gazania ciliaris DC. tended to increase with the addition of N and P, compared with those in the unfertilized plots. No significant differences in the biomass of the total vegetation and the major growth form categories (ericoid, restioid and proteoid) were found. However, total necromass tended to increase in response to the fertilizer additions. Phosphorus concentrations tended to increase in the phytomass of all growth forms in response to P addition. Herbaceous and shallow rooted plants showed a greater growth increase and nutrient uptake, in response to nutrient additions, than the deeper rooted shrubs, indicating that these species are more plastic in their responses to nutrient additions than the shrubs.

INTRODUCTION

Lowland and mountain fynbos vegetation is a fire-adapted and fire dependent vegetation (Van-Wilgen 1982) dominated by evergreen sclerophyllous shrubs and hemicryptophytes of the Restionaceae (Taylor 1978) on nutrient-poor acidic, sandy soils (Witkowski & Mitchell 1987). During a fire, the vegetation, surface litter and the organic matter in the surface soil layer are combusted, with the vegetation and litter remains deposited as ash on the soil surface. Thereafter plant available forms of phosphorus and nitrogen remain significantly higher in the soil for approximately 4-9 months after the fire (Brown & Mitchell 1986; Stock & Lewis 1986b). The decomposition of plant litter between fires and nitrogen and phosphorus turnover is very slow and a steady state may not be attained between fires (Mitchell *et al*. 1986; Mitchell & Coley 1987).

Fynbos vegetation biomass reaches a peak from 5-30 years after a fire and varies with age and vegetation type (Kruger 1977a; Van Wilgen 1982). Above-ground biomass of 14580 kg ha^{-1} occurred in an 11 year-old sand-plain lowland fynbos site (Low 1983), of which 90 % consisted of shrubs of *Phylica cephalantha* Sonder. Soil nutrients, particularly phosphorus, have been shown to limit vegetation productivity in edaphically similar mediterranean and other heathlands of Australia (Specht 1963; Heddle & Specht 1975; Specht *et al*.

1977). Over a period of twenty years, applications of 13.4 g phosphorus m^{-2} to an Australian heathland resulted in a complete change in species and growth form composition from predominantly sclerophyllous evergreen shrubs to herbaceous species (Heddle & Specht 1975). Applications of nitrogen and nitrogen plus phosphorus to mediterranean shrublands of the Californian chaparral resulted in increased proportions of annuals and graminoids (McMaster et al. 1982). Although phytomass and major nutrient pools have been determined in an 11 year-old lowland fynbos (Low 1983) and 12 and 21 year-old post-fire mountain fynbos communities (Van Wilgen & Le Maitre 1981), the effects of nutrient additions on phytomass in the field have not been investigated. This paper reports on the effects of the addition of nitrogen (N), phosphorus (P) and thirdly a mixture of all essential nutrients excluding N and P (M) on above ground phytomass, nitrogen and phosphorus contents of the representative plant growth forms in a 4-5 year-old sand-plain lowland fynbos ecosystem at Pella, south-western Cape.

THE STUDY AREA

The study site was the CSIR fynbos biome intensive study site at Pella, on the Burgherspost Farm (33° 31' S, 18° 32' E; 160-220 m altitude; 269 ha) 62 km north of Cape Town on the western Cape coastal forelands. It has a typical mediterranean climate with warm dry summers and

predominantly winter rainfall. Mean annual temperature is 17.3^{o} C and mean annual rainfall at the site is 522 mm.

The soil from which vegetation was harvested is a leached aeolian sand of the Clovelly soil form, Geelhout series (MacVicar et al. 1977) of approximately 2 m depth. This soil is low in both total and available phosphorus and nitrogen, the highest concentrations of which occur at the surface (Mitchell et al. 1984; Stock & Lewis 1986b). The soil is acidic (pH 4.1 - 5.1), with low organic matter content (0.5 - 1.5 %) and consists predominantly of medium textured sand. The specific study area was positioned in an approximately 1 ha area in the middle of a 26 ha patch of Clovelly soil and has a gentle 5^{o} easterly slope.

The vegetation is described as a Leucospermum parile-Thamnochortus punctatus mid-high open shrubland of Phylica cephalantha fynbos (Boucher & Shepherd 1987). This vegetation is typically dominated by ericoid, narrow leptophyllous, evergreen divaricately branched shrubs and rhizomatous hemicryptophytes. Shrubs of the Proteaceae are the third most important growth form. Lowland fynbos is more uniform in composition than mountain fynbos because of the uniformity of the terrain compared to that in the mountains (Boucher 1983). In both sand-plain lowland fynbos at Pella and mountain fynbos vegetation, it has been found that proteoid shrubs were the deepest rooting,

followed by the ericoid, while the restioids were generally shallow rooted (Jongens-Roberts & Mitchell 1986; Higgins et al. 1987; Stock et al. 1987; Chapter 3).

MATERIALS AND METHODS

A complete factorial field fertilizer study was initiated at the Pella site during September 1984. Plots, 10 x 5 m in size, and separated by 5 m wide strips were amended with 0.5 g phosphorus m^{-2} ($Ca_3(PO_4)_2$), 5 g nitrogen m^{-2} (NH_4NO_3) and a mixture of all essential nutrients excluding N and P. The amounts of P and N added were the approximate amounts returned to the soil after a moderate intensity wildfire at Pella in November 1980 (Brown & Mitchell 1986; Stock & Lewis 1986b). All other nutrients were based on a Long Ashton nutrient solution in proportion to the N and P additions (Chapter 2). Four replicate plots of each addition were layed-out at random in a grid pattern (8x4) and four additional control plots were positioned at the corners. Nutrients were added in spring, on the 15-17 September 1984. Above ground phytomass (biomass and necromass) was harvested in September 1985, one year after fertilizer addition, from four of the fertilizer additions, namely: unfertilized control (C), nitrogen only (N), phosphorus only (P) and a mixture of all essential nutrients excluding N and P (M). Phytomass was harvested from 5 m^2 (2.5 x 2 m) subplots positioned in the SE corner of each plot. Plant material

rooted in the plot was clipped as close to the soil surface as possible and subdivided into ericoid, restioid, proteoid, graminoid, succulents, annuals, geophytes and other. In addition a common root parasite, Thesium densiflorum A. DC.(Santalaceae), a low spreading shrub, Muraltia dumosa (Poiret) DC. (Polygalaceae), and a tufted perennial, Gazania ciliaris DC. (Asteraceae; Bond & Goldblatt 1984) were harvested separately. The ericoid, restioid, proteoid and graminoid phytomass were separated into live and dead components. Dead vegetation (necromass) consisted of dead branches and standing dead plants but not litter. Restioid and proteoid phytomass consisted only of Restionaceae and Proteaceae respectively. Ericoid biomass consisted of shrubs with 'ericoid' like leaves, ie: small needle like leaves. Important species were the resprouting P. cephalantha, P. stipularis L. (Rhamnaceae), Griesbachia plumosa (Klotzsch) (Ericaceae) and Aspalathus albens L. (Fabaceae) and the seed regenerating Metalasia adunca Less. and Lachnospermum fasciculatum (Thunb.) Baillon (Asteraceae). Proteaceae consisted predominantly of the obligate reseeder Leucospermum parile (Salisb. ex J. Knight) Sweet which germinates during the winter-spring period after fire and grows relatively slowly for the first 2-3 years, after which it becomes more dominant (Hoffman et al. 1987). Common examples of the Restionaceae were Thamnochortus punctatus Pill., Staberoha distachya (Rottb.) Kunch, Cannomois parviflora (Thunb.) Pill. and Calopsis impolitus

(Kunch) Linder ined. The graminoid phytomass consisted of examples from the Poaceae and Cyperaceae.

Plant material was oven-dried at 80° C in a forced draught oven for seven days and weighed. All plant material was ground in a Wiley mill to 10 mesh, thoroughly mixed and a 100 g subsample ground further to 40 mesh for the chemical analyses. The phosphorus concentration was determined on 0.1 g of plant material and digested by the method of Jackson (1958). The phosphate concentration of the digest was determined colorimetrically (Murphy & Riley 1962). For total nitrogen, 0.1 g plant material was digested using standard Kjeldahl procedures with selenium catalyst. Both salicylic acid and sodium thiosulphate were added to convert all nitrate and nitrite to ammonium which was determined colorimetrically (Smith 1980). Carbon content was determined as 58 % of ash-free weight of 1 g plant material ashed in a muffle furnace at 550° C for 5 h (Allen et al. 1976). All nitrogen and phosphorus analyses were performed in triplicate.

Differences between treatments in biomass and necromass, nitrogen and phosphorus content and concentration, of each growth form, were analyzed by one-way analysis of variance. Biomass and necromass and nitrogen and phosphorus contents were log transformed prior to statistical analyses.

RESULTS

The ericoid and restioid groups are the largest components of sand-plain lowland fynbos at Pella and together make up 83 % - 91 % of the total biomass and 97 % - 99 % of total necromass (Table 6.1). Total biomass was not significantly different between treatments (Table 6.1) and was lowest in the P amended plots (6272 kg ha^{-1}) and greatest in the M treatment (7697 kg ha^{-1}). The proportion of necromass as a percentage of total phytomass in the control plots was only 14.5 % compared with 17.2 - 20.7 in the nutrient amended plots. Few significant differences in biomass and necromass of the various growth forms and species were found between treatments (Table 6.1). Although significant differences in proteoid biomass were found between treatments ($P<0.10$; Table 6.1), this was due to the absence of the dominant proteoid shrub, L. parile, in the P amended plots. Annual plant biomass was significantly different between treatments and was highest in the three fertilizer treatments (Table 6.1). Graminoid biomass was approximately twice that of the control in the N and P amended plots and that of Gazania ciliaris was greater in the three fertilizer treatments than the control.

Total phosphorus content of the live vegetation was lowest in the N treatment (1.4 kg ha^{-1}) and greatest for the P and M treatments (1.8 and 2.0 kg ha^{-1} respectively; Table 6.2).

Table 6.1. Above-ground biomass (live) and necromass (dead) (kg ha^{-1}) of various components of five-year-old sand-plain lowland fynbos vegetation at Pella, south-western Cape in unfertilized control (C), phosphorus (P), nitrogen (N) and a mixture of all essential nutrients excluding N and P (M) amended plots, one year after fertilizer additions. Values are means ± S.E. NS denotes not significant.

GROWTH FORM	TREATMENTS C	P	N	M	F	d.f.	P
Ericoid (live)	2270 ±520	3370 ±930	3900 ±660	4630 ±1100	1.22	3,12	NS
Ericoid (dead)	754 ±352	1092 ±158	1529 ±180	1020 ±390	1.40	3,12	NS
Restioid (live)	3350 ±350	2210 ±420	2310 ±580	1910 ±340	1.69	3,12	NS
Restioid (dead)	364 ±94	174 ±81	219 ±113	844 ±46	0.75	3,12	NS
Proteoid (live)	520 ±219	2 ±2	46 ±21	460 ±377	3.13	3,12	<0.10
Proteoid (dead)	1 ±1	7 ±7	14 ±8	4 ±4	0.39	3,12	NS
Graminoid (live)	35 ±9	76 ±30	77 ±28	20 ±5	2.81	3,12	<0.10
Graminoid (dead)	19 ±3	33 ±13	28 ±14	8 ±4	0.96	3,12	NS
Succulent	33 ±31	16 ±10	14 ±8	34 ±13	0.62	3,12	NS
Annuals	1.4 ±0.4	5.7 ±2.7	10 ±5.4	11 ±2.4	3.59	3,12	<0.05
Geophytes	9.4 ±5.4	2.5 ±1.3	11 ±8.5	5.9 ±2.8	0.32	3,12	NS
Thesium densiflorum	154 ±89	352 ±211	310 ±109	192 ±81	0.20	3,12	NS
Muraltia dumosa	330 ±104	178 ±97	70 ±50	242 ±110	1.99	3,12	NS
Gazania ciliaris	0.7 ±0.7	15 ±8	10 ±7	6 ±2	2.03	3,12	NS
Other	34 ±13	49 ±27	88 ±36	180 ±66	2.16	3,12	NS
Total (live)	6737 ±453	6272 ±670	6839 ±1068	7697 ±1260	0.29	3,12	NS
Total (dead)	1138 ±341	1306 ±138	1787 ±226	1880 ±566	1.15	3,12	NS

Table 6.2. Above-ground biomass (live) and necromass (dead) phosphorus content (g Phosphorus ha^{-1}) of various components of five-year-old sand-plain lowland fynbos vegetation at Pella in unfertilized control (C), phosphorus (P), nitrogen (N) and a mixture of all essential nutrients excluding N and P (M) treated plots, one year after nutrient additions. Values are means ± S.E. NS denotes not significant.

GROWTH FORM	TREATMENTS C	P	N	M	F	d.f.	P
Ericoid (live)	539 ±91	1013 ±357	838 ±143	1191 ±400	1.20	3,12	NS
Ericoid (dead)	72 ±26	188 ±29	183 ±25	107 ±41	2.98	3,12	<0.10
Restioid (live)	579 ±115	510 ±108	838 ±100	107 ±51	2.04	3,12	NS
Restioid (dead)	24 ±7	22 ±13	20 ±9	67 ±36	0.59	3,12	NS
Proteiod (live)	231 ±116	0.7 ±0.7	17 ±8	211 ±163	3.29	3,12	<0.10
Proteoid (dead)	0.1 ±0.1	2.2 ±2.2	2.1 ±1.4	1.0 ±1.0	0.49	3,12	NS
Graminoid (live)	10 ±4	20 ±6	18 ±8	8.6 ±1.4	1.33	3,12	NS
Graminoid (dead)	2.6 ±0.6	4.3 ±1.8	6.2 ±4.3	1.4 ±0.5	0.76	3,12	NS
Succulent	11 ±11	12 ±7.5	5.4 ±3.1	17 ±6.8	0.63	3,12	NS
Annuals	0.6 ±0.1	2.5 ±1.2	3.0 ±1.4	6.0 ±2.2	3.50	3,12	<0.05
Geophytes	3.5 ±1.8	1.2 ±0.6	2.3 ±1.6	3.5 ±2.2	0.37	3,12	NS
Thesium densiflorum	68 ±39	157 ±95	108 ±38	92 ±40	0.15	3,12	NS
Muraltia dumosa	134 ±39	82 ±47	26 ±19	102 ±45	2.14	3,12	NS
Gazania ciliaris	0.1 ±0.1	6.6 ±4.6	2.1 ±1.2	2.5 ±1.2	1.68	3,12	NS
Other	11 ±4.4	21 ±12	28 ±13	73 ±22	3.35	3,12	<0.10
Total (live)	1586 ±111	1825 ±321	1384 ±158	2030 ±482	0.75	3,12	NS
Total (dead)	99 ±22	217 ±18	211 ±33	176 ±59	2.76	3,12	<0.10

Significant differences in total necromass phosphorus content were found between treatments ($P<0.10$). Phosphorus content of the necromass makes up only 6 % of the total phosphorus in the control plots compared with 8-13 % in the fertilizer treatments. Significant differences in phosphorus content were found between treatments for annuals, which were 4 - 10 times greater in the three fertilizer treatments compared with the control (Table 6.2). Significant differences in phosphorus concentration were found between treatments for restioid, succulent, and Thesium densiflorum biomass (Table 6.3). Mean phosphorus concentrations were higher in all growth forms and species sampled in the P amended plots except for proteoid shrub (live), graminoid (live and dead), annuals, geophytes, other, T. densiflorum and G. ciliaris, in all of which M addition resulted in higher phosphorus concentrations. Nitrogen addition resulted in depressed mean phosphorus concentrations in the biomass of all growth forms and species, except succulents and Gazania ciliaris, compared to that in the unfertilized plots. Shoot phosphorus concentrations of N amended L. parile shrubs were also depressed (Chapter 3). Ericoid, proteoid and restioid necromass exhibited only approximately half the phosphorus concentration of the corresponding biomass.

The nitrogen content of the above-ground total biomass and necromass ranged 49-78 kg ha^{-1} and 5-10 kg ha^{-1} respectively

Table 6.3. Phosphorus concentration (µg Phosphorus g^{-1} dry mass) of above-ground biomass (live) and necromass (dead) of various components of five-year-old sand-plain lowland fynbos vegetation at Pella, south-western Cape, in unfertilized control (C), phosphorus (P), nitrogen (N) and a mixture of all essential nutrients excluding N and P (M) amended plots, one year after nutrient additions. Values are means ± S.E. NS denotes not significant and - denotes not determined due to insufficient replication.

GROWTH FORM	TREATMENT C	P	N	M	F	d.f.	P
Ericoid (live)	250 ±12	300 ±19	218 ±10	260 ±15	1.34	3,12	NS
Ericoid (dead)	112 ±10	178 ±16	119 ±7	110 ±7	2.51	3,12	NS
Restioid (live)	168 ±9	235 ±15	145 ±8	173 ±8	4.01	3,12	<0.05
Restioid (dead)	67 ±3	101 ±11	94 ±6	94 ±8	1.23	3,12	NS
Proteoid (live)	422 ±34	400 -	346 ±19	515 ±27	2.40	2,6	NS
Proteoid (dead)	100 -	291 -	235 ±23	244 -	-	-	-
Graminoid (live)	264 ±24	351 ±47	219 ±9	500 ±61	2.55	3,12	NS
Graminoid (dead)	136 ±12	134 ±15	192 ±20	193 ±21	1.05	3,12	NS
Succulent	347 ±35	738 ±8	397 ±39	498 ±31	9.34	3,6	<0.05
Annuals	428 ±60	487 ±94	400 ±20	537 ±53	0.97	3,12	NS
Geophytes	399 ±37	488 ±23	281 ±32	583 ±73	2.69	3,12	NS
Thesium densiflorum	442 ±7	445 ±10	348 ±4	466 ±12	11.55	3,6	<0,01
Muraltia dumosa	425 ±12	442 ±12	376 ±6	437 ±13	2.24	3,12	NS
Gazania ciliaris	191 -	339 ±35	242 ±36	365 ±25	0.60	2,7	NS
Other	323 ±48	440 ±21	306 ±12	469 ±38	2.25	3,12	NS

(Table 6.4). Mean necromass nitrogen content was greater in the three fertilizer treatments than the control. The proportion of total nitrogen found in necromass was 9.9 % in the control compared with 17.6 % in the N amended plots. Significant differences in nitrogen content between treatments was only found for ericoid necromass, with the N and P amended plots having the highest nitrogen contents. Significant differences in nitrogen concentration between fertilizer treatments were found for ericoid biomass and graminoid necromass (Table 6.5).

Percentage carbon and carbon to nitrogen (C/N) and carbon to phosphorus (C/P) ratios of components of the vegetation ranged from 54-57, 53-170 and 1303-8420 respectively (Table 6.6). The C/N, C/P, and N/P ratios of the ericoid, restioid and proteoid necromass were all higher than those of the corresponding biomass. Nitrogen to phosphorus ratio was lowest for proteoid biomass and highest for ericoid necromass (Table 6.6). The C/N and C/P ratios of the graminoid necromass were also higher than in the corresponding biomass.

DISCUSSION

Total above-ground biomass of 6737 kg ha^{-1} for 5 year-old vegetation was found in unfertilized control plots compared with 7630 and 12090 kg ha^{-1} for 4 and 9 year-old vegetation

Table 6.4. Above-ground biomass (live) and necromass (dead) nitrogen content (kg nitrogen ha^{-1}) of various components of five-year-old sand-plain lowland fynbos vegetation at Pella, south-western Cape, in unfertilized control (C), phosphorus (P), nitrogen (N) and a mixture of all essential nutrients excluding N and P (M) amended plots, one year after nutrient additions. Values are means ± S.E. NS denotes not significant.

GROWTH FORM	TREATMENTS C	P	N	M	F	d.f.	P
Ericoid (live)	24.46 ±6.83	39.73 ±11.6	32.90 ±4.9	60.55 ±17.3	1.56	3,12	NS
Ericoid (dead)	3.79 ±1.1	8.29 ±1.6	9.09 ±1.3	4.31 ±1.3	3.43	3,12	<0.05
Restioid (live)	16.76 ±3.2	9.44 ±1.6	10.85 ±2.5	8.91 ±1.0	2.21	3,12	NS
Restioid (dead)	1.51 ±0.5	0.63 ±0.4	1.06 ±0.5	2.83 ±1.6	1.12	3,12	NS
Proteoid (live)	2.40 ±0.95	0.012 ±0.012	0.24 ±0.14	2.19 ±1.76	2.76	3,12	<0.10
Proteoid (dead)	0.005 ±0.005	0.038 ±0.038	0.081 ±0.054	0.026 ±0.026	0.79	3,12	NS
Graminoid (live)	0.25 ±0.08	0.40 ±0.14	0.44 ±0.15	0.13 ±0.03	1.75	3,12	NS
Graminoid (dead)	0.06 ±0.008	0.13 ±0.06	0.16 ±0.09	0.03 ±0.01	1.21	3,12	NS
Succulent	0.44 ±0.42	0.22 ±0.13	0.15 ±0.09	0.49 ±0.27	0.40	3,12	NS
Annuals	0.011 ±0.003	0.059 ±0.027	0.115 ±0.075	0.118 ±0.033	1.63	3,12	NS
Geophytes	0.114 ±0.062	0.025 ±0.014	0.110 ±0.09	0.065 ±0.03	0.52	3,12	NS
Thesium densiflorum	1.17 ±0.70	2.32 ±1.34	2.03 ±0.73	1.37 ±0.68	0.17	3,12	NS
Muraltia dumosa	2.90 ±0.88	1.61 ±0.84	0.93 ±0.45	2.21 ±1.00	0.92	3,12	NS
Gazania ciliaris	0.003 ±0.003	0.154 ±0.103	0.031 ±0.017	0.077 ±0.034	1.66	3,12	NS
Other	0.36 ±0.06	0.72 ±0.46	0.75 ±0.35	1.38 ±0.40	1.59	3,12	NS
Total (live)	48.86 ±5.9	54.71 ±11.1	48.54 ±6.3	77.50 ±17.6	0.98	3,12	NS
Total (dead)	5.36 ±0.71	9.09 ±1.25	10.39 ±1.75	7.20 ±2.28	2.09	3,12	NS

Table 6.5. Nitrogen concentration (mg N g^{-1} dry mass) of above-ground biomass (live) and necromass (dead) of various components of five-year-old sand-plain lowland fynbos vegetation at Pella, south-western Cape in unfertilized control (C), phosphorus (P), nitrogen (N) and a mixture of all essential nutrients excluding N and P (M) amended plots, one year after nutrient additions. Values are means ± S.E. NS denotes not significant and - not determined due to insufficient replication.

Growth Form	Treatment C	P	N	M	F	d.f.	P
Ericoid (live)	10.6 ±0.6	10.9 ±0.6	8.6 ±0.6	12.8 ±0.9	6.33	3,12	<0.01
Ericoid (dead)	6.4 ±1.8	7.9 ±1.9	6.1 ±2.0	5.6 ±1.5	0.41	3,12	NS
Restioid (live)	4.9 ±0.7	4.3 ±0.2	4.8 ±0.3	4.9 ±0.5	0.37	3,12	NS
Restioid (dead)	4.2 ±0.4	3.2 ±0.4	5.2 ±0.3	4.7 ±1.0	2.06	3,12	NS
Proteoid (live)	4.8 ±0.4	6.9 -	6.0 ±0.3	5.1 ±0.3	3.50	2,6	<0.10
Proteoid (dead)	4.4 -	5.1 -	8.9 ±1.7	6.0 -	-	-	-
Graminoid (live)	6.5 ±0.6	5.9 ±1.3	5.8 ±0.8	7.1 ±0.9	1.07	3,12	NS
Graminoid (dead)	3.3 ±0.2	3.6 ±0.5	5.2 ±0.4	4.4 ±0.6	3.94	3,12	<0.05
Succulent	13.2 ±0.3	14.8 ±2.5	10.4 ±1.2	12.9 ±3.2	0.43	3,6	NS
Annuals	7.9 ±0.5	10.2 ±0.6	9.1 ±1.3	10.9 ±1.0	2.06	3,12	NS
Geophytes	11.8 ±1.9	9.8 ±0.4	10.5 ±0.8	11.7 ±1.3	1.22	3,12	NS
Thesium densiflorum	7.5 ±0.9	6.8 ±1.2	6.5 ±0.5	6.6 ±1.2	0.19	3,6	NS
Muraltia dumosa	9.1 ±0.6	9.2 ±0.3	9.6 ±0.3	9.2 ±0.5	0.25	3,12	NS
Gazania ciliaris	4.6 -	8.5 ±1.2	7.0 ±0.7	11.2 ±1.0	3.28	2,7	<0.10
Other	8.1 ±1.6	12.0 ±2.2	8.1 ±0.5	9.5 ±2.3	1.09	3,12	NS

Table 6.6. Percentage carbon, C/N, C/P and N/P ratios of biomass (live) and necromass (dead) of various components of five-year-old sand-plain lowland fynbos vegetation at Pella, south-western Cape in unfertilized control plots. Values are means ± S.E. [1] pooled carbon analyses. - denotes not determined.

Growth Form	Carbon (%)	C/N	C/P	N/P
Ericoid (live)	55.8±0.3	53	2225	42
Ericoid (dead)	56.2±1.0	88	5007	57
Restioid (live)	56.8±0.1	116	3377	29
Restioid (dead)	56.8±0.2	135	8420	62
Proteoid (live)	55.0±0.7	115	1303	11
Proteoid (dead)	54.3 -	123	5405	44
Graminoid (live)	55.9±0.1	86	2114	25
Graminoid (dead)	56.2±0.4	170	4139	24
Succulents[1]	-	-	-	38
Annuals[1]	-	-	-	19
Geophytes[1]	54.8±0.4[1]	65[1]	1370[1]	30
Thesium densiflorum[1]	-	-	-	17
Muraltia dumosa[1]	-	-	-	21
Gazania ciliaris[1]	-	-	-	24
Other[1]	-	-	-	25

at Pella respectively, determined on a different soil type by Mitchell et al. (1986). The proportion of proteoid biomass was higher at 26 % and 38 % for 4 and 9 year-old vegetation compared with only 8 % in this study. The higher proteoid biomass probably explains the higher total biomass found by Mitchell et al. (1986). Litter production, which can be used as an indirect measure of productivity (Alexander 1982), was greater in Protea repens (Proteaceae) shrubs in mountain fynbos at Jonkershoek than at Pella (Mitchell & Coley 1987). The lower productivity of lowland fynbos in comparison to mountain fynbos is probably related to its greater aridity. Along a karoo-fynbos elevational gradient with vegetation greater than 10 years of age, total biomass ranged from 7564 kg ha^{-1} for succulent karoo to 14311 kg ha^{-1} for heathlands dominated by Restionaceae and the changes were related to elevation and rainfall (Rutherford 1978). The above-ground biomass of fynbos communities is similar to analogous communities in other areas with mediterranean-type climates (Kruger 1977a).

The low above-ground nutrient pools of phosphorus and nitrogen found in unfertilized five year-old vegetation in this study is indicative of a nutrient-poor fynbos ecosystem. The above-ground biomass pool of nitrogen is comparable with that found by Low (1983) but phosphorus is lower when compared on a mean dry mass basis.

The build-up of necromass in sand-plain lowland fynbos at Pella proceeds with the mortality of many of the early-successional dominant ericoid species such as Lachnospermum fasciculatum and Metalasia adunca and restionaceae such as Cannomois parviflora (Hoffman et al. 1987). The proportion of standing dead vegetation dry mass at Pella only increased from 16.5 % to 17.6 % as the vegetation aged from 4 to 9 years (Mitchell et al. 1986). Early successional shrub species begin to senesce and die back from 3-4 years, and mortality probably only increases significantly again with increasing interspecific competition for resources between nutrient stress-tolerant competitors (sensu Grime 1979) when the vegetation ages to 20 years. Standing dead vegetation made up 12 % of the total in an 11 year-old sand-plain lowland fynbos ecosystem (Low 1983). At the highest altitude restionaceous and Protea laurifolia communities of a karoo-fynbos gradient, dead individuals comprised only 1.4 % and 3.5 % of total phytomass respectively, but increased to 19.7 % in mountain renosterveld (Rutherford 1978). The increase in dead material with decreasing rainfall suggests a direct response to aridity (Rutherford 1978). In a southern Australian heathland, many understorey species reach their peak and die at 2-3 years of age and this was attributed either to natural senescence or competition for water and light (Specht et al. 1958). Foliar nutrient changes in the chaparral shrub Adenostoma fasciculatum associated with a

fire-induced age gradient, suggest that nutrient limitations may be a significant factor in senescence (Rundel & Parsons 1980).

The increase in the proportion of necromass in the fertilized plots compared with the control, may indicate that the vegetation is nutritionally stressed, probably as a result of a nutrient imbalance. Necromass in the fertilizer treatments tended to display higher nutrient contents than the control. Kummerow (1982) postulated that increased growth in chaparral shrubs, amended with nutrients, resulted in less drought resistant chaparral shrubs as a result of decreased root to shoot ratios in response to fertilizer addition.

Plants adapted to nutrient-poor soils have inherently slow growth rates which do not increase when nutrient availability is increased (Clarkson 1967). During periods of increased nutrient availability, these plants store nutrients (luxury consumption) which are used during periods of reduced availability (Stock et al. 1987). Increased mean concentrations of phosphorus, in response to P addition, were found in the biomass of all growth forms and species sampled except the proteoid shrubs. Increased mean biomass nitrogen concentrations with nitrogen addition were found only in proteoid, annuals, Muraltia dumosa and Gazania ciliaris. The addition of all essential nutrients other

than N and P tended to result in higher phosphorus concentrations and contents in many of the growth forms. Thus phosphorus uptake from the soil may be limited in many growth forms by a deficiency in nutrients other than N. However, nitrogen and not phosphorus addition resulted in increased shoot growth in Leucospermum parile and Phylica cephalantha (Chapter 3). Luxury consumption of nutrients is a feature of fynbos as well as chaparral (Rundel & Parsons 1980, 1984), and Australian heathlands (Specht et al. 1958).

The decrease in N/P ratio in the necromass of the three major plant growth forms, compared with their biomass, indicates reabsorption of a greater proportion of phosphorus than nitrogen prior to senescence. In the Proteaceae, internal recycling of nitrogen from senescing leaves of Australian heath plants such as Banksia ornata is not as efficient as for phosphorus, with only 30 % compared to 90 % recycled prior to leaf abscission (Specht 1981). For L. parile, a withdrawal of 41 % nitrogen and 25-50 % phosphorus was found during leaf abscission (Mitchell et al. 1986). For Protea repens, a common sand-plain lowland fynbos shrub, withdrawal of 33-66 % phosphorus and only 3-25 % nitrogen during leaf abscission was found in plants growing in lowland and mountain fynbos (Mitchell & Coley 1987).

The addition of fertilizers, particularly nitrogen, resulted in increases in annual and graminoid phytomass. These herbaceous and shallow-rooted plants showed a greater growth response than the deeper rooted shrubs, indicating that these species are more plastic in their responses to nutrient additions than shrubs. Geophytes were found to have relatively high nitrogen and phosphorus concentrations. Geophytes in western Australia have an extremely efficient (80-99 %) utilization of N, P and K resources in a parent corm or tuber at the start of the growing season and an almost equally efficient withdrawal of the same resources at the end of the growing season (Pate & Dixon 1982). The various growth forms appear to be better adapted for phosphorus than nitrogen conservation by enhanced luxury consumption of phosphorus and greater withdrawal prior to senescence and leaf abscission (Specht 1981; Mitchell et al. 1986; Mitchell & Coley 1987). Although the vegetative growth response of the various growth forms to nutrient additions was relatively low, with repeated nutrient inputs or additions of larger magnitude than applied in this study, the growth form composition of the vegetation may ultimately shift in favour of ephemeral, nutrient demanding species.

CHAPTER 7

RESPONSE TO NUTRIENT ADDITIONS BY THE REPRESENTATIVE PLANT GROWTH FORMS OF SAND-PLAIN LOWLAND FYNBOS, SOUTH AFRICA

(Submitted to Vegetatio in July 1988)

SUMMARY

The growth response (foliage projective cover; FPC) of the representative plant growth forms of lowland fynbos, South Africa to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) was monitored for two years. Ordination by correspondence analysis revealed a successional trend as the vegetation aged, with increases in proteoid, and to a lesser extent restioid, and decreases in reseeding ericoid, graminoid, geophyte and annual plant FPC but no discernible effects due to fertilizer application. Analysis of covariance revealed significant increases in restioid, graminoid and annual plant FPC with N addition, one- and two-years after fertilizer addition and of total FPC with N addition for only one year. Of the other nutrient treatments, only an increase in annuals with P addition and a reduction in the rate of decline of reseeding ericoid with M addition were found, both after two years. There were few significant interactions between nutrient treatments. Thus nitrogen may often limit vegetative growth of at least the herbaceous species. The herbaceous growth forms are more plastic in their morphological growth responses to nutrient additions than the slow-growing, stress tolerant, evergreen shrub species. Plant mortality as a result of nutrient additions was low and the vegetation appears to be resilient, at least in the short term, to a

disturbance of this magnitude. However, chronic nutrient applications and those of larger magnitude will probably result in long-term changes in species composition, with an increase in ephemeral, nutrient demanding species.

INTRODUCTION

The divergence in the structure and growth form composition of the Cape fynbos and Australian heathlands, compared with the northern hemisphere and Chilean matorral mediterranean-type ecosystems, has been attributed to the more nutrient-poor soils found in fynbos and Australian heathlands (Cody & Mooney 1978; Cowling & Campbell 1980; but see Moll 1985). The soils of the fynbos biome have been shown to have a low phosphorus and nitrogen status (Mitchell et al. 1984; Stock & Lewis 1986b; Witkowski & Mitchell 1987) and are edaphically more similar to the Australian heathlands than the other mediterranean-type ecosystems. The fynbos biome closely approximates the geographical area of the Flora Capensis (Goldblatt 1978; Taylor 1978; Kruger 1979), which has been described as the richest and smallest of the world's six floral kingdoms (Hall 1978). It is highly threatened by urbanization, agricultural development, artificially increased fire frequencies, invasive alien vegetation and nutrient pollution. Nutrient additions to Australian heathlands, particularly phosphorus, over a period of twenty years, resulted in a complete change in

species and growth form composition from predominantly sclerophyllous evergreen shrubs to herbaceous species (Specht 1963; Connor & Wilson 1968; Heddle & Specht 1975; Specht et al. 1977). Applications of nitrogen and nitrogen plus phosphorus to Californian chaparral vegetation resulted in increased proportions of annuals and graminoids (McMaster et al. 1982). The effects of nutrient additions on fynbos vegetation composition has not previously been studied, although the application of fertilizers onto adjacent agricultural land and particularly forest plantations (Schönau 1983) is prevalent. This study aimed to determine the growth response of the representative growth forms of sand-plain lowland fynbos to a factorial application of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M), one and two years after fertilizer application at Pella, south-western Cape Province, South Africa. It was hypothesized that the annual and graminoid growth forms would exhibit the greatest increases in vegetal cover as a response to nutrient additions. Evergreen shrub species and hemicryptophytes of the Restionaceae, the typical and dominant fynbos growth forms (Taylor 1978), were expected to exhibit a smaller growth response. Secondly, it was hypothesized, in accordance with the responses to fertilization in Australian heathlands, that the vegetation would exhibit a greater growth response to phosphorus than to nitrogen or M addition.

STUDY AREA

The CSIR fynbos biome intensive study site at Pella on the Burgherspost Farm 62 km north of Cape Town south-western Cape, South Africa (33°31' S, 18°32' E; 15 km inland from the west coast; altitude 160-220 m; 269 ha) was the study area. The climate is mediterranean (Csa and Csb) which is characterized by hot dry summers and wet winters (Schulz 1947). The 49 year mean annual rainfall for the Burgherspost Farm was 522. Mean annual temperature is 17.3° C and frost is virtually absent. The soils are well drained aeolian acidic sands of approximately 2 m depth and are classified as the Geelhout series of Clovelly (orthic A horizon overlying a yellow/brown apedal B) according to the South African soil classification system (MacVicar et al. 1977). The site was burnt by a moderately intense wildfire in November 1980. The vegetation is broadly classified as sand-plain lowland fynbos (Moll et al. 1984). An area of approximately 1 ha in the centre of a 26 ha patch of Clovelly soil was chosen at Pella for this study. It was positioned on a gentle 5° easterly slope in homogeneous four-year old post-fire vegetation which is classified as Leucospermum parile - Thamnochortus punctatus mid-high open shrubland of Phylica cephalantha fynbos (Boucher & Shepherd 1987). Phylica cephalantha and P. stipularis are ericoid shrub species, which resprout within one month after fire, and in conjunction with the reseeders Metalasia adunca and

Lachnospermum fasciculatum dominate the early post-fire succession. Restionaceae species such as Cannomois parviflora are also resprouters and early successional dominants but are replaced later in the succession by reseeding restios such as Thamnochortus punctatus. Leucospermum parile, a sclerophyllous and dominant proteoid shrub, is an obligate reseeder after fire. Seedlings germinate during the winter-spring period after fire and grow relatively slowly for the first 2-3 years compared to the ericoid species. However, from 4 years of age, Proteaceae become more dominant and the vegetation reaches maximum cover five years post-fire (Hoffmann et al. 1987).

METHODS

A complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) was applied to 10 x 5 m sized plots, separated by 5 m wide strips, in 4 year-old sand-plain lowland fynbos vegetation during September 1984. Five g nitrogen m^{-2} as NH_4NO_3 and 0.5 g phosphorus m^{-2} as $Ca_3(PO_4)_2$ were the amounts and forms of nitrogen and phosphorus applied, which were approximately the return to the surface soil and ash after a fire at Pella in November 1980 (Stock & Lewis 1986b; Brown & Mitchell 1986). All other nutrients were based on a Long Ashton nutrient solution (Hewitt & Smith 1975) in proportion to the N and P additions. Each

treatment combination was randomly assigned to four plots except the unfertilized control (C) which was replicated 8 times. Each plot was divided into a destructive and a non-destructive sampling half, each 5x5 m in size.

Foliage projective cover (FPC) has been defined as the proportion of the terrain covered by photosynthetic tissues projected vertically (Specht & Moll 1983) and was determined in the non-destructive half of each plot using 500 point samples. Five 5 m lines, 1 m apart were spread across the plot with points taken every 5 cm along each line. Foliage projective cover (FPC) was determined from the 36 plots prior to fertilizer addition during the late winter to early spring period of 1984 and at the same time of year during 1985 and 1986, 1 and 2 years after fertilizer addition respectively. A wildfire destroyed the vegetation in November 1986 and thus no further sampling was undertaken. The percentage of 'strikes' for each species was calculated and it was possible for a single 'strike' to hit more than one species because of the shading of understorey species. Species were grouped into 9 categories based on physiognomy (growth form) and mode of regeneration. The evergreen shrub component of the vegetation was separated into ericoid and proteoid. The ericoid growth form is dominant in lowland (coastal) fynbos of the western coastal forelands (Boucher 1983), and was further subdivided into those regenerating after fire by resprouting and those that are

obligate reseeding species. Similarly to Kruger (1977a), restioid consists only of Restionaceae and is separated from graminoid which consists of Poaceae and Cyperaceae. Ericoid shrubs are low evergreen leptophyllous shrubs, proteoid are tall sclerophyllous shrubs with broad isobilateral leaves and restioid elements comprise wiry aphyllous hemicryptophytes (Taylor 1978). Geophytes, succulents, annuals and 'other' are the remaining four growth forms.

Ordination by correspondence analysis (reciprocal averaging) was performed by a single analysis of all the data collected during the three years to determine trends due to vegetation age and the nutrient treatments. Three-way analysis of covariance of the responses of each growth form to the nutrient additions were analyzed separately, one and two years after nutrient application (SAS GLM procedure; SAS Institute 1985). The pre-fertilizer (1984) FPC values were used as a covariate in these analyses. Where significant differences were found between treatments, homogeneity of slope was tested by four-way ANOVA. Total FPC was analyzed in the same way.

RESULTS

Resprouting ericoid shrubs, followed by reseeding ericoid shrubs and restioids were the dominant growth forms found at

Pella during the study period, each accounting for more than 20 % of the FPC of the vegetation (Table 7.1). The FPC of the proteoid shrubs accounted for from 2 to 7 % of the total FPC before fertilizer addition in the plots assigned to the various fertilizer treatments (Table 7.1). Each of the other growth forms contributed less than 5 % of the total cover (Table 7.1). During the two year study period, a decrease in the proportion of reseeding ericoid (20 %), graminoid (49 %), geophytes (57 %) and annuals (31 %), and an increase in proteoid (148 %) and to a lesser extent restioid (11 %) FPC were found in the unfertilized control plots (Table 7.1), representing successional change in growth form composition during the study period. The FPC of resprouting ericoids, succulents and 'other' species remained essentially unchanged during this time period. Mean pre-fertilizer addition variation in total foliage projective cover ranged from 44 to 52 % in the plots assigned to the various fertilizer treatments (Table 7.2). Total foliage projective cover declined slightly during the two year study period in the unfertilized control plots (Table 7.2), largely as a result of the unusually hot and dry summer of the 1985-86 growing season (Jarman & Mustart 1987).

Graphical presentation of the first two ordination axes of correspondence analysis showed that the major trend in plant growth form composition as the vegetation aged was

Table 7.1. Percentage contribution to total foliage projective cover of the representative growth forms in 4-6 year-old sand-plain lowland fynbos vegetation, prior to (1984) and 1 and 2 years after amendment (1985 and 1986) with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) at Pella, South Africa. C denotes unfertilized control.

Growth Forms	Year	Treatment							
		C	N	P	M	NP	NM	PM	NPM
Ericoid resprouters	84	32.01	30.32	33.15	32.20	32.36	34.20	34.85	23.97
	85	32.26	24.87	31.48	28.00	24.41	30.48	26.23	19.53
	86	31.47	26.65	31.51	25.61	21.51	30.99	27.90	18.77
Ericoid reseeders	84	22.34	20.36	24.26	25.47	18.20	19.81	24.28	27.68
	85	20.71	17.56	21.29	28.32	15.57	16.47	23.73	21.95
	86	17.92	15.07	16.14	25.33	15.58	15.99	22.01	19.37
Proteoid	84	5.44	6.79	6.33	1.87	3.19	6.45	2.01	2.87
	85	9.14	7.49	9.08	4.11	6.50	10.05	7.23	8.93
	86	13.51	10.78	12.58	10.40	9.81	15.41	12.84	11.48
Restioid	84	22.99	22.08	19.46	22.38	23.45	17.30	19.91	25.32
	85	25.36	25.58	22.40	22.92	25.05	23.06	26.14	26.88
	86	25.55	29.94	23.25	17.86	28.06	22.04	21.33	25.79
Graminoid	84	4.44	2.99	4.96	3.24	2.53	3.38	1.57	4.30
	85	2.35	4.37	3.13	2.16	4.30	7.25	3.89	6.33
	86	2.27	4.49	1.15	3.12	5.42	3.73	3.19	5.40
Geophytes	84	3.98	1.27	3.68	2.51	3.00	3.46	5.24	1.52
	85	2.31	3.48	2.93	3.57	3.53	2.64	1.58	2.88
	86	1.71	2.89	2.88	3.88	2.41	3.31	1.06	2.66
Annuals	84	3.33	3.71	3.12	4.30	3.75	5.58	4.28	3.63
	85	2.45	5.17	1.92	3.14	6.74	3.71	2.50	5.58
	86	2.31	4.79	5.00	4.35	7.66	4.14	3.86	8.40
Succulents	84	1.19	1.99	1.76	1.14	1.41	0.55	1.92	3.12
	85	1.12	2.05	2.93	2.05	3.05	0.58	2.13	2.51
	86	1.10	0.40	2.88	2.65	1.89	0.66	3.28	2.06
Other	84	4.28	10.50	3.28	6.89	12.10	9.28	5.94	7.59
	85	4.31	9.45	4.84	5.72	10.83	5.76	6.58	5.39
	86	4.17	4.99	4.61	6.80	7.66	3.73	4.54	6.08

Table 7.2. Total live foliage projective cover (Mean ±S.E.) of 4-6 year-old post-fire sand-plain lowland fynbos vegetation prior to (1984) and 1 and 2 years after amendment (1985 and 1986) with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) at Pella, South Africa. C denotes unfertilized control.

Year	Treatment							
	C	N	P	M	NP	NM	PM	NPM
1984	48.3 ±1.5	43.9 ±3.3	49.1 ±2.4	52.1 ±3.6	46.8 ±2.3	46.2 ±1.3	44.1 ±1.7	47.2 ±2.3
1985	44.7 ±2.0	49.1 ±1.4	44.9 ±3.0	47.0 ±2.7	52.4 ±0.3	48.8 ±2.6	45.7 ±1.7	49.8 ±1.7
1986	42.1 ±1.1	44.9 ±1.1	46.0 ±4.6	47.5 ±4.9	50.1 ±0.4	50.4 ±2.9	45.6 ±2.0	49.4 ±2.7

successional. No discernible trend due to fertilizer additions was found when analyzing the data with correspondence analysis. It was concluded that changes in growth form composition in response to fertilizer additions may have been masked by the spatial heterogeneity of growth form composition in the 5x5 m sized plots prior to fertilizer addition.

Analyzing the data by covariance analysis overcomes the problem of pre-fertilizer addition spatial heterogeneity in growth form composition between plots because pre-fertilizer FPC values are entered as a covariate in the statistical analysis. Significant increases in restioid, graminoid and annual plant FPC were found with N addition one, and two years after fertilizer addition (Tables 7.1 & 7.3). An increase in total FPC was found with N addition for the first but not the second year after fertilizer addition (Tables 7.2 & 7.3). Of the other nutrient treatments, only an increase in annuals with P addition and a decrease in the rate of decline of reseeding ericoids with M addition, both two years after fertilizer addition were found (Table 7.3). Few significant interactions between nutrient treatments were found (Table 7.3).

Bonferonni conservative confidence intervals were also used to overcome the possibility of increased type one error with multiple comparisons (Morrison 1976). Using these

Table 7.3. Three-way analyses of co-variance of the live foliage projective cover of the representative plant growth forms of four-year old sand-plain lowland fynbos vegetation at Pella, South Africa as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M), 1- and 2-years after fertilizer addition.

Growth Forms	Year	Treatments							
		N	P	M	N^+P	N^+M	P^+M	N^+P^+M	Covariate
Ericoid (resprouters)	85	NS	NS	NS	NS	NS	NS	NS	***
	86	NS	NS	NS	NS	NS	NS	NS	***
Ericoid (reseeders)	85	NS	NS	NS	NS	NS	NS	NS	**
	86	NS	NS	*	NS	NS	NS	NS	*
Proteoid	85	NS	NS	NS	NS	NS	NS	NS	***
	86	NS	NS	NS	NS	NS	NS	NS	***
Restioid	85	**	NS	NS	NS	NS	NS	*	**
	86	**	NS	NS	NS	NS	NS	NS	*
Graminoids	85	***	NS	NS	NS	*	NS	NS	*
	86	***	NS	NS	NS	NS	NS	NS	***
Annuals	85	***	NS	NS	NS	NS	NS	NS	**
	86	**	**	NS	NS	NS	NS	NS	NS
Geophytes	85	NS	NS	NS	NS	NS	NS	NS	NS
	86	NS	NS	NS	NS	NS	NS	NS	NS
Succulents	85	NS	NS	NS	NS	NS	NS	NS	**
	86	NS	NS	NS	NS	NS	NS	NS	*
Other	85	NS	NS	NS	NS	*	NS	NS	*
	86	NS	NS	NS	NS	NS	NS	NS	*
Total	85	**	NS	NS	NS	NS	NS	NS	**
	86	NS	NS	NS	NS	NS	NS	NS	*

$^+$ denotes interaction
NS denotes not significant
*** $P<0.001$, ** $P<0.01$, * $P<0.05$

confidence intervals ($P<0.0025$), significant differences in FPC with N addition in graminoids, annuals and restioids one year after fertilizer addition were found, while only graminoids and annuals were significantly different after two years.

DISCUSSION

Most ecophysiological studies of necessity deal with the environmental response of one or a few, usually dominant, species rather than the entire community and conclusions are then extrapolated to the whole community (Chapin & Shaver 1985). In this study, species were grouped into nine representative growth forms to obtain a relatively complete community response to nutrient additions. These growth forms represent the main survival strategies of plants in these nutrient-poor and semi-arid mediterranean areas.

Successional trends during the study period, broadly depicted by correspondence analysis, are similar to those found by Hoffman et al. (1987) for sand-plain lowland fynbos vegetation of similar age at Pella. Despite the reported lower vegetation variability of sand-plain lowland fynbos compared to mountain fynbos (Boucher 1983), spatial heterogeneity is still high with coefficients of variation between 5 m^2 control plots of ericoid, restioid and proteoid above-ground biomass of 46, 22 and 84 % respectively

(Chapter 6). Using a destructive sampling method to determine the effects of nutrient additions on the vegetal cover of the various plant growth forms is thus not sufficiently sensitive to detect differences which may occur in response to nutrient additions. In this study, the use of both non-destructive sampling, before and after a disturbance, and covariance analysis provided a more sensitive approach to the analysis of the growth responses of the various plant growth forms of sand-plain lowland fynbos to nutrient additions.

The increased cover of annuals and graminoids was the result of both increased numbers of individuals and increased plant size while that of the Restionaceae appears to be largely due to increased growth of individual plants. It has been postulated that species of the Restionaceae occupy the niche normally filled by grasses and sedges in other ecosystems (Linder 1984). The results presented in this study provide support for this hypothesis. The FPC of geophytes appears to vary unpredictably from year to year. Their cover one and two years after fertilizer addition, in the 5 x 5 m sized plot, was found by covariance analysis to be unrelated to pre-fertilizer addition values (Table 7.3). An increase in geophyte FPC as a response to nitrogen addition was expected because of the exceptionally high concentrations of nitrogen in their seed-like aestivating organs (Dixon et al. 1983). The lack of a detectable response in geophytes to

fertilizer additions, may be due to an insufficiently large plot size to accurately determine variations in the FPC of geophytes because of their low FPC, or alternatively be the result of the controlling influence mole-rats have on geophyte abundance in the deep aeolian sands of sand-plain lowland fynbos (Lovegrove & Jarvis 1986).

The increase in total FPC with nitrogen addition during the first year after fertilizer addition corresponds with increased soil nitrogen concentrations in the N amended plots, which were no longer elevated during the second year (Chapter 2). The increase in total vegetal cover with N addition is largely the result of the increases in annuals and graminoids, which reach maximum FPC during early spring, and of restioids. Phosphorus addition had no effect on total FPC despite elevated soil phosphorus concentrations in the P fertilized plots throughout the two year study period (Chapter 2). Similarly the addition of M had little effect on vegetation FPC. Thus the vegetation of sand-plain lowland fynbos at Pella may often be nitrogen limited. This contrasts with the greater growth response to phosphorus addition rather than nitrogen by the vegetation of the Australian heathlands (Specht 1963).

The responsiveness to nutrient additions of the various growth forms studied appears to be inversely related to rooting depth and possibly also plant longevity. In

mountain fynbos vegetation, Higgins et al. (1987) found that proteoid shrubs were the deepest rooting, followed by the ericoid, while the restioids were generally shallow rooted. Studies in sand-plain lowland fynbos at Pella agree with these findings (Moll & Sommerville 1985; Jongens-Roberts & Mitchell 1986).

The herbaceous growth forms, such as the graminoid, annual and restioid, responded to fertilizer additions with increased vegetative growth and appear to be more plastic in morphological growth than the slow growing, stress tolerant evergreen shrubs which showed little growth response to increased nutrient availability. In other nutrient stressed ecosystems such as tundra communities, Lechowicz & Shaver (1982) found that graminoid species had a greater growth response to NPK factorial fertilizer addition than deciduous and evergreen shrub species, while Henry et al. 1986) found that the growth response to N addition of forbs > graminoids > deciduous dwarf shrubs > evergreen dwarf shrubs. Species characteristic of favourable habitats show greater plasticity in allocation patterns than do species from stressful habitats (Grime 1979). However, in unproductive habitats, long-lived plants such as evergreen shrubs express plasticity through reversible physiological changes such as nutrient storage (Bloom et al. 1985; Grime et al. 1986). Storage of nutrients in response to fertilizer addition has been demonstrated for resprouting

ericoid, proteoid and restioid elements (Chapters 3 & 4), whereas seasonal storage of nitrogen has been shown for a restioid element (Stock et al. 1987) at Pella.

In this study, nutrient additions resulted in little change in plant mortality patterns, and it appears that the vegetation is resilient to a nutrient input perturbation of this magnitude. Fertilizer application is one of the most economically viable management practices in South African forestry (Schönau 1983) and is also vital for high agricultural productivity in these nutrient-poor ecosystems. Indigenous patches of fynbos, situated in close proximity to forest plantations and agricultural land, are susceptible to accidental inputs of fertilizers broadcast from adjacent areas or seepage of nutrients in soil. Although the dominant short-term growth response by the vegetation was with nitrogen addition, long-term changes may be greater with phosphorus addition because of the greater residence time of phosphorus in the soil compared with nitrogen (Chapter 2). With chronic nutrient inputs or additions of larger magnitude than applied in this study, it is likely that the growth form composition of the vegetation may ultimately shift in favour of ephemeral, nutrient demanding species. This occurred in the Calluna heathlands of Europe with increased soil nitrogen concentrations as a result of nitrogen input in acid rain, resulting in the replacement of Calluna scrub with graminoids such as Molinia (Heil &

Diemont 1983; Berendse & Aerts 1984; Heil & Bruggink 1987). Atmospheric inputs (0.19 kg P ha^{-1} and 1.89 kg N ha^{-1}, Brown et al. 1984; Stock & Lewis 1986a respectively) at Pella appear to be presently too low to be having a similar effect. Similarly, large phosphorus additions to Australian heathlands, resulted in a complete change in species composition over a period of twenty years (Heddle & Specht 1975).

CHAPTER 8

THE EFFECTS OF NUTRIENT ADDITIONS ON INFLORESCENCE AND SEED PRODUCTION OF *LEUCOSPERMUM PARILE* (PROTEACEAE) IN A NUTRIENT-POOR FYNBOS ECOSYSTEM, SOUTH AFRICA

(To be submitted to Journal of Ecology)

SUMMARY

The effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) on inflorescence and seed, production, dry mass, nitrogen and phosphorus contents in the evergreen shrub, Leucospermum parile (Proteaceae), growing in a nutrient-poor fynbos ecosystem, south-western Cape Province, South Africa was studied for two growing seasons. Leucospermum parile is monoecious, non-serotinous and regenerates from seed after fire.

Nitrogen addition resulted in reduced inflorescence production and increased vegetative growth and nitrogen accumulation in shoots during the first year. During the second year, inflorescence production was significantly increased in response to N addition (ie. population marginal means of 101 and 70 flowers on N-amended and unfertilized shrubs respectively). Nitrogen addition also resulted in reduced dry mass per seed (21 mg compared with 38 mg for seeds from unfertilized control plants) and seed dry mass per inflorescence during the first, although not the second year. Seed size variation in L. parile was higher than that found in Australian Proteaceae. Resource allocation to seed production in L. parile may be controlled at several stages during inflorescence and seed development, providing

a high degree of maternal control over seed production during any one growing season.

INTRODUCTION

With the expansion in recent years of the wildflower industry of the fynbos biome, concern has been expressed about overexploitation of proteaceous and other plant species, which are largely harvested from wild populations (Davies 1984; Low & Lamont 1986; Van Wilgen & Lamb 1986). The soils of the fynbos biome are of a low nitrogen and phosphorus status (Stock & Lewis 1986b; Witkowski & Mitchell 1987), and it has been postulated that flowering and reproduction of shrubs of the Proteaceae are limited by resources, particularly mineral nutrients (Lamont et al. 1985). These shrubs display all the features characteristic of nutrient-stress tolerant plants (Grime et al. 1986), except that they possess persistent seed banks. This feature is an adaptation to recurrent fires (Bond et al. 1984) which occur at 4-50 year intervals in most fynbos vegetation categories (Kruger 1977b). In addition, these plants produce relatively large seeds with high nutrient contents (Kuo et al. 1982; Mitchell & Allsopp 1984; Pate et al. 1986), which is suggested as a mechanism to enable seedlings to establish in the impoverished soils.

Studies on the effects of nutrient additions on flower production and reproduction in uncultivated fynbos plants in the field have not previously been attempted, while detailed studies of the response of uncultivated species to the nutrient supply of the mother plant in other ecosystems are also few in number (Roach & Wulff 1987). Seed production may be limited by extrinsic factors such as resource availability, pollination, predation on flowers, fruit and leaves, and weather conditions, as well as intrinsic factors such as age and size of the plant, genetic constitution and maternal control (Lloyd 1980; Stephenson 1981; Wiens 1984; Sutherland 1986; Wiens et al. 1987; Krusi & Debussche 1988). This study aimed to determine the effects of a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) on flower and seed production (both mass and number), and their nitrogen and phosphorus contents in Leucospermum parile (Salisb. ex J. Knight) Sweet (Proteaceae) shrubs, during two growing seasons, in a nutrient-poor sand-plain lowland fynbos ecosystem at Pella, south-western Cape Province, South Africa. This species has been recommended for cultivation (Hall & Veldhuis 1985). Most studies of seed production dynamics in the Proteaceae have been undertaken on serotinous (canopy stored seed) species, because of the ease of determining annual seed production compared with non-serotinous species such as L. parile (eg. Bradstock & Myerscough 1981; Cowling et al. 1987).

STUDY AREA AND SPECIES

The study area is the CSIR fynbos biome intensive study site at Pella on the Burgherspost Farm, 62 km north of Cape Town, south-western Cape Province, South Africa (33° 31' S, 18° 32' E; 15 km inland from the west coast; altitude 160-220 m; 269 ha). The climate, soils and vegetation have been described, while the nutrient dynamics of fertilizer input to these soils and climate during the study period have been described in detail (Chapter 2).

Leucospermum parile is a monoecious shrub endemic to the Malmesbury region of the south-western Cape. It is a mid-late successional dominant growing up to 1.3 m in height and attaining a density of 1630 plants ha^{-1}, four years after fire by regenerating from seed. Seeds of this and other Leucospermum species are passively released onto the soil during spring and summer, where they are either predated by rodents (Bond & Breytenbach 1985), or buried by myrmecochorous ants (Bond & Slingsby 1983; Brits 1987), which seldom disperse the seed more than 2-3 m. Germination and establishment occurs during the winter period after fire, resulting in an even-aged stand of shrubs. Growth of L. parile is largely maintained during the first year by nutrient reserves within the cotyledons of the developing seedlings and approximately 20 % of the total phosphorus content of reproductively mature plants is

allocated to inflorescences each year (Jongens-Roberts & Mitchell 1986).

METHODS

Field fertilizer layout

A complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) was applied to 10 x 5 m plots, arranged in a grid pattern (8x4) with 5 m wide strips separating the plots. Five g N m^{-2} as NH_4NO_3 and 0.5 g P m^{-2} as $Ca_3(PO_4)_2$ were the forms and amounts of nitrogen and phosphorus applied, these being the approximate return of nitrogen and phosphorus to the surface soil and ash after a wildfire at Pella in November 1980 (Brown & Mitchell 1986; Stock & Lewis 1986b). All other nutrients were based on a Long Ashton nutrient solution in proportion to the nitrogen and phosphorus inputs (Hewitt & Smith 1975). Fertilizers were applied during the period 15-17 September 1984. Each treatment combination was replicated four times except the control which was replicated eight times. A full description of the plot layout, chemical fertilizers used and mode of application is provided in Chapter 2.

Plant sampling

Plants of L. parile were approximately three-years of age at the start of the study in September 1984. During November-

December 1984, the number of inflorescences on each L. parile shrub in the plots was counted. A mean of eight mature inflorescences were harvested from 59 plants. During November-December 1985, the number of inflorescences growing on two L. parile shrubs per plot were counted and 10 inflorescences harvested from one of them. Further sampling was not possible because the vegetation was destroyed by a wildfire in November 1986. Seeds (nut-like achenes; Brits 1986) were removed from the inflorescences and each weighed separately. Plump (assumed viable) and damaged (assumed predated or diseased) seeds were counted separately. The plump seeds harvested from each nutrient treatment combination were pooled for nutrient analyses. The number of flower buds per shoot was counted on 10 shoots, randomly chosen from one plant per plot during June 1985 and 1986. The canopy volume and area of these shrubs was also determined during November-December 1984 and 1985 as described in Chapter 3.

Nutrient analyses

All plant material was oven-dried at 80^{o} C for 48 h, weighed, ground to 40 mesh in a Wiley mill and analyzed for nitrogen and phosphorus in triplicate. Nitrogen was determined on 0.1 g plant material by Kjeldahl digestion using a selenium catalyst, sodium thiosulphate and salicylic acid to convert nitrate and nitrite to ammonium, which was determined colorimetrically (Smith 1980). Total phosphorus

was determined on 0.1 g plant material by the methods of Jackson (1958) and Murphy and Riley (1962).

Statistical analyses

Three-way analysis of variance was used to test differences in mean seed and inflorescence, mass, nitrogen and phosphorus contents, inflorescence bud number per shoot and mean seed number per inflorescence between fertilizer treatments (SAS GLM procedure; SAS Institute 1985). Three-way analysis of covariance was used to compare the number of inflorescences produced per shrub between treatments. Either shrub canopy volume or canopy area were used as the covariate in separate analyses. Where significant differences were found between treatments, homogeneity of slope was tested by four-way ANOVA. Comparisons of dry mass per seed between treatments was analyzed by three-way analysis of variance with nesting.

RESULTS

Flowering phenology

In L. parile, inflorescence buds are produced towards the end of the shoot growing season, from March to June and inflorescences are produced from June-July to November-December. In the spring of 1984, 122 or 42 % of the 293 L. parile shrubs in the 36 plots were flowering, while 94 % were flowering in 1985. The percentage of plants flowering

in 1984 was unlikely to have been influenced by the nutrient additions because flowering had commenced before the nutrients were applied. It was the smaller sized shrubs which were not flowering during 1984 and 1985. Inflorescences are axillary, forming clusters immediately below the terminal shoots of the current year's growth flush. Only a proportion of the inflorescence buds produced inflorescences and aborted buds were recovered from litter traps during spring. Inflorescence buds on each shoot developed asynchronously into inflorescences from winter until the end of spring. The number of inflorescence buds per shoot in control plants during May-June 1985 was linearly related to shoot dry mass ($I = 2.33\ S - 2.48$, $r^2 = 0.74$, $P<0.01$, $n=80$; I denotes number of inflorescence buds, and S denotes shoot dry mass (g)).

Inflorescence production

The mean number of inflorescence buds per shoot was not significantly different between treatments in 1985 and 1986, although tending to be higher and more variable with N addition than the other treatments in 1985 (Fig. 8.1, Table 8.1). A log-log relationship was found between inflorescence production and shrub canopy volume (Fig. 8.2), which is similar to that found for *Protea lorifolia* (Bond *et al.* 1984). Nitrogen addition resulted in a significant decrease in inflorescence production in 1984 ($F_{1,113} = 4.31$ & 4.24, $P<0.05$, using canopy area and canopy volume as

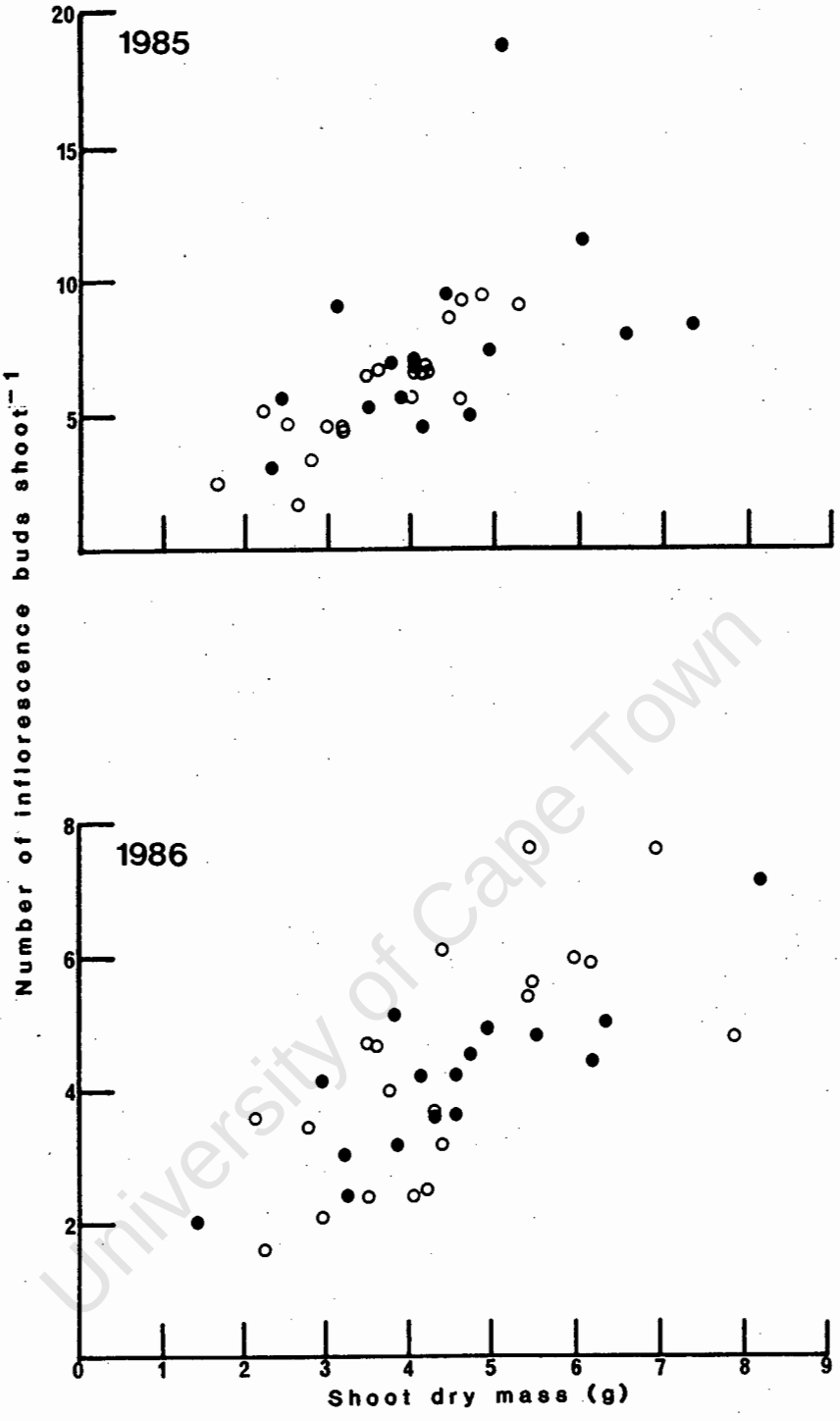

Fig. 8.1. Mean number of inflorescence buds produced per shoot in relation to shoot dry mass during May-June 1985 and 1986 in Leucospermum parile shrubs amended with nitrogen (●) on 15-17 September 1984 and not amended with nitrogen (○). In 1985, I = 1.91 S - 0.98, n=20, r^2=0.72, P<0.01, for shrubs not amended with nitrogen; and, I = 1.14 S + 2.55, n=16, r^2=0.19, P>0.05, for nitrogen amended shrubs. In 1986, I = 0.79 S + 0.84, n=20, r^2=0.48, P<0.01, for shrubs not amended with nitrogen; and, I = 0.65 S + 0.72, n=16, r^2=0.72, P<0.01 for nitrogen amended shrubs. I denotes inflorescence number per shoot, and S denotes shoot dry mass (g).

Table 8.1. Variations by three-way analysis of variance of inflorescence dry mass, nitrogen and phosphorus contents and concentrations, mean seed dry mass and seed number per inflorescence in 1984 and 1985, and mean number of inflorescence buds per shoot in 1985 and 1986, of *Leucospermum parile* shrubs after amendment with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M), applied on 15-17 September 1984 at Pella, South Africa. Values are *F* values, *d.f.* =1,51; 1,28 and 1,28 for determinations in 1984, 1985 and 1986 respectively. ***, $P<0.001$; **, $P<0.01$; *, $P<0.05$; $^{+}$, denotes interaction; [1], denotes not analyzed due to insufficient sample size.

Treatments	N	P	M	$N^{+}P$	$N^{+}M$	$P^{+}M$	$N^{+}P^{+}M$
Inflorescence buds							
Number per shoot (mean)							
1985	0.14	0.40	0.19	0.23	0.64	0.84	0.55
1986	0.66	0.25	0.84	0.95	0.35	0.11	0.75
Inflorescence							
Dry mass							
1984	1.32	0.21	2.90	1.22	0.11	4.79*	1.73
1985	0.34	0.05	1.59	3.56	2.33	1.30	2.44
Nitrogen concentration							
1984	12.39***	0.85	0.87	0.18	0.70	1.35	0.06
1985	0.30	0.19	0.51	0.56	0.02	0.03	0.21
Phosphorus concentration							
1984	0.83	3.77	0.07	6.16*	0.96	2.95	3.92
1985	7.10*	0.01	1.77	0.00	1.47	0.01	0.02
Nitrogen content							
1984	1.48	0.06	4.78*	0.67	0.53	6.28*	1.58
1985	0.50	0.08	0.13	3.86	1.24	0.32	2.06
Phosphorus content							
1984	1.44	2.49	1.95	4.73*	0.00	5.05*	3.08
1985	4.63*	0.01	0.26	1.23	3.08	0.08	1.03
Seed (including testa)							
Dry mass (mean)							
1984	4.59*	3.22	0.49	1.07	1.94	0.69	0.35
1985	0.00	2.23	0.01	1.45	4.51*	2.81	3.38
Number per inflorescence							
1984	0.07	2.38	0.37	3.41	0.41	1.34	2.00
1985[1]							
Inflorescence plus seed							
Dry mass							
1984	1.82	0.43	2.70	1.35	0.24	4.52*	1.71
1985	0.34	0.07	1.61	3.71	2.52	1.42	2.61

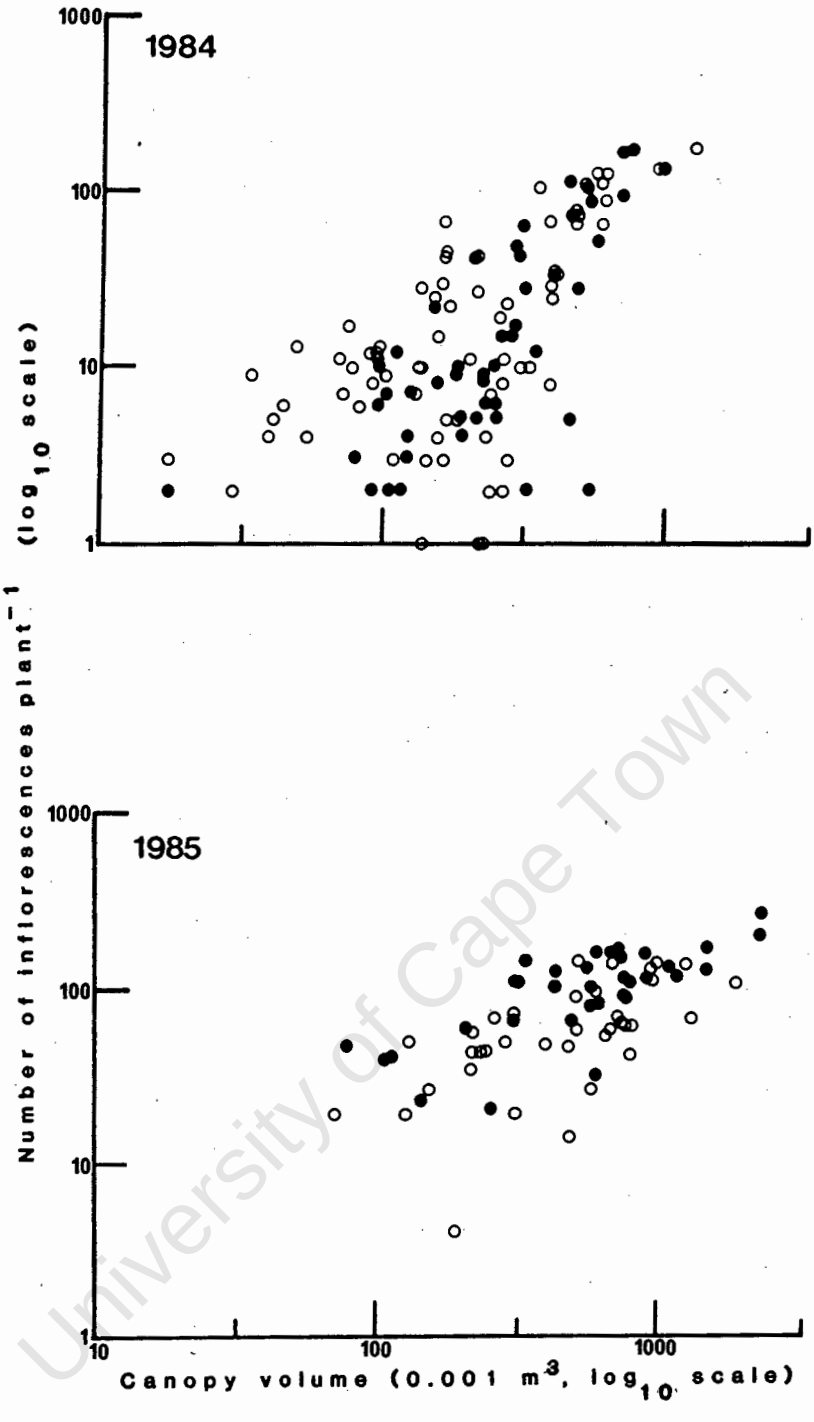

Fig. 8.2. Number of inflorescences produced in relation to shrub canopy volume during November-December 1984 and 1985 in reproductive Leucospermum parile shrubs amended with nitrogen (●) on 15-17 September 1984 and those not amended with nitrogen (○). In 1984, log I = 0.90 log V - 0.88, n=71, r^2=0.34, P<0.01, for shrubs not amended with nitrogen; and, log I = 1.28 log V - 1.91, n=48, r^2=0.49, P<0.01, for nitrogen amended plants. In 1985, log I = 0.61 V + 0.12, n=40, r^2=0.36, P<0.01, for shrubs not amended with nitrogen; and, log I = 0.57 log V + 0.41, n=32, r^2=0.57, P<0.01, for nitrogen amended shrubs. I denotes inflorescence number per shrub, and V canopy volume (0.001 m^3).

covariates, respectively; Fig. 8.2). Population marginal means (also called least squares means; Searle et al. 1980) of inflorescence production in response to each fertilizer treatment combination were calculated (Table 8.2). These show that N addition resulted in reduced inflorescence production in 1984, particularly with the sole addition of N. The sole addition of P tended to result in increased inflorescence production compared with the control plants (Table 8.2). During the second year (1985), a significant increase in inflorescence production was found with N addition ($F_{1,63}$ = 18.16 and 14.49, $P<0.001$, for canopy area and canopy volume as covariates, respectively; Fig. 8.2, Table 8.2). Mean inflorescence dry mass varied significantly with the interaction of P and M addition in 1984 ($P<0.05$), whereas no significant differences were found in 1985 (Fig. 8.3, Table 8.1). In addition, no significant differences in the mean inflorescence dry mass of the control plants were found between years ($t=-1.11$, $d.f.=20$, $P>0.05$; Fig. 8.3).

Seed production

The percentage of barren inflorescences found in control plants was 23 % in 1984. With the sole addition of N, 69 % of inflorescences were barren, while the sole addition of P and P plus M addition, resulted in only 17 % and 16 % barren inflorescences respectively (Table 8.3). In 1985, the percentage of barren inflorescences varied between 82 % and

Table 8.2. Population marginal means (least squares means; Searle et al. 1980) of numbers of inflorescences produced during 1984 and 1985 by Leucospermum parile shrubs amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. These were calculated using either shrub canopy volume or canopy area as a covariate in the analyses. C denotes unfertilized control.

		Treatments							
Year	Covariate	C	N	P	M	NP	NM	PM	NPM
1984	Canopy area	32	7	39	29	23	32	27	24
	Canopy volume	33	7	39	29	24	32	24	27
1985	Canopy area	76	101	58	62	112	87	82	102
	Canopy volume	77	97	59	62	115	84	85	107

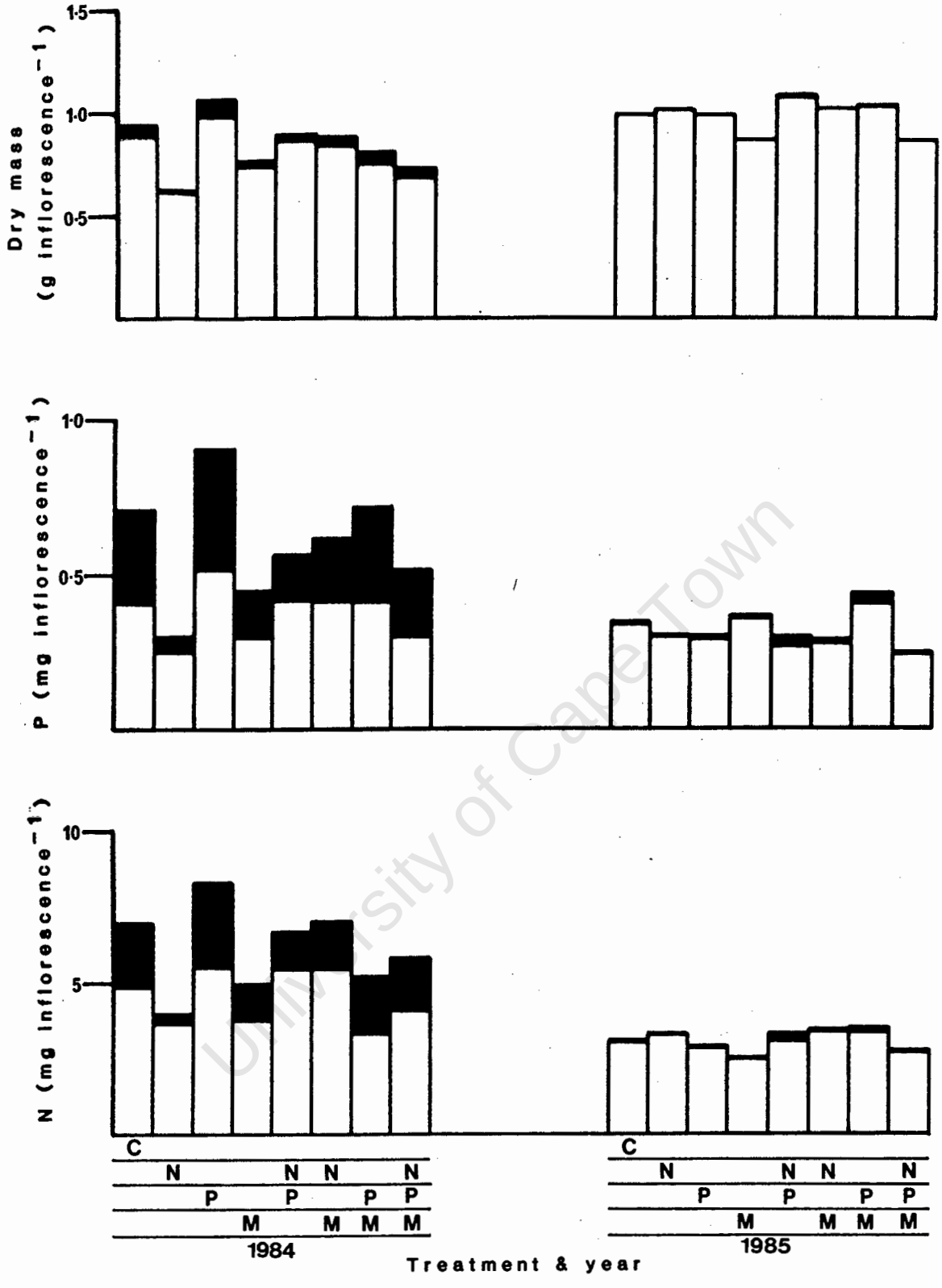

Fig. 8.3. Mean inflorescence (□) and seed (per inflorescence; ■) dry mass, phosphorus and nitrogen contents of Leucospermum parile during November-December 1984 and 1985 as a response to a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrient excluding N and P (M) applied on 15-17 September 1984 at Pella, South Africa. C denotes unfertilized control.

Table 8.3. Numbers of plants and flowers sampled, mean numbers of plump (assumed viable) and damaged seeds recovered per inflorescence, dry mass per seed (mean ± S.E.), % of barren inflorescences, and inflorescence nitrogen and phosphorus concentrations (mean ± S.E.) in 1984 and 1985 and seed nitrogen and phosphorus concentrations in 1984, of Leucospermum parile shrubs amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M), applied on 15-17 September 1984 at Pella, South Africa. C denotes unfertilized control.

Treatment	C	N	P	M	NP	NM	PM	NPM
Total No. of plants sampled								
1984	14	4	7	8	4	8	7	7
1985	8	4	4	4	4	4	4	4
Total No. of flowers sampled								
1984	111	36	40	51	39	57	38	36
1985	80	40	40	40	40	40	40	40
Total No. of plump seeds								
1984	183	14	74	34	44	96	59	50
1985	9	3	7	2	14	6	3	5
Total No. damaged seeds								
1984	11	1	5	8	0	13	18	4
1985	1	1	0	1	0	1	0	0
Mean No. of plump seeds per inflorescence								
1984	1.54	0.75	1.94	0.77	1.34	1.71	1.64	1.47
1985	0.10	0.08	0.18	0.05	0.35	0.15	0.08	0.13
Barren inflorescences (%)								
1984	23	69	17	51	46	19	16	33
1985	90	92	90	92	85	82	85	90
Seed mass per seed (mg)								
1984	38±1	21±6	36±2	33±3	27±3	30±2	38±2	32±2
1985	23±6	13±7	13±3	38	21±4	18±7	11±2	11±2
Seed P concentration (mg P g^{-1} dry mass)	5.38	5.46	4.66	4.91	4.68	4.55	5.53	4.87
Seed N concentration (mg N g^{-1} dry mass)	36.2	37.5	32.9	37.3	37.2	34.1	33.9	39.1
Inflorescence P concentration (µg P g^{-1} dry mass)								
1984	455±26	389±58	513±30	415±45	487±25	490±35	544±20	437±31
1985	345±56	299±34	321±31	428±65	292±78	281±70	431±47	283±25
Inflorescence N concentration (mg N g^{-1} dry mass)								
1984	5.52 ±0.34	5.74 ±0.76	5.53 ±0.08	5.26 ±0.44	6.42 ±0.25	6.58 ±0.35	4.43 ±0.25	6.10 ±0.43
1985	3.02 ±0.21	3.12 ±0.03	2.84 ±0.32	2.89 ±0.37	2.87 ±0.40	3.28 ±0.20	3.17 ±0.31	3.13 ±0.21

92 % for all treatments. The number of plump seeds recovered per inflorescence varied from 0 to 5, with a mean of 1.54 for control plants, and was greatest for plants amended with only P (1.94) and lowest for plants amended with only N (0.75; Table 8.3). However, the mean number of plump seeds per inflorescence was not significantly different between treatments (Table 8.1). Mean seed dry mass per inflorescence was reduced in response to N addition ($P<0.05$) in 1984, particularly the sole addition of N (Tables 8.1 & 8.3). Dry mass per seed ranged from 9-77 mg for control plants (coefficient of variation = 47 %). In 1984, dry mass per seed was reduced in response to N addition ($P<0.001$; Tables 8.3 & 8.4), and was particularly low and variable with the sole addition of N (coefficient of variation = 108 %; Table 8.3). The viability of different sized seeds was not tested.

Only 0.136 plump seeds per inflorescence were recovered during November-December 1985 compared with 1.19 in 1984. Inflorescences matured earlier in 1985 compared with 1984 and had probably already released a large proportion of their seeds when harvested. Seeds not enclosed in inflorescences were recovered from October 1985 to March 1986 from litter traps placed under the shrubs, although most of the released seeds would have been removed by myrmecochorous ants and rodent seed predators. Seeds harvested from control plants were significantly smaller, on

Table 8.4. Results of a nested three-way analysis of variance of dry mass per seed in 1984 of Leucospermum parile shrubs amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M), applied on 15-17 September 1984 at Pella, South Africa. NS, denotes not significant; $^{+}$, denotes interaction between treatments.

Treatments	d.f.	F	P
N	1,478	70.81	<0.001
P	1,478	4.63	<0.05
M	1,478	1.25	NS
$N^{+}P$	1,478	0.04	NS
$N^{+}M$	1,478	14.83	<0.001
$P^{+}M$	1,478	0.04	NS
$N^{+}P^{+}M$	1,478	0.99	NS
Within plants ($N^{+}P^{+}M$)	49,478	18.38	<0.001

a mean dry mass basis, in 1985 compared with 1984 (t=2.65, $d.f.$=20, P<0.01; Table 8.3). Only 5.7 % and 10.0 % of the seeds recovered from the control plants were damaged during 1984 and 1985 respectively, with a mean of 9.8 % and 7.5 % for all treatments respectively (Table 8.3).

Inflorescence and seed nutrient contents

Seed nitrogen and phosphorus concentrations of L. parile were similar to that of other Cape Proteaceae (Pate et al. 1986) and varied little between fertilizer treatments (Table 8.3). In 1984, inflorescence phosphorus content varied significantly with the interaction of N and P addition, as well as that of P and M, but was reduced in the N amended plants during 1985 (Table 8.1, Fig. 8.3). Significant differences in inflorescence phosphorus concentration were found with the interaction of N and P addition in 1984, whereas a reduction with N addition was found in 1985 (Tables 8.1 & 8.4). Inflorescence nitrogen content was significantly increased with M and varied with the interaction of P and M addition during 1984, while it varied with the interaction of N and P addition in 1985 (Table 8.1; Fig. 8.3). Inflorescence nitrogen concentration increased with N addition (P<0.001) in 1984, whereas no significant differences were found between treatments in 1985.

DISCUSSION

This study shows that inflorescence production of L. parile is matched with resource availability within the plant, in particular nitrogen levels. Nitrogen addition during the first year (1984) resulted in reduced inflorescence production and increased vegetative growth and nitrogen storage in shoots (Chapter 3). During the second year (1985), N amended plants displayed significantly increased inflorescence production compared with the other treatments. This may be due to the allocation of stored nitrogen to increased inflorescence production during 1985. At the end of the 1985-86 growing season, shoot nitrogen concentrations of N-amended plants were no longer elevated, and thus the nitrogen reserves accumulated during the previous season had been utilized. In addition, soil nitrogen concentrations had also returned to pre-fertilizer levels by June 1985 (Chapter 2).

Seed number per inflorescence in unfertilized control plants in 1984 was similar to that found for L. parile by Jongens-Roberts & Mitchell (1986). In 1984, nitrogen addition resulted in significantly reduced dry mass per seed as well as seed mass per inflorescence and the sole addition of N also tended to reduce inflorescence size (Fig. 8.3). In many species, seed size increases with increased nutrient supply (Willson & Price 1980; Parish & Bazzaz 1985; Wulff 1986) whereas in others, seed size is unchanged despite

increased nutrient supply and increased parent plant growth (Fenner 1986).

Australian Proteaceae have larger more nutrient rich seeds than Cape Proteaceae and, for any particular species, have low variation in seed size (Lamont et al. 1985; Pate et al. 1986). Variation in seed size of Grevillea leucopteris from 18 localities in Western Australia (Hocking 1986) was less than for L. parile seeds harvested from a single population of unfertilized plants in 1984. The asynchronous development of seeds in L. parile may result in differential seed size because of variation in resource availability during the seed production period (eg. Wulff 1986). The smallest seeds may have been produced as a result of a decrease in resource availability towards the end of the flowering season. The reduced dry mass per seed in response to N addition found in this study, may be due to physiological interruption of seed development as a result of the timing of fertilizer application during the period of seed development (Roach & Wulff 1987). Relatively large nutrient inputs of this type is not a typical disturbance for these plants at this stage in their life-cycle. When nutrient addition to the annual, Abutilon theophrasti, was delayed until fruit maturation had begun, seed numbers and total seed mass were reduced (Benner & Bazzaz 1985).

The unusually hot dry period which occurred during mid-November 1985 (Jarman & Mustart 1987), probably triggered

earlier than normal seed release from these dehydrating inflorescences in 1985 compared with 1984. Field observations suggest that in most non-serotinous Cape Proteaceae, seeds are mostly released during periods of warm, dry weather (Bond & Breytenbach 1985). The smaller seeds recovered from inflorescences in 1985 compared with 1984, suggests that seeds produced at the end of the flowering season are smaller than those produced earlier. This may be due to reduced nutrient availability for reproduction as these plants begin to allocate more resources to shoot growth, which commences during the late October-early November period (Chapter 3).

Investment of resources in flowering and fruiting can be regulated at any one of several stages (Lloyd 1980). In L. parile, not all shoots produce inflorescence buds at the end of the shoot growing season and larger shoots have more buds than smaller ones (Fig. 8.1). Secondly, inflorescence buds are aborted in early spring. Seed production can also be controlled throughout the inflorescence production period by abortion of immature inflorescences because of their asynchronous development on any particular shoot. Finally, resource allocation to reproduction may also be altered by producing fewer and smaller sized seeds. These features enable this species to maintain high levels of seed production in any one year without detrimentally reducing its resource allocation to the vegetative growth which follows, even if unfavourable climatic conditions occur.

In L. parile, stored nutrients in shoots may provide these plants with an ability to pre-determine levels of reproduction from year to year. In addition, floral structures, such as buds and inflorescences may be relatively inexpensive to produce (Chaplin & Walker 1982; Bookman 1983) and thus their abortion would not entail a high cost in scarce resources. Seed set in L. parile is probably within the range found for other Leucospermum spp. (1.2 % to 17.0 %; Collins & Rebelo 1987). This low seed set may be due to most florets in an inflorescence being functionally andromonoecious, serving as pollen donors and attractants to pollinators (Collins & Rebelo 1987).

In conclusion, nitrogen addition resulted in reduced inflorescence production during the year of application, while increasing shoot growth and nutrient storage. Stored nitrogen was utilized for increased inflorescence production during the following year. Nitrogen addition also increased variation in seed size and the production of smaller seeds during the first year, probably due to interruption of physiological growth processes. Seed production in L. parile may be altered at several stages during the flowering period in response to variable environmental conditions, thus ensuring relatively high levels of seed production within the constraints of the nutrient-poor soils and mediterranean climate.

CHAPTER 9

THE EFFECTS OF NUTRIENTS ON THE DISTRIBUTION OF DRY MASS, PHOSPHORUS AND NITROGEN IN SEEDLINGS OF *PROTEA REPENS* (L.) L. (PROTEACEAE)

(To be submitted to The New Phytologist)

SUMMARY

The response of Protea repens seedlings to increasing concentrations of phosphorus (P), nitrogen (N) and a mixture of all essential nutrients excluding P and N (M) was determined in potted Clovelly soil collected from a lowland fynbos site at Pella, south-western Cape, South Africa. Pot culture resulted in increased soil mineral nitrogen, in particular nitrate, and decreased available (resin-extractable) phosphorus concentrations compared to the field soil. High levels of N (4-64 g N m^{-2}) and M addition resulted in seedling mortality. Leaf, stem and total plant dry mass increased with increasing P application level, while increased nitrogen resulted in reduced total plant dry mass in surviving plants. Leaf, stem, root and total plant phosphorus contents increased with P application level and decreased with N. Leaf, stem and total plant nitrogen contents increased with P application level and root nitrogen content decreased with that of N. Plant leaf area increased with P application level, whereas it decreased with N. These results are compared to the responses of adult shrubs to fertilizer additions in the fynbos and responses of pot-grown plants from other mediterranean-type ecosystems.

INTRODUCTION

Protea repens (L.) L. is a common and widespread species in mountain and lowland fynbos vegetation of the south-western Cape, South Africa, in contrast to most other Cape species of the Proteaceae which are more restricted in their distributions (Bond & Goldblatt 1984). It is a slow growing evergreen shrub of 1-4 m in height and is prevalent in the late stages of fynbos succession. Its large seeds are mainly released from the flowerheads after the parent plants have been exposed to fire (Bond 1985) and contain high nutrient reserves, particularly nitrogen and phosphorus (Mitchell & Allsopp 1984; Pate et al. 1986) which allow seedling growth to be independent of external supplies of nutrients. When the nutrient reserves in the cotyledons are almost depleted, nutrient uptake from the soils of low nutrient status is facilitated by proteoid roots (Lamont 1982; Lamont et al.1984). As a further adaptation to soils of low nitrogen status, P. repens has a low rate of NO_3^- and NH_4^+ assimilation, a poor nitrate reductase activity in both roots and shoots and a low rate of nitrogen metabolism (Lewis & Stock 1978; Stock & Lewis 1982; 1984).

The aim of this study was to examine the effects of a range of concentrations of phosphorus (P), nitrogen (N) and a mixture of all essential nutrients excluding P and N (M) on the distribution of dry mass, phosphorus and nitrogen in

seedlings of P. repens. Comparisons of plant available forms of phosphorus and nitrogen between the field and in the pots were determined to establish whether the results of this experiment could be extrapolated to the field.

MATERIALS AND METHODS

Plant growth procedure

Protea repens seeds were obtained from shrubs growing in mountain fynbos vegetation on the Honingklip farm, 65 km southeast of Cape Town. Seeds were germinated by immersion in 10 % H_2O_2 for 6 h and then planted into asbestos trays (10 cm depth) containing an autoclaved (121 ^{o}C for 15 minutes) mixture of 50 % 2 mm sieved Clovelly soil and 50 % acid-washed sand on 1st October 1984. The Clovelly soil (orthic A horizon overlying a yellow-brown apedal B; MacVicar et al. 1977) was collected from Pella (0-20 cm depth), a sand-plain lowland fynbos site, 62 km north of Cape Town on the western coastal forelands, which has an annual rainfall of 522 mm per annum. This soil is of a low phosphorus and nitrogen status and consists predominantly of medium textured sand (Mitchell et al. 1984; Stock & Lewis 1986b) and was the same sand used in the studies of Mitchell & Allsopp (1984) and Lamont et al. (1984). Acid-washed sand was obtained from Industrial Sand & Engineering Company, Cape Town. The trays were incubated at 0 ^{o}C for 4 days and then transferred to a well ventilated glasshouse at

the Botany Department, University of Cape Town. Seeds germinated after 3 weeks (55 % germination). Each seedling was transplanted after a further 5 weeks into plastic bags (surface area of 270 cm^2 and depth of 30 cm) and grown in the glasshouse until June 1985 when at the age of 8 months the cotyledons were chlorotic as the reserves were depleted. The greenhouse was east-facing and had unrestricted light throughout the day, with midday light intensities on clear days ranging from 800 - 1500 μEinsteins m^{-2} $second^{-1}$. Temperatures ranged from 10 to 32° C and relative humidity from 50 - 95 %. The plants were watered with deionized water to saturation at three day intervals.

Nutrient applications

Seedlings were amended only once with one of three treatments, applied randomly at various concentrations on 14th June 1985 and replicated five times:

1. Phosphorus ($Ca_3(PO_4)_2$) at 0, 0.2, 0.4, 0.8, 1.6, 3.2, 6.4 and 12.8 g P m^{-2}.
2. Nitrogen (NH_4NO_3), at 0, 2, 4, 8, 16, 32 and 64 g N m^{-2}, (based on the N : P ratio of a Long Ashton nutrient solution which is 10; Hewitt & Smith 1975).
3. A mixture of all essential nutrients excluding N and P (M) based on a Long Ashton nutrient solution (Hewitt & Smith 1975) in proportion to the N and P additions. It consisted of K_2SO_4, $MgSO_4$, $CaCl_2$, $NaCl_2$, Fe Citrate $5H_2O$, $MnSO_4$ $4H_2O$, H_3BO_3, $ZnSO_4$ $7H_2O$ and $CuSO_4$ $5H_2O$

Soil analyses

Soil samples were taken from the pots (0-5 cm depth) 21, 96 and 171 days after fertilizer addition as well as from the field site (0-20 cm depth). All soils were analyzed for resin-extractable and Bray No. 2 phosphorus, ammonium and nitrate. Total nitrogen, total phosphorus, organic matter and pH were determined on the potted soil samples taken 21 and 171 days after fertilizer addition and from the field site. Resin-extractable and Bray No. 2 phosphorus, nitrate, ammonium and pH were determined on fresh soil immediately after collection whereas the others were determined on air-dried soil. The soil analytical methods were the same as those used in Mitchell et al. (1984) and Stock & Lewis (1986b).

Statistical analyses

Statistical analyses were performed separately for each treatment. Comparisons between potted soils were analyzed by analysis of variance with repeated measures (SAS GLM procedure, SAS Institute 1985) and between unfertilized field and pot samples by t-tests. Soil mineral nutrient concentrations were $\log_{10}$ (X+1) transformed and all percentage values were arcsin transformed prior to statistical analysis (Zar 1984). Plant responses to nutrient applications were determined by regression analyses (SAS regression procedure: SAS Institute 1985). Both the

independent and the dependent variables were $\log_{10}$ (X+1) transformed.

RESULTS

Soil responses

A decrease in ammonium and resin-extractable phosphorus concentrations and an increase in nitrate concentration were found in unfertilized, eight month-old potted soil supporting P. repens, compared to field soil (Table 9.1). Soil organic matter, pH, total nitrogen and total phosphorus remained unchanged (Table 9.1). After the application of nutrients to the pots, an increase in soil pH with time and with P application level (from 5.2 to 5.6 at 12.8 g P m^{-2}) and a decrease with N application level (from 5.2 to 5.0 at high N application levels of 32-64 g N m^{-2}) were found (Table 9.2). Soil organic matter decreased with incubation time, except with M application, where it increased from 0.9 % in unfertilized pots to 1.4 % at high M application levels. There was a rapid decrease in soil ammonium and nitrate concentrations with time in the N amended pots (Fig. 9.1). The nitrate to ammonium ratio and total mineral nitrogen concentration in unfertilized pot incubated soils was approximately one order of magnitude higher than that found in the field (Fig. 9.1, Table 9.1). Total nitrogen concentrations decreased with time in the N amended pots (Fig. 9.1). No significant differences in total and Bray

Table 9.1. Comparison of the chemical properties of unfertilized Clovelly soil (mean ± SE) in the field and after 8 months in a glasshouse pot experiment supporting *Protea repens* seedlings. Significant differences by t-test (*d.f.*=8, NS denotes not significant). Figures in parentheses are arcsin transformations ± SE.

	Field	Pot	t	P
Organic matter (%)	0.84 (5.3±0.06)	0.89 (5.4±0.09)	0.61	NS
pH	5.3±0.06	5.2±0.09	-0.28	NS
Ammonium ($\mu g\ N\ g^{-1}$ dry mass)	1.2±0.13	0.6±0.10	-3.34	<0.01
Nitrate ($\mu g\ N\ g^{-1}$ dry mass)	0.5±0.09	6.8±3.5	2.43	<0.05
Resin-extractable-P ($\mu g\ P\ g^{-1}$ dry mass)	0.3±0.07	0.1±0.01	-3.47	<0.01
Bray No. 2-P ($\mu g\ P\ g^{-1}$ dry mass)	2.6±0.3	3.3±0.4	1.24	NS
Total nitrogen ($\mu g\ N\ g^{-1}$ dry mass)	245±9	276±15	1.79	NS
Total phosphorus ($\mu g\ P\ g^{-1}$ dry mass)	28.5±0.4	29.5±0.8	1.10	NS

Table 9.2. Analyses of variance with repeated measures of chemical properties of potted Clovelly soil, supporting Protea repens seedlings, and amended with a range of concentrations of phosphorus (P), nitrogen (N) and a mixture of all essential nutrients excluding N and P (M). ***, P<0.001; **, P<0,01; *, P<0.05.

	Nutrient Concentration		Time		Nutrient Concentration x Time	
	d.f.	F	d.f.	F	d.f.	F
Organic matter						
P-amended	7,32	0.81	1,32	36.99***	7,32	3.37**
N-amended	6,28	0.80	1,28	9.67**	6,28	2.10
M-amended	6,28	3.44*	1,28	17.58***	6,28	1.26
pH						
P-amended	7,32	3.18*	1,32	19.34***	7,32	0.74
N-amended	6,28	2.77*	1,28	9.20**	6,28	0.69
M-amended	6,28	1.12	1,28	11.94**	6,28	1.05
Resin-extractable-P						
P-amended	7,32	44.96***	2,64	25.77***	14,64	2.20*
Bray No. 2-P						
P-amended	7,32	45.51***	2,64	2.49	14,64	1.49
Total phosphorus						
P-amended	7,32	24.52***	1,32	1.84	7,32	1.12
Nitrate						
N-amended	6,28	8,34***	2,56	10.55***	12,56	2.19*
Ammonium						
N-amended	6,28	14.34***	2,56	37.87***	12,56	3.18*
Total nitrogen						
N-amended	6,28	4.97*	1,28	12.08**	6,28	0.83

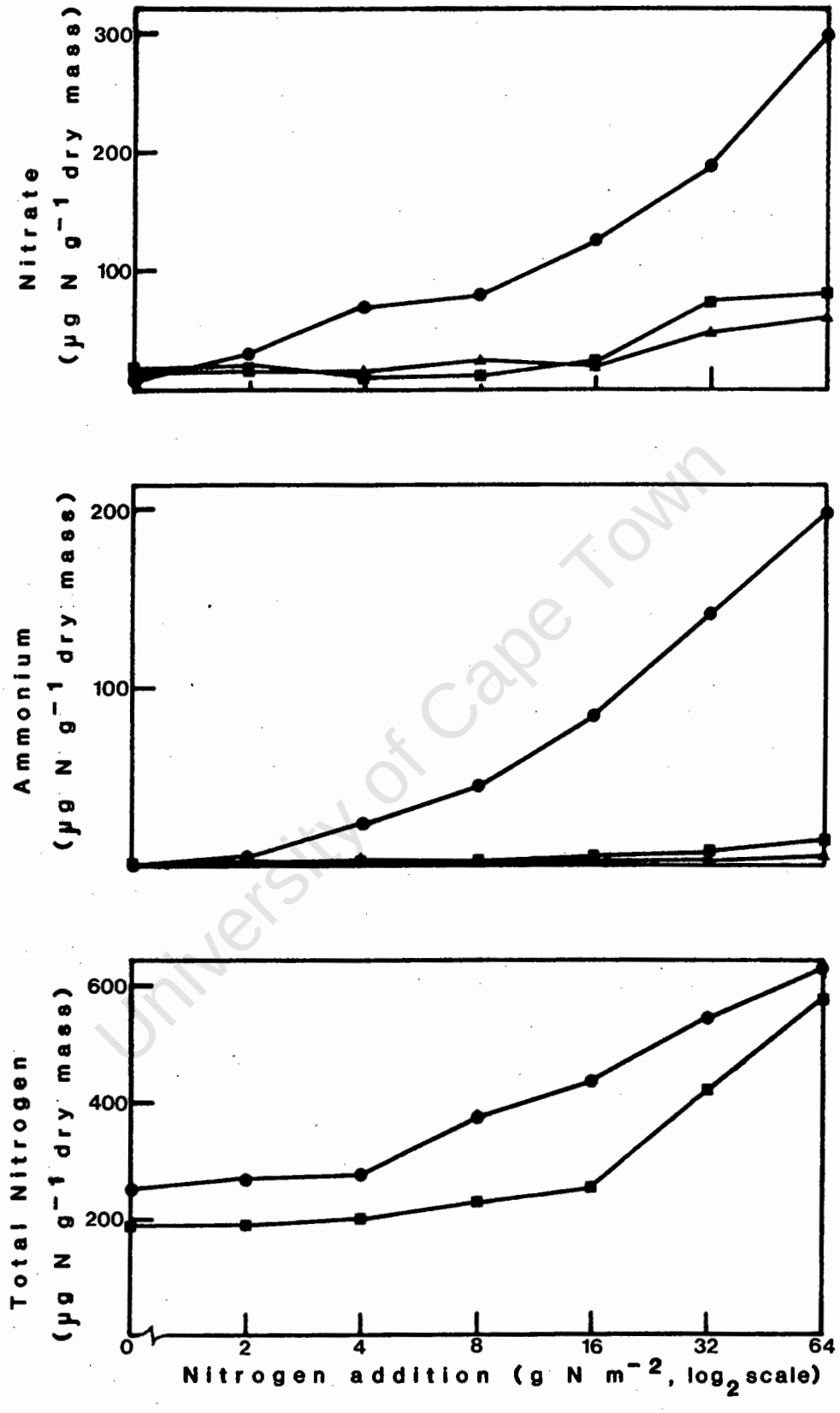

Fig. 9.1. Nitrate, ammonium and total nitrogen concentrations (●—●) 21, (▲—▲) 96 and (■—■) 171 days after amendment with a range of nitrogen concentrations in potted Clovelly soil supporting Protea repens seedlings.

No. 2 phosphorus concentrations were found in the P amended pots with incubation time (Table 9.2), whereas resin-extractable phosphorus concentrations declined (Fig. 9.2).

Plant responses

Three days after nutrients had been applied, several plants amended with 32 and 64 g N m^{-2} became necrotic and subsequently died. These plants were found to have high nitrogen concentrations, in the range of 46-66 mg N g^{-1} dry mass, compared to a mean and S.E. of 16±1 mg N g^{-1} dry mass for unfertilized control plants harvested at the same time. In addition, further plants amended with N (4-64 N g m^{-2}) and some amended with high levels of M became necrotic and some of these subsequently died during November when temperatures were high (Fig. 9.3). No mortality of *P. repens* seedlings in response to P addition was found (Fig. 9.3). In the surviving plants, the proportion of normal leaves per plant, ie. those that were not necrotic, partially necrotic or abscissed, was significantly reduced with increasing N and higher with increasing P application levels ($F_{1,22}$=4.88 & $F_{1,38}$=5.31 respectively, $P<0.05$). No significant trends in plant height and leaf number per plant with nutrient application level were found for any of the treatments.

Leaf, stem and total plant dry mass increased significantly with increasing P application level ($F_{1,38}$= 18.19, 7.93 &

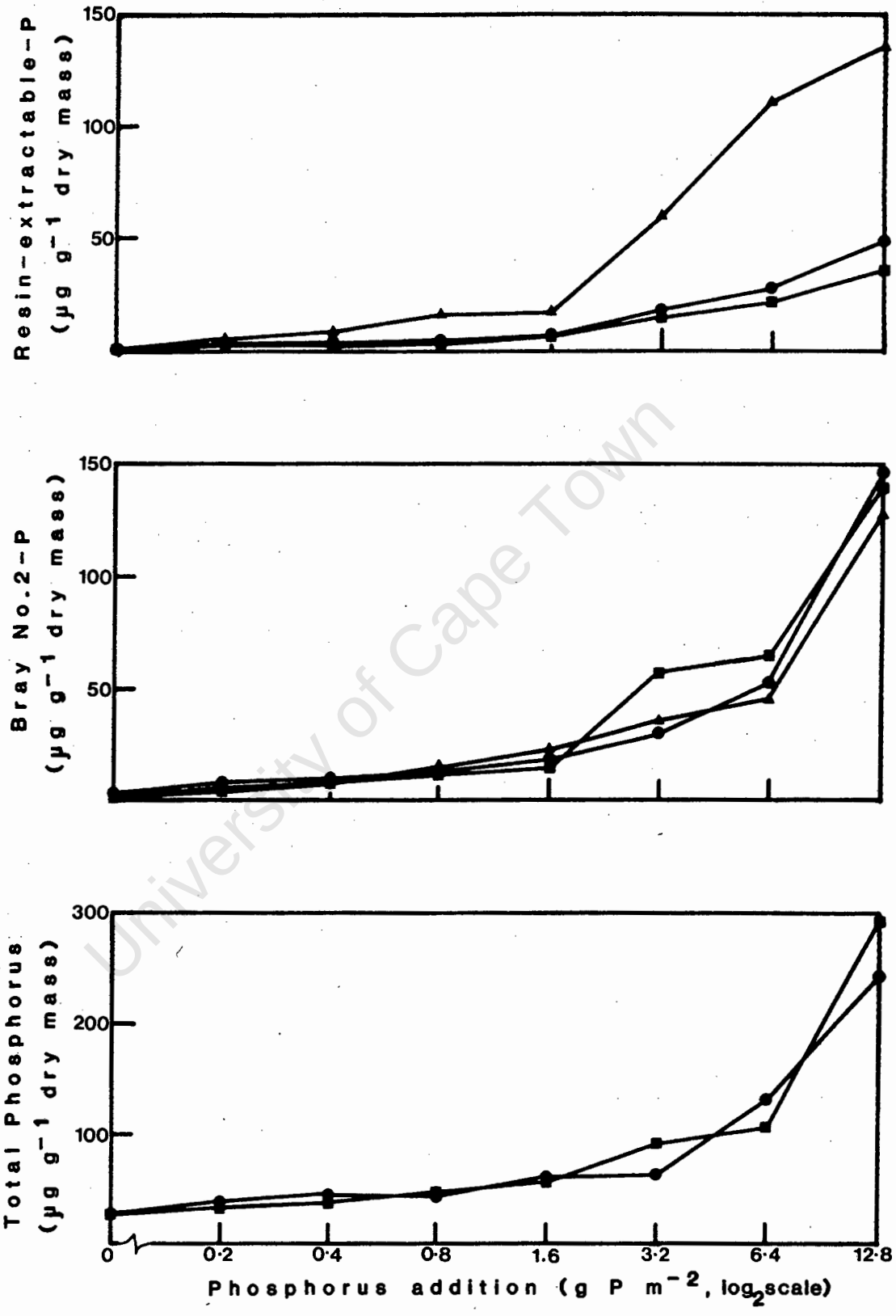

Fig. 9.2. Resin-extractable, Bray No. 2 and total phosphorus concentrations (●—●) 21, (▲—▲) 96 and (■—■) 171 days after amendment with a range of phosphorus concentrations in potted Clovelly soil supporting Protea repens seedlings.

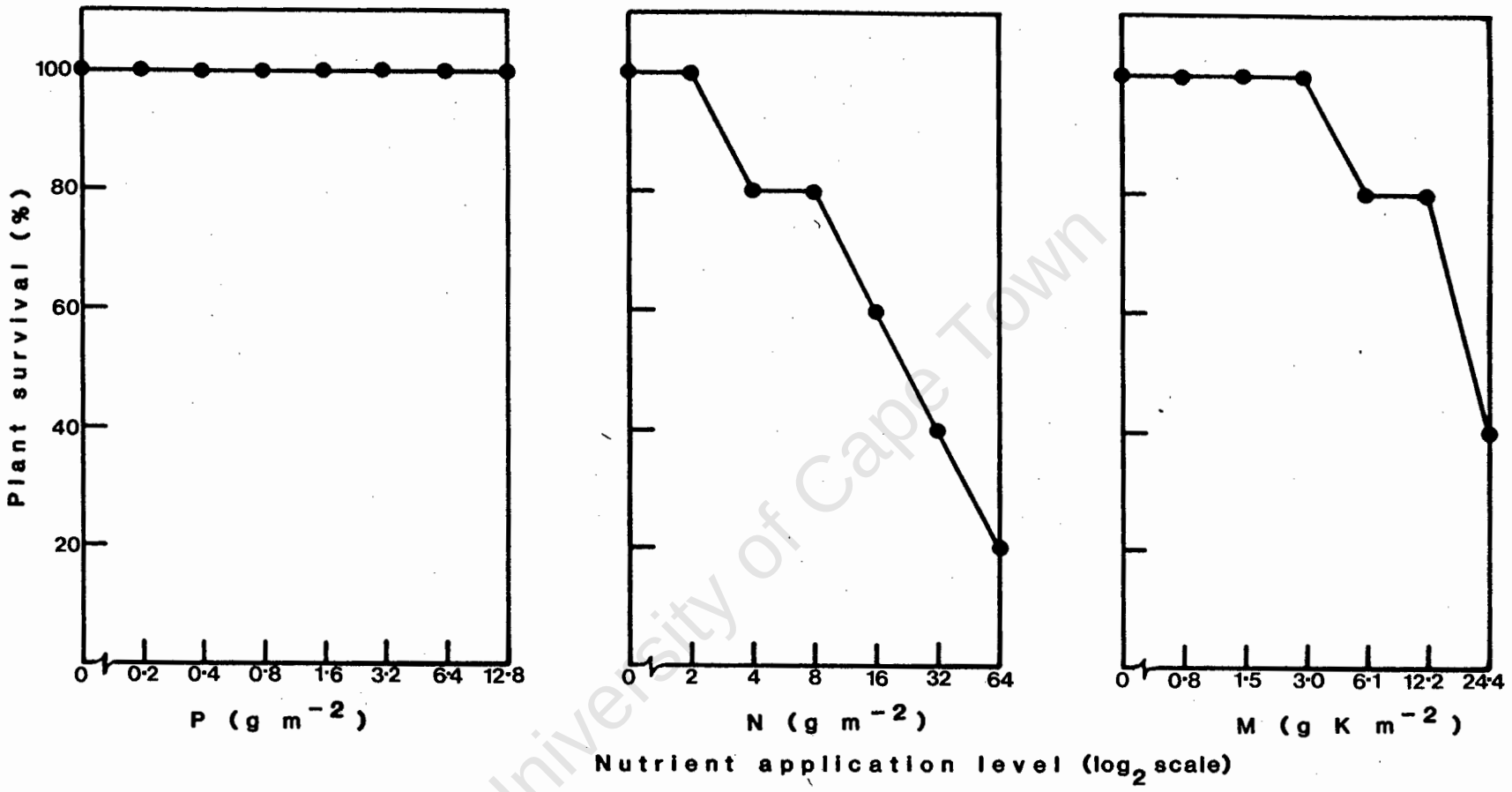

Fig. 9.3. Survival of 16 month-old Protea repens seedlings after eight months growth in a range of concentrations of phosphorus (P), nitrogen (N) and a mixture of all essential nutrient excluding N and P (M). Additions of P, N and M are in the same proportions found in a Long Ashton nutrient solution (Hewitt & Smith, 1975) with M presented as K additions.

7.96 respectively, $P<0.01$; Fig. 9.4) whereas increased nitrogen resulted in reduced total plant dry mass ($F_{1,22}=8.86$, $P<0.01$; Fig. 9.4). Leaf, stem, root and total plant phosphorus contents increased with P application level ($F_{1,38}$= 26.07, 14.52, 14.93 & 22.07 respectively, $P<0.001$) and decreased with that of N ($F_{1,22}$= 4.58, 4.34, 8.79 & 6.43 respectively, $P<0.05$; Fig. 9.5). Total plant, leaf and stem nitrogen contents increased significantly with P application level ($F_{1,38}$= 4.22, 6.02, & 10.66 respectively, $P<0.05$), while root nitrogen content decreased with N application level ($F_{1,22}=7.19$, $P<0.05$; Fig. 9.6). Leaf specific mass tended to decline in response to increasing application level of all three treatments, although not significantly. However, plant leaf area increased with P application level ($F_{1,38}=24.79$, $P<0.001$) and decreased with N ($F_{1,22}=4.76$, $P<0.05$; Fig. 9.7).

The root to shoot ratio of dry mass decreased significantly with increasing application levels of both N ($F_{1,22}=15.44$, $P<0.001$) and P ($F_{1,38}=3.95$, $P<0.05$). The root to shoot nitrogen ratio increased with increasing N ($F_{1,22}=10.56$, $P<0.01$) and M ($F_{1,28}=4.52$, $P<0.05$) application level, whereas no significant trends in root to shoot phosphorus ratio were found with increasing application level of any of the three treatments.

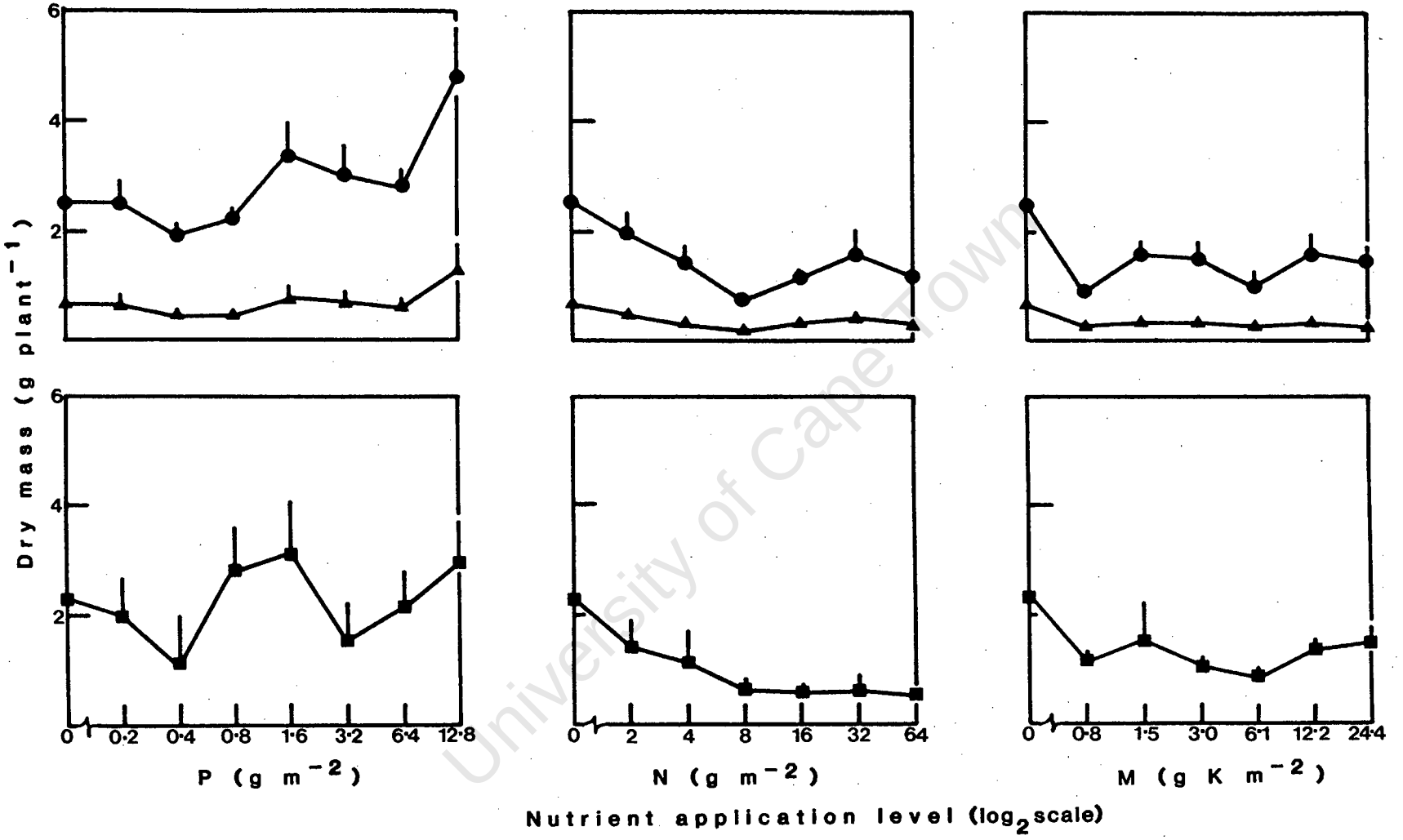

Fig. 9.4. Dry mass of Protea repens seedlings grown in a range of concentrations of phosphorus (P), nitrogen (N) and a mixture of all essential nutrients excluding N and P (M) in potted Clovelly soil. Additions of M are presented as K addition. Symbols: (●—●), leaf; (▲—▲), stem; (■—■), root. Vertical bars represent S.E.

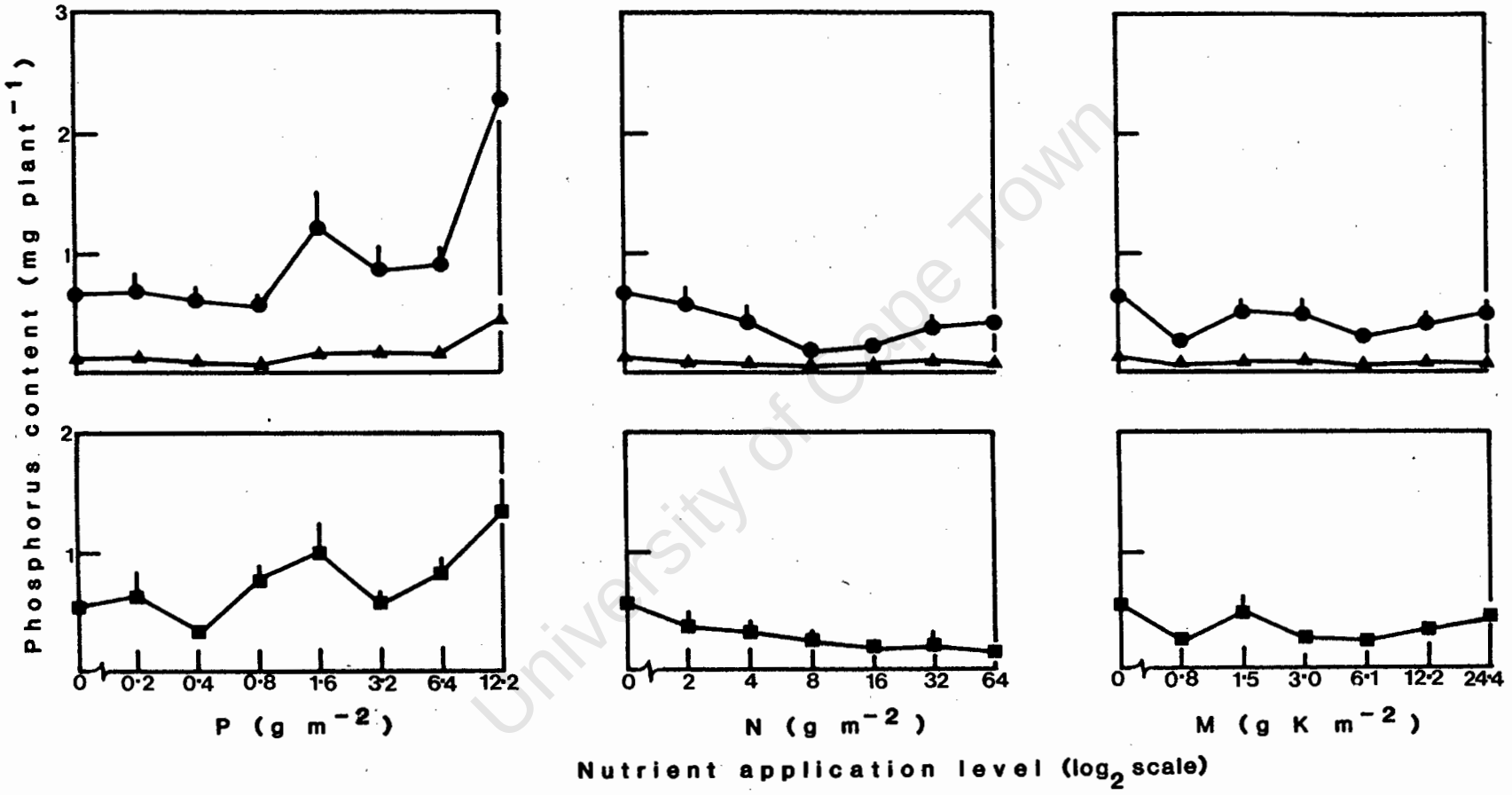

Fig. 9.5. Phosphorus content of Protea repens seedlings grown in a range of concentrations of phosphorus (P), nitrogen (N) and a mixture of all essential nutrient excluding N and P (M) in potted Clovelly soil. Additions of M are presented as K additions. Symbols: (●—●), leaf; (▲—▲), stem; (■—■), root. Vertical bars represent S.E.

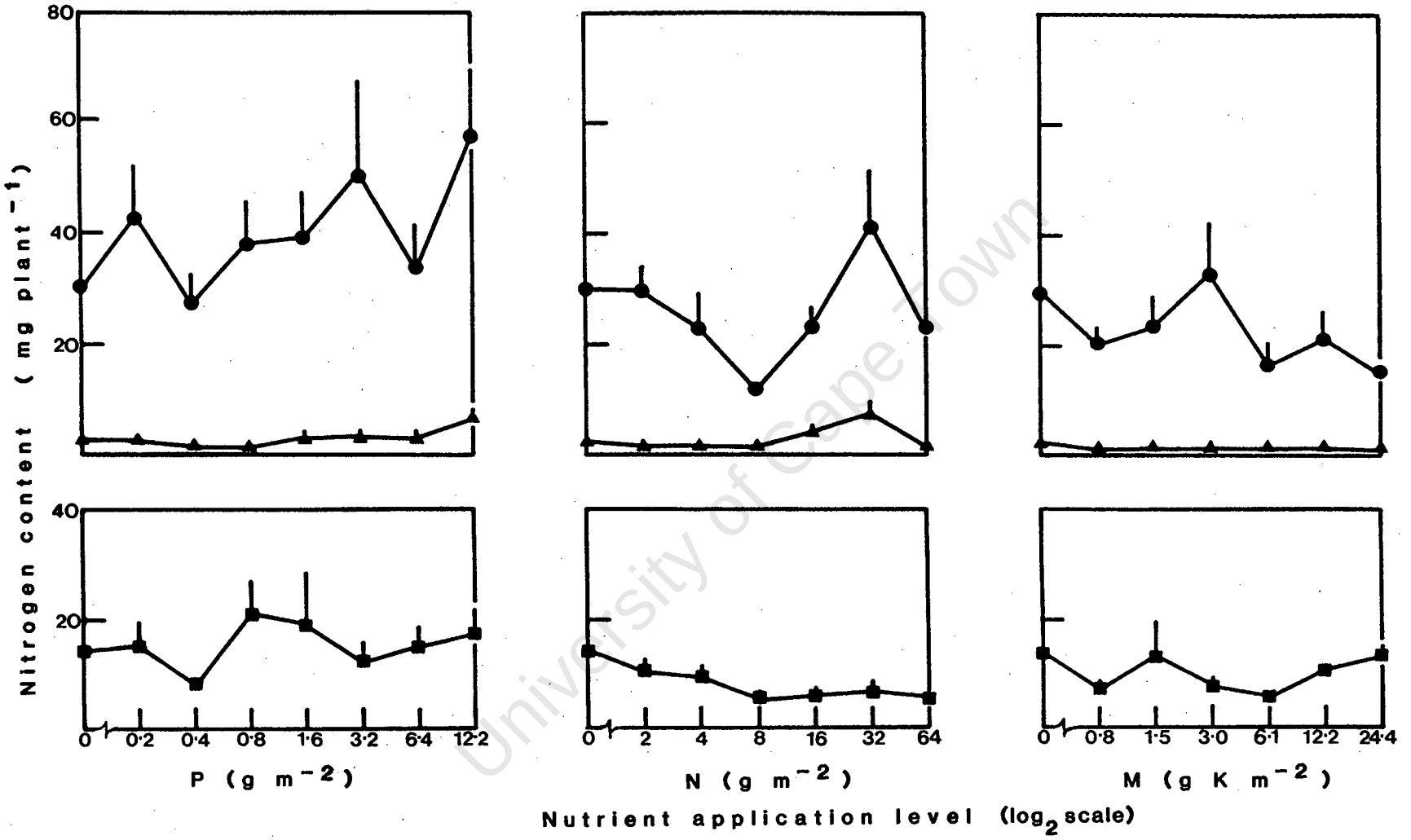

Fig. 9.6. Nitrogen content of Protea repens seedlings grown in a range of concentrations of phosphorus (P), nitrogen (N) and a mixture of all essential nutrient excluding N and P (M) in potted Clovelly soil. Additions of M are presented as K additions. Symbols: (●—●), leaf; (▲—▲), stem; (■—■), root. Vertical bars represent S.E.

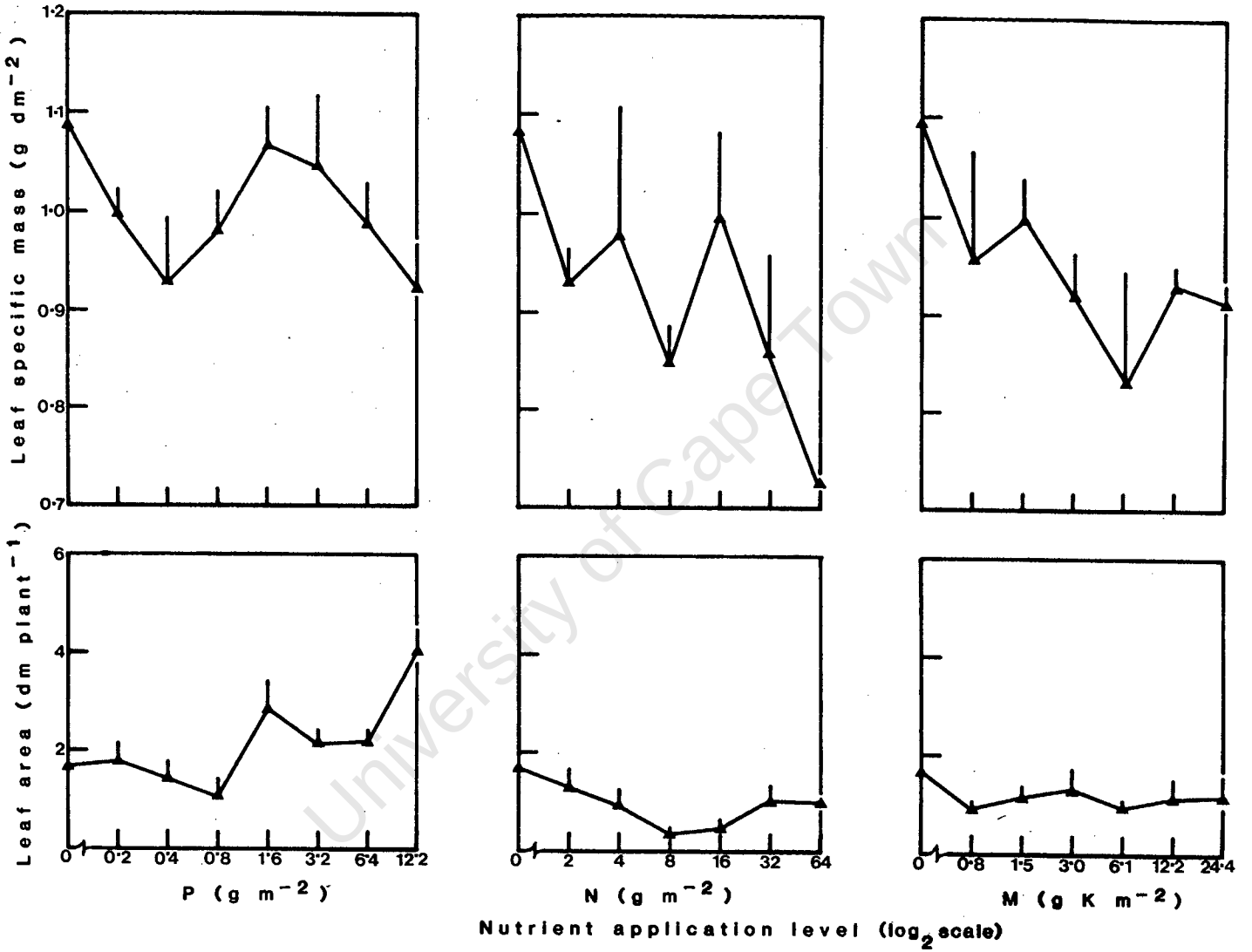

Fig. 9.7. Leaf area and leaf specific mass of Protea repens seedlings grown in a range of concentrations of phosphorus (P), nitrogen (N) and a mixture of all essential nutrient excluding N and P (M) in potted Clovelly soil. Additions of M are presented as K additions. Vertical bars represent S.E.

DISCUSSION

This study has shown that the growth of Protea repens seedlings in Clovelly soil pot culture is stimulated by phosphorus additions of 0.2-12.8 g P m^{-2}, whereas additions of 4-64 g N m^{-2} and high M additions resulted in seedling mortality and reduced growth. In a field fertilizer experiment, 4 year-old shrubs of Leucospermum parile (Proteaceae) and Phylica cephalantha (Rhamnaceae), growing in the same Clovelly soil, responded to a factorial fertilizer addition, of the same three treatments applied in this study (0.5 g P m^{-2}, 5 g N m^{-2} and 1.9 g K m^{-2}), with increases in shoot growth of both species in response to nitrogen and not phosphorus addition (Chapter 3). The different responses between potted P. repens and the shrubs at the field site can be explained by differences in nutrient availability between potted and field soils. Unfertilized potted soil exhibited greater concentrations of mineral nitrogen, particularly nitrate, and reduced concentrations of resin-extractable phosphorus, compared with field soil. Incubation studies on this soil have shown that relatively high soil moisture contents stimulated nitrogen mineralization (Stock et al. 1988). Although moderate soil moisture contents of 9-18 % of field capacity enhanced phosphorus mineralization, incubation at 50-100 % of field capacity resulted in reduced concentrations of resin-extractable phosphorus (Baker & Witkowski submitted).

Thus the ratio of available nitrogen to available phosphorus is increased by approximately one order of magnitude in potted soil. Similar results were found by Kachi & Hirose (1983) for coastal sand dune soil in Japan, suggesting that the ratio of plant available nitrogen to phosphorus may be at least as important, in determining the range of a species, as the absolute amounts of available N and P. The reduced growth of surviving P. repens seedlings amended with N and M was thus a response to a nutrient imbalance.

In Australian heathlands, which are edaphically similar to those of the fynbos biome (Witkowski & Mitchell 1987), phosphorus fertilizer addition caused increased growth in both surviving seedlings and mature heath plants (Specht 1963; Heddle & Specht 1975). Although seed germination was not affected by high levels of phosphate supply, survival of seedlings was markedly reduced. Heath plants showed little response to N addition (Specht 1963). Pot culture of three Banksia spp. (Proteaceae; Siddiqi et al. 1976) and other heath species (Grundon 1972; Specht & Groves 1966) in P amended heathland soil, resulted in reduced growth and phosphorus toxicity symptoms. A similar study of three sclerophylls grown in washed fine quartz sand, showed mortality of seedlings at high levels of application of both N and P (Groves & Keraitis 1976), and P toxicity symptoms were usually associated with leaf P concentrations of 0.8 % and above (Ozanne & Specht 1981). In this study on P.

repens, leaf phosphorus concentrations of only 0.06 % were found with addition of 12.8 g P m^{-2}. Phosphorus toxicity was found to be alleviated by the supply of N and K (Grundon 1972) and K (Siddiqi et al. 1976), indicating that a nutrient imbalance may again be involved.

In P. repens seedlings, no significant differences in leaf specific mass were found with increasing level of application of any of the three treatments, although it tended to decrease (Fig. 9.7). Leaf specific mass has been shown to vary with water supply (Miller 1983), nutrient availability (Loveless 1962; Gulmon & Chu 1981), light intensity during growth (Bjorkman 1981) and has been used as a measure of sclerophylly. It is positively correlated with leaf duration and the longest leaf durations generally occur on plants occupying the most nutrient-poor soils (Mooney 1983). In a range of growth forms studied, evergreen sclerophylls were found to have the highest leaf specific mass and the lowest photosynthetic capacities (Field & Mooney 1983).

Increasing levels of application of both N and P resulted in a trend of decreasing root to shoot dry mass ratio. Similar trends have been found in response to imposed nutrient and moisture stress in graminoids and other herbaceous plants (Davidson 1969; Hunt & Nicholls 1986; Hunt et al. 1987). An increase in root to shoot dry mass ratio

in 2-year old Thamnochortus punctatus (Restionaceae) with M (1.9 g K m^{-2}) and a decrease with N (5 g N m^{-2}) addition was found in Clovelly soil at the Pella field site (Chapter 4).

Although P. repens is a widely distributed species and has a broader ecological niche then most other members of the Proteaceae in the fynbos biome, the degree of response of these seedlings to nutrient additions is low compared with that found in graminoid species (Davidson 1969; Hunt et al. 1987). This study confirms that this species has a conservative response to nutrient additions which corresponds to its slow growth habit and is thus similar to nutrient stressed evergreen shrubs from many parts of the world (Chapin 1980).

CHAPTER 10

GENERAL DISCUSSION

In this chapter, the information described in the preceding eight chapters is synthesized and compared with existing literature to obtain an overall picture of the effects of nutrient additions on nutrient cycling and other ecosystem processes in sand-plain lowland fynbos.

SOILS

Monitoring the nutrient dynamics in the soil after fertilizer addition confirms the trends found in the Australian heathlands (Specht 1963, Heddle & Specht 1975), that P added to the soil has a long residence time in comparison to N, and thus will have more profound long-term effects on nutrient cycling processes and plant species composition. As phosphorus is a relatively immobile element in the soil (Bieleski 1976), different forms of inorganic phosphorus addition will behave in a similar manner. In this study, soil ammonium and nitrate concentrations in the N amended plots decreased by approximately 80 % within one month after fertilizer application. It appears that these soils, of low clay and silt contents, cation exchange capacity and soil organic matter content, are incapable of preventing leaching of nitrate applied in relatively large concentrations (in comparison to their average soil concentrations). This is also the case for potassium, another highly mobile element in the soil. In finer textured soils; ie. those derived

from granite and shales (Witkowski & Mitchell 1987, Appendix 1), leaching will be less. The 5 g N m^{-2} added to the soil in this study, resulted in a small, transient increase in total N concentration of the soil. Although total nitrogen reserves in the soil are low, over 90 % of the ecosystem nitrogen reserves of sand-plain lowland fynbos are in the soil (Low 1983; Stock & Lewis 1986b). Total nitrogen concentrations at various depths down the 2 m soil profile at Pella were highly correlated with soil organic matter (Stock & Lewis 1986b), and thus most of the nitrogen is contained within decomposing organic matter, unavailable to plants. Immobilization of applied nitrogen and phosphorus by the soil organic matter is a common problem in fertilizer studies, resulting in limited responses in the vegetation (Chapin et al. 1986). Monitoring soil nutrient concentrations after fertilizer addition provides essential information which is necessary for the interpretation of vegetational responses to applied nutrients.

RESPONSES OF AN ERICOID, A PROTEOID & A RESTIOID SPECIES

Phenotypic plasticity is the ability of an individual organism to alter its morphology and physiology in response to changes in the environment (Schlichting 1986). Plastic responses represent changes in developmental sequences due to the interaction of the organism's genotype with the environment. Plastic responses have three main

characteristics; the amount, the direction and the response time (Kuiper & Kuiper 1988). In addition, phenotypic plasticity in response to environmental changes may vary during the life cycle of a plant species; eg. between seedlings and mature shrubs (Schlichting 1986). Plasticity in the responses to nutrient additions of the three dominant growth forms of sand-plain lowland fynbos are compared below.

The application of nutrients had no discernible effects on the timing of the various phenophases of the evergreen sclerophyllous shrubs such as the mid-late successional dominant, Leucospermum parile, or the early successional dominant, Phylica cephalantha. Studies in the Australian heathlands have shown earlier flowering in some sclerophyllous shrubs, both in terms of season and plant age, in response to large additions of phosphorus (Specht 1963). In this study, small increases in shoot growth in response to the application of N were found during the first growing season, while P addition tended to result in a decline in both species during both growing seasons. However, shoot nitrogen contents increased by 66 % and 55 % in L. parile and P. cephalantha respectively during the first year, whereas phosphorus contents increased only slightly. Nitrogen addition also resulted in a 31 % increase in total inflorescence dry mass per shoot in P. cephalantha during the first year. In P. cephalantha,

irrespective of the nutrient additions, an approximately 50 % reduction in shoot growth and a 66 % decrease in inflorescence dry mass per shoot were found in the second year when compared with the first. This may be explained by either the hotter and drier conditions during the second year resulting in increased plant moisture stress, or the depletion of internal reserves (nutrients and carbohydrates) due to the large fruit crop produced during the first year. Plasticity in shoot nutrient concentrations (nutrient storage) and inflorescence production were found in response to nutrient additions, rather than large increases in shoot growth in both these evergreen shrubs species. However, variation in shoot growth of P. cephalantha, between growing seasons, is relatively plastic compared with L. parile. The evergreen habit may be viewed as a means of nutrient conservation (Bazzaz et al. 1987).

The dioecious restioid plant, Thamnochortus punctatus, was found to be more plastic in its responses to raised soil nutrient concentrations than the shrub species. Nitrogen application resulted in increased dry mass and nitrogen allocations in the shoots of pre-reproductive plants, whereas decreased allocations of resources to the culms and inflorescences (mature characters) and increased allocations to vegetative branches (juvenile character), were found in reproductively mature male plants. Therefore N addition appears to slow down the life-cycle of this species,

favouring vegetative growth at the expense of reproductive allocation. The addition of P tended to increase the allocation of resources to the inflorescences, while that of M resulted in increased allocation of resources to the below-ground organs. Increased below-ground growth at the expense of above-ground growth is probably an adaptation to increase the acquisition of a limiting soil resource, in particular nitrogen. Phenotypic plasticity in T. punctatus was found in terms of nutrient storage and allocation patterns, as well as reproductive effort and the partitioning of resources between the roots and the shoots. The three fynbos species studied in detail in this thesis, represent the typical ericoid, proteoid and restioid growth forms of the fynbos. All displayed increased vegetative growth in response to N, rather than P or M addition. In addition, the degree of morphological plasticity was inversely related to the maximum rooting depth of these species.

In terms of the hypothesis of resource limitation of vegetative growth and reproductive output tested in this thesis, the null hypothesis of no responses to nutrient additions in species representing the dominant ericoid, restioid and proteoid growth forms of the fynbos is rejected. However, this hypothesis was not fully tested in the case of T. punctatus (restioid), because nitrogen addition appears to delay reproduction in this species.

Reproductive output of T. punctatus may have increased during the third year after fertilizer addition, but this could not be tested because a wildfire destroyed the vegetation during that year. Storage of nitrogen in the shoots of the species representing the three dominant growth forms, and subsequent utilization of these nutrients during the following year, tends to confirm the theoretical predictions of Clarkson's (1967) hypothesis.

Several studies of allocation have converged on the theme of cost - benefit analysis (Bloom et al. 1985; Bazzaz et al. 1987). Debate still continues on the ideal currency of allocation (Abrahamson & Caswell 1982; Reekie & Bazzaz 1987a,b,c). However, carbon appears the most useful as exchange rates between carbon and limiting nutrient elements can be determined for environments of differing nutrient deficiency. Thus carbon can integrate the costs of acquiring growth limiting nutrients (Bloom et al. 1985). For example, nitrogen limitation results in increased carbon allocation to root growth in T. punctatus, thus increasing nitrogen acquisition from the soil. The increase in the carbon cost per unit of nutrient acquired, as the nutrient becomes more scarce, implies that total carbon allocation tends to be biased towards the resource or resources most limiting to plant growth (Reekie & Bazzaz 1987b). The allocation pattern of a plant defines its ecological roles

and is therefore an important factor in understanding plant distribution and adaptation.

LITTER PRODUCTION AND NUTRIENT RETURN

Litter production at Pella was positively correlated with wind-run and absolute maximum monthly temperature, and tended to increase in response to the addition of N and M. Phosphorus return increased with P addition during the first year, whereas it increased in response to N and M during the second year. Relative to the other nutrient treatments, nitrogen return in response to N addition, only increased during a period of moisture stress experienced by the vegetation. Significant differences in the growth form composition of litter and its interaction with vegetation age, highlights the successional changes in the vegetation during the study period. The most apparent increase was that of the proteoid component.

The litter layer dry mass, nitrogen and phosphorus contents increased in response to nutrient treatment combinations containing N and M. Increased concentrations of nitrogen and phosphorus in the litter layer may increase the rate of decomposition and nutrient return to the soil. The return of nitrogen and phosphorus to the soil from decomposing plant material is probably the rate limiting step in the cycling of nutrients in nutrient-poor fynbos ecosystems

(Mitchell et al. 1986; Mitchell & Coley 1987). A positive feedback towards the maintenance of nutrient stress in nutrient-poor ecosystems has been postulated (Shaver & Melillo 1984; Vitousek 1982). This argument is based on the assumptions that in nutrient-poor ecosystems, increased efficiency of both nutrient use and reabsorption of nutrients from senescing leaves prior to abscission, results in litter of a high C : N ratio, which is relatively resistant to decomposition, and thus further reduces soil nutrient availability (Lajtha & Klein 1988). This may be the case in the nutrient-poor soils of the fynbos biome and Australian heathlands, where most of the ecosystem reserves of nitrogen and phosphorus are held within decomposing organic matter in the soil (Groves 1983; Read & Mitchell 1983; Stock & Lewis 1986b; Witkowski & Mitchell 1987; Appendix 1).

VEGETATION GROWTH FORM COMPOSITION

Few significant differences in the above-ground phytomass of the representative growth forms of sand-plain lowland fynbos were found between treatments. This is because the growth rates of these plants are low, the growth responses to the application of nutrients of most of the growth forms are small, and the spatial heterogeneity in growth form composition, in the 5 m^2 plots used for harvesting phytomass, is relatively high. Measuring foliage

projective cover (FPC) in 25 m^2 plots, to monitor growth form composition between years, and the use of pre-fertilizer addition FPC as a covariate, proved to be a much more sensitive procedure to determine plant responses to nutrient applications than destructive sampling. In this study (Chapter 7), the annual, graminoid and restioid growth forms were found to increase in FPC in response to N addition. However, this study only provided information on the short-term responses of the various growth forms to the application of nutrients. Long-term fertilizer studies, using annual applications of limiting nutrient elements, are necessary to test the resilience of indigenous plant species to raised soil nutrient levels. In addition, the effects of fertilizer input from adjacent agro-ecosystems could be determined by monitoring the growth form composition and soil nutrient concentrations of indigenous stands of vegetation at various distances from the boundary with the agro-ecosystem.

Fertilizer (nitrogen) addition to plant communities have one of four possible results (Lee et al. 1983):

1) No change in overall plant production or species composition.
2) An increase in overall plant production with little change in species composition or relative abundance.
3) A change in species composition or relative abundance with little change in overall plant production.

4) A change in species composition and a marked increase in overall plant production.

Lee et al. (1983) argue that only result 2. (above) demonstrates nutrient (nitrogen) deficiency, since results 3. and 4. effectively produce new communities. However, where an increase in plant production in response to fertilizer addition is observed, a change in species composition is usual.

REPRODUCTIVE TRAITS OF LEUCOSPERMUM PARILE

In L. parile, it appears that a minimum shrub size has to be attained for an individual plant to become reproductive. Some plants became reproductive three years after germination, whereas others were not reproductive even after five years. Plant size and not age was also found to determine onset of reproduction in other plant species (Lacey 1986). In addition, Lacey (1986) suggested that the ability to accumulate resources, which is directly related to plant size, determines onset of reproduction in plants. Nitrogen addition resulted in decreased inflorescence production in shrubs of L. parile during the year of application, while the nitrogen stored in the shoots was utilized for increased flowering during the second year. This increased N supply resulted in an increase in inflorescence production of approximately 44 % compared with the unfertilized control plants. In addition, the

application of N resulted in reduced dry mass per seed during the year of application, probably because of the interruption of physiological processes involved with seed development, as nutrients were applied during the inflorescence production period. It appears that smaller sized seeds are produced towards the end of the flowering period, at which point shoot growth commences for that season. This suggests that reproduction and vegetative growth may be competing for scarce resources during this period. Seasonal variations in seed size have also been described for other species (Fuller et al. 1983). Seed size variation in unfertilized L. parile shrubs was higher than in Australian members of the Proteaceae, which display little variation in seed size (Hocking 1986; Pate et al. 1986).

Seed production in L. parile can be altered at several developmental stages and times during the 5-6 months long flowering period in response to variable environmental conditions, thus ensuring relatively high levels of seed production within the constraints of the nutrient-poor soils and mediterranean climate. This study supports the hypothesis of Lamont et al. (1985), that inflorescence production in the nutrient-poor soils of the fynbos biome is (resource) nutrient-limited.

Seed dispersal of serotinous species (canopy stored seeds) of the Proteaceae occurs after fire and is thus a largely synchronous event (Bond 1984). This synchronous release of seeds has been attributed to a predator satiation strategy (O'Dowd & Gill 1984). In non-serotinous species, such as L. parile, release of seeds occurs over an extended time period of several months, corresponding to the sequential development of the inflorescences. This allows efficient dispersal and burial of seeds by myrmecochorous ants (Slingsby & Bond 1985), thus reducing seed predation by rodents (Bond & Breytenbach 1985). Asynchronous fruit development in L. parile, may thus have two main functions: firstly to provide a high degree of maternal control over resource allocation to reproduction, and secondly to reduce post-dispersal seed predation.

Concern has been expressed about overexploitation of proteaceous plants in the wildflower industry and L. parile has been recommended for cultivation (Hall & Veldhuis 1985). To maintain long-term yields of flowers from proteaceous plants, aspects of their life histories, degree of serotiny, seed viability, variation in cone production and responses to fire and picking intensity, as well as long-term responses to fertilizer addition, need to be understood. In a study of nutrient accumulation in developing infructescences (cones) of Protea compacta and P. obtusifolia (Proteaceae), it was found that accumulations of

high levels of nitrogen and phosphorus were delayed until seed ripening (Esler et al. submitted). This has important implications for ecosystem losses of N and P associated with cone and flower harvesting.

RESPONSES OF PROTEA REPENS SEEDLINGS

Protea repens seedlings grown in potted Clovelly soil exhibited increased dry mass, nitrogen and phosphorus acquisition in response to increasing application level of P. Increasing application level of N, and to a lesser extent M, resulted in plant mortality and a reduction in growth and phosphorus acquisition. The ratio of available nitrogen to available phosphorus in the soils of the control plants, was approximately one order of magnitude higher than in the field, and total mineral nitrogen concentrations were also increased. This explains the positive plant growth response to P in the pot experiment compared with the response to N at the field site. Phenotypic plasticity in these seedlings was found in terms of plant leaf area, nutrient contents and resource allocation patterns. Although no significant differences in leaf specific mass (LSM) were found, it tended to decrease in response to increasing application level of all three nutrient treatments. In another proteoid species, Leucadendron laureolum, increasing application level of P resulted in a significant reduction ($F_{1,38}$=61,35, P<0.001) in LSM, which

decreased from 0.85 to 0.53 g dm^{-2} in response to the application of 12.8 g P m^{-2} (unpublished data). Hirose (1987) shows how plasticity in dry mass partitioning and LSM enables a plant to compensate for growth limiting conditions and presents three postulates, namely:

1) The partitioning of dry mass and nitrogen between organs is controlled by the nitrogen concentration of the whole plant.
2) Leaf specific mass (LSM) is controlled by leaf nitrogen concentration.
3) Net assimilation rate is a function of nitrogen concentration per unit leaf area.

Plants show different partitioning of dry mass between and within component organs depending upon the environmental conditions under which they grow. Under nutrient (or moisture stress), root growth is promoted and leaf growth retarded, while LSM increases (Chapin 1980). Hirose (1987) found that plants with plasticity in both dry matter partitioning and LSM always attained the higher growth rate under various availabilities of nitrogen, and plasticity also contributed to the efficient use of nitrogen in plant growth. In Leucadendron laureolum seedlings, LSM was more strongly correlated with leaf phosphorus concentrations than with leaf nitrogen (r=-0.72 and -0.56 respectively, P<0.01, n=40). In addition, soil phosphorus concentrations were found to be limiting the growth of this plant rather than

nitrogen, and thus the concentration of the growth limiting element may control LSM and not nitrogen per se.

NITROGEN LIMITATION AND NITROGEN USE EFFICIENCY

The availability of nitrogen is the primary factor limiting plant growth in many other natural environments (Berendse & Aerts 1987; Lee et al. 1983). This has been determined from both correlation studies (eg. Vermeer & Berendse 1983; Pastor et al. 1984) as well as fertilizer experiments in the field (eg. Bradshaw et al. 1964; McMaster et al. 1982; Tilman 1984, 1987; Vermeer 1985). Wild plant species vary widely in their efficiency of nitrogen uptake and nitrogen use (Chapin 1980). Berendse & Aerts (1987) define a measure of nitrogen use efficiency which includes two components. Firstly the mean residence time of the nitrogen in the plant; ie. the period during which the absorbed nitrogen can be utilized for carbon fixation. Secondly, the instantaneous rate of carbon fixation per unit of nitrogen (nitrogen productivity). It has been shown that a long residence time of nitrogen in the plant is favourable under nutrient-poor conditions, whereas a high nitrogen productivity is favourable under relatively nutrient-rich conditions (Berendse 1985). It seems that there is an evolutionary trade-off between features that lead to a high nitrogen productivity and those that lead to a long mean residence time of nitrogen in the plant. The

mean residence time of N and P may be relatively high in fynbos sclerophylls, and those of the other mediterranean-type ecosystems, because of relatively long leaf longevities (Kruger 1981; Mooney 1983). Nitrogen fertilization resulted in a reduction of the leaf longevities of L. parile and P. cephalantha in this study (Chapter 5). In addition, Shaver (1981, 1983) found reduced longevities of leaves of the tundra shrub, Ledum palustre subsp. decumbens, in response to nitrogen addition, as well as in unfertilized stands of this species growing in more nitrogen-rich soils.

EXTRAPOLATION OF RESULTS

The results from the field study in this thesis may be directly extrapolated to other fynbos areas with similar soil nutrient concentrations, in particular those having soils with similar N : P ratios, and annual precipitation. The N : P ratio of the soil, in sandy acidic fynbos ecosystems, is affected by annual precipitation, fire frequency and biological nitrogen fixation between fires, as well as nutrient pollution. Where soil N : P ratios are higher than at Pella, a positive plant growth response to P rather than N addition would be predicted (see Chapter 3), assuming that no other nutrient elements are also limiting. Thus for example, in mesic mountain fynbos vegetation growing on nutrient-poor soils derived from Table Mountain Sandstone, it is predicted that applications of P, rather

than N would increase inflorescence production of *Protea* shrubs or other species. The ability of finer-textured soils to prevent leaching of nitrate and the effects of high soil pH on the availability of ammonium for plant uptake (Haynes & Goh 1978; Taylor & Havill 1981), are likely to result in very different plant and soil responses to the application of nutrients than found in this study. In addition, these soils tend to be more nutrient-rich than sandy acidic soils (Specht & Moll 1983).

Fire is considered to be an evolutionary feature of the fynbos biome (Moll *et al*. 1980) and fire appears to deplete soil N reserves with little apparent loss of P, thus altering the soil N : P ratio. However, there is still little data on volatilization of nutrients from fires of different intensities in the fynbos biome. Further experimental work is necessary to determine the limiting nutrient elements in fynbos soils of different N : P ratio.

IMPORTANCE OF OTHER FACTORS AND ECOSYSTEM PROCESSES

The small increases in plant size in response to nutrient addition found in this study, may be due to the limitations of other resources, notably soil moisture. Miller (1981) suggested that in mediterranean-type ecosystems, the fraction of precipitation which is received in the spring and summer and the amount of water stored in the soil at the

beginning of spring are more important for annual transpiration and production than the total amount of precipitation received throughout the year. Measurements in the fynbos supported this hypothesis (Miller et al. 1983). Under controlled conditions, various chaparral shrubs were found to produce higher fine root surface to leaf area ratios under moisture stress (Kummerow 1982). In addition, Kummerow (1982) postulated that biomass increase with fertilizer addition may result in shrubs with high moisture loss through transpiration and a relatively small fine root surface area and thus less drought resistant (chaparral) shrubs. Studies on the effects of the interaction of nutrient and moisture stress on vegetation productivity in fynbos ecosystems have not been undertaken, but would be a fruitful avenue for future research.

A topic not considered in this thesis but which is very relevant to plants growing in nutrient-poor soils, is the allocation of resources to defence against herbivores. High levels of defence compounds are associated with resource limiting environments (Bryant et al. 1983), evergreen plants (Mooney & Gulmon 1982; Coley 1983) and plants with slow growth rates (Coley et al. 1985), as well as other plant characteristics and environmental features (Bazzaz et al. 1987). No studies on the effects of herbivory on the allocation of resources to defence have been undertaken in the fynbos biome.

Some of the responses to nutrient additions by the various plant species studied, may have differed if larger inputs or repeated applications of the same inputs of nutrients had been tested. In addition, responses may have differed if vegetation of younger or older post-fire age had been studied (Chapin et al. 1986). However, by applying nutrients in similar concentrations to simulate what was released after a fire, the responses measured in the vegetation and soils in this study are more ecologically meaningful.

A final conclusion is that the experimental approach used in this study to elucidate some of the characteristics of sand-plain lowland fynbos, in terms of nutrient cycling, proved to be a very fruitful one.

CHAPTER 11

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CHAPTER 12

APPENDICES

APPENDIX 1

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VARIATIONS IN SOIL PHOSPHORUS IN THE FYNBOS BIOME, SOUTH AFRICA

E. T. F. WITKOWSKI AND D. T. MITCHELL*

Department of Botany, University of Cape Town, Rondebosch 7700, South Africa

SUMMARY

(1) The phosphorus composition of the main soils of the dominant vegetation categories of the fynbos biome, south-western Cape, South Africa was studied.

(2) Total, Bray No. 2 and resin-extractable phosphorus, pH and organic matter varied significantly between the soils with the Fernwood soils of the strandveld vegetation containing the highest total (338–422 $\mu g\ g^{-1}$ dry mass) and resin-extractable (13–40 $\mu g\ g^{-1}$ dry mass) phosphorus concentrations.

(3) Organic phosphorus was only 10–15% of total phosphorus in the Fernwood soils of strandveld but was 58–77% in the soils of the other vegetation categories.

(4) On the west coast, a gradient of soil texture, bulk density and phosphorus status occurred along a 2-km transect from the coastal dunes inland, through strandveld vegetation, vegetation infested with *Acacia cyclops* and into sand plain lowland fynbos.

(5) A significant decrease in the proportion of calcium-bound and increases in iron-bound and saloid fractions of inorganic phosphorus and organic phosphorus occurred along the 2-km transect.

(6) Litter phosphorus concentrations declined from the coastal dunes inland through strandveld and sand plain lowland fynbos but there were peaks in foliage projective cover, ground litter mass and soil phosphorus concentrations in *A. cyclops* invaded strandveld.

(7) The phosphorus status of the soils of the south-western Cape excluding the Fernwood soils of the strandveld and the alluvial soils of limestone lowland fynbos is low.

INTRODUCTION

The fynbos biome closely approximates the geographical area of the Flora Capensis (Goldblatt 1978; Taylor 1978; Kruger 1979), which has been described as the richest and smallest of the world's six floral kingdoms, covering only 0·04% of the earth's surface (Hall 1978). The vegetation is divided into the Cape Floral Kingdom and Cape-Palaeotropical Floral Kingdom transition (Moll *et al.* 1984). The former consists of mountain and lowland fynbos, whereas the latter is divided into Cape-transitional small-leafed (renosterveld) and Cape-transitional large-leafed shrublands (strandveld). Soil nutrients, in particular nitrogen and phosphorus are very low, and may act as determinants in the structure and function of the vegetation (Kruger, Mitchell & Jarvis 1983). Total and available phosphorus of Clovelly soil, the prominent one in coastal (lowland) fynbos vegetation varied with depth and seasonally at the soil surface (Mitchell, Brown & Jongens-Roberts 1984). Although the granite-derived soils of mountain fynbos (Joubert 1965; Campbell 1983) and the aeolian soils of coastal fynbos (Low 1983; Mitchell, Brown & Jongens-Roberts 1984) are low in phosphorus, there is generally a lack of data for the whole fynbos biome (Groves 1983). This paper presents the soil phosphorus composition in the major vegetation categories of the fynbos biome. Along the west coast, a 2-km transect from the coastal dunes through strandveld and lowland fynbos was examined in detail.

* Present address: Department of Botany, University College, Dublin 4, Ireland

vegetation from 800 m inland. At 1500 m inland, an exposed ridge was dominated by *A. saligna*, *A. cyclops* and *Thamnochortus spicigerus* (Thunb.) Sprengel. Finally, from 1700 m inland the vegetation changed to sand plain lowland fynbos invaded by *A. saligna*. The indigenous strandveld contained *Eragrostis cyperoides* (Thunb.) Beauv. on the sand dunes above the HWM, and palaeotropical shrubs (*Olea exasperata* Jacq., *Euclea racemosa* Murray and *Clutia daphnoides* Lam.) with patches of *T. spicigerus* characterized the indigenous strandveld inland.

METHODS

Soil sampling

Soil samples were collected from the most common soils occurring in each vegetation category and along the 2-km transect at Melkbosstrand (Table 1). These were soil cores (67 mm diameter and 100 mm depth) taken from the surface during June to October 1983 in undisturbed open areas and at Melkbosstrand the rhizosphere of four dominant species. The soils were classified according to the South African binomial system (Macvicar *et al.* 1977) which is based on the recognition of diagnostic soil horizons.

Vegetation sampling

Foliage projective cover, vegetation height and litter layer at Melkbosstrand were determined along two 50-m lines 5 m apart at right angles to the transect at 0, 100, 250, 400, 575, 700, 1000, 1500 and 2000 m inland. Foliage projective cover was measured using 1000 points equidistant along the two 50-m lines. Foliage projective cover has been defined as the proportion of the terrain covered by photosynthetic tissue projected vertically (Specht & Moll 1983). The mean maximum height of the vegetation was measured from fifty consecutive 1-m^2 quadrats. Surface litter samples were collected from a series of ten 0·3-m × 0·3-m quadrats placed every 5 m along the 50-m line and bulked.

Soil and plant analyses

Each soil sample was thoroughly mixed and sieved through a 2-mm mesh. Bray No. 2 and resin-extractable phosphorus and pH were analysed on fresh soil within three days of collection. Total organic and inorganic phosphorus and nitrogen were determined on air-dried soil. Total, Bray No. 2 and resin-extractable phosphorus were extracted using methods similar to those of Hesse (1971), Bray & Kurtz (1945), and Sibbesen (1977), respectively. Bray No. 2 and resin-extractable phosphorus are both measures of plant available phosphorus. The Chang & Jackson (1958) method fractionated the soil for inorganic phosphorus and organic phosphorus was determined by the method of Steward & Oades (1972). The Murphy & Riley (1962) method was the routine colorimetric assay for phosphorus. Total nitrogen was determined on the Melkbosstrand soils only. Soil (1 g) was digested by standard Kjeldahl procedures using selenium catalyst, and both sodium thiosulphate and salicyclic acid converted NO_3^--N to NH_4^+-N. The NH_4^+-N was then determined colorimetrically (Smith 1980). Soil pH, organic matter and bulk density were determined using the same methods as those of Mitchell, Brown & Jongens-Roberts (1984). Soil texture was analysed by mechanically sieving air-dried soil (approximately 1000 g) through 0·5- and 0·2-mm sieves, then dispersed in Calgon (0·1 M sodium hexametaphosphate) and analysed by the Bouyoucos hydrometer method (Day

1965). Plant litter was oven-dried at 80 °C for 48 h, weighed and ground through a Wiley Mill (60-mesh). The phosphorus content was determined by the methods of Jackson (1958) and Murphy & Riley (1962).

Statistical analyses

Each analysis was replicated at least four times. All percentage values were converted to their arcsin transformations before they were statistically analysed. Analysis of variance was computed to compare variations between soil types and sites.

TABLE 2. Mean particle sizes (%) of the soils from the vegetation categories of the fynbos biome, South Africa.

	Coarse sand	Medium sand	Fine sand	Silt	Clay
Strandveld					
Melkbosstrand					
Fernwood	25	34	40	1	0
Nortier					
Fernwood	8	74	18	<1	<1
Renosterveld					
Tygerberg					
Swartland	8	17	28	30	17
Lowland fynbos					
Melkbosstrand					
Fernwood	25	24	50	2	<1
De Hoop					
Hutton	3	8	76	11	2
Mispah	7	16	62	13	2
Mountain fynbos					
Bain's Kloof					
Fernwood	37	38	22	2	<1
Hutton	24	40	25	8	3
Clovelly	20	35	34	8	4
Clovelly	32	41	22	4	<1
Zachariashoek					
Clovelly	53	26	16	3	1
Champagne	42	25	25	6	1
Jonkershoek					
Clovelly	32	19	30	12	7
Clovelly*	30	28	28	12	2

* Denotes shallow soils less than 100 mm depth.
Percentages were arcsin transformed and the mean coefficient of variation is 12%.

RESULTS

Physical properties of the soils

Apart from the Swartland soil (orthic A, pedocutanic B overlying saprolite) of the renosterveld vegetation, the soils of the major vegetation categories of the fynbos biome are sandy (Table 2). Mountain fynbos soils have coarse to medium textured sands, while the sands of lowland fynbos are fine-textured. Of the sandy soils, the Mispah (orthic A

TABLE 3. Mean ± 1 S.E. of total, Bray No. 2 and resin-extractable phosphorus concentrations, pH and organic matter of the surface soils (0–100 mm) of the main vegetation categories of the fynbos biome, South Africa.

Vegetation	Phosphorus ($\mu g\ g^{-1}$ dry mass) Total	Bray No. 2.	Resin-extractable	pH	Organic matter (%)
Strandveld					
Melkbosstrand					
Fernwood	422 ± 49	72 ± 6	40 ± 7	7·5 ± 0·1	2·2
Nortier					
Fernwood	338 ± 24	68 ± 6	13 ± 2	6·6 ± 0·1	1·4
Renosterveld					
Tygerberg					
Swartland	159 ± 7	4·0 ± 0·4	0·4 ± 0·06	5·8 ± 0·2	7·9
Lowland fynbos					
Melkbosstrand					
Fernwood	29 ± 13	2·9 ± 0·7	1·6 ± 0·5	5·2 ± 0·2	2·4
De Hoop					
Hutton	108 ± 14	5·9 ± 2	0·9 ± 0·2	7·1 ± 0·1	5·4
Mispah	207 ± 24	8·3 ± 1·2	1·0 ± 0·2	7·6 ± 0·1	10
Dundee	403 ± 108	5·7 ± 1·0	3·2 ± 1·2	8·0 ± 0·7	5·2
Mountain fynbos					
Bain's Kloof					
Fernwood	35 ± 7	0·8 ± 0·1	0·1 ± 0·05	3·4 ± 0·2	5·6
Hutton	46 + 27	2·2 ± 1·5	0·1 ± 0·01	4·5 ± 0·2	3·6
Clovelly	46 ± 4	1·0 ± 0·3	0·1 ± 0·01	3·9 ± 0·1	3·5
Clovelly*	12 ± 2	0·4 ± 0·1	0·2 ± 0·1	3·3 ± 0·1	1·8
Zachariashoek					
Clovelly	56 ± 1	2·7 ± 0·2	0·1 ± 0·02	3·9 ± 0·1	1·4
Champagne	120 ± 24	1·9 ± 0·1	0·3 ± 0·02	3·2 ± 0·2	10
Jonkershoek					
Clovelly	181 ± 31	3·7 ± 0·8	0·2 ± 0·02	4·1 ± 0·1	5·4
Clovelly	120 ± 6	1·9 ± 0·3	0·2 ± 0·06	4·6 ± 0·1	12
Clovelly*	81 ± 7	1·7 ± 0·5	0·4 ± 0·2	4·0 ± 0·1	7·1
Potberg					
Hutton	180 ± 28	3·8 ± 0·3	0·3 ± 0·03	5·1 ± 0·1	11
F	5·60	11·80	4·13	168·07	26·73
d.f.	16,93	16,89	16,93	16,93	16,93
P	≤0·01	≤0·01	≤0·01	≤0·01	≤0·01

* Denotes shallow soil less than 100 mm depth. Percentages were arcsin transformed and the mean coefficient of variation is 14%.

overlying hard rock or a hardpan horizon) and Hutton (orthic A, red apedal B) soils had the highest silt and clay contents and were found on higher topographic positions in the landscape. The Clovelly soil (orthic A, yellow-brown apedal B) was the most common one in both lowland and mountain fynbos, and occurred on slopes below Hutton and Griffin (an intermediate type) soils. Fernwood (orthic A overlying regic sand) and Champagne (organic O) were found on bottomlands and seepage zones. The Fernwood soils of strandveld are deep aeolian sands (about 2 m deep). The Swartland soils of renosterveld have lower bulk densities (0·9 kg l^{-1}) compared with a range of 1·1–1·8 kg l^{-1} for the other soils. Significant variations in pH and organic matter were found between soils (Table 3).

TABLE 4. Fractionation of inorganic phosphorus as a percentage of total inorganic phosphorus and organic phosphorus as a percentage of total P in the soils of the main vegetation categories of the fynbos biome, South Africa.

	Inorganic phosphorus						Organic
	Saloid	Al	Fe	Reductant soluble	Occluded	Ca	
Strandveld							
Melkbosstrand	9	1	2	<1	<1	87	15
Nortier	50	18	24	0	6	2	10
Renosterveld							
Tygerberg	3	1	6	0	51	40	67
Lowland fynbos							
Melkbosstrand	57	0	19	0	11	14	68
Pella	7	1	88	0	1	3	70
De Hoop							
Hutton	41	0	13	0	9	37	—
Mispah	11	0	2	0	35	52	58
Dundee	5	1	7	0	1	86	—
Mountain fynbos							
Bain's Kloof	78	12	1	2	3	4	76
Zachariashoek	6	4	79	4	2	6	77
Jonkershoek	4	6	67	0	0	23	60
Potberg	48	0	22	0	13	17	—

— Denotes not determined. Percentages were arcsin transformed and the mean coefficients of variation for inorganic and organic phosphorus were 20 and 12%, respectively.

Soil phosphorus

Variations in total and available soil phosphorus occurred between vegetation categories (Table 3). Strandveld soils contained the highest available phosphorus contents whereas the soils of all other vegetation categories had less than 8·5 $\mu g\ g^{-1}$ dry mass Bray No. 2 and 3·5 $\mu g\ g^{-1}$ dry mass resin-extractable phosphorus. Total soil phosphorus contents were highest in strandveld and the alluvial soils of the De Hoop Nature Reserve.

The inorganic phosphorus in the Fernwood soils at Melkbosstrand was mainly Ca-bound (87%) compared with only 2% Ca-bound phosphorus in similar soils at Nortier (Table 4). Limestone derived soils of lowland fynbos also had high Ca-bound phosphorus fractions but mountain fynbos soils had either high saloid or Fe-bound phosphorus or both (Table 4). Occluded and Ca-bound inorganic phosphorus were the main forms in the Swartland soils of renosterveld (Table 4). Significant differences in organic phosphorus were found between soils of the vegetation categories ($F_{11,75} = 46{\cdot}51$, $P \leqslant 0{\cdot}01$). Strandveld soils had low proportions of organically-bound phosphorus (10–15%) compared with the other vegetation types containing 58–77% organic phosphorus (Table 4).

Vegetation and soils at Melkbosstrand

The foliage projective cover of the vegetation increased from about 25% at high water mark (HWM) to between 40 and 70% inland. Mean vegetation height also increased significantly from 0·3 m at HWM to 5·2 m in the *A. saligna* invaded sand-plain lowland fynbos ($F_{8,441} = 218{\cdot}2$, $P \leqslant 0{\cdot}01$). Both foliage projective cover and vegetation height were greater in depressions due to protection from wind. Soil texture changed from coarse and

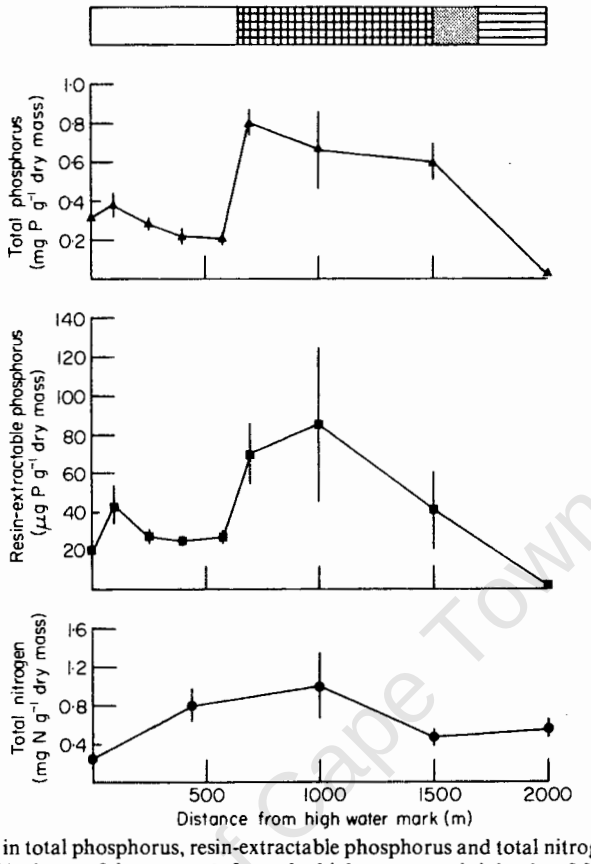

FIG. 1. Variation in total phosphorus, resin-extractable phosphorus and total nitrogen of the soil (0–100 mm depth) along a 2-km transect from the high water mark inland at Melkbosstrand, South Africa. Shading: (□), indigenous strandveld; (▦), strandveld infested by *Acacia cyclops*; (▨), *A. cyclops*, *A. saligna* and *Thamnochortus spicigerus* strandveld; (▤), sand plain lowland fynbos infested by *A. saligna*. Vertical bars represent twice S.E.

medium sands at HWM to fine sands inland with significant differences in fine sand along the transect ($F_{3,8} = 24{\cdot}77$, $P \leqslant 0{\cdot}01$). Soil bulk density declined from HWM inland and soil organic matter content was low throughout the transect. Soil pH was about 7·5 in the strandveld vegetation, but then dropped to pH 5·2 in sand-plain lowland fynbos. There were no significant variations in soil organic matter and pH in the strandveld soils ($F_{3,22} = 1{\cdot}35$ and 0·02, respectively).

Total and resin-extractable phosphorus varied significantly in the soils along the transect in the strandveld vegetation ($F_{3,22} = 14{\cdot}83$, $P \leqslant 0{\cdot}01$ and $F_{3,22} = 3{\cdot}75$, $P \leqslant 0{\cdot}05$, respectively; Fig. 1). Total soil phosphorus increased in indigenous strandveld invaded by *Acacia cyclops*, but declined to 29 $\mu g\ g^{-1}$ dry mass in the sand-plain lowland fynbos (Fig. 1). Resin-extractable soil phosphorus followed a similar pattern. Total soil nitrogen content was lowest at HWM and highest in *A. cyclops* dominated strandveld (Fig. 1). There was no significant difference in nitrogen concentration between strandveld and sand-plain lowland fynbos soils ($F_{1,27} = 0{\cdot}18$).

No significant differences were found in total and available phosphorus and organic matter contents between the rhizospheres of four indigenous strandveld plant species

TABLE 5. Mean ± 1 S.E. of resin-extractable, Bray No. 2 and total phosphorus, organic matter and pH in the rhizosphere of four dominant indigenous strandveld species at Melkbosstrand, South Africa. Figures in parentheses are arcsin transformations ± 1 S.E.

Species	Phosphorus ($\mu g\ g^{-1}$ dry mass) Resin-extractable	Bray No. 2	Total	Organic matter (%)	pH
Euclea racemosa	18 ± 1	58 ± 11	262 ± 49	5·0 (13 ± 2)	7·2 ± 0·03
Clutia daphnoides	29 ± 7	100 ± 29	284 ± 48	3·0 (10 ± 2)	7·2 ± 0·03
Olea exasperata	32 ± 4	85 ± 18	260 ± 33	2·8 (10 ± 1)	7·4 ± 0·05
Thamnochortus spicigerus	35 ± 21	73 ± 16	277 ± 101	1·5 (7 ± 1)	7·5 ± 0·13
F	0·50	0·85	0·28	3·53	4·60
d.f.	3,8	3,8	3,8	3,8	3,8
P	N.S.	N.S.	N.S.	N.S.	⩽0·05

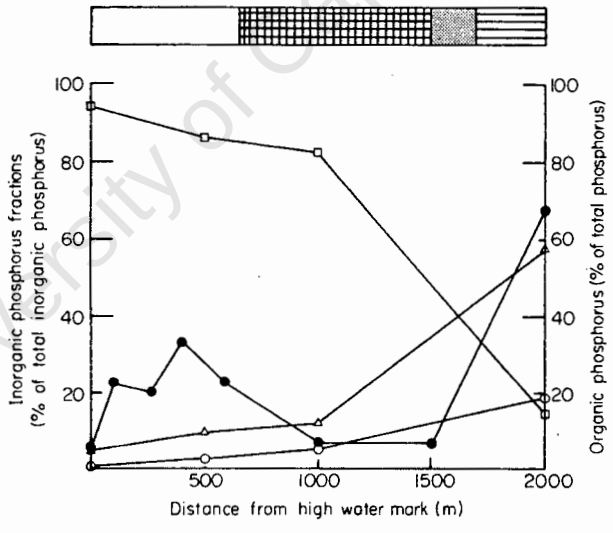

FIG. 2. Variation in organic phosphorus as a percentage of total phosphorus and inorganic phosphorus of the soil (0–100 mm depth) along a 2-km transect from the high water mark inland at Melkbosstrand, South Africa. Shading: (□), indigenous strandveld; (▦), strandveld infested by *Acacia cyclops*; (▨), *A. cyclops*, *A. saligna* and *Thamnochortus spicigerus* strandveld; (▤), sand plain lowland fynbos infested by *A. saligna*; (●——●), organic phosphorus; (□——□) calcium-bound; (△——△) saloid; (○——○), iron-bound.

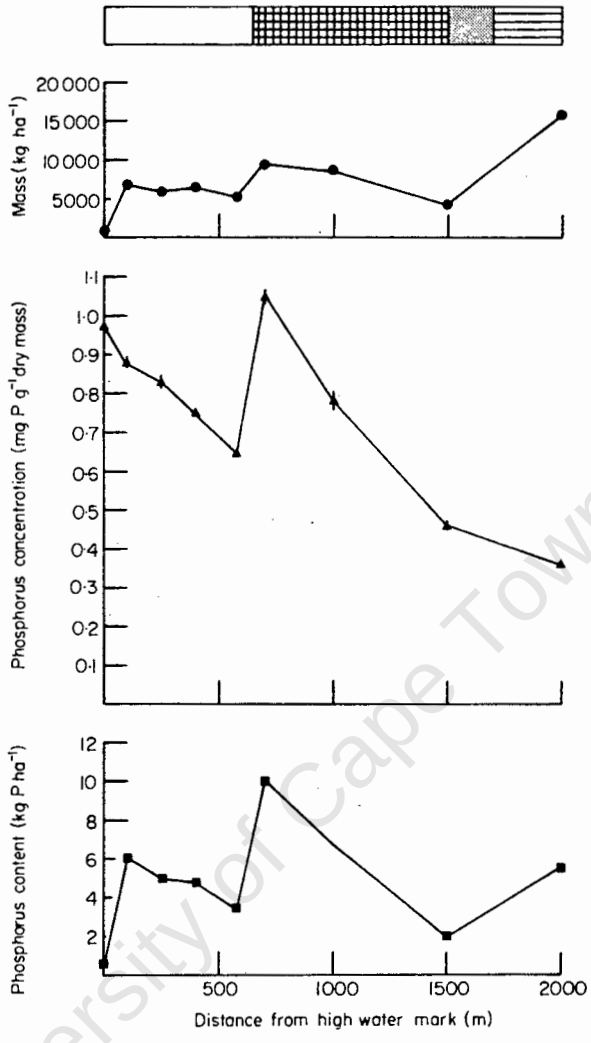

FIG. 3. Variations in dry mass and phosphorus of the litter layer along a 2-km transect from the high water mark inland at Melkbosstrand, South Africa. Shading: (□), indigenous strandveld; (▦), strandveld infested by *Acacia cyclops*; (▨), *A. cyclops*, *A. saligna* and *Thamnochortus spicigerus* strandveld; (▤), sand plain lowland fynbos infested by *A. saligna*. Vertical bars of phosphorus concentration represent twice S.E.

(*Euclea racemosa*, *Clutia daphnoides*, *Olea exasperata* and *Thamnochortus spicigerus*; Table 5). Only soil pH was significantly different between the rhizospheres and open soil samples ($F_{1,23} = 15{\cdot}26$, $P \leqslant 0{\cdot}01$).

Calcium-bound, Fe-bound, saloid and organic phosphorus showed significant variations along the transect ($F_{3,14} = 19{\cdot}34$, 10·68 and 14·28, respectively, and $F_{4,41} = 42{\cdot}7$, $P \leqslant 0{\cdot}01$; Fig. 2). Calcium-bound phosphorus decreased whereas occluded, Fe-bound and saloid phosphorus increased from negligible proportions at HWM to 11, 18 and 57% of total inorganic phosphorus, respectively, 2 km inland (Fig. 2).

Standing litter varied from only 500 kg ha^{-1} at HWM to 15 600 kg ha^{-1} 2 km inland in the sand plain lowland fynbos infested with *Acacia cyclops* (Fig. 3). There was less litter in the wind exposed sites whereas the sites invaded by *Acacia* spp. contained the greatest litter dry mass, consisting predominantly of *Acacia* leaves and seed pods. The phosphorus concentration of the litter declined from HWM inland with a peak in the *A. cyclops*-invaded strandveld (1·05 mg P g^{-1} dry mass) and was only 0·36 mg P g^{-1} dry mass 2 km inland. The phosphorus contained in litter on an area basis was highest in *A. cyclops*-invaded strandveld (Fig. 3). Litter phosphorus content was equivalent to 14·4% of the 0–0·1 m soil total phosphorus in sand-plain lowland fynbos, but only 0·1–1·4% in the surface Fernwood soils in strandveld. At the other sites, ground litter mass was low in the renosterveld vegetation (4 200 kg ha^{-1}) and high in mountain fynbos (11 000 kg ha^{-1}). Phosphorus content of litter was low in renosterveld (0·3 mg P g^{-1}; 1·2 kg ha^{-1}) and mountain fynbos (0·2 mg P g^{-1}; 1·9 kg ha^{-1}), and was equivalent to only 1·2 and 1·3% of the total 0–0·1 m depth soil phosphorus content.

DISCUSSION

Along the west coast inland of the south-western Cape, a gradient of soil texture and phosphorus status occurred from the coastal dunes through the strandveld vegetation into sand plain lowland fynbos. The soil phosphorus status was altered by infestations of alien legumes, e.g. *Acacia cyclops* and *A. saligna*, and was essentially due to large litter accumulations and rapid turnover rates. The annual litterfall of alien Australian acacias was about 704 g m^{-2} (Milton 1981), being greater than that of indigenous sand plain lowland fynbos vegetation (Mitchell *et al.* 1986). The phosphorus content of the acacia litter exceeded that of litter from the indigenous vegetation. Ground litter masses of the indigenous vegetation in this study were similar to those of Kruger (1977) and van Wilgen (1982). It has been postulated that plants adapted to low nutrient conditions do not compete successfully on fertilized soils (Specht 1963; Grime 1979). Thus, infestations of the fynbos biome by acacias may make the environmental less suitable for the indigenous plants by enriching the soil with nutrients.

The Fernwood soils of the strandveld vegetation contained the highest levels of both total and available phosphorus where there are extensive deposits of phosphorites of marine origin, aluminium and aluminium-iron phosphate and phoscrete (Birch 1977). Inorganic phosphorus changed from Ca-bound along the coast to Fe-bound and saloid phosphorus with an increase in the proportion of organic phosphates inland agreeing with those studies on a chronosequence of sandy soils of stabilized dunes in New Zealand (Syers & Walker 1969a,b; Williams & Walker 1969). The transformations of soil phosphorus can be indicators of pedogenic weathering processes (Smeck 1973), and the fate of phosphorus during pedogenesis has been correlated with soil age (Walker & Syers 1976). The ageing of coastal sands was not undertaken in this study, but the aeolian sands along the coast are of Holocene and late Pleistocene origin whereas the acidic soils inland became decalcified by leaching (Schloms, Ellis & Lambrechts 1983).

The organic phosphorus contents of the soils varied from a small proportion of total phosphorus occurring in the Fernwood soils along the west coast to high proportions in soils of the other vegetation categories. Many factors are known to affect soil organic phosphorus (Dalal 1977), but in the south-western Cape, they appear to be due to the type of parent material and age of soil. Soil organic phosphorus is primarily accumulated as a result of microbial activity and in solution is more mobile than inorganic phosphorus

(Dalal 1977), but movement of phosphorus through soils is slow (Russell 1973; Bieleksi 1976). Although organic phosphorus may be absorbed by plants directly, it is made available by mineralization to organic phosphorus (Dalal 1977). In this study, available phosphorus contents of the rhizosphere soils of the four indigenous plant species of the strandveld compared with the open were similar. This is different from the rhizosphere soils of the sand plain lowland fynbos where resin-extractable phosphorus varied between the physiognomic groups of the vegetation, but was found in lower concentrations (Mitchell, Brown & Jongens-Roberts 1984).

In conclusion, the soils of the south-western Cape are either derived directly from the parent rock material or consist of wind-blown sand. The Fernwood soils of the strandveld vegetation are distinguished from the rest by having higher total and available phosphorus contents and a low proportion of organic phosphorus. These wind blown soils along the coast change to more acidic and leached ones inland. On the limestone outcrops of the southern Cape, the Mispah and Dundee soils are characterized by calcium phosphates as the predominant inorganic form and high total phosphorus contents, but low in available phosphorus. The soils of the mountain fynbos are derived from either sandstones or granites, the granite-derived soils being higher in total phosphorus content than those from sandstone. The lowest concentrations of available phosphorus were found in soils of mountain fynbos as a result of the steep slopes and high rainfall. Finally, the Swartland soils of the renosterveld vegetation have a phosphorus status similar to those of granite-derived soils of mountain fynbos, but differ in texture.

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Variation by three-way analysis of variance with nesting of shoot extension and dry mass of Leucospermum parile and Phylica cephalantha shrubs amended with a complete factorial fertilizer addition of nitrogen (N), phosphorus (P) and a mixture of all essential nutrients excluding N and P (M) at the end of the 1984-85 and 1985-86 growing seasons at Pella, South Africa. Values are F values. Main effects and interaction d.f.=1,28. Values in parentheses are within treatment d.f. $^{+}$, denotes interaction; ***, significant differences at P<0.001, **, P<0.01; *, P<0.05.

Source		Treatments							
		N	P	M	N+P	N+M	P+M	N+P+M	Within (N+P+M)
Shoot extension									
L. parile 1984-85	(28,328)	18.42***	1.77	2.60	1.50	1.81	2.79	6.75+++	8.46***
1985-86	(28,321)	1.31	30.46***	1.67	24.31***	0.53	17.11***	0.12	2.95***
P. cephalantha 1984-85	(28,315)	14.45***	0.37	2.16	0.01	2.06	0.09	3.07	6.14***
1985-86	(28,315)	2.04	2.42	2.07	9.81**	0.70	18.43***	9.92**	4.04***
Shoot dry mass									
L. parile 1984-85									
Leaf	(28,319)	9.88**	5.01*	2.76	0.76	2.17	5.29*	2.57	3.28***
Stem	(28,319)	9.61**	0.06	0.81	0.17	3.56	2.24	5.82*	2.77***
Total shoot	(28,319)	10.14**	2.54	2.04	0.09	2.70	4.26*	3.64	3.09***
L. parile 1985-86									
Leaf	(28,318)	0.48	20.26***	3.81	2.66	0.02	17.62***	0.02	3.03***
Stem	(28,318)	0.32	13.13***	0.39	2.94	0.23	11.80***	0.32	2.76***
Total shoot	(28,318)	0.02	17.42***	1.88	2.88	0.09	15.35***	0.12	2.88***
P. cephalantha 1984-85									
Leaf	(28,298)	11.79***	0.08	0.73	3.51	6.04*	2.47	3.95*	3.14***
Stem	(28,298)	6.70**	1.01	4.07*	0.57	1.68	0.11	1.89	3.09***
Inflorescence	(28,298)	5.12*	0.93	4.58*	0.84	0.59	5.75*	0.01	5.84***
Total shoot	(28,298)	10.83**	0.17	2.73	1.12	2.54	0.03	2.44	3.54***
P. cephalantha 1985-86									
Leaf	(28,280)	4.30*	0.00	2.32	5.37*	0.00	21.41***	10.49**	3.42***
Stem	(28,280)	3.14	0.14	0.66	8.16**	0.64	10.17**	6.56*	2.64***
Inflorescence	(28,280)	7.90**	0.00	9.39**	7.23**	0.20	1.88	7.98**	2.71***
Total shoot	(28,280)	1.74	0.00	0.86	11.21***	0.40	16.11***	5.80*	2.81***