ASPECTS OF THE PLANT, SOIL MICROBIAL AND NUTRIENT ECOLOGY OF SELECTED MOUNTAIN FYNBOS COMMUNITIES AT THE CAPE OF GOOD HOPE NATURE RESERVE

BY

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SUMMARY

1. The mountain fynbos investigated in this study at the Cape of Good Hope Nature Reserve fell into six plant communities. Site 1 : Metalasia brevifolia - Leucospermum hypophyllocarpodendron (Community 1.1) and Metalasia brevifolia - Serruria furcellata (Community 1.2); Site 2 : Elegia parviflora - Chondropetalum nudum - Erica clavisepala (Community 2.1) and Elegia parviflora - Berzelia intermedia - Simocheilus depressus (Community 2.2); Site 3 : Elegia parviflora - Chondropetalum nudum - Simocheilus depressus (Community 2.3) and Elegia parviflora - Erica pulchella - Simocheilus depressus (Community 2.4).

2. Live above-ground phytomass data for Communities 1.1 and 1.2 were 825,4 and 967,4 gm^{-2} respectively, the bulk comprising low nanophanerophytes (87,7 and 93,3%). In Sites 2 and 3 where the hemicryptophytic Restionaceae were dominant, phytomass was lower by two to three times. Total dead material was highest in Sites 2 and 3.

3. Soils were all acidic (pH 3,34 to 4,14, highest in Site 1). In winter soils were moist (Site 1) to waterlogged (Sites 2 and 3), drying out in summer. Site 1 possessed highest amounts of organic matter, and total N and P compared with those of Sites 2 and 3. (Organic matter: 2,8 to 10,9 x 10^4, 0,7 to 8,3 x 10^4 and 0,2 to 5,3 x 10^4 kg ha^{-1} respectively; total N: 492 to 2371, 161 to 1107 and 183 to 722 kg ha^{-1} respectively; total P : 18,20 to 58,11 , 6,36 to 47,85 and 4,68 to 23,30 kg ha^{-1} respectively for all three depths studied Organic matter and total N and P all decreased with soil depth and there were irregular fluctuations with season . Bray no. 2 P on the other hand displayed similar quantities for each site (1,25 to 10,33 , 0,00 to 11,30 and 0,78 to 8,24 kg ha^{-1} respectively) with marked summer peaking in Sites 2 and 3. C/N ratios were high, all exceeding 24.

4. Leaf N and P exhibited the following concentrations - N : 5126 (Leucospermum - Community 1.1), 6679 (Serruria - Community 1.2), 6800 (Erica - Community 2.1) and 5333 µg g^{-1} (Simocheilus - Community 2.3) and P : 384, 555, 404 and 328 µg g^{-1} respectively. These were higher than in the aphyllous photosynthetic

stems of Elegia - N : 2978 (2.2) and 4168 (2.4) $\mu g\ g^{-1}$ and P : 155 and 167 $\mu g\ g^{-1}$ respectively. Erratic seasonal trends in both N and P were observed.

5. Three major rooting types were found. These were the long, well-developed tap root systems of Leucospermum and Serruria, the shorter, less developed tap root system of Erica and the fibrous system of Elegia arising from a rhizome. Both the first two species possessed proteoid roots, while Elegia was shown to have capillaroid root - like structures. Both Erica and Simocheilus were heavily mycorrhizal.

6. 41 soil microfungal isolates were obtained from profiles in each of the three sites. Dominant groups were Penicillium spp., members of the Mucorales and Peronosporales and mycelia sterilia. Each site displayed a specific mycoflora. Numbers (per g soil dry mass) were greatest in the top soil of Site 1 (67000) compared with Sites 2 (37000) and Site 3 (12000), and tended to decrease with depth. There was strong correlation between numbers and organic matter, and total N and P.

7. Although no members of the Azotobacteriaceae were isolated, free-living nitrogen-fixation was demonstrated in the top soils of Site 1 (0,1), Site 2 (153,8) and Site 3 (8,6 g N fixed ha^{-1} day^{-1}).

"It is usual to designate the plants of dry localities.....
as xerophytes, but in this due attention is not paid
to the fact that the characteristics of organisms are
physiological, those of habitats are physical, and
that there is no necessary connection between the two."

(Schimper 1903, p2)

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CHAPTER 1

INTRODUCTION

Vegetation growing in habitats influenced by winter rainfall (and dry summer) regimes are subject to seasonal moisture stress and commonly possess leaf xeromorphic features which are absent in mesomorphic vegetation of more temperate and wet areas (Grieve 1955). Schimper (1903), the father of plant ecophysiology, had already recognized this phenomenon and stated that, "The mild temperate districts with winter rain and prolonged summer drought are the home of evergreen xerophilous woody plants which, owing to the stiffness of their thick, leathery leaves, may be termed sclerophyllous plants". These plants are generally associated with hard leaves which are often reduced in size and have a similar basic leaf anatomy (Kummerow 1973). Other features common to sclerophyll leaves include reduced cell size, submerged stomata and higher stomatal frequencies, thicker cell walls, thicker cuticles, more veins per unit surface area and possession of secondary chemicals such as phenols and terpenoids (Kummerow 1973). Sclerophylly appears to be characteristic of vegetation found in mediterranean-type climate

zones (see definition in Appendix A). Areas occurring outside the bounds of a mediterranean-type climate may also harbour a vegetation with a similar leaf morphology and anatomy; these include the tropical Amazonian rain forests (Jordan and Uhl 1978) and the summer rainfall heathlands in south eastern Australia (Beadle 1968).

Sclerophylly was originally thought to have arisen in direct response to a consistent moisture stress during part of the year, especially over the summer months. This hypothesis is supported by Grieve (1955). However Andrews (1916) suggested that many xeromorphic taxa arose from a more mesomorphic habit through adaptations to an environment of lower ferti lity. He proposed that before and after the isolation of Australia (i.e. on the breaking up of Gondwanaland during the late Mesozoic), trees were driven by competition, and with their own inherent ability to migrate, from the more mesic northern Australia to the south- onto the (low nutrient) sandy soils. Andrews (1916) suggestion is supported by Mothes (1932) findings that a decrease in soil nitrogen gave rise to leaf xeromorphy. A similar effect was

demonstrated by Beadle (1966) who fed plants with varying concentrations of nitrate and phosphate. Wood (1934) also suggested that a decrease in certain soil nutrients might be responsible for xeromorphism in western Australian vegetation.

More recently Small (1973) has proposed that physiological properties inherent in xeromorphy are adapted to both drought stress as well as permitting growth on a nutrient deficient soil.* He based this hypothesis on the observation that characters found in plants growing under arid conditions also occurred in those on soils low in nutrients (in non-arid areas).

In addition to specific leaf characters, sclerophylls on oligotrophic soils very often possess certain rooting morphologies which enable a more efficient mineralization of phosphorus compounds and nutrient uptake. Included

* Nutrient deficient and like terms such as nutrient limiting imply a nutrient climate which may be detrimental to the plant. On the whole, plants growing under these conditions appear to survive if not thrive quite adequately. Terms such as "oligotrophic" or "low in nutrients" are therefore preferred and have been adhered to in this thesis.

in this category is the proteoid root, chiefly found in the Australian (Purnell 1960 and Lamont 1981) and western Cape (Low 1980) Proteaceae. These arise as bottle-brush structures on lateral roots and they have been shown to enhance the nutrient status of Banksia and Hakea which are typical sclerophyllous genera of the Proteaceae (Jeffrey 1967) and Lamont (1972, 1981).

Other modified roots include the capillaroid structures of the Restionaceae (Lamont 1982) and the dauciform root common in the Cyperaceae (Lamont 1981). Capillaroid roots are named because of their ability to retain soil moisture.

The mycorrhizal associations are perhaps of greater importance as these appear to be universally associated with plant roots (Harley 1969, Nicholson 1967). Harley (1969) recognized both ecto- and endomycorrhizas in his comprehensive classification of this group. The latter predominate in heathlands where the ericoid, orchid and vesicular-arbuscular types are found (Malajczuk and Lamont 1981). In many cases they play an obligatory role in the survival of plants growing in oligotrophic soils (Hacskaylo 1972). Mycorrhizal fungi are important

to the host by providing an external hyphal network in the soil and by the presence of mineralizing enzymes eg. phosphatases (Baylis 1967, Harley 1971, Mitchell and Read 1981, Read and Stribley 1973). Plant water status may also be enhanced by the mycorrhizal association (Safir et al.1972) particularly under water-stressed conditions (Reid and Bowen 1979).

Acidic sandy heaths may also possess a mycoflora unique to this specific environment. The distribution of soil microorganisms is of course dependent on the soil pH, water content and availability of nutrients. Correspondingly the soil mycoflora will play an obligatory role in nutrient cycling processes - after above ground litter is finally incorporated into the upper layer of the soil.

In the past considerable work has been concentrated on the relationships between the plant and microorganisms in agricultural soils. Little attention has been given to the microbiology of natural ecosystems (Borut 1960, Stenton 1953, Tresner et al.1954). Studies have focused on fungi although bacterial investigations have formed an additional aspect of microbiological work in these systems.

Many natural soils tend to be acidic at a pH which favours the growth of fungi. The heathlands of Australia and Britain are no exception (McLennan and Ducker 1954, Sewell 1959a, Warcup 1955) and their podzols attain pH's as low as 3 (Williams and Parkinson 1964). Bacteria and actinomycetes on the other hand prefer alkaline conditions, and their growth is restricted at pH values below 5.

Another group of soil microorganisms which has been found to be extremely important to the nutrient cycle in nutrient poor soils is the free-living nitrogen-fixing bacteria. As early as 1893, Winogradsky discovered that the free-living bacterium, Clostridium pasterianum fixed gaseous nitrogen. Shortly after this, Beijerinck (1901) found the same for several members of the Azotobacteriaceae. Since then (e.g. Jurgensen and Davy 1970, Virtanen and Miettinen 1963) evidence suggests that certain species in this family can contribute in a positive fashion to the soil nitrogen input.

Mountain fynbos in the western Cape winter rainfall region is characterized by its sclerophyllous nature and its ubiquitous presence on oligotrophic soils, the latter

displaying a summer moisture deficit (Kruger 1979, Taylor 1978). As such it provides an ideal example of a South African vegetation type which possesses the major heathland criteria as described by Specht (1979).

In the Fynbos Biome (see Kruger (1978) for a description) little has been published on plant-soil-microbial aspects. There is limited data on the nutrient status of the soil (Low 1978, Low 1980, Mitchell 1980) and even less on the presence of root adaptative strategies (Low 1980) or on the soil microbiology (Coley and Mitchell 1980).

The study outlined in this thesis therefore sets out to establish the nutrient, microbial and root strategy phenomena in several homogeneous mountain fynbos communities at the Cape of Good Hope Nature Reserve. The project entails the characterizing of the major soil parameters, including N and P levels, and how these varied with the season. Further, leaf N and P levels of dominant species were investigated on a seasonal basis. The microbiological aspect of the study involved the isolation of soil microfungi and free-living nitrogen-fixing bacteria, as well as the estimation

of soil nitrogen-fixation. Finally, plants were examined for their respective rooting strategies and whether specialized rooting structures were present.

The overall aim of the study was thus to provide chemical characterization of mountain fynbos soils and leaves and to ascertain dominant plant rooting strategies and adaptations which may be important in a potentially low nutrient environment. Microbiological investigations were aimed at providing an insight into microfungal characteristics of acid fynbos soils, and whether these soils could supplement nitrogen input into the soil through free-living nitrogen-fixing bacteria.

CHAPTER 2

THE STUDY AREA

An area along the western part of the Cape Peninsula in the Cape of Good Hope Nature Reserve was selected for this study. This area contained some of the most accessible homogeneous fynbos communities near to Cape Town and occurred on soils derived from Table Mountain Sandstone (TMS). The S.H. Skaife field station at Olifantsbos (long. 34°30' S, lat. 18°15' E) provided a suitable base from which to conduct field work.

Climate is typically mediterranean (Fig. 2.1) with an average annual rainfall of 819 mm (Simonstown) and 356 mm (Cape Point). Mean annual rainfall at Klaas-jagersberg, the rangers' station, is 605 mm. The latter rainfall data collection point is the closest to the study sites (rainfall data supplied by G. Wright).

Geologically the southern Peninsula is dominated by unfolded sediments of the Table Mountain group, with the Peninsula (lower sandstone) formation being

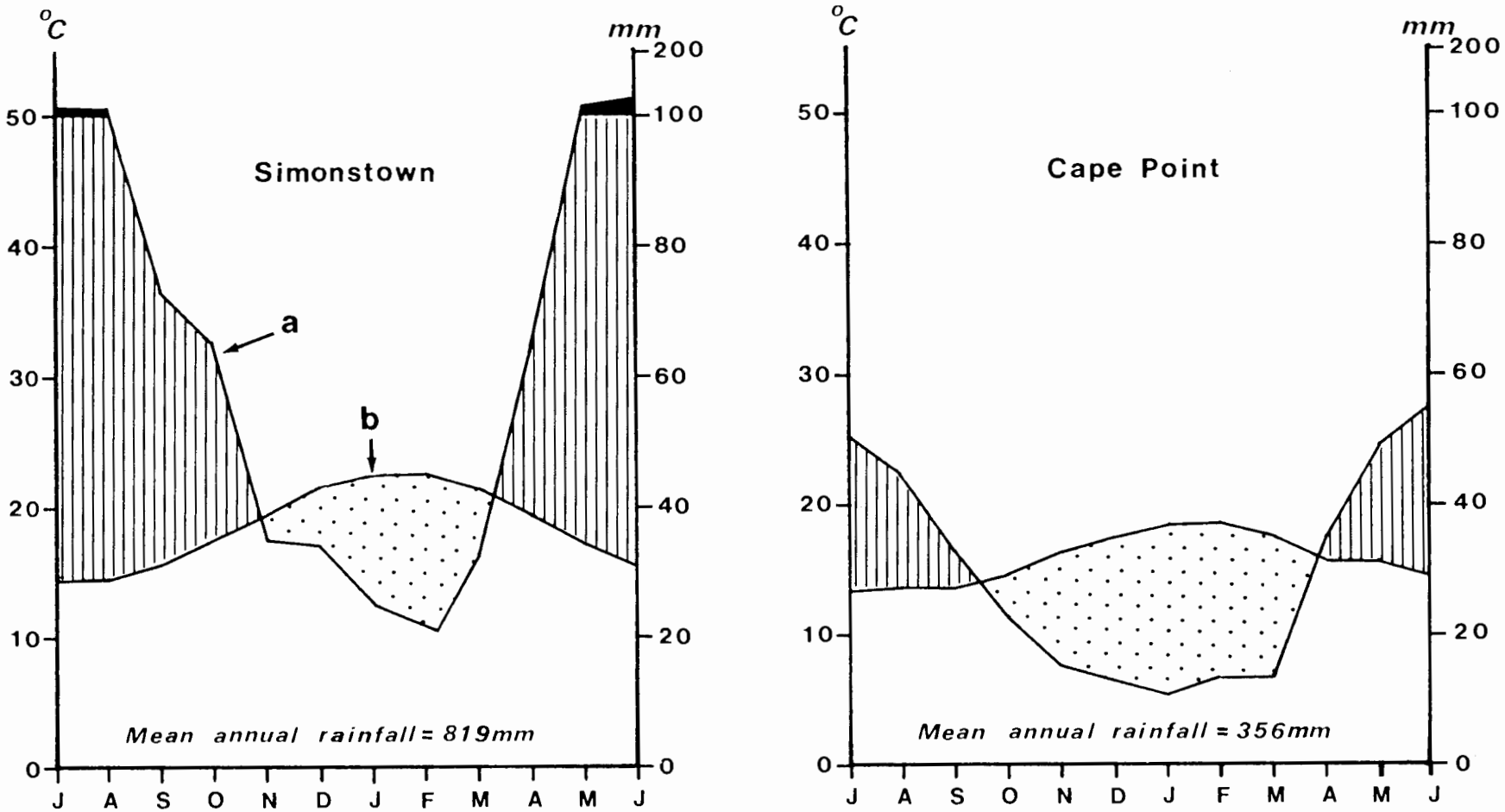


Fig. 2.1 Climate diagrams for Simonstown and Cape Point. The study area lies between the two localities, but closer to Simonstown (see Fig. 2.2). a = rainfall; b = temperature.

predominant. Coastal and inland dunes of Quarternary to Recent age are also found in localized places (Taylor 1969).

Taylor (1969) classified the vegetation of the Reserve into two broad categories: a Fynbos Formation (Coastal alliance and Inland alliance) and a Broad Leaved Scrub Formation. Both the latter and the Inland alliance tend to occur on soils derived from TMS, while the Coastal alliance is found mainly on sandy calcareous dune fields. Three sites were chosen in the Fynbos Formation, and contain the characteristic physiognomic elements of the vegetation. The position of each site is illustrated in Fig. 2.2. Soil forms at the three study sites were identified after Mac Vicar et al. (1977).

General description of Site 1

Site 1 was approximately 61 m above sea level on a well-drained plateau north-east of the field station (Plates 2.1 and 2.2). The plateau was about 2000 m^2 in area, bounded on two sides by rocky outcrops. Soils were 0,5 to over 0,75 m deep and were derived from TMS. Shallower soils were of the Mispah form with the Cartref form in the deeper parts (Plate 2.3).

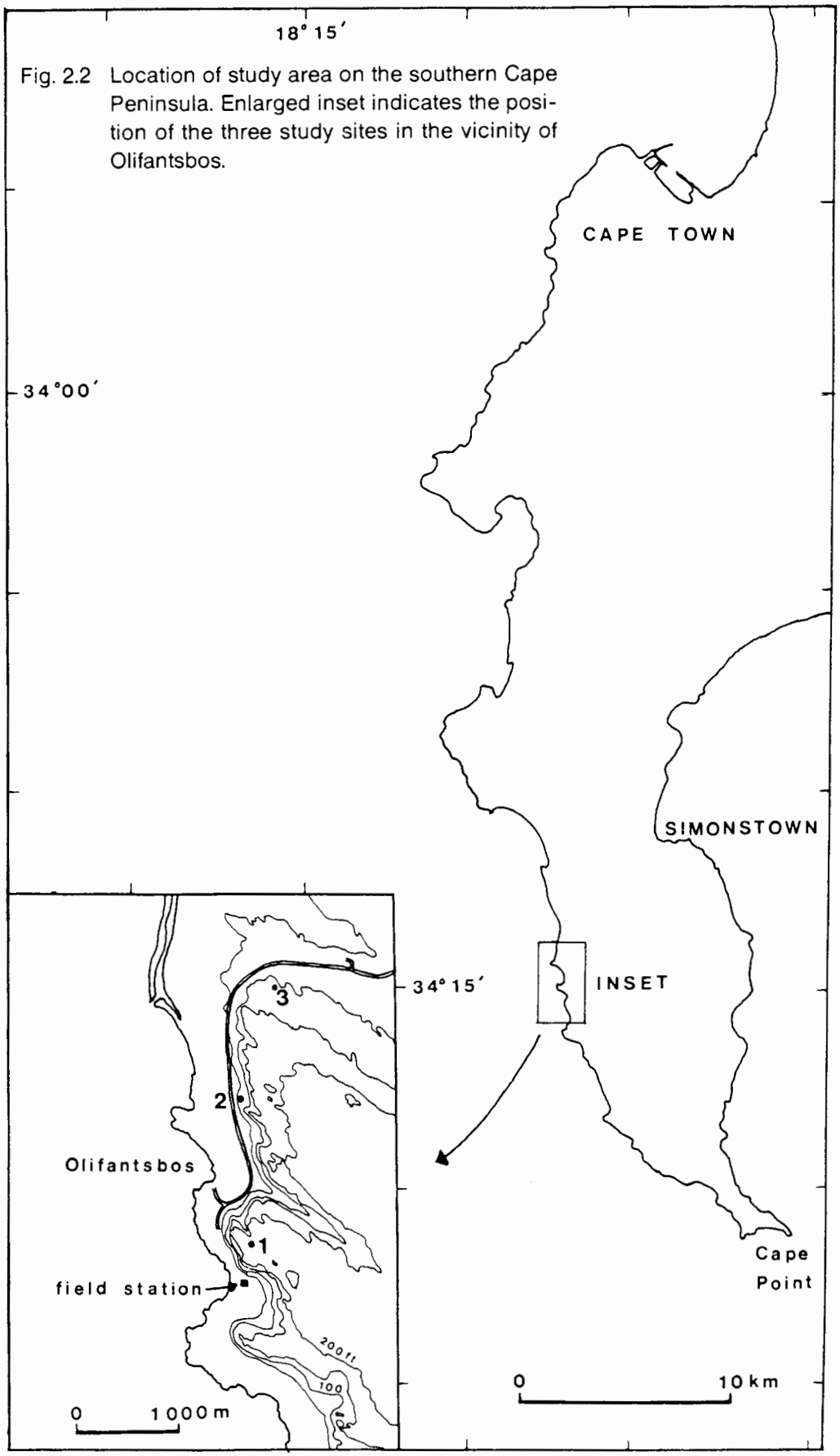


Fig. 2.2 Location of study area on the southern Cape Peninsula. Enlarged inset indicates the position of the three study sites in the vicinity of Olifantsbos.

Plate 2.1 View of Site 1 showing mixed fynbos of Community 1 dominated by **Metalasia brevifolia** (white flowers). The site forms a sandy plateau bounded by rocky sandstone outcrops which can be seen in the far distance, right. Species 300 — 600 mm tall.

Plate 2.2 **Metalasia brevifolia** (white flowers) (M.b) and **Serruria vallaris** (S.v) occurring in Community 1.2. Heights approximately 600 and 450 mm respectively.

Plate 2.3 Soil profile in Site 1 showing A (top) and bleached E horizon. Partially decomposed bedrock (Table Mountain sandstone) at the bottom of the soil pit. Markings on stick represent 100 mm intervals. Profile dug in late spring.

General description of Site 2

Site 2 (Plates 2.4 and 2.5) was located in a shallow depression on the landward side of the tar road to Olifantsbos, 1,7 km from the field station. The area of the depression was approximately 1500 m^2. Soils were TMS-derived with the possible inclusion of aeolian sand from the coastal zone to the west. Soil depth was more than 1,5 m and classified as the Fernwood form (Plate 2.6). The site was seasonally wet to waterlogged, the latter during the winter months.

General description of Site 3

Site 3 (Plates 2.7 and 2.8) was located 3,0 km from the field station along the tar road to Olifantsbos, also on the landward side. Area of the site was approximately 1200 m^2 and also seasonally wet to waterlogged, despite the fact that it was situated on a slight north-west facing slope (c. 3°). Soils were again TMS-derived, over 1,5 m deep and also of the Fernwood form, with a similar profile to that shown in Plate 2.6

A detailed description of the plant communities appearing in each site is presented in Chapter 4.

Plate 2.4 View of Site 2 showing **Elegia** community (Community 2) in shallow depression. Vegetation includes restioid (**Elegia, Chondropetalum**) and ericoid (**Erica, Simocheilus**) components of 350 — 450 mm in height.

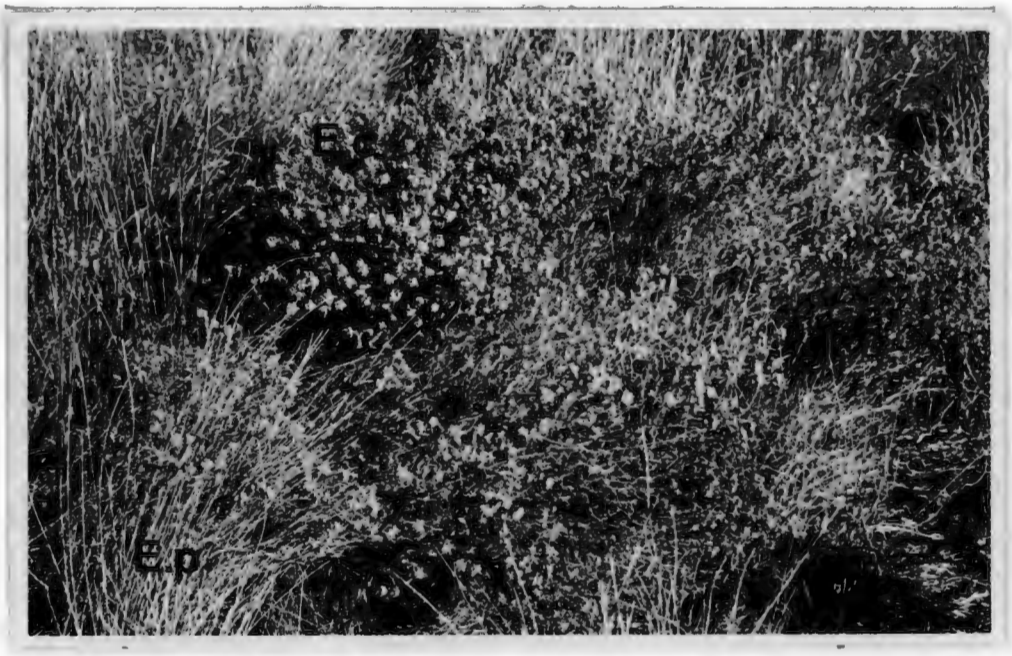


Plate 2.5 **Erica clavisepala** (E.c) and **Elegia parviflora** (E.p) in Community 2.1. Heights approximately 400 and 450 mm respectively.

Plate 2.6 Soil profile in Site 2 and underlying water table showing A horizon over deep sand. Markings on stick represent 100 mm intervals. Profile dug in late spring.

Plate 2.7 View of Site 3 with **Elegia** dominated vegetation (Community 2). The site slopes gently from right to left, over deep sand. Vegetation 350 to 500 mm tall.

Plate 2.8 **Elegia parviflora** occurring in Community 2.4. Height 450 mm.

CHAPTER 3

METHODS AND MATERIALS

VEGETATION

The vegetation of the study sites was described using the Braun-Blanquet technique (Westhoff and Van der Maarel 1973). Eight 5mx5m releves (minimum size determined by the minimal area method (Hopkins 1957)) were subjectively placed in Site 1 and six in each of Sites 2 and 3. Species and cover abundance values from each quadrat were recorded.

PHYTOMASS

Above-ground phytomass was determined by cropping 1mx1m quadrats (5 in each of Communities 1:1 and 1:2 (Site 1) and 4 in each of Communities 2:1 and 2:2 (Site 2) and 2:3 and 2:4 (Site 3). Plant material was divided into live, dead-standing and litter components. The former was further divided into sclerophyllous nanophanerophytes, Restionaceae, grasses (both hemicryptophytic) and other fractions (including nanophanero-

phytic succulents. Life forms were described after Raunkiaer (1934). All material was laid on the floor of a laboratory, dried next to asbestos heaters for two weeks at a temperature of 25°C to 30°C and then weighed. After this period all plant material had dried sufficiently so as to be comparable mass-loss wise with similar material dried for 48h at 80°C. Succulents would not dry out after the two week period and were consequently weighed after heating to constant mass at 80°C.

SOIL ANALYSIS

Soils were sampled at three-monthly intervals during July and October, 1976, and February, May and August, 1977, covering five seasons from winter to winter (Table 3.1).

TABLE 3.1 Dates and seasons of soil sampling

DATE	SEASON
31 July 1976	Winter
4 November 1976	Spring
3 February 1977	Summer
7 May 1977	Autumn
7 August 1977	Winter

Soil cores (20x23 mm), placed in a random "Z" pattern through each community, were taken from each site and from each of three arbitrary depths (0-150, 150-300 and 300-450 mm) and bulked by placing immediately into plastic bags and sealed. Within 24h, mass loss (48h at 80°C) was determined. Soils were then air-dried for one week and passed through a 2 mm mesh sieve to remove stones, roots and larger pieces of organic debris. Very few stones were encountered in Site 1 and none in Sites 2 and 3. The following analyses (six replicates on the bulked samples) were performed on the sieved soil (after a week of air-drying the mass of a unit volume of soil was comparable with that of the same volume of soil dried at 80°C). The latter temperature may effect changes in the soil which are not desirable for the methods discussed below:

pH (adapted after Schofield and Taylor 1955).

Soil (10 g) and 25 cm^3 of 0,01-M $CaCl_2$ were mixed with a glass rod. After standing for 1h, pH was determined using a glass electrode connected to a T and C digital pH-meter (Model 900), standardized at pH 4.

Organic Matter

Soil (5 g) was placed in a porcelain crucible, transferred to a Muffle furnace for 8h at 450°C and the mass-loss determined.

Nitrogen (modified after Hesse (1971) to include NO_2^- ions)

Total nitrogen was determined using the micro-Kjeldahl technique. Soil (4 g) and finely ground sodium thiosulphate (0,5 g) were placed in a 50 cm^3 pear-shaped digestion flask. Concentrated sulphuric acid containing salicyclic acid (34 g dm^{-3}), and a Merck selenium catalyst tablet containing 0,1 g selenium and 1 g sodium sulphate were added and the sample left to stand for 20 min. Flasks were then placed on a six-place heating mantle on low heat to digest. The heat was gradually increased until the acid boiled vigorously. After initial charring the sample cleared to a white to pale yellow colour (1-1,5h) and heating was continued for a further 30 min. after which the flask was allowed to cool. The digest was then filtered with three washings of distilled water through

a pad of glass wool and made up to 50 cm^3 with distilled water. An aliquot (5 cm^3) together with approx. 40 cm^3 NaOH was steam-distilled through a Kjeldahl distillation apparatus into 2 cm^3 of 0,02M-HCl, with approx. 20 cm^3 of distillate being collected. This was titrated against 0,005M-NaOH using three drops of Tshiro's indicator (0,125 g methyl red and 0,083 methylene blue in 100 cm^3 absolute alcohol). The amount of nitrogen (as NH_4^+) originally present in the aliquot was calculated from:

$$1\ cm^3\ 0{,}005M\text{-}NaOH \equiv 70\ \mu g\ N$$

C/N ratio

Samples (10-15 mg) (from the 0-150 mm horizon only) were analysed on a Hewlett-Packard 185-B C-H-N analyzer by the Department of Geochemistry, University of Cape Town. The analyzer was calibrated using a synthetic mixture of quartz and calcium carbonate (C) and NBS 141 B acetanilide (N). Total carbon was determined from the CO_2 released on igniting the sample; likewise the total nitrogen from the nitrous gases released.

Phosphorus

Total phosphorus was extracted using a wet digestion method modified from Hesse (1971) and Jackson (1958). Soil (5 g) was placed in a 50 cm^3 pear-shaped flask together with 5 cm^3 60% perchloric acid. The mixture was digested on medium heat until white, and dense, white fumes were emitted, and subsequently for a further 30 min. pH of the digest was adjusted to 3 by adding two drops 0,5%, 2-4 dinitrophenol in 80% ethanol and neutralising by adding 33% ammonia solution until the digest colour just turned yellow, and then 6M-HCl dropwise until the colour had disappeared. The digest was then filtered with three washings of distilled water through a Whatman no. 41 filter paper and made up to 50 cm^3 with distilled water.

Bray no. 2 ("available") phosphorus. No universal method exists for "available" phosphorus determination (Hesse, 1971, p273). Most extraction techniques give different results for the amount of so-called available P in the soil (mild acid extractants - eg. Metson (1961), Truog (1930), Warren and Cooke (1962);

alkaline extractants - eg. Das (1930), Olsen *et al.* (1954). These techniques can only approximate the soil-plant root phosphorus interface state but without giving a precise reflection of what is available to the plant. Various dilute acid solutions (see Hesse 1971, Chapter 12) have been used to determine the available P fraction in the soil. However it is generally conceded that without a direct bioassay of the availability (and subsequent uptake by plants) of the various forms of soil P, accurate determinations cannot be made.

The Bray no. 2 method which employs a mild acid extraction (0,1M-HCl, 0,03M-NH_4F) is commonly used in the determination of P in South African agricultural soils (Anon 1974; G Thompson pers. comm.). Because of its wide use in the western Cape, it was decided to employ this method in the study.

Soil (4 g) was shaken for 1h in a 50 cm^3 conical flask with 30 cm^3 Bray no. 2 extractant (see Table 3.2.1 for the extractant's recipe). This was then filtered through a Whatman no. 30 filter paper containing approx. 0,3 g P-free activated charcoal.

TABLE 3.2.1 Composition of Bray no. 2 P-extractant

Ammonium fluoride stock solution

Ammonium fluoride (185,5 g) made up to 5 dm^3 with distilled water.

Bray extractant solution

Ammonium fluoride stock solution (600 cm^3) and 200 cm^3 31% HCl made up to 20 dm^3 with distilled water.

Assay of phosphorus using the molybdenum blue method (modified after Anon 1974).

To a sample digest of extract (10 cm^3) was added 35 cm^3 1,5% ammonium molybdate solution followed by 5 cm^3 freshly prepared 0,12% stannous chloride solution (see Table 3.2.2 for the composition of both the latter). The resultant blue colour was read after 10-15 min. on a Bausch and Lomb Spectronic 20 spectrophotometer at 670 nm. The blank consisted of 10 cm^3 distilled water, and 35 cm^3 ammonium molybdate and 5 cm^3 dilute stannous chloride reagents. A typical standard curve of standard phosphorus solutions vs OD units using this method is shown in Fig. 3.1.

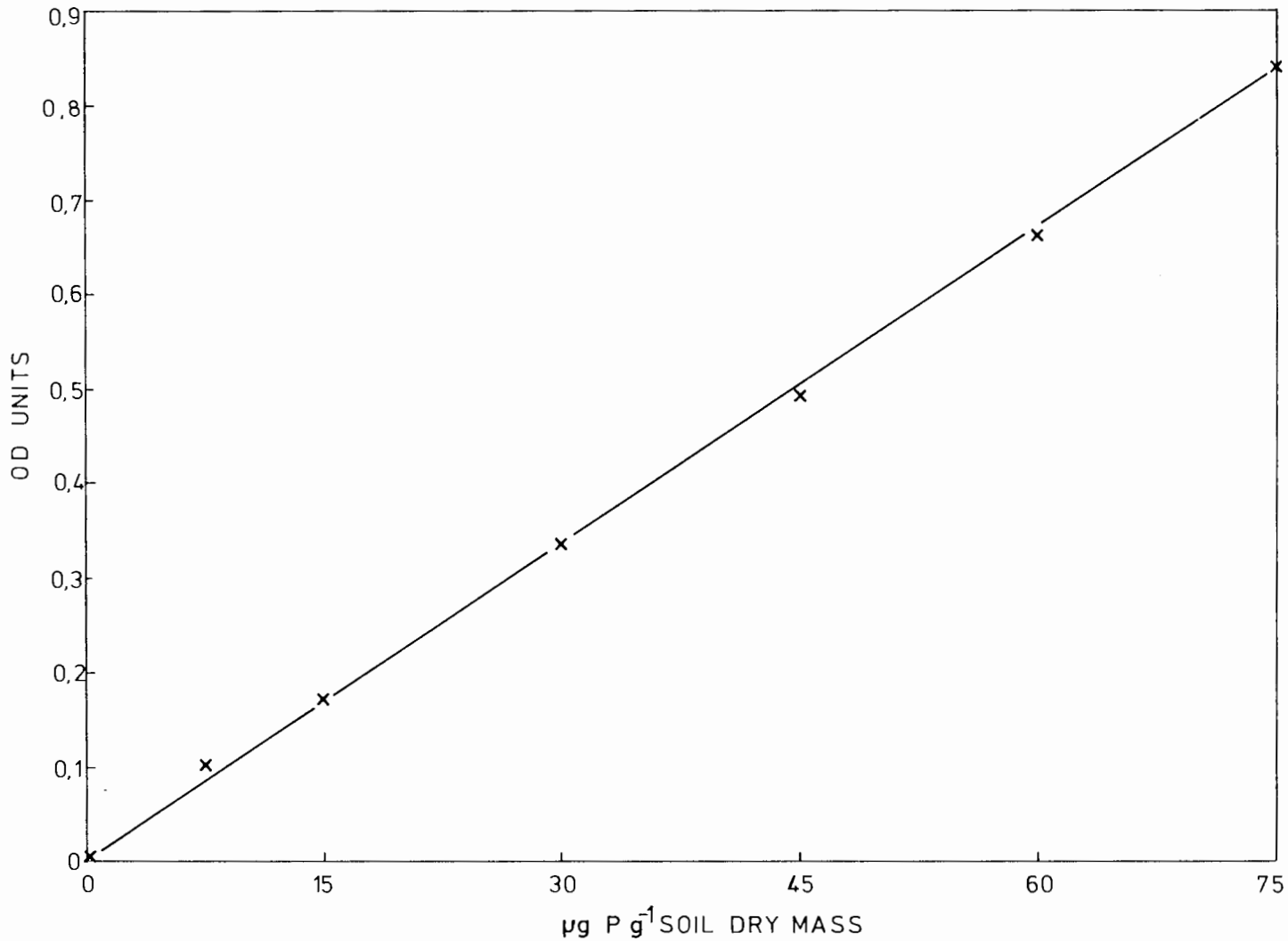


Fig. 3.1 Standard curve of phosphorus concentration vs OD used in the molybdenum blue method of assay. Readings along x - axis represent soil P levels (converted from concentration in extract) for the Bray no. 2 method. A fresh curve was prepared every approximately 100 samples.

TABLE 3.2.2 Composition of solutions for molybdenum blue P determination

Boric acid solution

400 g made up to 20 dm^3 with distilled water.

Ammonium molybdate solution

300 g made up to 7 dm^3 with distilled water.
Added to 31% HCl (7 dm^3) and made up to 20 dm^3 with distilled water.

Final solution for P determination prepared from 2 dm^3 boric acid, 2 dm^3 ammonium molybdate solution and 3 dm^3 distilled water.

Stannous chloride solution for P determination

Stock: $SnCl_2.2H_2O$ (20 g) dissolved in 50 cm^3 conc. HCl and stored in a fridge at 0^oC.

Diluted: Stock $SnCl_2$ (0,75 cm^3) diluted to 250 cm^3 with distilled water (active for 1h only).

PLANT ANALYSIS

Leaves or aphyllous photosynthetic stems (Elegia) from five dominant species (Table 3.3) in the three study sites were sampled on 4 November 1976, 3 February 1977, 7 May 1977 and 7 August 1977. Approx. 50 g fully expanded leaves (whole stems in Elegia) were randomly sampled from a minimum of six plants from each species. All material was dried for 24h at 80°C and then ground in a Wiley mill to pass through a 0,2 mm mesh sieve.

TABLE 3.3 Species sampled for analysis

Site	Community no.	Species	Family
1	1.1	Serruria vallaris Knight	Proteaceae
1	1.2	Leucospermum hypophyllocarpodendron Druce	Proteaceae
2	2.1	Erica clavisepala Guthrie & Bolus	Ericaceae
2	2.2	Elegia parviflora Kunth	Restionaceae
3	2.3	Simocheilus depressus (Lichenst.) Benth.	Ericaceae
3	2.4	Elegia parviflora Kunth	Restionaceae

Nitrogen

The same method for total nitrogen was used in the soils except that the sample size was 0,5 g and the digest (not filtered) was made up to 100 cm^3.

Phosphorus

Ground material (0,5 g) was digested in a 50 cm^3 pear-shaped flask using 10 cm^3 of a tri-acid mixture (10 conc. HNO_3 : 1 60% $HClO_4$: 4 conc. H_2SO_4). The heating procedure was similar to that used in the digestion of soil. When the digest had cleared, it was heated for a further 30 min., then filtered through a Whatman no. 41 filter paper and made up to 100 cm^3. Phosphorus levels were determined using the molybdenum blue method similar to that described for the assay of soil phosphorus, except that the blank and standard P solutions were made up to volume with dilute (10x) tri-acid mixture.

ROOTING SYSTEMS

The rooting systems of *Serruria* (Community 1:1), *Leucospermum* (1:2), *Erica* (2:1) and *Elegia* (2:2) were examined by excavating their respective rooting systems during December 1976, and subsequently diagrammatically recording their gross rooting morphologies.

Proteoid-type roots

Lateral rooting systems of *Serruria*, *Leucospermum*, *Erica*, *Simocheilus* and *Elegia* were excavated during December 1976 and presence or absence of proteoid root or proteoid root-like structures recorded.

Mycorrhiza

Terminal rootlets of all the species mentioned above were examined for endomycorrhizas using a modification of the technique of Phillips and Hayman (1970). Rootlets were heated at 90°C for approx. 5h in 10% KOH, and then washed in clean 10% KOH. This was followed by emersion for 30-120 min. in 2,5% H_2O_2 and then rinsing in tap

water. After acidification with 10% HCl rootlets were stained by simmering for 5 min. in 0,05% trypan blue in lactophenol. Excess stain was removed with clear lactophenol. Pieces of rootlet were mounted in lactophenol and examined for the presence of intracellular mycorrhizal hyphae. Photographs were taken of appropriate sections using a Zeiss photomicroscope Model 3 and Ilford FP4 125 ASA black and white film.

SOIL FUNGI

On 30 June 1977 a 450 mm soil profile was dug at the centre of each site. Soil was removed using sterile glass tubes (25 mm wide and 150 mm long) which were inserted horizontally at depths of 25, 110, 225 and 375 mm. These depths corresponded to the midpoints of the arbitrarily chosen depths: 0-50, 50-150, 150-300 and 300-450 mm. After removal, the tubes were immediately stoppered with cotton wool bungs and transferred to the laboratory. Within six hours of removal from the field, dilution (1 g in 1000 cm^3 sterile distilled water) and soil plates were prepared. The plating medium was Merck Czapek Dox agar to which had been added rose bengal (1:30 000) and streptomycin

(1:15 000) to prevent the growth of bacterial colonies. Molten agar (50°C) was poured into sterile petri dishes containing 1 cm^3 soil suspension in the dilution plate method or 0,05 - 0,15 mg soil in the soil plate method. Plates were triplicated at each soil depth. Both sets of petri dishes were incubated in the dark at 25°C and checked regularly for the appearance of colonies. Colonies were sub-cultured using either the droplet technique (Miss L Oliver pers. comm.) or re-plated onto Czapek Dox agar in petri dishes. Individual colonies were identified and numbers from each taxonomic entity were counted.

NITROGEN-FIXATION

Isolation of Azotobacteriaceae

An attempt was made to isolate *Azotobacter* and *Beijerickia* spp. from the soil and rhizospheres of selected plants in the three sites. Soil and root samples from each site and the major species in Table 3.3 were collected on 4 November and 11 November 1976 respectively. The latter were taken from various regions of the root system, including tap, laterals and

terminal rootlets. Aliquots of soil (0,5 - 1,0 g) from a 0-150 mm core or approx. 20 mm sections of root were placed in separate 100 cm^3 conical flasks each containing 20 cm^3 enrichment medium for Azotobacter or Beijerinckia (see Table 3.4 for composition of media) and stoppered with cotton wool bungs. The flasks were left indoors next to a sunny north-facing window, and regularly checked for any characteristic surface film which is produced by these bacteria.

TABLE 3.4 Enrichment media for the culturing of Azotobacter and Beijerinckia.

Azotobacter	Beijerinckia
2% mannitol	2% mannitol
2% $CaCO_3$	-
0,1% K_2HPO_4	0,1% K_2HPO_4
0,05% $MgSO_4$	0,05% $MgSO_4$

Both were made up in tap water and allowed to cool after autoclaving.

Determination of the nitrogen-fixation capacity of soils

Work by Schöllhorn and Burris (1966, 1967), and Dilworth (1966) led to the discovery that nitrogenase preparations preferentially reduced acetylene to ethylene, competitively inhibiting nitrogen-fixation. The requirements for acetylene reduction were similar to that of gaseous nitrogen reduction and in addition the ethylene was not reduced.

The acetylene reduction technique was developed by Hardy et al. (1968) for use in several biological systems and is more sensitive than the isotopic $^{15}N_2$ method. The main drawback however, is that the ratio of acetylene to nitrogen reduced varies: on average a factor of 3 is used when converting from moles acetylene reduced to moles nitrogen fixed. Various ratios have been provided by Brouzes and Knowles (1973). As the main purpose of this study was to determine whether or not a soil fixed gaseous nitrogen, no serious consideration was given to an accurate ratio.

The final methodology employed was based partly on that of Hardy et al. (1973) but chiefly on suggestions made by Drs J H Staphorst and B W Strijdom, Dept Agricultural Technical Services, Pretoria. Intrinsically it involved the incubation of a given sample in a 10% acetylene, 90% air atmosphere, and the subsequent determination of ethylene produced from acetylene reduction. Initially 10 cm^3 rubber-stoppered glass tubes or 30 cm^3 McCartney bottles (with rubber septa and holes drilled in the tops) were used for incubating experimental material. A small amount of the latter was placed in either container, air withdrawn to 0,9 atm. with a syringe and 0,1 atm. acetylene added. The acetylene was first passed through four traps containing water, Brady's reagent, sulphuric acid and $CaCl_2$ respectively, so as to remove traces of acetone, PH_3, H_2S and other impurities. Acetylene was stored at 1 atm. in a rubber bladder, thus facilitating the addition of known pressures of the gas. The tubes and bottles were left for various lengths of time at room temperature. After the required period had elapsed, 0,5 or 1,0 cm^3 aliquots were removed and injected into a Pye (Unicam) Series 104 gas-liquid chromatograph, with a 2,8 m length, 4 mm

diameter glass column packed with "Porapak R". The carrier gas was nitrogen with a flow rate of 25 cm^3 min^{-1}. Oven and detector temperatures were set at 50°C and 100°C respectively. Attenuation was set at $8x10^3$ for ethylene and $8x10^3$ to $128x10^3$ for acetylene, with the former peak having a retention time of approx. 6 min. and the latter approx. 8 min. Acetylene and ethylene peaks were recorded on a Philips PM 8000 recorder run at a speed of 5 mm min^{-1}.

The method was initially assessed and refined by testing materials from various local biological sources including soil, roots and root nodules. Nitrogen-fixation determinations in the study sites were however concentrated on the soils as nodulated plants were not a dominant component of the plant communities (see Table 4.1a in Chapter 4). Preliminary studies described in Chapter 9 indicated that larger volumes of material in Consul jars had to be used. Glass Consul jars of approx. 1200 cm^3 capacity were fitted with special lids which allowed for the removal and injection of gases (Fig. 3.2). Allowing for the volume of a 0-150 mm soil core in the Consul jar,

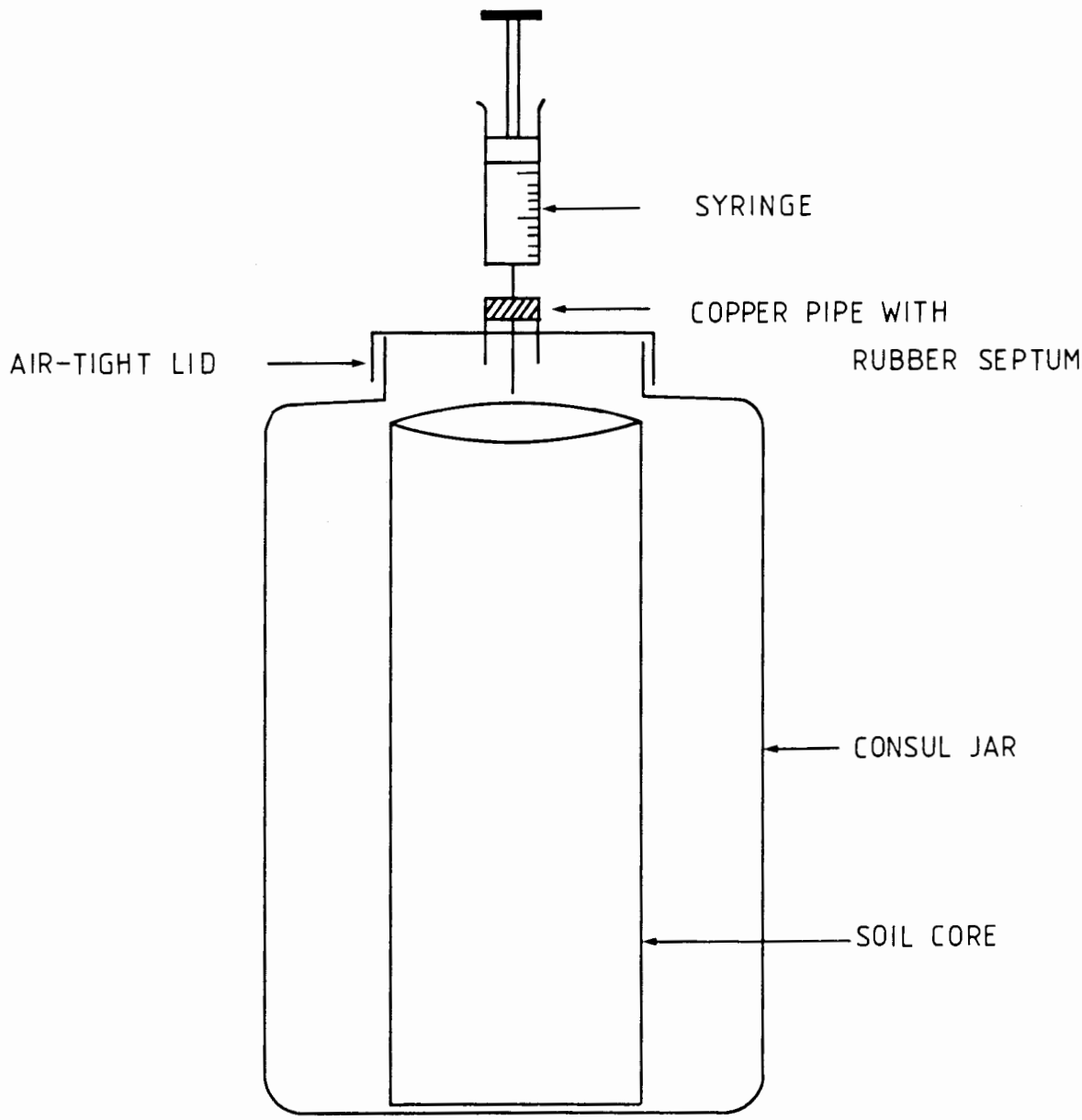


Fig. 3.2 Diagram of Consul jar system used for incubation of soil cores in a 0,1 atmosphere acetylene atmosphere.

extracting 80 cm^3 of air and replacing with 80 cm^3 1 atm. acetylene provided an atmosphere in the jar of about 0,1 atm. acetylene. In addition stainless steel soil cores (72 mm internal diam. x 150 mm length) were constructed which just fitted into the jars so facilitating easy collection and incubation of selected soils. A standard curve for peak height vs cm^3 ethylene was prepared. 0,1; 0,25; 0,5; 0,75 and 1,00 cm^3 aliquots (triplicated) of 0,2 atm. ethylene/0,2 atm. acetylene were analyzed (Table 3.5). A standard curve of peak height vs µmol 0,2 atm. ethylene was then prepared (Fig. 3.3) which gave a linear relationship of $y = 1,940 + 19,506x$ (s.e. = 2,298); $x = -0,091 + 0,051\ y$ (s.e. = 0,118) and a correlation coefficient of 0,998 ($p = 0,01$) for 0,10; 0,25 and 0,50 cm^3 ethylene.

TABLE 3.5 Standard 0,2 atm. ethylene volumes and corresponding peak heightsafter analysis.

0,2 atm. ethylene		mean
cm^3	µmol	peak height (mm)
0,10	0,83	19
0,25	2,08	45
0,50	4,16	82
0,75	6,24	113
1,00	8,32	132

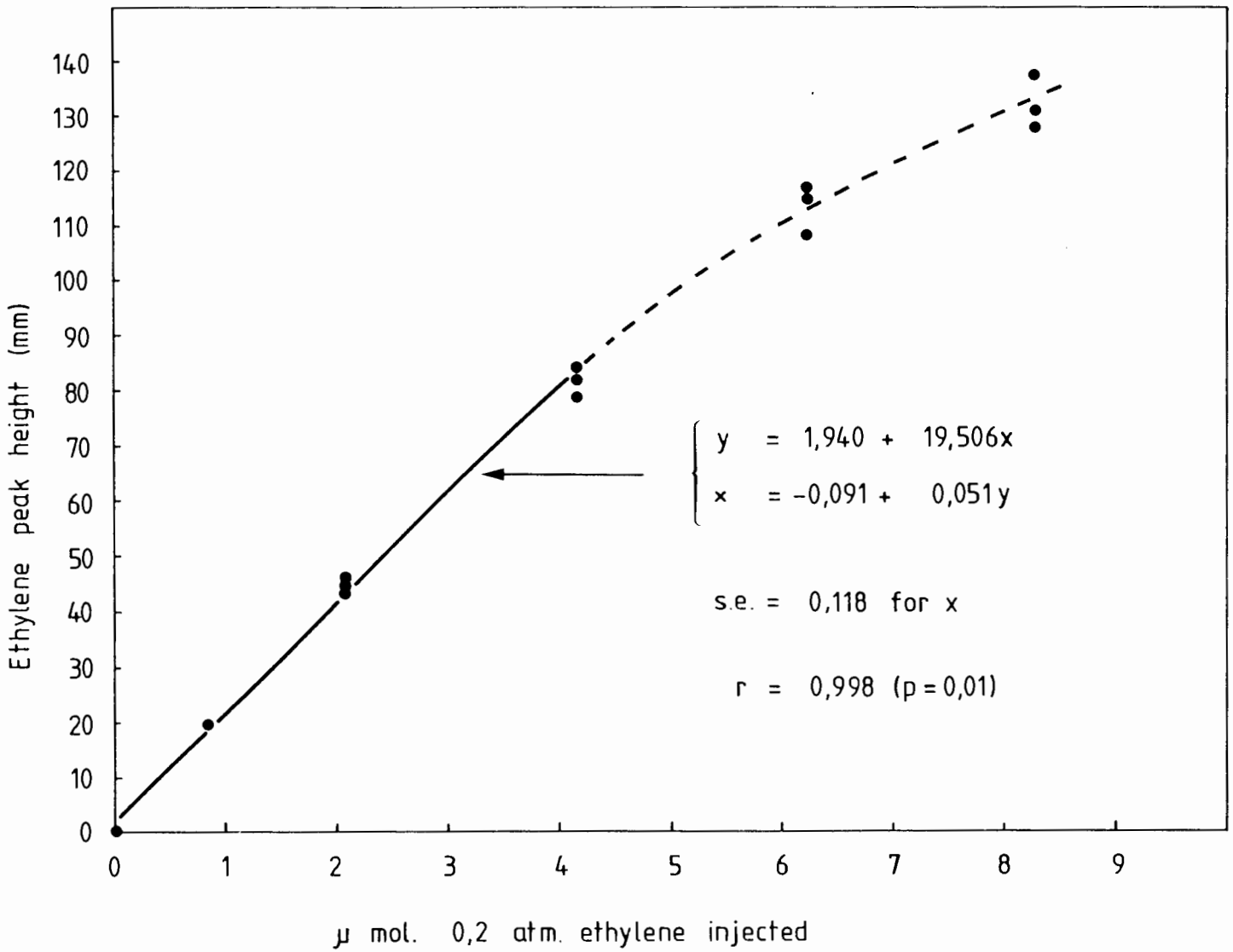


Fig. 3.3 Standard curve of 0,2 atmosphere ethylene **vs** peak height.

CHAPTER 4

VEGETATION AND PHYTOMASS

DESCRIPTION OF MAJOR PLANT COMMUNITIES

Following a Braun-Blanquet phytosociological analysis of the vegetation at the three sites (Chapter 3) the following major communities (Table 4.1a) were derived. Minor or tail species appear in Table 4.1b. A list of species names and authors used below, appears in Table B.1 in Appendix B.

Site 1

1. *Metalasia brevifolia* community (see Plate 2.1)

1.1 *Metalasia brevifolia* - *Leucospermum hypophyllocarpodendron* community

1.2 *Metalasia brevifolia* - *Serruria vallaris* community (see Plate 2.2)

TABLE 4.1a

Phytosociological table of major species occurring in the three sites. Soil data presented as mean of four seasons (Spring 1976 to Winter 1977). Cover-abundance values as follows: r = one or two individuals with negligible cover; + = <1% cover, individuals sparsely present; 1 = 1-5% cover, individuals few or plenty; 2a = 6-12% cover, individuals very numerous; 2b = 13-25% cover, individuals very numerous; 3 = 26-50% cover, any number of individuals; 4 = 51-75% cover, any number of individuals; 5 = 76-100% cover, any number of individuals.

Site number	1								2								3					
Community number	1.1				1.2				2.1				2.2				2.3			2.4		
Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Species per relevé	14	16	19	3	19	15	15	10	6	5	4	6	7	7	8	6	10	9	11	11	9	12
Soil (0-15 cm)																						
Moisture (kg ha^{-1})	106000				115000				341000				255000				162000			176000		
pH	4,31				4,33				3,41				3,46				3,65			3,59		
Organic matter (kg ha^{-1})	94000				106000				71000				50000				39000			47000		
Total nitrogen (kg ha^{-1})	1843				1940				1004				759				529			640		
Total phosphorus (kg ha^{-1})	55,5				46,8				37,1				26,7				18,2			18,6		
Bray no. 2 phosphorus (kg ha^{-1})	7,8				6,2				5,5				5,0				3,0			4,0		
Phytomass (kg ha^{-1})																						
Above-ground, live	8254				9674				4363				3868				3344			2970		
Above-ground, dead	3400				1740				6883				6173				2150			4220		
Ruschia sarmentosa	+	+	+	+																		
Tetraria sylvatica	+	+	+	+																		
Pentaschistis curvifolia	+	r	+	+																		
Ficinia deusta	+	+	+																			
Petalacte coronata	+		+																			
Staavia radiata					1	+	+															
Aspalathus capensis					+	1	+															
Carpobrothus acinaciformis					+	+	+															
Hypodiscus willdenowianus					+			1														
Erica cerinthoides					+	1																
Ehrharta calycina					r	1																
Aristea glauca	r				+	+																
Leptocarpus gracilis						+	+															
Stylapterus fruticosus							+	+														
Anaxeton asperum							+	+														
Restio cuspidatus	+	r	+				+															
Cullumia setosa		r	+			+																
Pseudopentameris macrantha			+				+															
Lampranthus falcatus			r		r			+														
Ficinia secunda		+			+																	
Agathosma imbricata	+	+	+		+	1																
Serruria vallaris		+		+	2a	2a	2b	1														
Phylica stipularis	+	1	+		+		+	+														
Leucospermum hypophyllocarpodendron	1	1	2a	1	1		1	+														
Thamnochortus fruticosus	+	+	+	+	+	+	+															
Phillipia chamissomis	+	+	r	+	1	1																
Metalasia brevifolia	2b	2b	2b	2a	2b	1	2a	2a														
Berzelia intermedia													1	+	+	1						
Erica glliva														+	+	+						
Scyphogyne mucosa													+			+						
Erica corifolia														+	+							
Erica imbricata																	+	+	+	+	1	+
Thamnochortus gracilis																	+	+	+	+	+	+
Erica pulchella																	+		+	1	2a	1
Erica coarctata																	+	+	+	1		+
Staberoha cernua																	+	+	+	+	+	
Struthiola ciliata																	+	+			+	
Stilbe ericoides																		+				+
Elegia stipularis																			+		+	
Erica articularis																			+	+		
Hypodiscus aristatus																					+	+
Simocheilus depressus													1	1	2a	1	2a	2a	2b	2a		1
Elegia parviflora									2b	1	1	2a	3	3	3	2b	+	1	+	2a	2b	2b
Chondropetalum nudum									+	1	1	+	+		+		+	1	1			+
Restio bifurcus									+		+	r		+	+	+				+	+	+
Restio quinquefarius									+				+	+								+
Erica clavisepala									2b	3	3	3	+		+							
Metalasia muricata		2a			+	+	+	+	+	2a		+										

TABLE 4.1b Minor species occurring in the three Sites. Braun Blanquet cover abundance values as per Table 4.1a.

Community number	1.1				1.2				2.1				2.2				2.3			2.4		
Relevé numbers	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Passerina vulgaris		+																				
Asparagus rubicundus			+																			
Chironia linoides			r																			
Rhus laevigata			+																			
? Amphithalea ericifolia			+																			
Anaxeton laeve					+																	
Diosma oppositifolia					+																	
Pelargoniun sp.						+																
Selago scabrida						r																
Anthospermum sp.							+															
Aspalathus hispida/ericifolia							r															
Helichrysum vestitum								+														
Phylica imberbis								+														
Chondropetalum tectorum										+												
Erica laeta												r										
Disparago lasiocarpa																	+					
Thamnochortus obtusus																			+			
Struthiola ? dodecandra																				+		

These communities comprised elements which typified the mixed fynbos of Taylor (1969), containing ericoid-leaved, proteoid and restioid components. Phylica stipularis, Thamnochortus fruticosus and Phillipia chamissomis were common in both communities. Differential species in 1.1 included Ruschia sarmentosa, a succulent, and the grass, Pentaschistis curvifolia, and in 1.2, Staavia radiata, Asparagus capensis and Carpobrotus acinaciformis. The vegetation in this site had been burnt in about 1972/1973 (G. Wright pers. comm.) but no fire records were available.

Sites 2 and 3

2. Elegia parviflora community (see Plates 2.4 and 2.7)

2.1 Elegia parviflora - Chondropetalum nudum - Erica clavisepala community (see Plate 2.5)

2.2 Elegia parviflora - Berzelia intermedia - Simocheilus depressus community

2.3 Elegia parviflora - Chondropetalum nudum - Simocheilus depressus community

2.4 *Elegia parviflora* - *Erica pulchella* - *Simocheilus depressus* community (see Plate 2.8)

Communities 2.1 and 2.2 were found at Site 2, and 2.3 and 2.4 at Site 3. Although both ericoid-leaved and hemicryptophytic restioid elements dominated both sites a distinction (based on cover) between predominantly ericoid (2.1 and 2.3) and predominantly restioid (2.2 and 2.4) was recognized.

The vegetation in Sites 2 and 3 appears to be a climax form of fynbos found in seasonally wet to waterlogged habitats and compares with those described in Taylor (1978) and Low (1981).

It is clear that the vegetation of Site 1 differs from that in Site 2 and 3, the former essentially typical early post-fire succession mixed fynbos, and being found on a seasonally moist, well-drained soil. Sites 2 and 3 on the other hand represent a more extreme situation with very wet conditions prevailing during the winter months (see Figs. 5.1(b) and 5.1(c) in Chapter 5). Despite overall comparable heights and

lack of stratification, community structure in Site 1 was more complex than in the other two sites. This is borne out by the greater diversity in leaf morphology (broad- and dissected leaf forms of the Proteaceae, various ericoid-type leaves and succulence) and the low importance of the Restionaceae. In addition species richness was higher in Site 1 (14,5 species per 25 m^2 relevé) as opposed to Sites 2 (6,1) and 3 (10,3).

PHYTOMASS OF THE DIFFERENT COMMUNITIES

Dry above-ground masses (g m^{-2}) of the different growth forms and fractions from the various communities appear in Table 4.2. Histograms depicting the relationships between live, dead-standing and the litter components appear in Fig. 4.1.

It is apparent that Communities 1.1 and 1.2 (Site 1) displayed the greatest live above-ground phytomass (825,4 and 967,4 g m^{-2} respectively) with nanophanerophytes (on average 300-600 mm tall) dominating (87,7 and

TABLE 4.2 Phytomass of above-ground live, dead standing and litter material from Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Amounts in g m^{-2}.

	Nanophanerophytes		Restionaceae		Poaceae		Other		Litter		Total	
Community	L	D	L	D	L	D	L	D			Live	Dead
1:1	724,7 * (333,3)	- **	51,7 (26,4)	22,7 (14,6)	19,6 (13,8)	25,0 (14,4)	29,4 *** (61,4)	-	292,3 (77,7)		825,4	340,0
1:2	902,8 (299,3)	1,2 (1,5)	45,0 (27,7)	10,4 (6,8)	1,4 (0,4)	2,0 (1,5)	19,9 (27,2)	0,2 (0,5)	160,4 (49,1)		967,4	174,2
2:1	387,2 (150,7)	110,0 (71,5)	58,1 (57,9)	171,3 (115,4)	-	-	-	-	407,0 (70,3)		436,3	688,3
2:2	49,3 (30,6)	56,0 (59,0)	335,9 (103,9)	314,6 (128,2)	-	-	2,1 (1,3)	-	246,7 (20,4)		386,8	617,3
3:1	243,7 (79,0)	18,5 (14,9)	90,2 (25,7)	85,9 (44,9)	-	-	0,5 (0,5)	0,1 (0,2)	110,5 (33,6)		334,4	215,0
3:2	78,7 (31,5)	18,0 (12,2)	217,4 (44,6)	247,3 (70,1)	-	-	0,9 (1,0)	2,1 (3,5)	154,6 (57,7)		297,0	422,0

* Mean; standard deviation in parentheses (n = 5 in 1:1 and 1:2; n = 4 in 2:1, 2:2, 2:3 and 2:4)
** Fraction not present
*** Chiefly leaf succulents

L = live
D = dead-standing

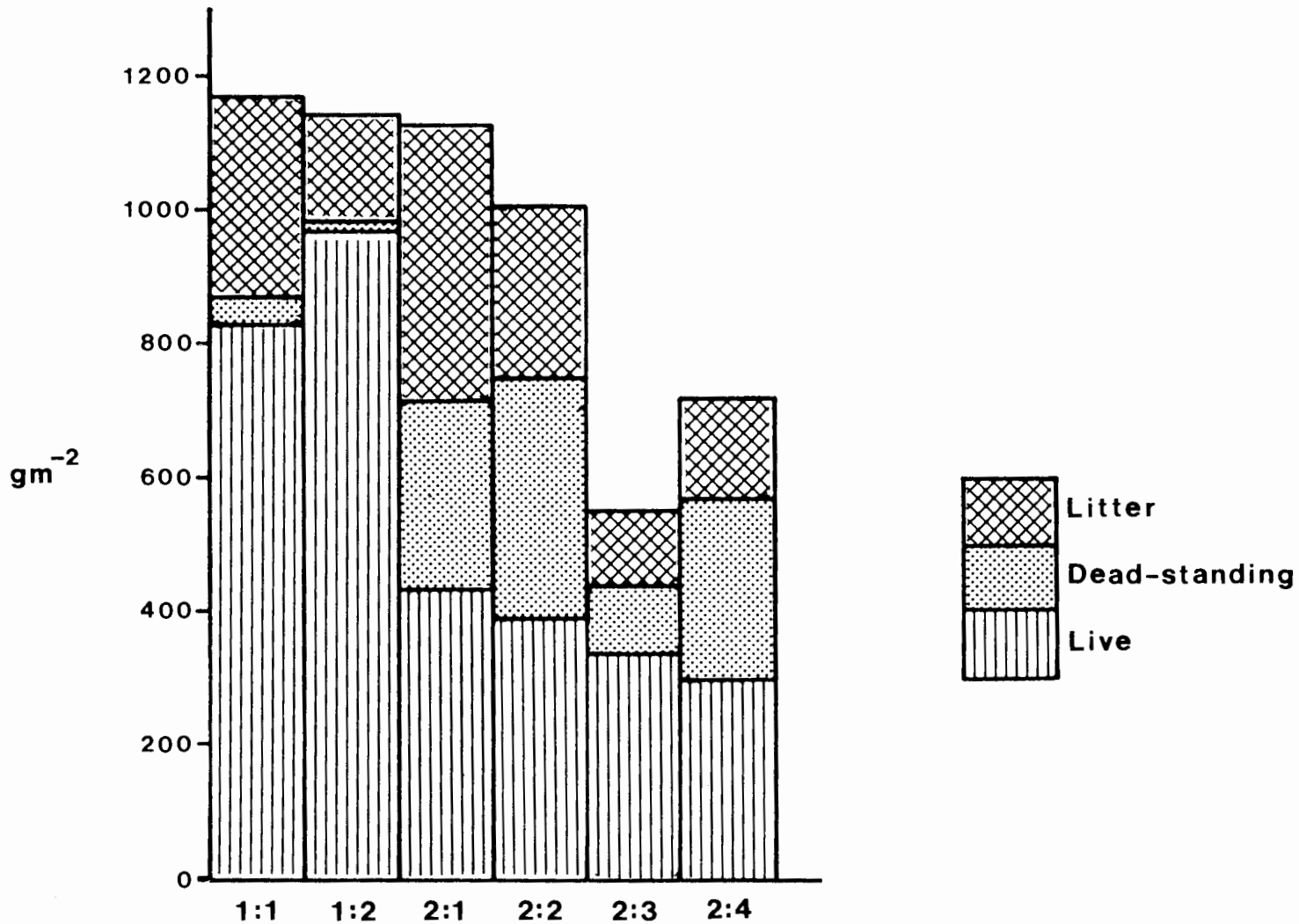


Fig. 4.1 Phytomass of live, dead - standing and litter components at Sites I, (dry), 2 and 3 (both wet). Plant community numbers appear at the base of each column (Site 1 = 1:1 and 1:2; Site 2 = 2:1 and 2:2; Site 3 = 2:3 and 2:4).

93,3% respectively). Communities 2.1 and 2.3 (Sites 2 and 3) whilst possessing a high proportion of nanophanerophytes (350-450 mm) (87,8 and 72,9% respectively) also had a greater restionaceous mass (13,3 and 27,0%) as opposed to Site 1. As is reflected in their cover abundance values in Table 4.1a, live Restionaceae (400-500 mm) dominated in Communities 2.2 and 2.4 (Sites 2 and 3) (86,8 and 73,2% respectively). Total live mass was lower in Sites 2 and 3 by a factor of two to three when compared with that of Site 1.

The quantity of litter was similar in Sites 1 and 2 but lowest in Site 3. The least dead-standing material was found in Site 1. In addition the dead-standing fraction comprised a larger proportion in Sites 2 and 3 relative to the litter mass.

Comparison with western Cape fynbos and other heathlands of the world

Kruger (1977) found amounts of 606,5 to 922,6 g m^{-2} aerial phytomass for 4,0 to 4,3 yr old mountain fynbos in the Jonkershoek, Zachariashoek and Jakkalsrivier

catchment areas. Van Wilgen (1982) recorded live aerial phytomass of 660 and 590 g m^{-2} for two 4 yr old mountain fynbos sites at Jonkershoek. Figures from both these sources compare with those obtained in Site 1 (724,4 and 902,8 g m^{-2}) allowing for the extra year in age. Litter totals (including dead-standing material) were on the other hand lower in Kruger's (1977) (trace amounts) and Van Wilgen's (1982) (53 and 33 g m^{-2}) sites. However litter masses from two of Kruger's (1977) approx. 6 yr old mountain fynbos communities (495,0 and 238,5 g m^{-2}) compare with those from Site 1 (340,0 and 174,2 g m^{-2}) in this study. Kruger's (1977) and Van Wilgen's (1982) work also reported far higher percentages of restionaceous and graminoid components (52-78%) than those from Site 1 (9 and 5%). 3,5 and 6 yr post-fire coastal fynbos near Mamre and Kraaifontein displayed above-ground phytomass levels of 174 and 513 (live), and 77 and 99 (dead) g m^{-2} respectively (Low unpub. data). Live mass was lower than mountain fynbos here or recorded elsewhere. Litter was also far lower than that recorded in Site 1.

There are no published aerial phytomass accounts of seasonally wet to waterlogged climax fynbos sites. Low (unpub. data) has however recorded some 354 (live) and 497 (dead) g m^{-2} for a restioid community growing on a seasonally wet sandy plain in the Winterhoek valley east of Porterville. These figures compare favourably with Communities 2.1 to 2.4 which displayed above-ground phytomass of 297,0 to 436,3 (live) and 215,0 to 617,0 (dead) g m^{-2}.

Live aerial mass of 5 yr Calluna heath in NE England was 1268 g m^{-2} (litter = 536,7 g m^{-2}) (Robertson and Davies 1965), 300-400 g m^{-2} higher than that of Site 1. However data from 6 yr old Calluna stands in NE Scotland (836,0 - Miller, in Gimingham, 1972), NE England (600,0 - Bellamy and Holland 1966) and SE England (723,0 - Chapman, in Gimingham 1972 and 361,6 g m^{-2} - Chapman 1967) were similar to those obtained here, despite dissimilarities in climate (colder and wetter) and lack of hemicryptophytes.

In Australia, 5 yr old sand heath at Keith gave a low mass of approx. 350 g m^{-2} whereas wet heath at Tidal River, Barry's Creek and Toolara displayed levels of approx. 650, 900 and 550 g m^{-2} respectively (Groves and Specht 1965). A sand heath at Frankston gave a figure of approx. 800 g m^{-2} (Jones, 1968). The wet Australian heath masses were also comparable with Site 1 in the Cape of Good Hope Nature Reserve.

In summary, aerial phytomass data from Site 1 on the whole displayed broad similarity with British Calluna, Australian as well as Cape mountain fynbos heaths, although there was some disparity in amounts of litter. The wetter Sites 2 and 3 showed similar masses to those occurring in a seasonally wet restioid plain elsewhere in mountain fynbos. Wet heath masses in Australia were however higher than these sites, chiefly due to the presence of a prominent shrub component.

CHAPTER 5

SOIL ANALYSES

The results presented in this chapter are from the analyses described in Chapter 3.

Bulk density

Bulk density values at the three sites appear in Table 5.1 Inter-site differences in bulk density were insignificant, although there were minor increases with soil depth. Seasonal variations were also negligible.

Moisture content

Seasonal variations in moisture content occurred at Sites 2 and 3 but were not marked in Site 1 (Fig. 5.1(a) - (c) and Table C.1 in Appendix C). Highest levels (0-150 mm) were recorded during the winter months at Sites 2 and 3, with values of 53,0 and 47,1x10^4 kg ha^{-1} respectively. With

TABLE 5.1 Bulk density (g cm^{-3}) of soils occurring at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Data recorded seasonally, between winter 1976 and winter 1977.

Community no.	Depth (mm)	Winter (1976)	Spring	Summer (1977)	Autumn	Winter
	0-150	1,31	1,33	1,29	1,29	1,24
1:1	150-300	1,43	1,39	1,37	1,38	1,40
	300-450	1,54	1,46	1,44	1,49	1,50
	0-150	1,23	1,23	1,22	1,22	1,18
1:2	150-300	1,28	1,32	1,34	1,33	1,44
	300-450	1,46	1,39	1,36	1,43	1,48
	0-150	1,25	1,20	1,27	1,26	1,27
2:1	150-300	1,41	1,39	1,41	1,45	1,44
	300-450	1,50	1,51	1,51	1,49	1,48
	0-150	1,28	1,34	1,31	1,28	1,28
2:2	150-300	1,40	1,42	1,44	1,46	1,44
	300-450	1,43	1,49	1,48	1,50	1,51
	0-150	1,39	1,39	1,41	1,39	1,41
2:3	150-300	1,46	1,43	1,44	1,48	1,43
	300-450	1,52	1,49	1,47	1,49	1,52
	0-150	1,36	1,37	1,38	1,28	1,36
2:4	150-300	1,45	1,41	1,46	1,41	1,41
	300-450	1,50	1,45	1,47	1,47	1,53

* Refer to Chapter 2 for a description of the three sites.

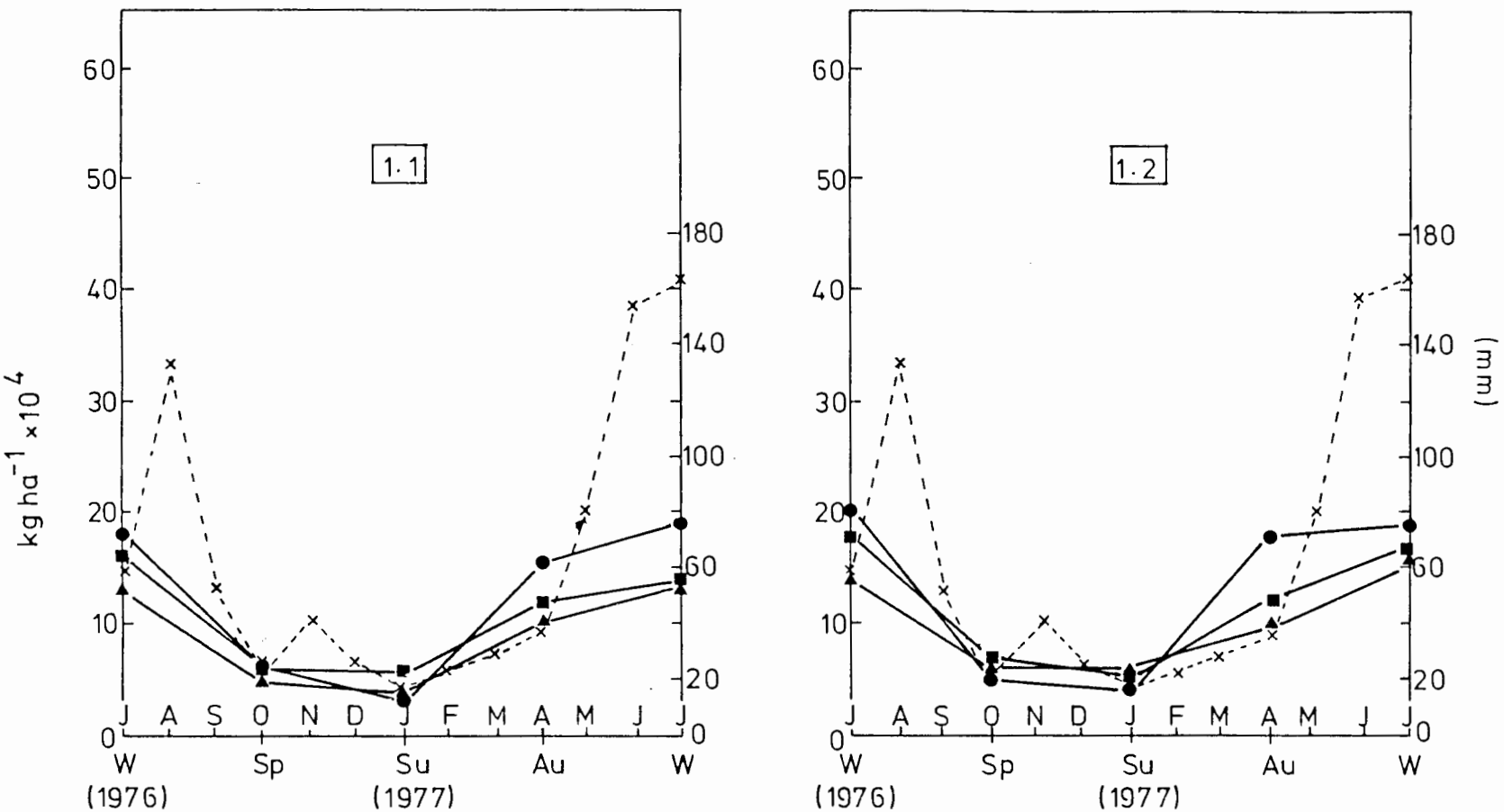


Fig. 5.1 (a) Moisture content (kg ha $^{-1}$ × 10^4) of soils at Site 1 (Communities 1:1 and 1:2). Seasonal variation (winter 1976 to winter 1977) at 0—150 (●——●), 150—300 (■——■) and 300—450 (▲——▲)mm. (×——×) indicates rainfall.

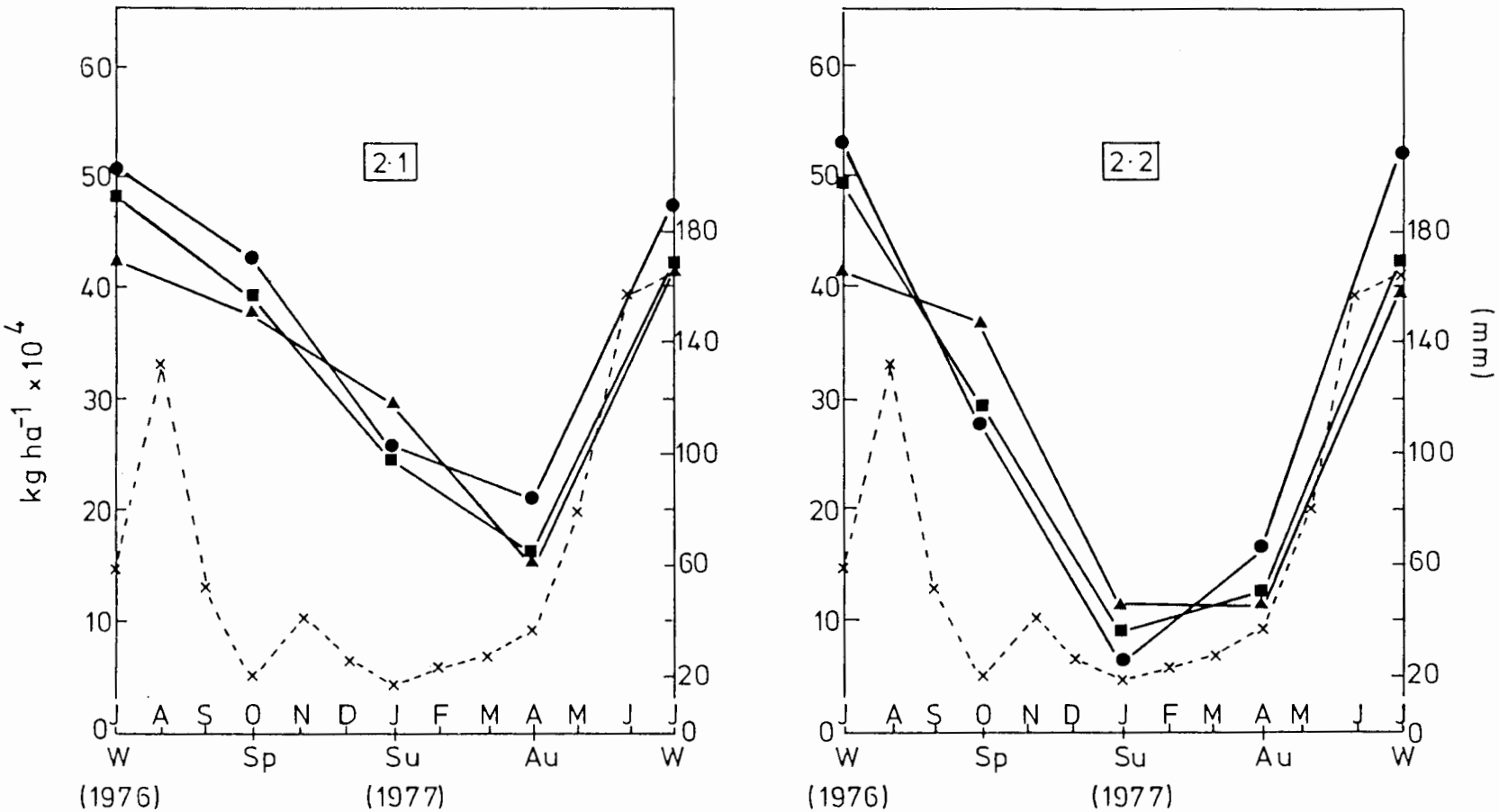


Fig. 5.1 (b) Moisture content (kg ha $^{-1} \times 10^4$) of soils at Site 2 (Communities 2:1 and 2:2). Seasonal variation (winter 1976 to winter 1977) at 0—150 (●——●), 150—300 (■——■) and 300—450 (▲——▲) mm. (×——×) indicates rainfall.

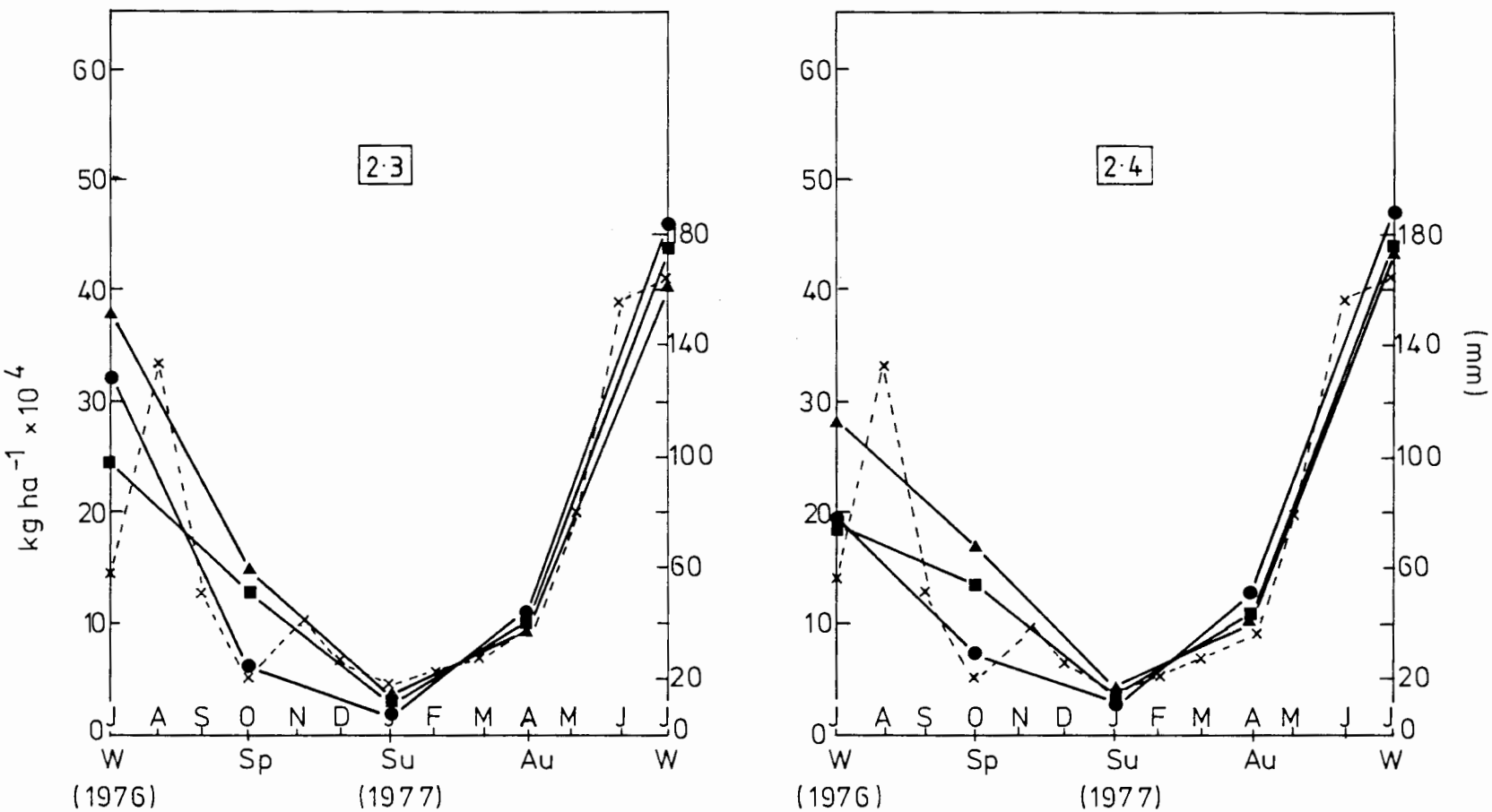


Fig. 5.1 (c) Moisture content (kg ha $^{-1}$ × 10^4) of soils at Site 3 (Communities 2:3 and 2:4). Seasonal variation (winter 1976 to winter 1977) at 0—150 (●——●), 150—300 (■——■) and 300—450 (▲——▲) mm. (×——×) indicates rainfall.

few exceptions, moisture content decreased with soil depth throughout the year, seasonal changes being correlated with variation in rainfall.

Amounts for all horizons varied from 3,3 to 20,1x10^4 kg ha^{-1} in Site 1, 6,1 to 53,0x10^4 kg ha^{-1} in Site 2 and 1,9 to 47,1x10^4 kg ha^{-1} in Site 3. All lowest levels were recorded in summer and the highest in winter.

pH

pH values of the soils at the three sites were all found to be acidic, ranging from 3,67 to 4,55 at Site 1, 3,34 to 3,76 at Site 2 and 3,51 to 4,14 at Site 3. (see Table C.2 in Appendix C). There was a decrease in pH with soil depth at Site 1, whereas at Sites 2 and 3 increases occurred down the soil profiles. Little seasonal variation was displayed: at Site 1 there was a detectable rise during summer while soil pH values at Site 3 declined slightly during the period of study, from winter, 1976 to winter, 1977 (Fig. 5.2).

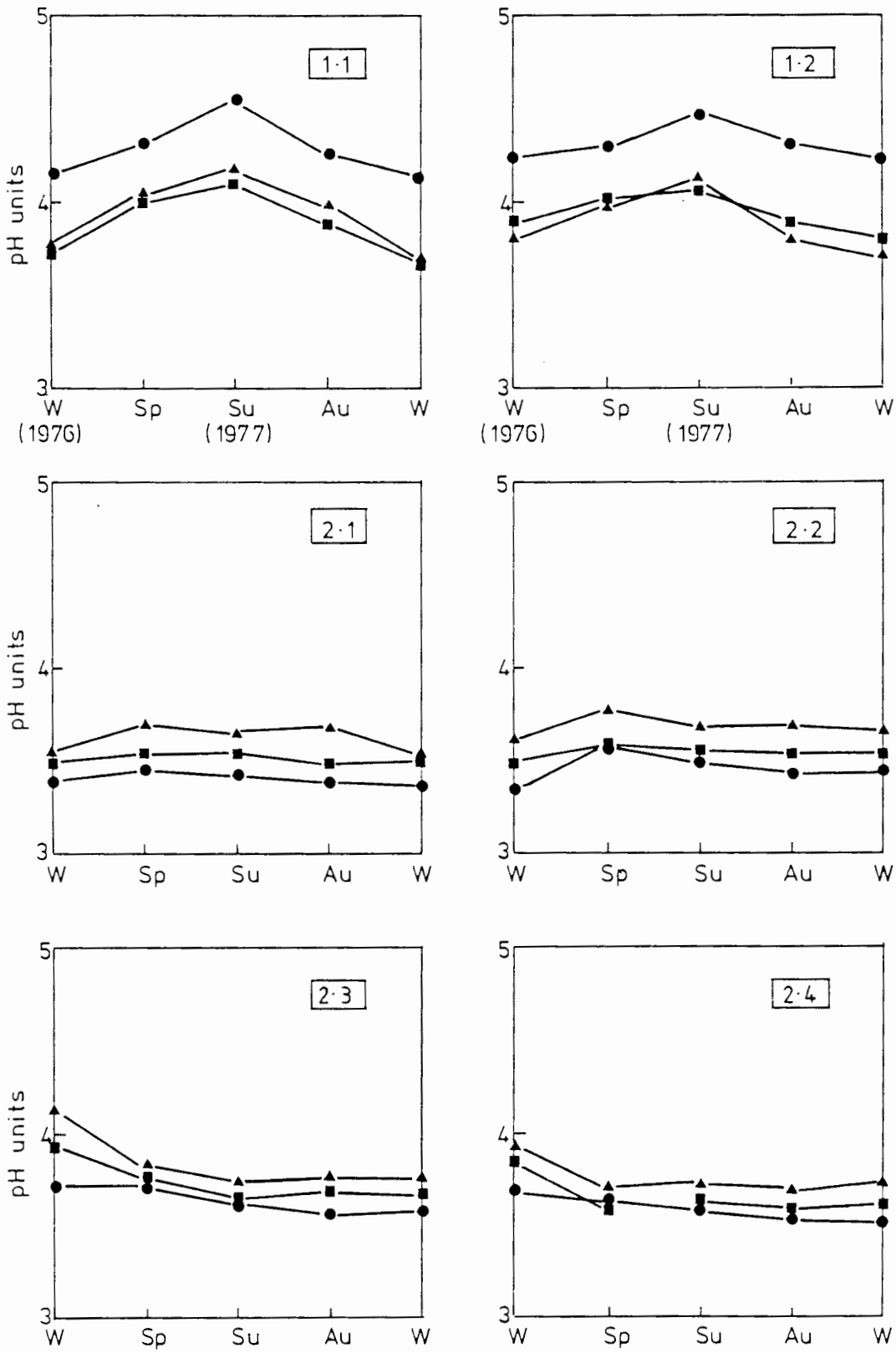


Fig. 5.2 pH of soils at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Seasonal variation (winter 1976 to winter 1977) at 0—150 (●——●), 150—300 (■——■) and 300—450 (▲——▲) mm.

Organic matter

Amounts recorded for all horizons were in the order of 2,8 to 10,9x10^4 kg ha^{-1} (Site 1) which were higher than those for Site 2 (0,7 to 8,3x10^4 kg ha^{-1}) and Site 3 (0,2 to 5,3x10^4 kg ha^{-1}) (see Table C.3 in Appendix C). In all sites, organic matter decreased with soil depth (Fig. 5.3). Seasonal variation was most apparent in the lower horizons of Site 1 where a summer maximum was observed. Site 2, in particular Community 2.1, showed a gradual decrease from winter, 1976 to winter, 1977 (Fig. 5.3).

Total nitrogen

Total nitrogen contents appear in Table C.4 in Appendix C. Levels of nitrogen were highest in Site 1 (492 to 2371 kg ha^{-1}) with Site 2 having amounts of 161 to 1107 kg ha^{-1} and Site 3, 183 to 722 kg ha^{-1}. A decrease in nitrogen was found down each profile and was most marked in Site 1 (Fig. 5.4). Apart from 150-450 mm in Community 1.1 and all depths in Community 1.2, little seasonal trends in nitrogen variation were apparent (Fig. 5.4).

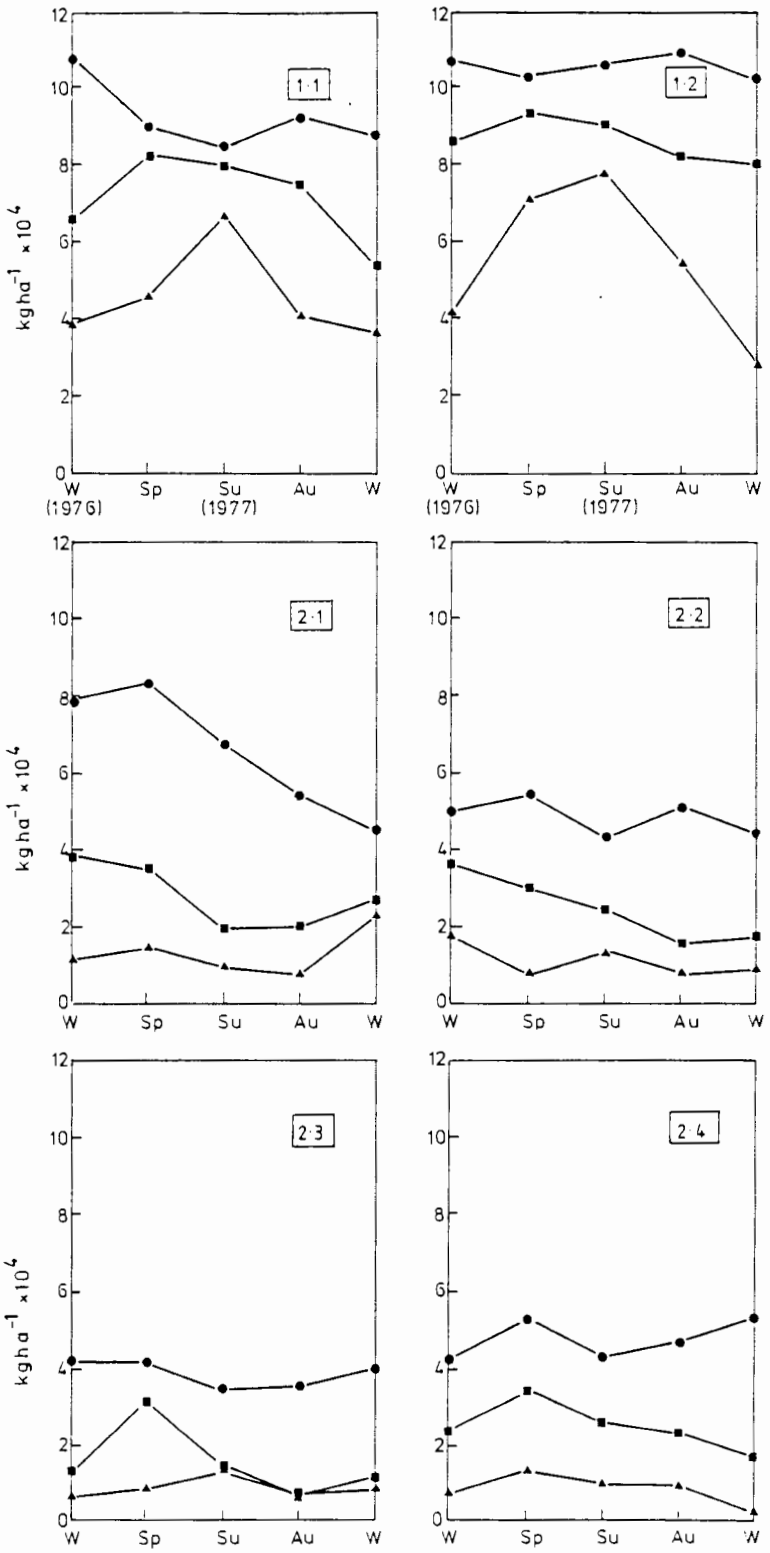


Fig. 5.3 Organic matter content (kg ha $^{-1}$ × 10^4) of soils at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Seasonal variation (winter 1976 to winter 1977) at 0—150 (●—●), 150—300 (■—■) and 300-450 (▲—▲) mm.

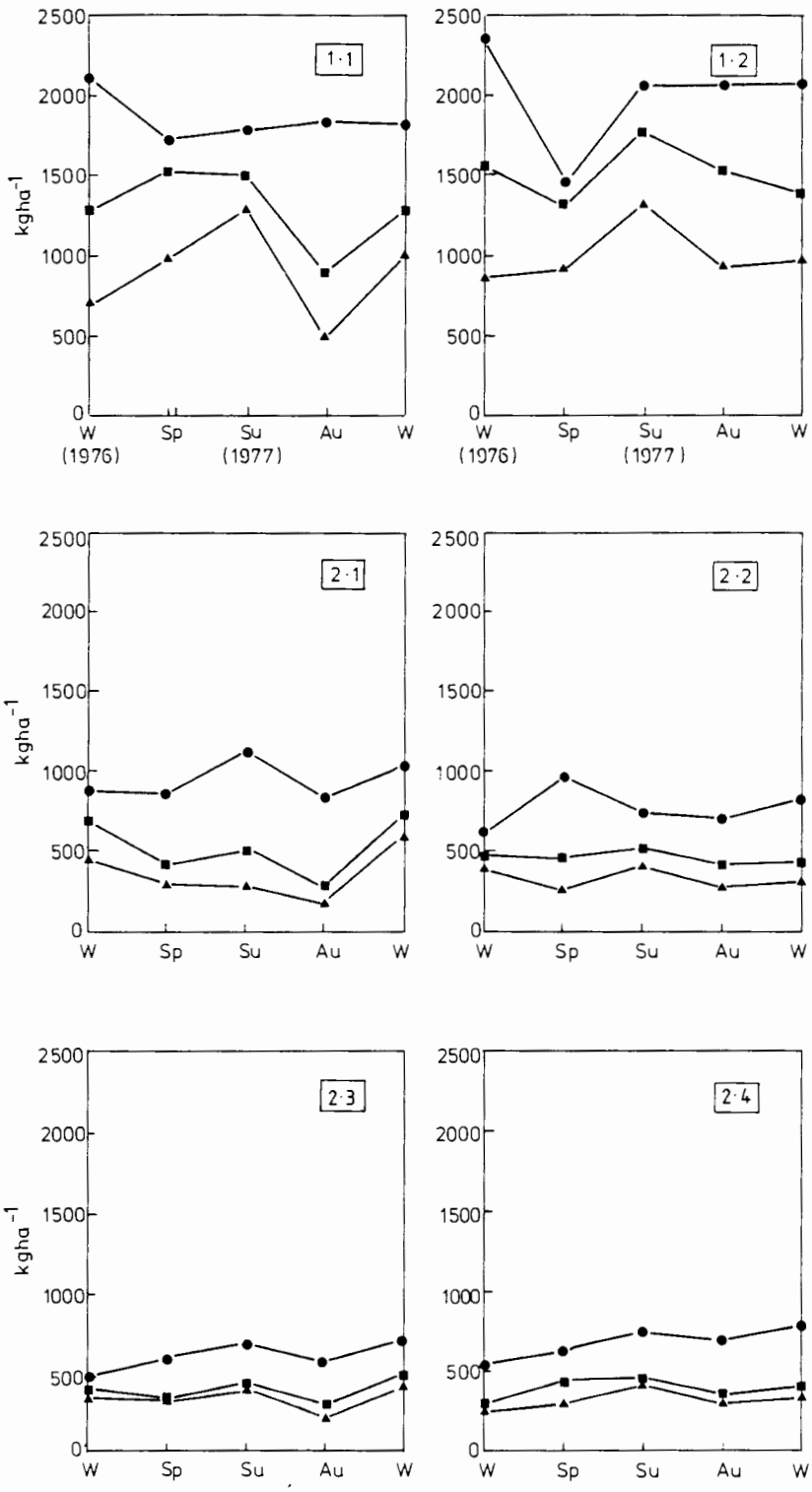


Fig. 5.4 Total nitrogen content (kg ha $^{-1}$) of soils at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Seasonal variation (winter 1976 to winter 1977) at 0—150 (●—●), 150—300 (■—■) and 300—450 (▲—▲) mm.

C/N ratio

$^{C}/_{N}$ values (see Table C.5 in Appendix C) were highest in Site 2 (29,8 to 44,3) followed by Site 3 (29,0 to 37,0) and Site 1 (24,1 to 29,3) (Fig. 5.5). There were indications of seasonal fluctuations in Sites 2 and 3 (Fig. 5.5).

Total phosphorus

Highest amounts of total phosphorus occurred in the soil at Site 1 (18,20 to 58,11 kg ha^{-1}) with levels of 6,36 to 47,85 kg ha^{-1} and 4,68 to 23,30 kg ha^{-1} for Sites 2 and 3 respectively (see Table C.6 in Appendix C). A decrease in total phosphorus with soil depth occurred in all three localities and was most apparent in Sites 1 and 2 (Fig. 5.6). From the latter, seasonal variation was apparent in the 150-300 mm and 300-450 mm depths of Site 1, and there was generally a peak during summer. A similar situation was observed at the 0-150 mm depth of Site 2, but there was a decrease during autumn at the 150-450 mm depths of Community 2.1 (Site 2) (Fig. 5.6).

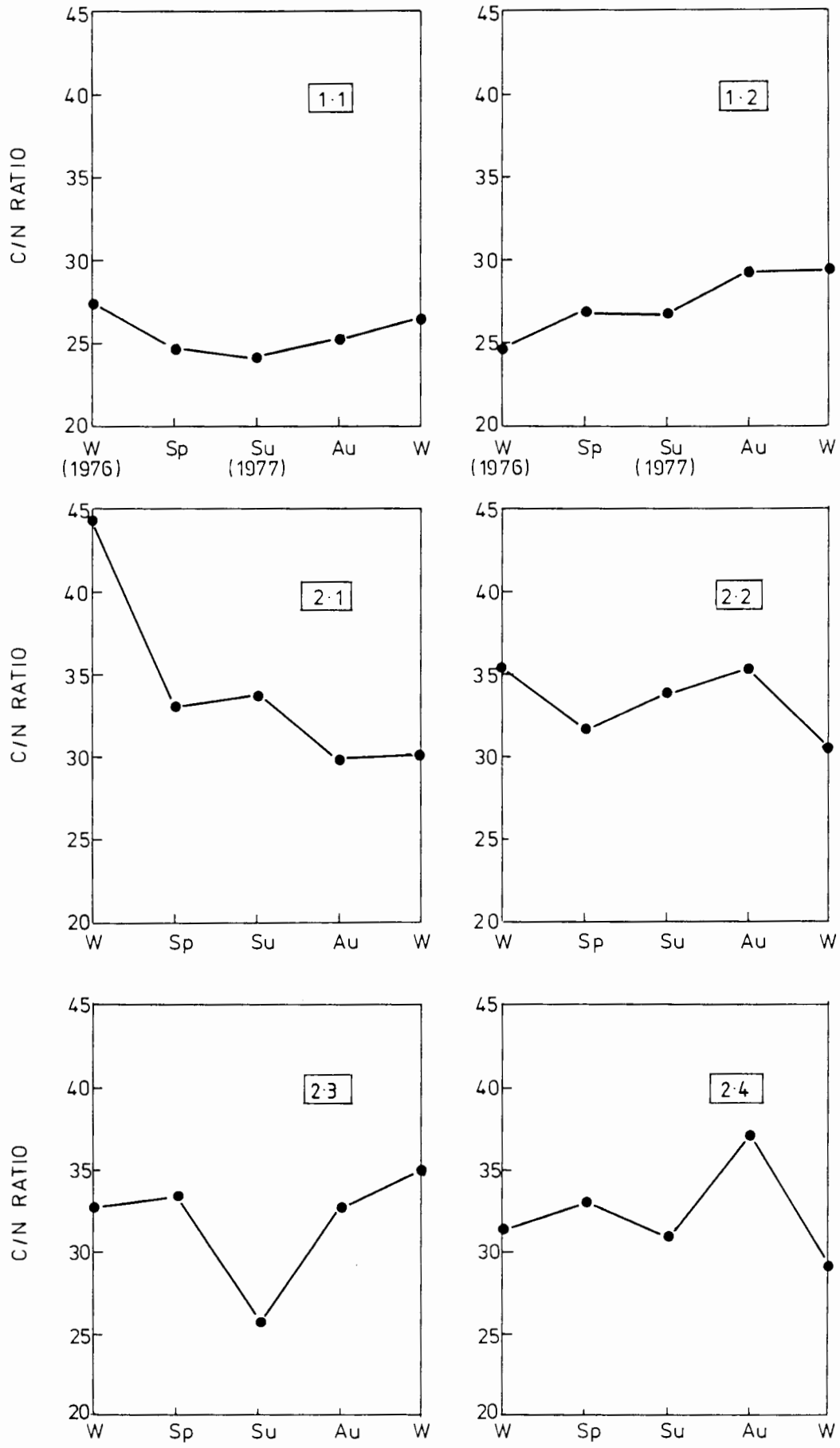


Fig. 5.5 C/N ratios of soils at Sites 1, 2 and 3. Seasonal variation (winter 1976 to winter 1977) at 0—150 mm.

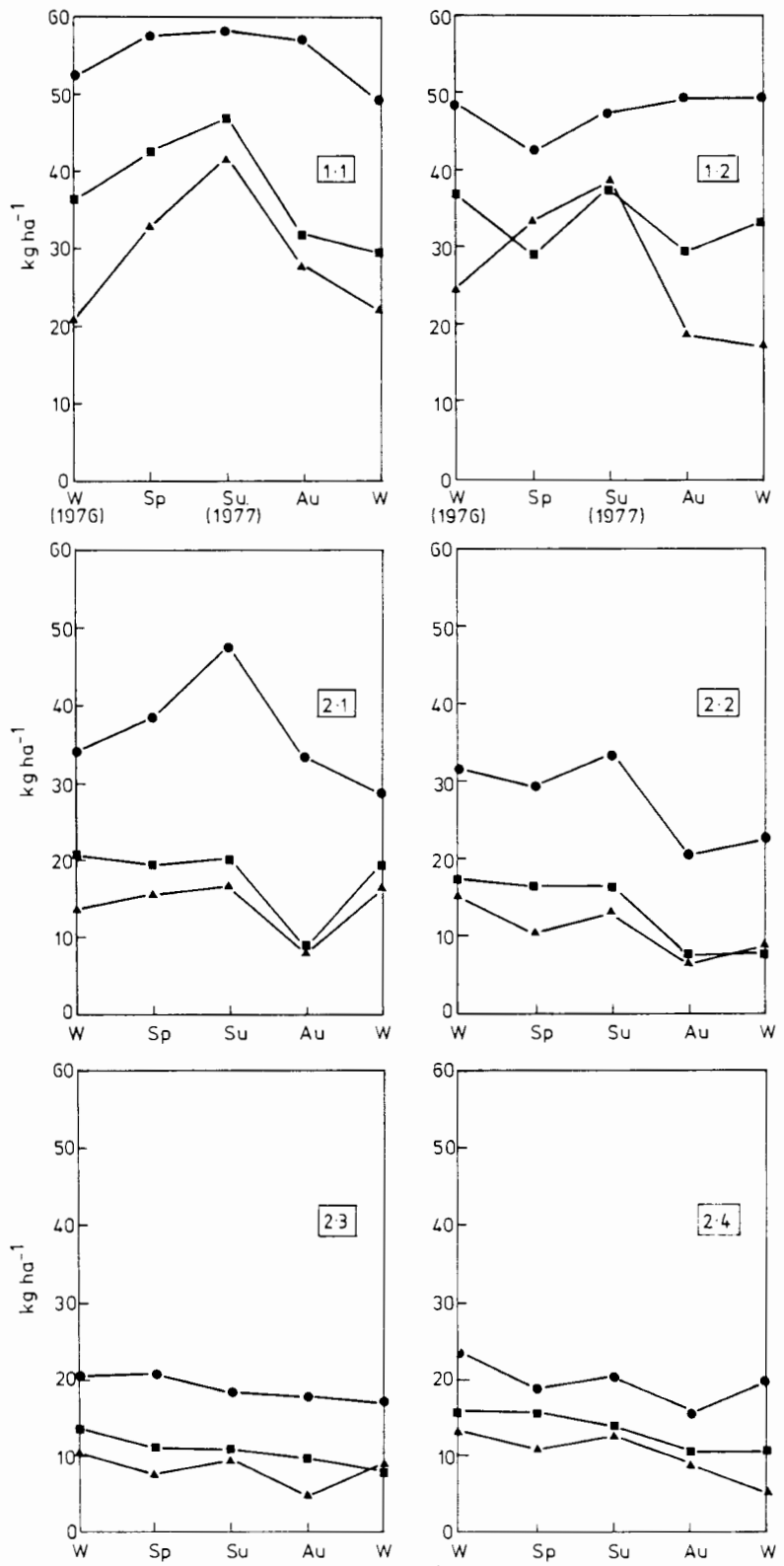


Fig. 5.6 Total phosphorus content (kg ha $^{-1}$) of soils at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Seasonal variation (winter 1976 to winter 1977) at 0—150 (●——●), 150—300 (■——■) and 300—450 (▲——▲) mm.

Bray no. 2 phosphorus

Bray no. 2 phosphorus levels were slightly higher in Site 1 (1,25 to 10,33 kg ha^{-1}) than Site 2 (0,00 to 11,30 kg ha^{-1}) and Site 3 (0,78 to 8,24 kg ha^{-1}) (see Table C.7 in Appendix C). Decrease with soil depth was not always marked and sometimes the 300-450 mm depth would display higher levels than the 150-300 mm (Communities 2.1 and 2.2, Site 2) or 0-150 mm and 150-300 mm depths (Community 2.3, Site 3) (see Fig. 5.7). Seasonal fluctuation in this form of phosphorus was prominent in Sites 2 and 3 where summer peaks were succeeded by fall-offs in autumn with further decreases during winter (Fig. 5.7).

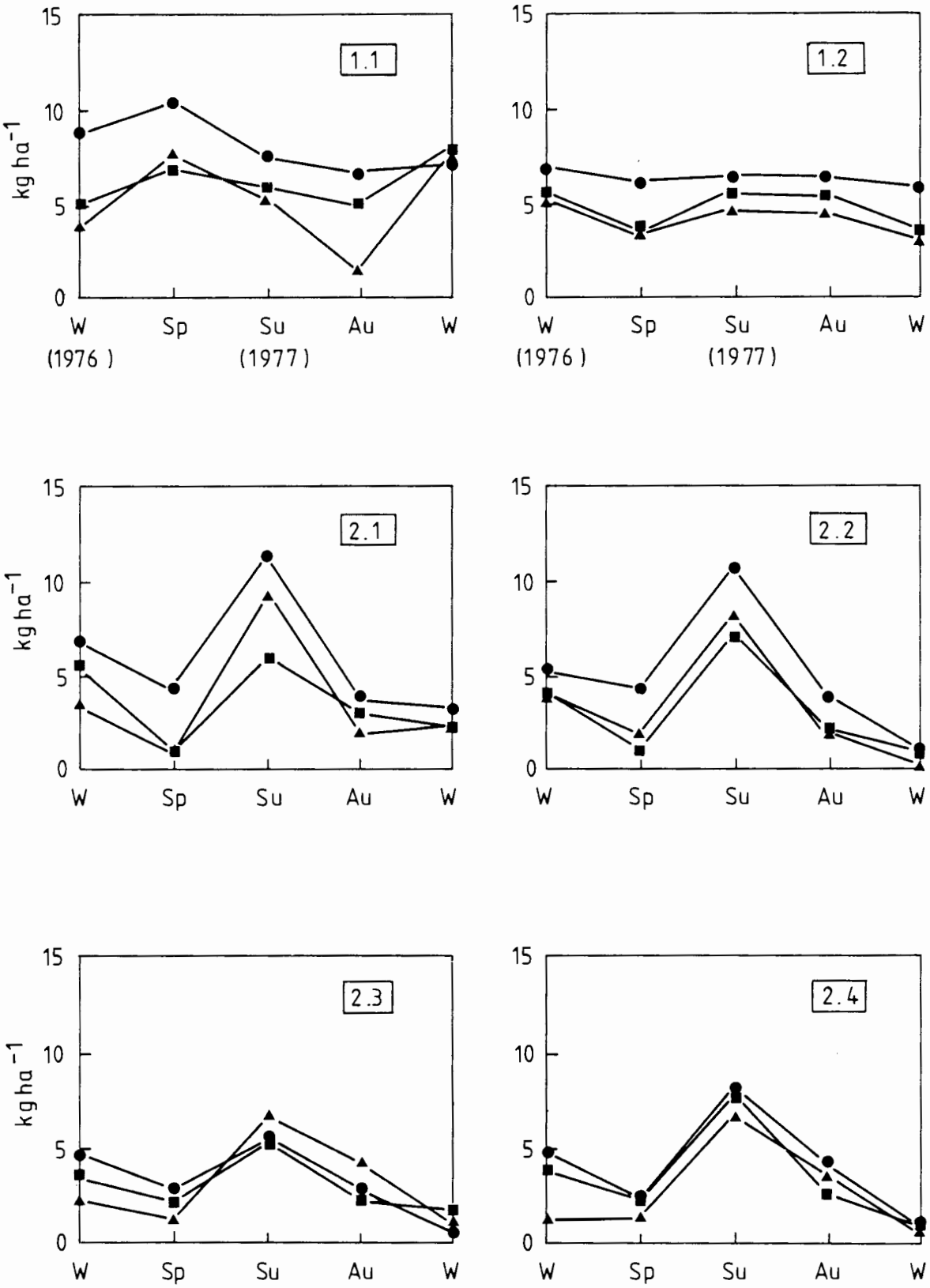


Fig. 5.7 Bray no. 2 phosphorus content (kg ha $^{-1}$) of soils at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Seasonal variation (winter 1976 to winter 1977) at 0—150 (●——●), 150—300 (■——■), 300—450 (▲——▲) mm.

CHAPTER 6

PLANT ANALYSIS

The results presented in this chapter are from the analyses described in Chapter 3. Seasonal variation in leaf tissue N and P for the five species is shown in Fig. 6.1, and Table C.8 in Appendix C. In all cases leaf N was higher than that of P, by a factor of 11 or more.

Mean N levels were greatest in *Leucospermum hypophyllocarpodendron* (Community 1.1), *Serruria vallaris* (1.2), *Erica clavisepala* (2.1) and *Simocheilus depressus* (2.3) (5126, 6679, 6800 and 5322 $\mu g\ g^{-1}$ leaf dry mass respectively) and lowest in *Elegia parviflora* (2.2 and 2.4) (2978 and 4168 $\mu g\ g^{-1}$). P followed a similar pattern with the first four species possessing mean amounts of 384, 555, 404 and 328 $\mu g\ g^{-1}$ respectively) and *Elegia* containing 155 and 167 $\mu g\ g^{-1}$). There was also evidence of seasonal fluctuations in leaf N and/or P. N and P variation in Site 1 (*L. hypophyllocarpodendron* and *S. vallaris*) displayed similar trends with

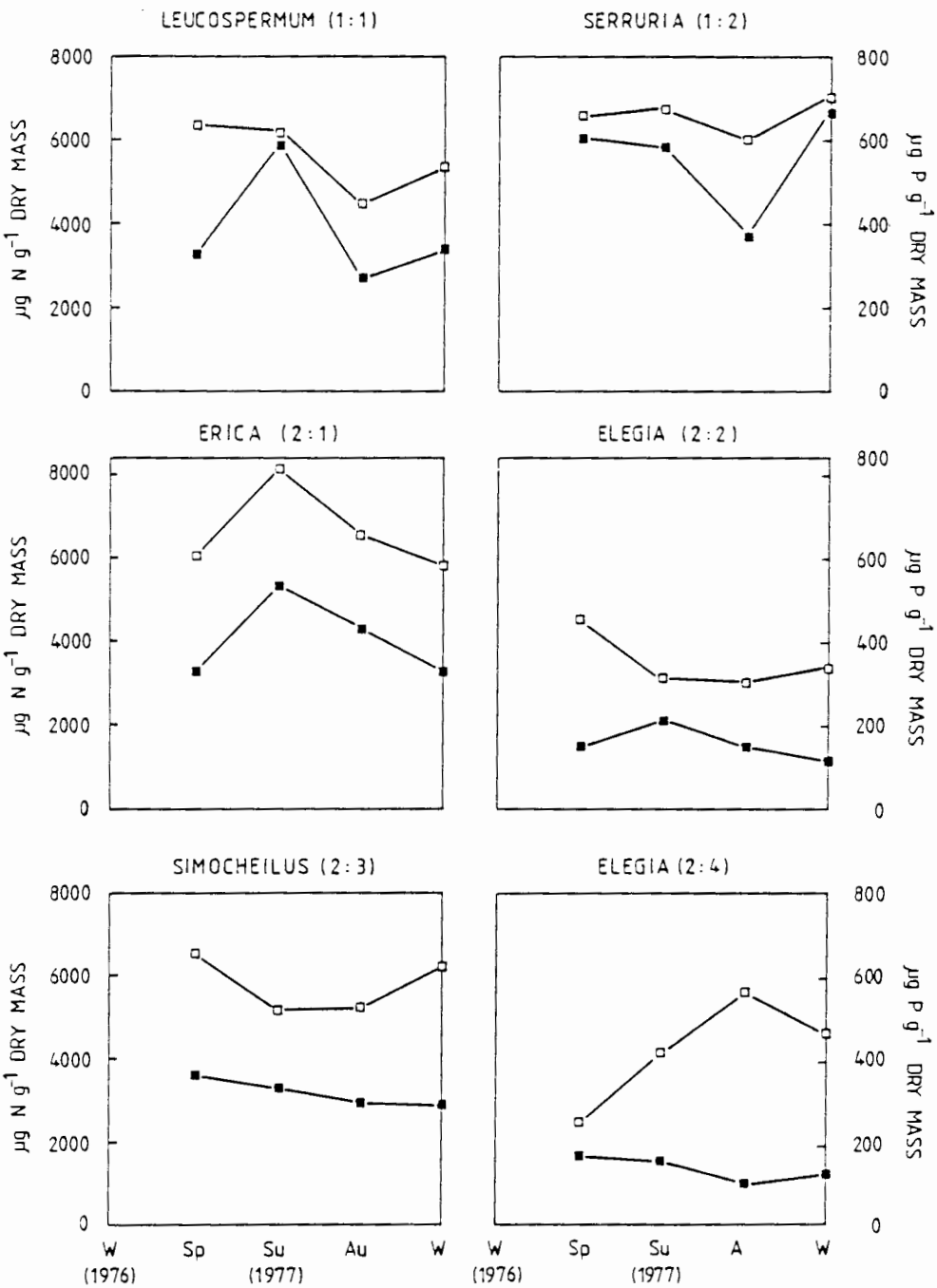


Fig.6.1 Seasonal variation in leaf or photosynthetic stem (*Elegia*) nitrogen (□——□) and phosphorus (■——■) of five species from Site 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:1 2:2) and 3 (2:3 and 2:4).

a notable trough in autumn followed by a rise to winter. An exception was the low spring level of P in Leucospermum. E. clavisepala (Community 2.1) was the only species to produce a marked summer peak in both N and P. However, E.parviflora (2.2) and S. depressus (2.3) displayed a spring/winter peak for N, with P showing a gradual decrease from spring to winter and with no obvious seasonal variation. Finally, in the case of E. parviflora (2.4) the only peak for N was observed in autumn with P displaying little change.

CHAPTER 7

ROOTING SYSTEMS

Gross rooting morphologies

Diagrams of the rooting systems excavated appear in Figs. 7.1, 7.2 and 7.3. *Serruria vallaris* (Plate 7.1) and *Leucospermum hypophyllocarpodendron* both displayed stout suberized tap root systems (400-500 mm and 450-550 mm deep respectively with strong laterals. These became thinner at their point of origin on the tap root with an increase in soil depth (Figs. 7.1 and 7.2). Lateral roots, which radiated in all directions from the tap root, tended to be more or less evenly concentrated with soil depth. The upper individuals were the longest, some with lengths of more than 3 to 4 m.

Erica clavisepala also possessed a tap-lateral root system (Fig. 7.3). The differences in thickness between tap and lateral were not as apparent as in the previous two species and the whole rooting system was

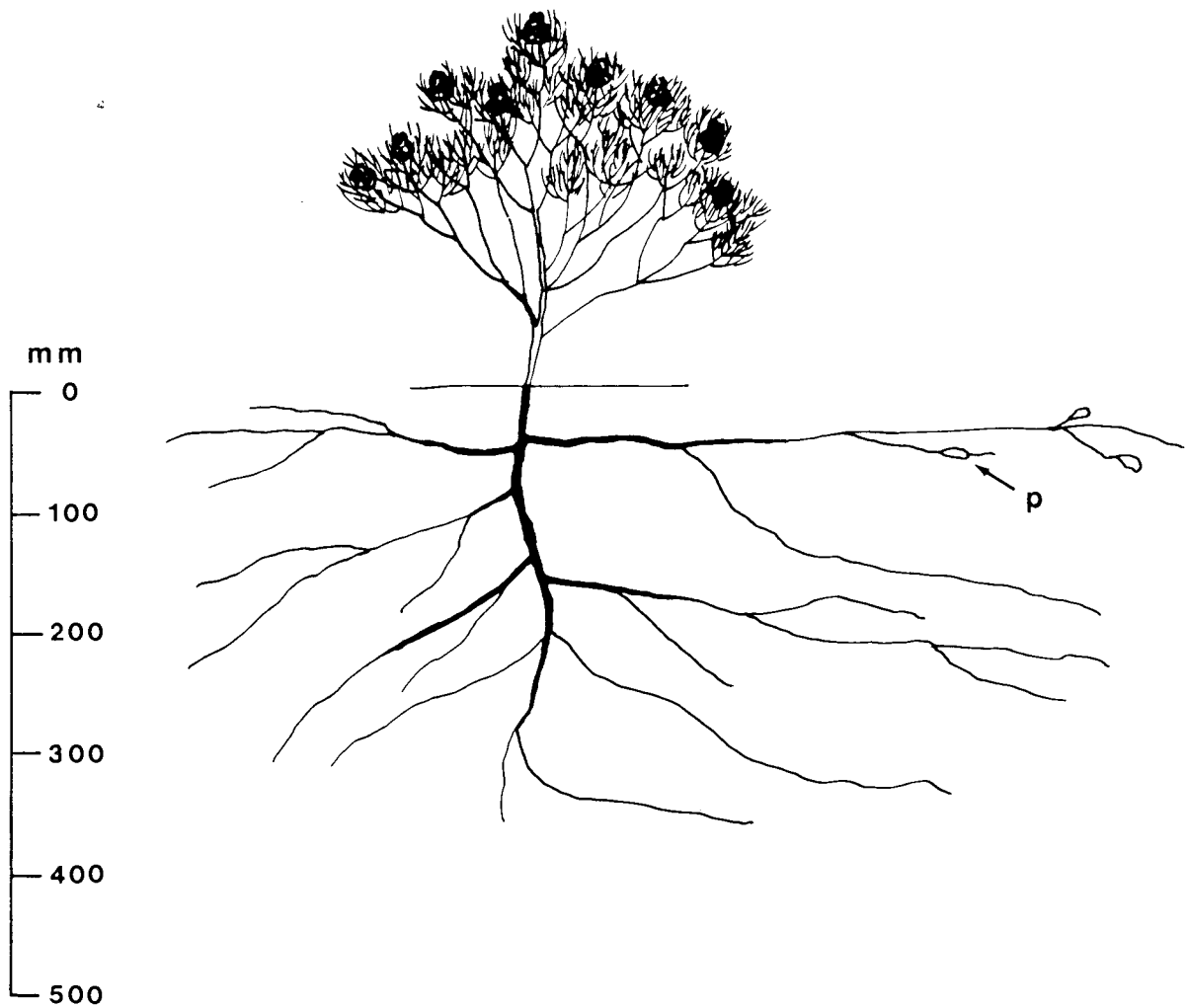


Fig. 7.1 Diagrammatic representation of the rooting system of **Serrura vallaris. p** = proteoid roots.

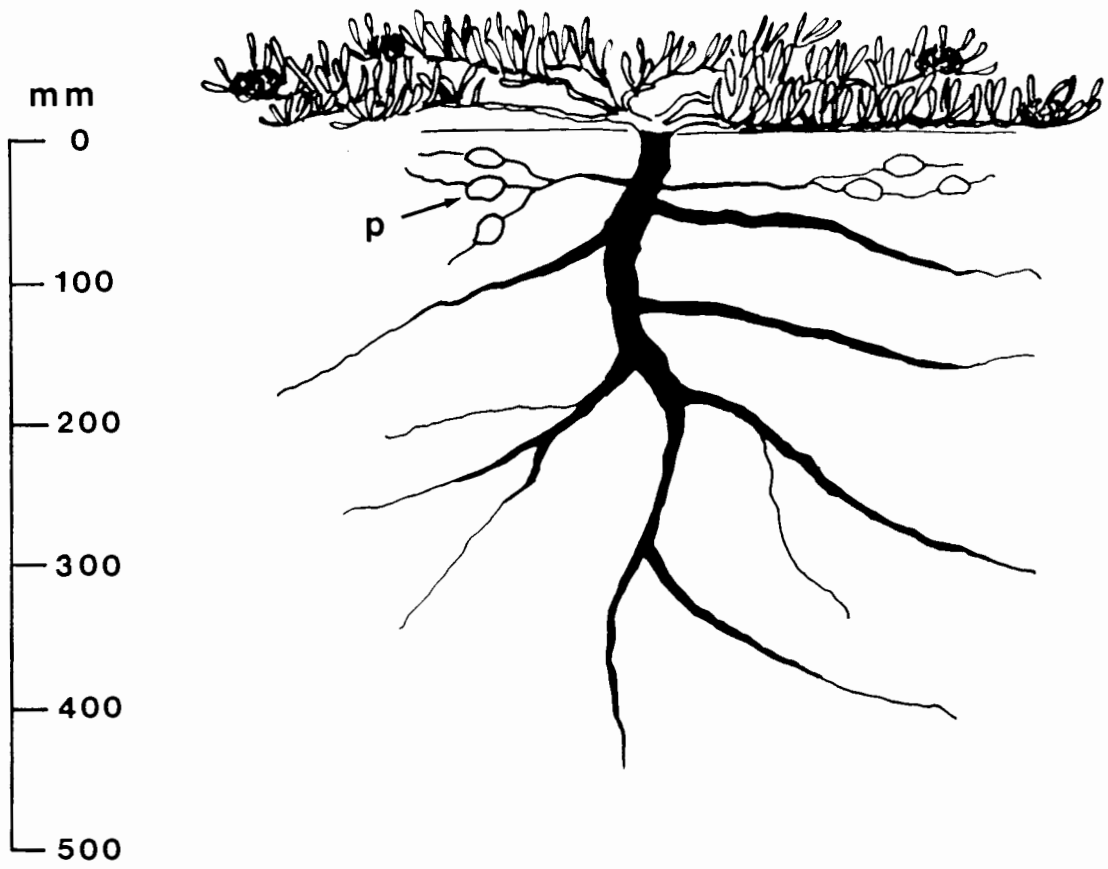


Fig. 7.2 Diagrammatic representation of the rooting system of **Leucospermum hypophyllocarpodendron. p** = proteoid roots.

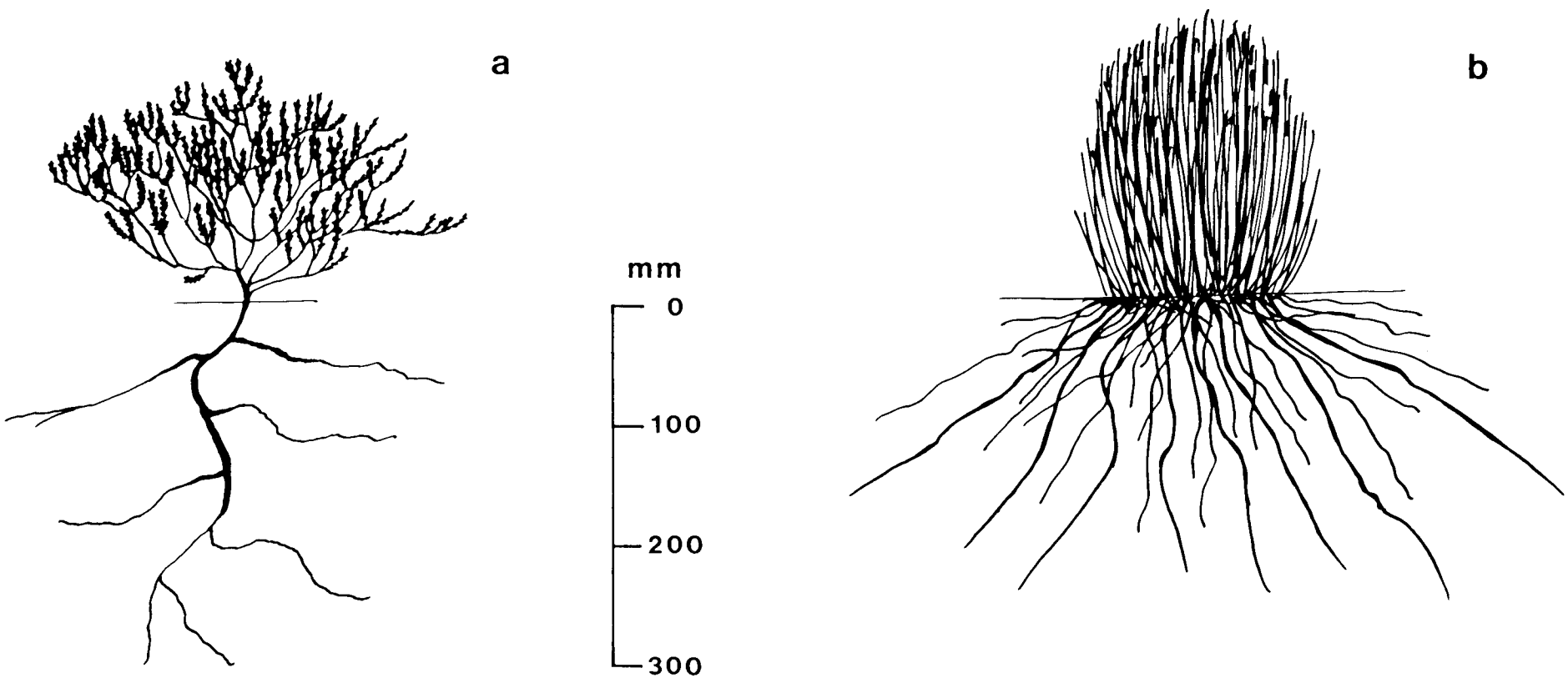


Fig. 7.3 Diagrammatic representation of the rooting systems of **Erica clavisepala** (a) and **Elegia parviflora** (b).

Plate 7.1 Partially excavated root system of **Serruria vallaris** showing stout taproot (500 mm) with horizontally projecting laterals.

more contorted and woody. The rooting depth was fairly shallow (about 250 to 350mm) and unlike Serruria and Leucospermum a profusion of lighter coloured terminal "feeding" rootlets was found. Laterals radiating out from around the tap root were fairly short, rarely extending beyond 1 or 2 m in the upper zone, and were fairly evenly distributed through the soil profile. Elegia parviflora displayed a different system which did not possess a tap root (Fig. 7.3). Rather it comprised a dense mat of fibrous laterals which radiated out from a rhizomatous structure to a depth of some 150-250 mm. Older laterals were dark brown in colour, while the younger forms appeared to be suberized and were light brown. The latter were covered in dense masses of root hairs (see below under "specialized structures").

Specialized structures

Two major morphological specializations were found after examining various roots.

S. vallaris and L. hypophyllocarpodendron (both

Proteaceae) together possessed proteoid roots in fairly dense clusters (Plate 7.2) on lateral or secondary lateral roots which tended to be concentrated in the top 50 mm to 75 mm of soil. Microscopic investigation of these structures revealed that they comprised a mass of 10 to 20 mm long root hairs radiating out from the lateral root axis and for lengths of about 15 to 40 mm.

E. parviflora also possessed a profusion of root hairs extending along certain sections of apparently younger lateral roots. These were unlike the "bottle-brush" type found in the proteaceous members examined as they were not localized on thinner lateral or secondary lateral roots and were not as long (generally under 5 to 8 mm). As they occurred to the tips of the roots, their distribution was also deeper.

E.clavisepala and Simocheilus depressus did not possess any morphological root adaptations but were both found to be highly mycorrhizal. Endotrophic mycorrhiza (Plate 7.3) were concentrated in the terminal feeding

Plate 7.2 Proteoid roots of the type found in **Serruria vallaris** and **Leucospermum hypophyllocarpodendron.**

Plate 7.3 A photomicrograph of root squash showing heavily infested root of **Erica.** Shaded parts of cells contain intracellular hyphae of ericaceous mycorrhiza.(×570)

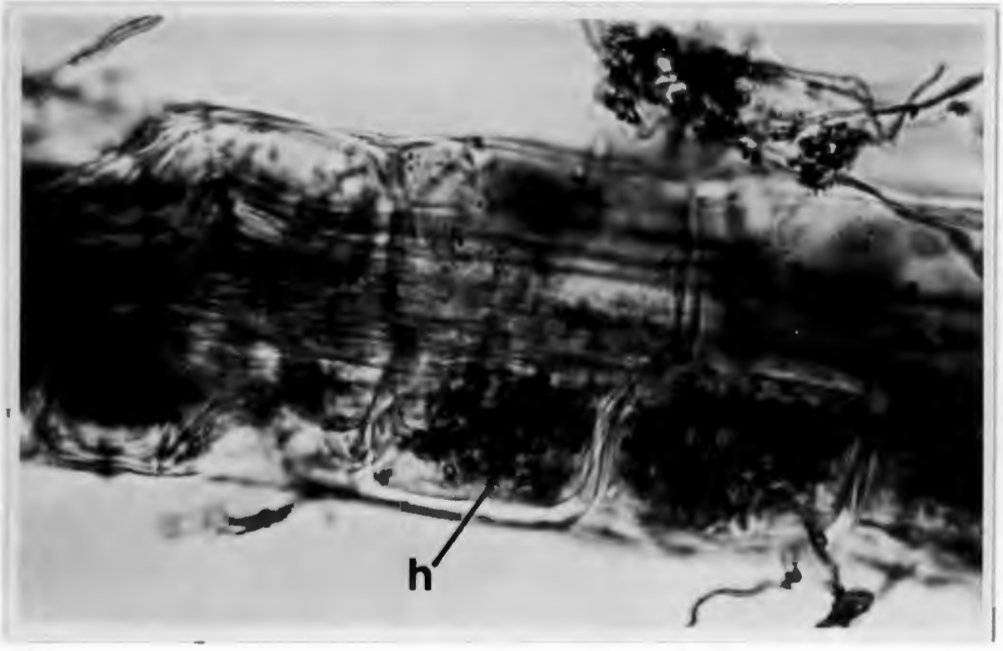


Plate 7.4 A photomicrograph of root squash showing intracellular mycorrhizal hyphae(**h**) in cortical cells of **Erica.** (×800)

rootlets of these species and infection was demonstrated by dense intracellular hyphal masses in the root cortex (Plate 7.4). Sand grains clinging to the terminal, infected rootlets provided evidence of external hyphae emanating from the mycorrhizal fungus.

No endotrophic associations were found in S. vallaris, L. hypophyllocarpodendron and E. parviflora.

CHAPTER 8

SOIL MICROFUNGI

Choice of method

One of the major problems in studying soil fungi has been to select methods of isolating fungi which will provide a true reflection of the (soil) mycoflora (Harley 1971). The two methods used in this study i.e. dilution plate (after Waksman and Fred 1922) and Warcup's soil plate (Warcup 1950) appear to be the ones most frequently used (Table 8.1). Sewell (1959b) maintained that the plate method was more effective in isolating the active mycelial constituents of the soil, whereas other workers, including Warcup (1951), have argued that more than one method is required to obtain a realistic account of the mycoflora. The results discussed below have thus been obtained utilizing the methodology most commonly employed.

Fungi isolated by the soil and dilution plate methods are shown in Table 8.2. Inter-site comparison was facilitated by placing fungi into ten of Ainsworth et al.'s (1973)

TABLE 8.1 Examples of isolation methods used in the study of soil microfungi in some natural ecosystems

		METHOD OF ISOLATION									
SYSTEM	AUTHOR	SOIL	DIL	DIR	WASH	IMM	SLIDE	HEMP	AGAR	OBS	ROSS
Arid zone	Borut (1960)		ab								
Sand dune	Brown (1958)	b		b			b	b			
	Dickinson and Kent (1972)	b									
	Phelps (1973)	b		b							
	Wohlrab et al.(1963)	b									
Grassland	Warcup (1951)	b						b			
Savannah	Eicker (1974)	b	b		b						
Marshland	Stenton (1953)	b									
Heathland	Jeffreys et al. (1953)		b								
	McLennan and Ducker (1954)	b	ab			b				a	
	Sewell (1959a)	b									
	Sewell (1959b)	b				b	b				b
Forest	Christenson (1969)		b								
	Eicker (1969, 1970)	b	ab								
	Morrall (1974)		b								
	Parkinson and Williams (1964)			b	ab						
	Tresner et al. (1954)		ab	b							
	Wicklow et al. (1974)	b	b			b					
	Widden and Parkinson (1973)				b				a		

[a] numbers determined

[b] species determined

METHODS

SOIL - Soil plate (Warcup 1950)
DIL - Dilution plate (Waksman and Fred 1922)
DIR - Direct inoculation (Waksman 1916)
WASH - Soil washing (Gams and Domsch 1967)
IMM - Immersion tube (Chesters 1940)
SLIDE - Slide-trap (Chesters 1940)
HEMP - Water and hemp seed (Butler 1907)
AGAR - Agar film (Jones and Mollison 1948)
OBS - Direct observation (Jones and Mollison 1948)
ROSS - Rossi-Cholodny slide (Cholodney 1930)

TABLE 8.2 Distribution of soil microfungi in each of the three sites and at four different depths. + represents presence of isolates using the soil plate method and numerals (per 10^{-3} g soil dry mass) the numbers of colonies isolated using the dilution plate technique.

	Site 1				Site 2				Site 3			
Depth (mm)	25	100	225	375	25	100	225	375	25	100	225	375
Absidia spinosa	+ + +	+ + +										
Gongronella sp.										+ + + 6 3 2	15 9 7	4 1 5
Mortierella sp.		7 6 8	8 8 9	+ + + 8 1 8	+ + + 8 2 2	+ + + 3 3 4	+ + 2 + 3	+ + + 3 2 1				
Mucor hiemalis		1	2 2 2									
Mucor plumbeus			1									
Mucor sp. 1		2 2 2	+	+ + +	1 1 1	+ + + 3 4 1	1					
Mucor sp. 2									+ + + 2 2 2	+ + + 1		+ + +
Mucor sp. 3									+ + + 2	+ + +		+ + +
Other Mucorales				2			+	+ 1 +			+ 1 +	+
Phytophthora sp.	4 3 4											
Unidentified Plectomycete		+										
Aspergillus sp. 1	1 1											
Aspergillus sp. 2	1											
Aspergillus sp. 3	2 10											
Penicillium sp. 1	+ + + 25 26 21	4 + 2 + 3	3 + 3 3	1								
Penicillium sp. 2	4 2 2	+ 5 1 +	7 1									
Penicillium sp. 3		8 2 6										
Penicillium sp. 4			1 4 1									
Penicillium sp. 5			+	+ + + 2 5 7			1	1				
Penicillium sp. 6					+ + + 6	3						
Penicillium sp. 7					1 1				+ + 2	1	2 3	
Penicillium sp. 8					+ + +	+ + + 1 5 3						
Penicillium sp. 9						1	1					
Penicillium sp. 10										+		
Penicillium sp. 11											+	
Penicillium sp. 12											+	
Penicillium sp. 13												+
Gliocladium sp.	1											
Paecilomyces sp.					+ + + 13 7 4							
Trichoderma sp.	+ + + 1	+	+			1						
Cladosporium sp.	1 1				2 3 + 2	+ +		+ +		1		
Ulocladium sp.	+ + 3											
Other Dematiaceae		8 1 4										
Fusarium sp.	1 2 1		+	+ + +		+ + +	+	+ + +	3 2 2	2 1		
Yeasts	+ 1	+	+ 6 + 3 + 3	+ 1	2					+ 3 1	2 2	2 + 2 + 2
Mycelia sterilia sp. 1	27 + + 17 19	+ + +	+ +	+ 2 + 1	14 8 7							
Mycelia sterilia sp. 2									+ + + 2 3 5	+ + + 1	+ + + 1 2 2	1 1 1
Mycelia sterilia sp. 3										+ 1	+ 1 2	
Mycelia sterilia sp. 4										+ + +	+	
Mycelia sterilia sp. 5										+		
Mycelia sterilia sp. 6												+ +
Number of different isolates	25	100	225	375	25	100	225	375	25	100	225	375
(i) at each depth	11	9	8	6	8	6	3	3	5	8	5	6
(ii) at each site	24				14				17			

Isolates identified using Alexopoulos (1962), Gilman (1957) and Von Arx (1970)

groups. Taxonomic entities in each group generally represent individual species; however several, including "Other Mucorales", may contain more than one species. "Yeasts" and "mycelia sterilia" (colonies not producing sporulating structures within an incubation period of three to four weeks after sub-culturing) were not identified further.

A total of forty one different taxonomic entities were isolated from the four depths, twenty four in Site 1, fourteen in Site 2 and seventeen in Site 3 (Table 8.2) to give a total of 41 for the three sites. Although certain similarities existed between sites, a specific mycoflora was isolated from each site. Similarities in Ainsworth *et al.*'s (1973) groups were most marked between Sites 2 and 3 (Fig. 8.1); all of these groups were present in Site 1 but the number of groups in Sites 2 and 3 were seven and six respectively. Site 1 was dominated by members of the "Mucorales and Peronosporales" (25,0%) and "*Penicillium* spp." (20,9%) and to a lesser extent by "*Aspergillus* spp." and examples from the "Dematiaceae" (both 12,5%). Sites 2 and 3 also exhibited a relatively high proportion of "Mucorales and

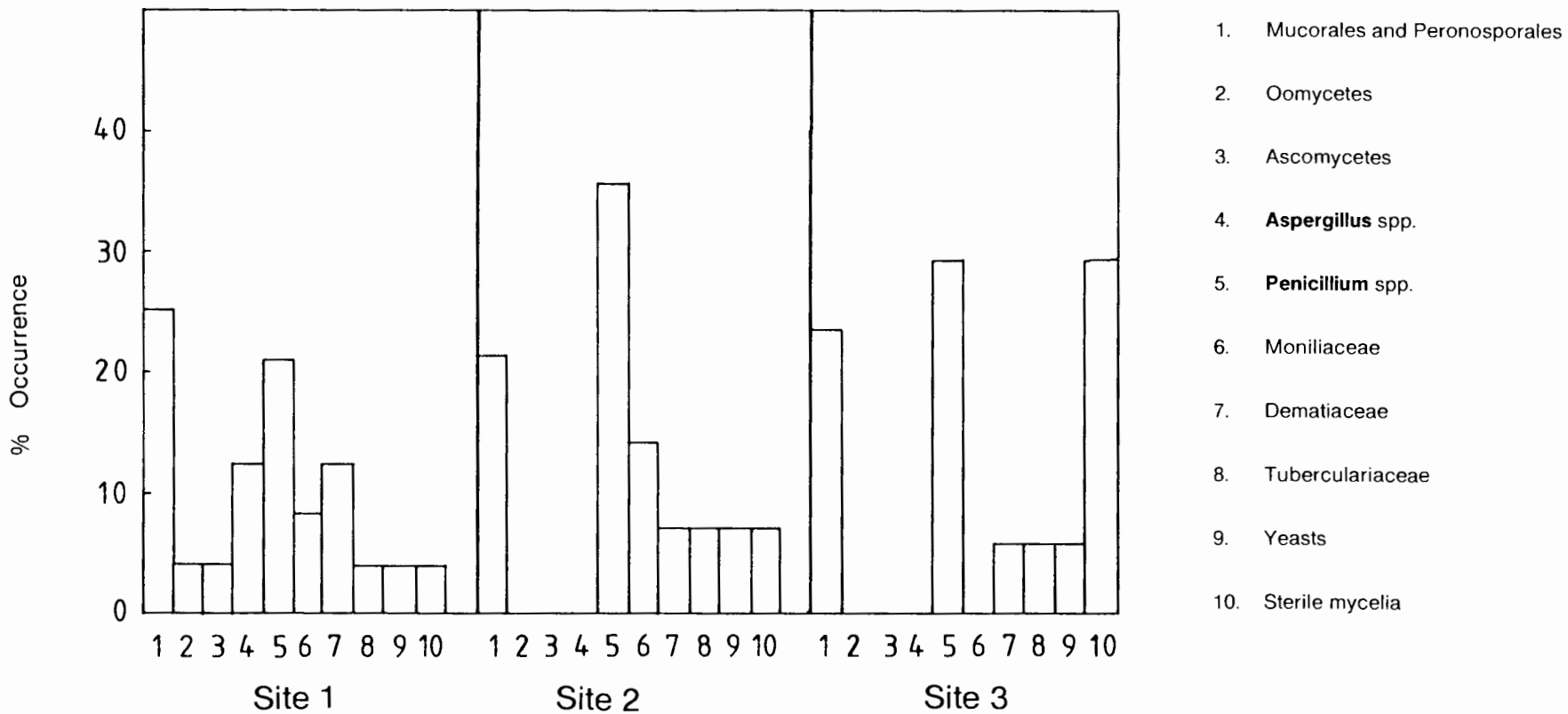


Fig. 8.1 Occurrence of fungal insolates in soils from Sites 1, 2 and 3.

Peronosporales" (21,5% and 23,5% respectively) and were most abundant in species of Penicillium (35,8% and 29,4% respectively). Mycelia sterilia accounted for 29,4% at Site 3.

Site 1 possessed isolates belonging to fifteen species which did not occur elsewhere. These included Absidia spinosa, Mucor hiemalis, Phytophthora sp., Aspergillus spp. and Penicillium spp. Four species were exclusive to Site 2, including several Penicillium spp. and Paecilomyces sp., whereas twelve species, including Gongronella and several mycelia sterilia were only found in Site 3.

Examples of species occurring in all Sites (irrespective of depth) were a member of the Mucorales, Cladosporium sp. and Fusarium sp. Several fungi were present in two of the three sites only, these being Mortierella sp., Mucor sp. and a mycelia sterilia (Sites 1 and 2) and yeasts (Sites 1 and 3). The above broad species distribution is arranged in Fig. 8.2.

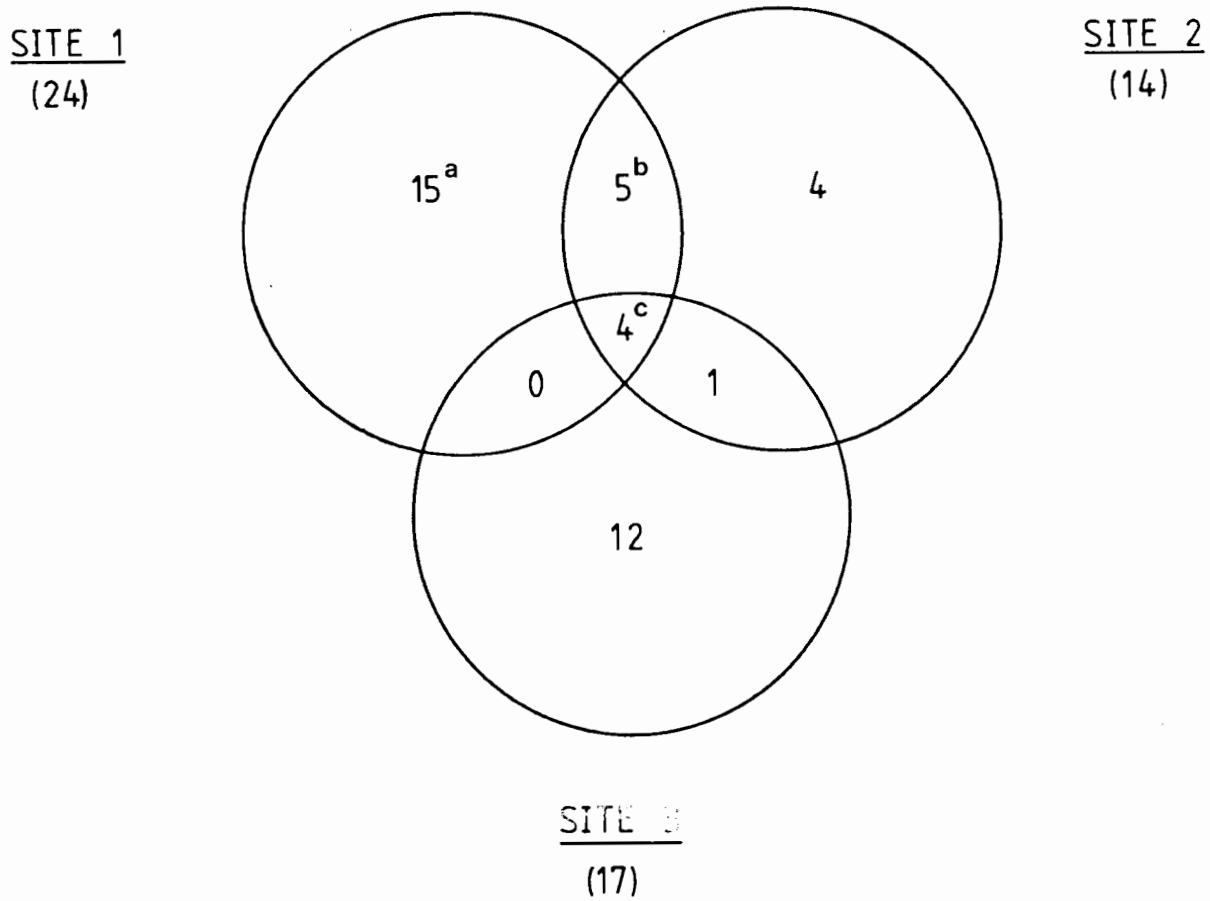


Fig. 8.2 Distribution of soil microfungi within and between sites. Total number of different isolates in each profile appears in parentheses.

[a] Number of isolates exclusive to one site.

[b] Number of isolates common to two sites.

[c] Number of isolates common to all sites.

The number of species also tended to vary with depth with a slight concentration in the upper layers (25 and 100 mm) which was most marked in Site 2 (Table 8.2). Several species including Absidia spinosa, Phytophthora sp. and Aspergillus spp. in Site 1 and Paecilomyces sp. in Site 2 were confined to the upper layers, while a few species ("Other Mucorales" and several species of Penicillium (Sites 1, 2 and 3) seemed to prefer the lower depths. Gongronella sp., Mortierella sp., Mucor spp., certain Penicillium spp., one Fusarium sp., and several yeasts and mycelia sterilia were found throughout the soil profile.

Total colony numbers were derived from those appearing in Table 8.2 and are recorded in Table 8.3. Although numbers are generally expressed per gram soil dry mass, this is rather misleading as the fungi are isolated from moist soil. Figures for both wet and dry soil mass are therefore given. In addition, numbers have been determined on a volume basis (i.e. per cm^3 dry soil), using bulk density values for each depth and profile. In this way direct comparison of

TABLE 8.3 Numbers of fungal colonies occurring in each site at four different depths (numbers calculated from dilution plates).

DEPTH (mm)	SITE 1			SITE 2			SITE 3		
	per g soil wet mass	per g soil dry mass	per cm^3 dry soil	per g soil wet mass	per g soil dry mass	per cm^3 dry soil	per g soil wet mass	per g soil dry mass	per cm^3 dry soil
25	60 000*	67 000	83 000	28 000	37 000	45 000	10 000	12 000	17 000
105	24 000	26 000	32 000	11 000	13 000	17 000	9 000	11 000	15 000
225	22 000	24 000	32 000	3 000	3 000	5 000	14 000	17 000	24 000
375	13 000	13 000	20 000	3 000	3 000	5 000	6 000	7 000	11 000
TOTAL	119 000	130 000	167 000	45 000	56 000	72 000	39 000	57 000	67 000

* To nearest thousand

numbers can be made more practicable, and they can be related to soil nutrient status (see Appendix C).

Total colony numbers ranged from $83x10^3$ to $20x10^3$ (Site 1), $45x10^3$ to $5x10^3$ (Site 2) and $24x10^3$ to $11x10^3$ (Site 3) per cm^3 dry soil. In Sites 1 and 2, numbers tended to decrease with soil depth, whereas in Site 3 this trend was not apparent. The total fungal isolates at Site 1 was $167x10^3$, i.e. more than twice that of Site 2 ($27x10^3$) or Site 3 ($67x10^3$). The higher numbers in the former may have been due to the presence of strongly sporulating individuals eg. Penicillium spp.

In conclusion, a comparison between species isolated by the two methods revealed the following (Table 8.4):

42-50% of the isolates in all sites were isolated using both techniques. In Sites 1 and 2, using the dilution plate method only, 50 and 43% respectively of the total number of species isolated were obtained. In Site 3 the situation was however reversed with the soil plate method being responsible for isolating 41% of the total number of species. Although a

realistic explanation for this is not presently apparent, this phenomenon may have been due to the dilution plate method being able to select for the strongly sporulating isolates of which few were present in Site 3, a fair proportion of the latter being made up of yeasts and mycelia sterilia .

TABLE 8.4 Comparison between species isolated by the dilution and soil plate methods

		No. taxa isolated	%
Site 1	Dilution	12	50
	Soil	2	8
	Both	10	42
	TOTAL	24	100
Site 2	Dilution	6	43
	Soil	1	7
	Both	7	50
	TOTAL	14	100
Site 3	Dilution	2	12
	Soil	7	41
	Both	8	47
	TOTAL	17	100

CHAPTER 9

NITROGEN - FIXATION

The results detailed below focus upon the occurrence of free-living nitrogen-fixers and the ability of these organisms to fix gaseous nitrogen in the soils from this study. While this group, represented here by two genera of the Azotobacteriaceae, was preferentially examined due to the overall aerobic nature of the topsoils, it should be borne in mind that other groups of free-living nitrogen-fixers may also be prominent in the soil. Of note is the genus Clostridium which may be common in waterlogged soils where anaerobic conditions would be expected. Soils showing marked seasonal variation in moisture status, as do Sites 2 and 3, might therefore show concurrent seasonal changes in the quantitative and possibly qualitative composition of the nitrogen-fixing bacteria. The same trend would most probably also apply to seasonality in the amount of nitrogen fixed.

Isolation of Azotobacteriaceae

After six weeks, none of the flasks with culture media had produced a surface film which is characteristic of the Azotobacteriaceae and which normally develops within two weeks of incubation. Consequently it was assumed that these bacteria were not present in the soil and on the roots examined, or had in some way escaped Azotobacteriaceae isolation.

Determination of nitrogen-fixation

In determining nitrogen-fixation by the acetylene reduction method (Hardy *et al.* 1973), two size classes of container - 30 cm^3 McCartney bottles/10 cm^3 glass tubes or 1,2 dm^3 Consul jars were used.

Tests using the smaller containers were on the whole negative with only one sample (*Acacia longifolia* nodules) reducing acetylene (Table 9.1). Greater success was obtained when using the Consul jars and a positive response was shown to the soil, root and nodule experimental material (Table 9.2). While the *Acacia* nodules displayed an immediate reduction of

TABLE 9.1 Preliminary testing of the acetylene reduction method for detection of nitrogen-fixation in various materials. 1. Using 10 cm^3 glass tubes and 30 cm^3 McCartney bottles (14.2.77 - 3.3.77). Ethylene produced (+) or not (-).

Soil/plant system	Material	Source	Incubation period	Ethylene produced
Myrica cordifolia	nodules	Olifantsbos,		-
	roots	C. of G. H. Nat. Res.*	24 h	-
	soil	(dune)		-
Erica clavisepala	roots	Olifantsbos,	"	-
	soil	C. of G. H. Nat. Res. (TMS soil)	"	-
Elegia parviflora	roots	"	"	-
	soil	"	"	-
Leucospermum hypophyllocarpodendron	roots	"	"	-
	soil	"	"	-
Serruria vallaris	roots	"	"	-
	soil	"	"	-
Thamnochortus sp.	roots	"	"	-
	soil	"	"	-
Cycad	nodules	UCT** glasshouse	"	-
Acacia longifolia	nodules	UCT campus	½ to 19 h	+
Garden soil		"	7 days	-
Pine forest soil		"	"	-
Ammophila arenaria	roots	Rooiels (dune)	2¼ h	-
	soil	"	"	-

* Cape of Good Hope Nature Reserve
** University of Cape Town

TABLE 9.2 Preliminary testing of the acetylene reduction method for detection of nitrogen-fixation in various materials. 2. Using 1,2 dm^3 Consul jars (23.6.77 - 20.8.77). Ethylene produced (+) or not (-).

Material	Source	Incubation period	Ethylene produced
Acacia spp.			
nodules	UCT campus	½, 2, 17, 96 h	+
roots		1, 17, 96 h	+
Garden soil	"	13, 86 h	-
		11, 15, 18 days	+
Pine forest soil (0 - 150 mm)	"	3, 13, 10, 86 h	+
		6½, 11½, 15, 18 days	+
Protea repens seedlings (roots)	Grown from seed	½, 3, 70 h	-
		11, 15, 18 days	-
Leucospermum sp.	Cape of Good Hope Nature Reserve		
roots		2, 5, 26½, 96 h	-
soil		7 days	-

acetylene, the soils had to be incubated for several days to produce a marked response. The pine forest soils (Fig. 9.1) displayed a generally sigmoid curve of ethylene production with time whereas ethylene production by the Acacia nodules (Fig. 9.2) levelled off rapidly.

Having established that the system employing a larger container was capable of detecting acetylene reduction in a given soil, it was decided to employ it in the nitrogen-fixation assessment of the soils in the study site.

A trial incubation of soils from the study area in the Cape Point Nature Reserve was then undertaken. Two soil cores were sampled from each of Sites 2 and 3 as well as one from a recent burn outside the latter. The resultant ethylene production is shown in Table 9.3. The soils from Sites 2 and 3 revealed traces of ethylene production after 72h and amounts of the gas increased until the incubation was halted after 292h. Prior to incubation, all soil cores in this and subsequent tests were removed from the cylinders.

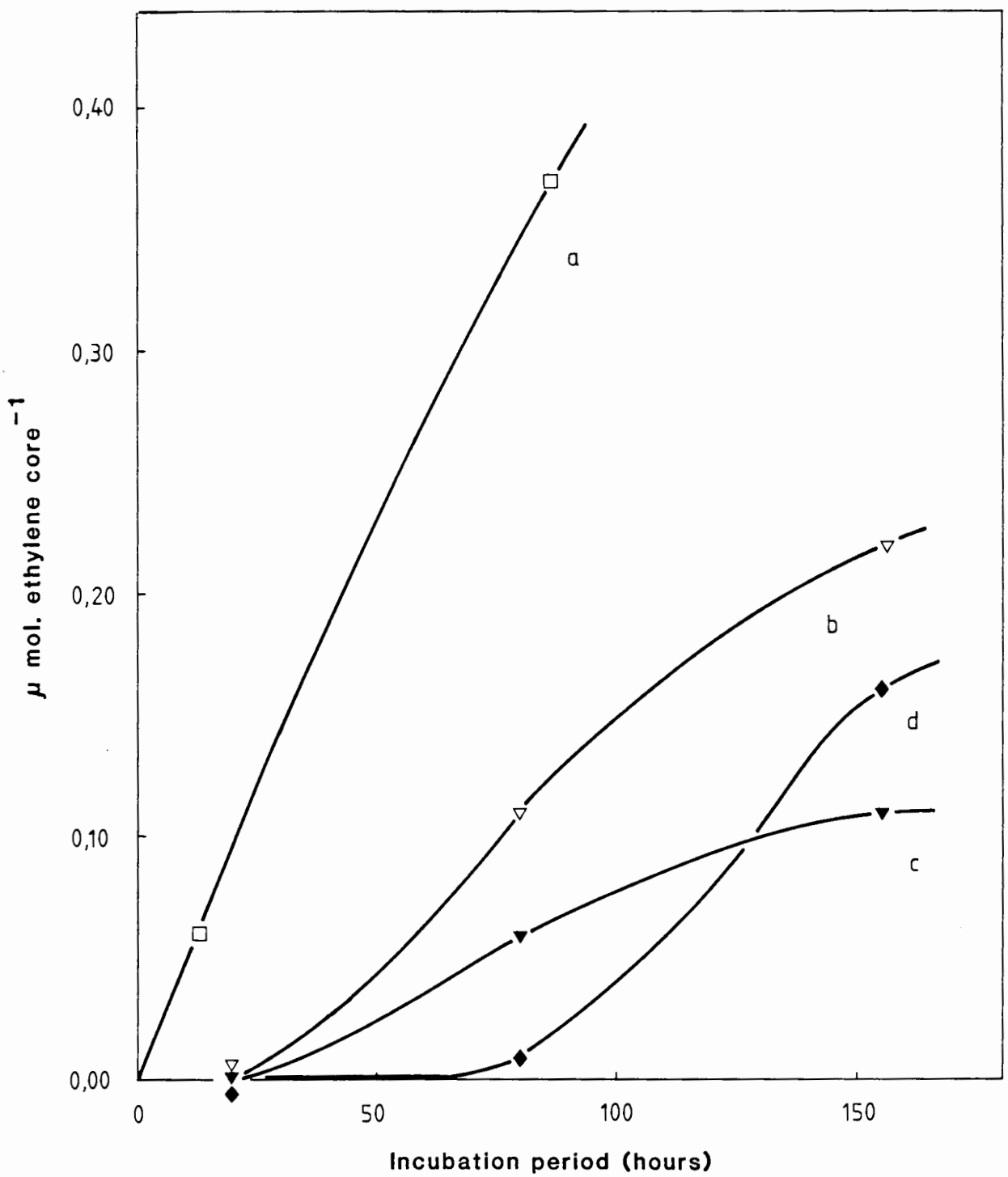


Fig. 9.1 Ethylene production with time in two soils from University of Cape Town campus. **Pine forest soils**: (a) 0 — 150 mm core (first run); (b) 0 — 150 mm core (second run); (c) 0 — 50 mm core. **Grassland soil adjacent to pine forest:** (d) 0 — 150 mm core.

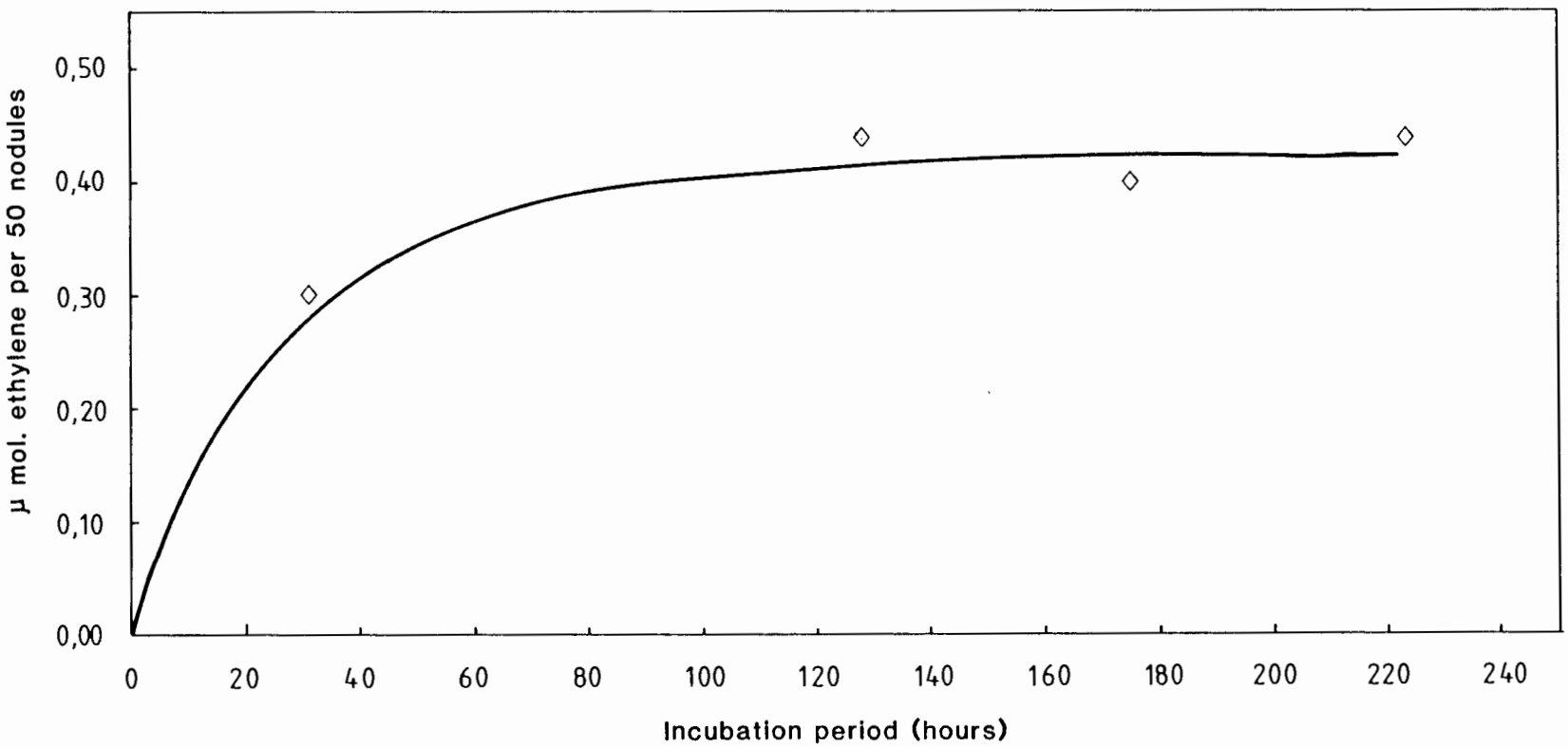


Fig. 9.2 Ethylene production with time of **Acacia longifolia** root nodules incubated in a 0,1 atmosphere acetylene atmosphere. Incubation in a 1,2 dm^3 Consul jar with approximately 50 nodules.

TABLE 9.3 Preliminary acetylene reduction tests on soils from Sites 2 and 3

Commencement of incubation = 7.8.77.

Hours of incubation	24					72					112					185					213					292				
Sample no.	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Ethelyne peak height (mm)	-	-	-	-	-	T	T	-	-	-	3,5	1,5	T	1,5	-	5	5	1	4	-	9	6	1	4,5	-	11	8	1	6	-
Mean (mm)						T					2,5		0,8			5		2,5			7,5		2,8			9,5		3,5		

1 and 2 = Community 2.1 (Site 2)

3 and 4 = Community 2.3 (Site 3)

5 = Recent burn near Community 2.3 (Site 3)

Finally soils (moisture contents of 2,5 (Site 1), 20,9 (Site 2) and 19,1% (Site 3)) from all three sites (four controls and four with 10% acetylene atmospheres for each site) were incubated at room temperature ($\pm 20^0$C) in the dark. Aliquots (1 cm^3) were run through the GLC at one week intervals for three weeks. None of the controls reduced acetylene while all but two of the jars (from Site 1) produced ethylene. Ethylene produced was greatest in Site 2 (82,88 µmol. per core after 3 weeks), followed by Site 3 (4,16 µmol. per core after 3 weeks) and Site 1 (only trace amounts).

Graphs of ethylene produced with time were drawn for each site and appear in Figs. 9.3 and 9.4. Curves from trial incubations showed an initial lag period but the final runs revealed a more linear response between the amount of ethylene produced and time.

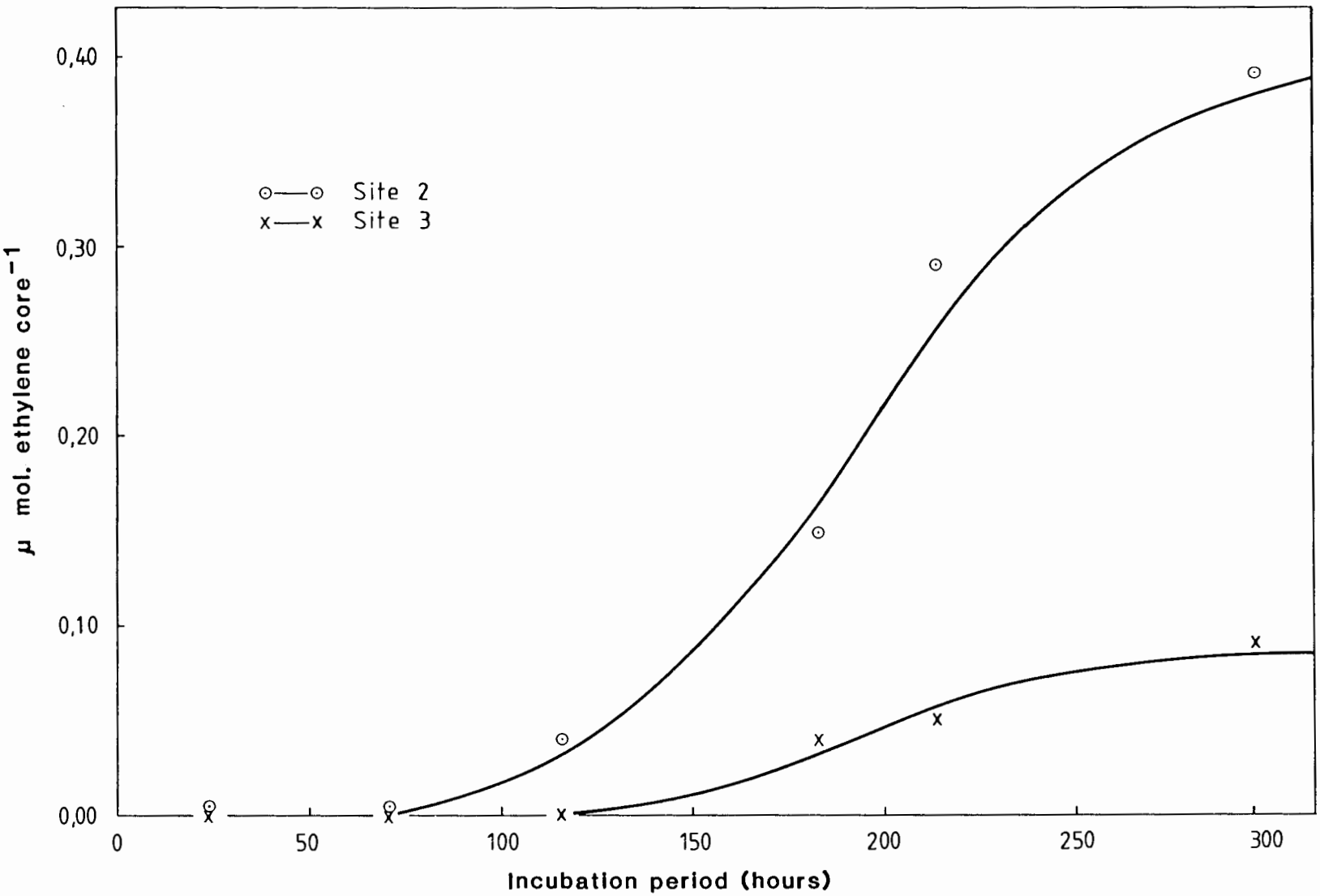


Fig. 9.3 Ethylene production with time after trial incubation of soils from Sites 2 and 3.

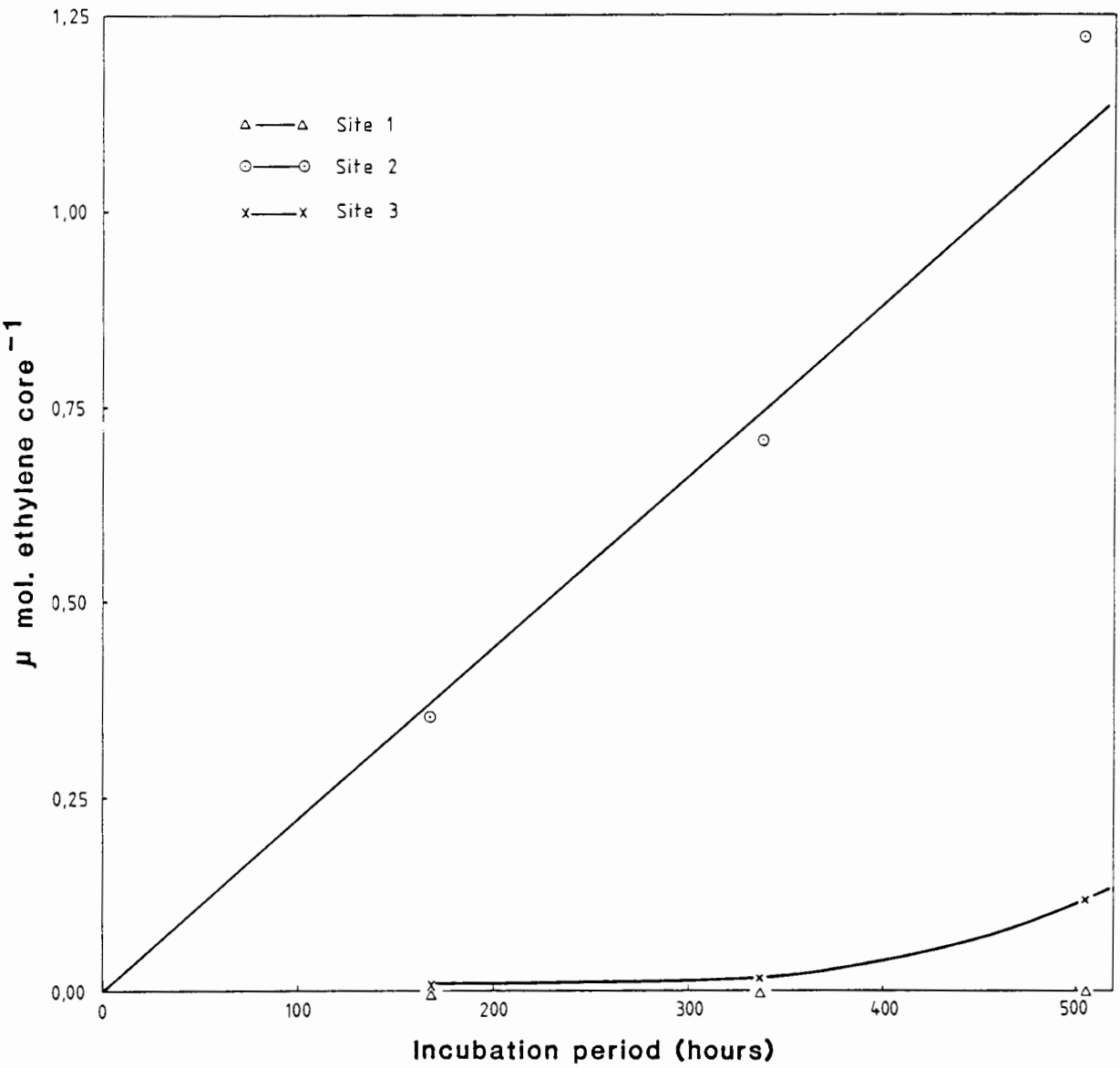


Fig. 9.4 Ethylene production with time after final incubation run on soils from Sites 1, 2 and 3.

CHAPTER 10

DISCUSSION

This study demonstrated that three mountain fynbos communities at the Cape of Good Hope Nature Reserve displayed soil and plant physical and chemical properties which were characteristic of heathlands in the western Cape and Australia (Low 1980, Specht 1979). The inter-site differences in certain parameters such as soil nutrients however showed that heathland systems may be extremely variable within their overall oligotrophic framework. Furthermore microbial aspects of the study revealed a soil microflora of the type found in (podzolised) acid soils. Free-living nitrogen-fixers, while not isolated were shown to have the potential of contributing to the nitrogen status of the soil.

The soils at the study sites were acid and of a low nutrient status similar to those of other mountain fynbos sites in the western Cape (Table 10.1) and heathlands in Australia (Table 10.2). Soils in the Cape show strong chemical affinities with their respective parent materials (Table 10.3) those from Table Mountain Sandstone owing their low nutrient contents and acidity to the siliceous nature and lack of feldspars, micas and clay (Du Toit 1966, Furon 1963, Wellington 1955).

TABLE 10.1 Topsoil analytical data from mountain fynbos sites in the western and southern Cape.

Author	Locality	No. samples	pH	% OM	% C	% N	µg g^{-1} P Total	µg g^{-1} P Bray no. 2	µg g^{-1} Ca	µg g^{-1} Mg	µg g^{-1} K	µg g^{-1} Na	µg g^{-1} S[b]	me 100 g^{-1} CEC
Juritz (1909)	Western and southern Cape	46					160		240[a]		250			3,78
Taylor (1969)	Cape of Good Hope Nature Reserve	10	4,8		1,60				245	66	16	55	382	57,2
Neethling (1970)	Southern Cape	4	4,8		1,57	0,16			305	124	149	41	619	14,32
Kruger (1974)	Jakkalsrivier	4	4,1		6,82								2,94[c]	
Low (1975)	Jonkershoek	1	3,5	5,5		0,06		11						
	Orange Kloof	1	3,4	7,7		0,42		2						
	Riebeek Kasteel	1	3,1	12,4		0,38								99[d]
Durand (1981)	Kogelberg	2	4,1		0,58	0,035		5	33	23	14	17	87	
Low (1981)	De Tronk wet sandy plain	8	3,85	1,44		0,048	36		86[a] 44	14 19	34 19	241 24	106	
	mixed fynbos	4	3,90	1,45		0,032	20		144[a] 124	57 21	32 17	183 9	171	
S Jongens-Roberts (pers. comm.)	Bainskloof	1		5,0			22,0							
	Kirstenbosch	2		5,5			24,6							
Low (this thesis)[e]	Site 1	8	4,32	5,3		0,099	27,3	3,8						
	Site 2	8	3,45	3,0		0,046	16,9	2,8						
	Site 3	8	3,59	2,2		0,032	9,0	1,7						

[a] Total bases, rest exchangeable

[b] Total exchangeable cations

[c] me 100 g^{-1}

[d] µg g^{-1}

[e] 0-150 mm depth, mean of 4 seasons (spring 1976 to winter 1977)

TABLE 10.2 Topsoil analytical data from heathland sites in western and southern Australia.

			%	µg g^{-1}					
Author	Locality	pH	N[a]	P[a]	Ca[b]	Mg	K	Na	S[c]
Hosking and Burvill (1938)	W. Australia	4,2	0,84	20					
Hubble (1946)	N.E. Tasmania	5,9	0,083	20					
Coaldrake (1951)	S. Australia	5,9	0,013	20					
Specht and Rayson (1957)	Keith, S.E. Australia (1) Tasmania	4,7-7,9 4,0-6,5	0,003-0,013 0,02-0,46	5-90 10-90					
Specht et al. (1958)	Keith, S.E. Australia (2)	5,76	0,020	8	182	26	12	7	227
	" (3)		0,020	10	158	29	8	9	204
	" (4)		0,022	6	208	38	12	9	267
Specht et al. (1961)	Adelaide Hills, S. Australia[d]	5,70	0,074	70	617	168	110	34	929

[a] Total

[b] Exchangeable bases

[c] Total exchangeable bases

[d] Heath understorey

TABLE 10.3 Elemental content of parent material and topsoils in the western and southern Cape. Analysis by X-ray fluorescence spectrometry. Nitrogen by micro-Kjeldahl. Data derived from Low and Bristow (1983).

Element (%)	Malmesbury shale		Cape granite		Table Mountain sandstone	
	Rock	Soil	Rock	Soil	Rock	Soil
Si	30,58	40,41	34,83	30,71	44,74	43,97
N	-	0,09	-	0,14	-	0,10
P	0,06	0,02	0,07	0,04	0,02	<0,01
Ca	0,49	0,11	1,07	0,41	<0,01	0,09
Mg	1,70	0,12	0,42	0,43	0,01	0,02
K	3,15	0,66	3,46	3,45	0,23	0,02
Na	1,39	0,25	2,08	0,88	0,01	0,03

Data from Mediterranean type shrubland soils are shown in Table 10.4 and illustrate the higher levels soils from these systems possess relative to those of the Mediterranean heathlands (Tables 10.1 and 10.2). The "nutrient - poor" - "nutrient - rich", heathland - shrubland dichotomy (Low and Bristow 1983, Specht 1979) is strongly apparent when comparing Cape and Australian heathland soils with those of Mediterranean-type areas in France, California and Chile. Of particular note are the marked differences in phosphorus concentration, thought by workers such as Specht (1963, 1979) to be a major limiting element to heathland growth.

Specific quantitative soil properties were distinguishable between Site 1, and Sites 2 and 3. During winter, soil moisture status was highest in the latter two sites due to impeded drainage. Here the water table rose above the soil surface. Apart from nutrients, organic matter content was greatest in Site 1, probably due to either a higher litterfall input from a greater above-ground phytomass (Table 4.2) and/or slower decomposition rates. Soil pH was highest in Site 1 and decreased down the profile. This reflects a process of podzolisation characteristic of the Cartref soil form which has a strongly leached E horizon (Mac Vicar et al. 1977). Acid soils occur throughout heathlands of the world (Dimbleby 1952, Gimingham 1972) and are also poor in bases.

TABLE 10.4 Topsoil analytical data from Mediterranean-type ecosystems supporting shrubland vegetation.

Author	Locality	pH	OM	C	N%	[a]P	Ca	Mg	K	Na	S	CEC [d]
CALIFORNIA												
Bradbury (1977)	Echo Valley	6,9	2,8			8,0	1703	170	196	115		15,6
	Camp Pendleton	6,0	2,2			2,1	1804	732	117	207		20,9
	Cabo Colnett	5,9	1,8			28,4	361	243	274	276		10,5
	Mt Laguna	6,5	1,8			10,2	1162	61	156	138		12,0
CHILE												
Specht (1969)	San Dimas				0,144	[b]715						
Bradbury (1977)	Fundo Santa Laura	6,6	7,9			15,1	2265	231	78	115		16,5
	Papudo/Zapallar	6,0	1,3			1,8	401	122	117	253		9,7
	Cerro Potrerillo 1	6,4	0,9			10,2	701	134	117	161		8,4
	Cerro Potrerillo 2	7,6	1,1			1,0	← C a l c a r e o u s →					4,6
	Cerro del Roble	6,3	2,5			17,5	822	85	156	138		10,6
SOUTH FRANCE												
Rapp (1971)	Montpellier (1)			5,19	0,33		8206	193	504	14		
	Montpellier (2)			3,29	0,32		11537	171	266	14		
Trabaud (1983)	Montpellier	6,5-7,5		5,43	0,37		9505	250	520	23		
Lossaint (1973)	Le Raquet	7,5-7,9	8,0-9,0		[c]0,003-0,006	30-70	3500-6300	50-100	120-200	3-8		

[a] "available" form [b] total [c] mineral N [d] me = 100 g^{-1}

Organic matter, total nitrogen and total phosphorus decreased with depth (typical of heathlands - Gimingham 1972, Specht and Rayson 1957), being most evident at Site 1. This may be related to podzolisation processes which lead to eluviation of nutrients below the A horizon. Decreases with depth in coastal fynbos were also demonstrated for total P at Pella (Mitchell et al. 1984) and for total N, P Ca, Mg and K at North Pine, Kraaifontein (Low unpub. data).

N must rely on its input from atmospheric precipitation, ground-water or nitrogen-fixation of some form. Inputs of the latter two are discussed below.

Of significance are the C/N ratios of the soils which were all in excess of 24 (Site 1), 29 (Site 2) and 25 (Site 3) (Table 10.5)

TABLE 10.5 Topsoil (0-150 mm) C/N, N/P and C/P ratios for Sites 1 (Communities 1.1 and 1.2), 2 (2.1 and 2.2) and 3 (2.3 and 2.4). Ratios are means of four seasons (spring 1976 to winter 1977).

Community no.	C/N	N/P	C/P
1.1	25,1	32,3	812
1.2	28,0	41,0	1146
2.1	31,6	25,7	807
2.2	32,8	29,9	977
2.3	31,6	32,8	1031
2.4	32,5	37,8	1229

Isaac (1935) records values of 11,2 to 22,9 in agricultural and natural soils of the south-western Cape derived from a range of parent materials. He also found TMS soils to have ratios of 20 to 25 and in a few examples, greater than 50. Duchafour (1948, 1950), states that C/N ratios of heath soils are often >15 and these maybe be generally deficient in available N. For appreciable net mineralization of organic N, Harmsen and Kolenbrander (1965) maintain that the C/N ratio of decomposing organic matter must be about 20 to 25 (ie. this will provide an excess of inorganic N after utilization by the soil microflora). Under low nutrient conditions there is marked competition between vegetation and micro-organisisms for essential nutrients (such as nitrogen) (Albrecht 1957).

Very acid or anaerobic conditions (compare the high seasonal water table in Sites 2 and 3) prevent the process of nitrification (Harmsen and Kolenbrander 1965). This situation is favourable to most heterotrophs as most prefer NH_4^+ as a nitrogen source. N/P and C/P ratios are also important when considering mineralization processes in the soil. N/P may reach 20 in leached forest soils, with C/P as high as 600 (Walker 1965). Table 10.5 summarizes soil C/N, N/P and C/P ratios for topsoils from the study

sites. The high N/P and C/P ratios may indicate an intense competition between plants and micro-organisims for available nutrients. Low P supplies may also limit the accumulation of N, particularly when the P is either in an organic or unavailable mineral form (Walker 1965). For example, much of the P fraction in acid coastal fynbos soils is either organically or iron bound (Mitchell et al. 1984). Walker (1965) also quotes a situation in New Zealand where, under increasing rainfall, inorganic P decreases with increasing organic P, organic C and N.

P levels in heathlands are low (Gimingham 1972, Specht et al. (1958), and see Tables 10.1 and 10.2) and the study sites at the Cape Point Nature Reserve were no exception. Total P in Site 1 was some 1,6 and 3,0 times higher than that found in Sites 2 and 3 respectively. Drops in total P have been reported for wetter areas (Kononova 1961, Turin 1956) which may explain the differences between Sites 1 (dry), and Sites 2 and 3 (wet).

P is regarded as a critical element in heathland growth and survival (Beadle 1966, Gimingham 1972, Specht 1979). Where P availability is low in natural ecosystems, the plants generally have low P requirements and are especially adapted to utilize this available P (mechanisms for this are discussed below).

Despite the disparity in amounts of total P between Site 1, and Sites 2 and 3, Bray no. 2 P levels were somewhat similar. The ratio of Bray no. 2 to total P was higher in Sites 2 and 3, probably due to the enhanced mobility of P under wet conditions (McConaghy, in Walker (1965) (Discussion)). Wild (1958) also found that poorly drained soils in south-western Australia had low total P levels, but that dilute acid - soluble P was high.

Amounts of Bray no. 2 P (<1-5 in Site 1, <1-6 in Site 2 and <1-4 $\mu g\ g^{-1}$ in Site 3) compare with those for leached acid sand from seven soil forms at Pella (1,7 to 4,6 $\mu g\ g^{-1}$) (Mitchell et al. 1984). These concentrations are all well below minimum agricultural limits (G. Thompson pers. comm.) and also compared with those presented by Low (1975) for other TMS soils under fynbos.

Acid soils readily fix inorganic P (Jackson 1967), particularly where waterlogging occurs (this leads to the release of Al^{3+} which binds with inorganic P (Brady 1974)). trace elements such as Mo also display a decreased availability under similar conditions, although the reverse occurs for Fe, Mn, Zn and Cu (Brady 1974, Jackson 1967). P replenishment is a major problem in oligotrophic soils, particularly where the geochemical content of parent material such as TMS (see Table 10.3) is very low. Input

from TMS is further retarded due to its strong resistance to weathering (J Marchant pers. comm.). P input through precipitation has been reported by Allen (1964) (0,5), Allen et al. (1969) (0,19 - 1,00), Chapman (1967) (0,01) and Crisp (1966) (0,4 kg ha^{-1} yr^{-1}) for various British heaths. Many of these sites are relatively close to industrial areas so these figures may be on the high side. However, Jones and Woodmansee (1979) demonstrated that P input for an annual grassland ecosystem was chiefly from the atmosphere under both dry and wet conditions.

Seasonal variation in soil parameters revealed the following : seasonal fluctuation in soil moisture correlated closely with monthly rainfall (Figs. 5.1(a), 5.1(b) and 5.1(c)).

The consistent summer peak in pH (Communities 1.1 and 1.2) is probably due to the drying out of the soils which leads to a decrease in soil metabolic activity and a lower release of organic acids (Brady 1974).

Organic matter, total nitrogen and total phosphorus showed appreciable variation at certain times of the year for the whole 0-450mm profile (Figs. 5.3, 5.4 and 5.6), and total N and total P correlated significantly with organic matter. Mitchell et al. (1984) demonstrated significant

seasonal variation in total P in acid coastal fynbos soils although as in this study, there was no apparent interaction between season and depth.

There were net changes over the five seasons (winter 1976 to winter 1977) for organic matter, and total N and P (Table 10.6). Organic matter and total P in all communities showed net losses of varying degrees over this period. In Site 1, where losses of N also occurred, these may be attributed to active growth in the early stages of post-fire succession and subsequent removal of soil nutrients (Specht et al. 1958). Losses due to leaching may also have occurred during the period of study. Total N, unlike organic matter and total P at Sites 2 and 3 showed increases from winter 1976 to winter 1977. This may have been due to the high levels of nitrogen-fixation (relative to Site 1) found here (see below).

Bray no.2 P in the soil changed seasonally in Sites 2 and 3 but not Site 1, with peaks occurring in winter 1976 and summer 1977. Mitchell et al. (1984) also found seasonal variation in amounts of this form of P, but with peaks during autumn and spring in the surface layers. Seasonal increases in inorganic N were demonstrated in summer and winter in a garrigue community south of France (Lossaint 1973). Harmsen and Lindenbergh (1949) recognized

TABLE 10.6 Net gains and losses (0-450 mm) of organic matter, total nitrogen and total phosphorus between winter 1976 and winter 1977 at the three sites. Amounts in kg ha^{-1}.

		Winter 1976	Winter 1977	% loss (-) or gain (+)	Site mean	
Organic matter ($x10^4$)	1:1[a]	21,3	17,7	-16,9	-14,0	1[b]
	1:2	23,5	20,8	-11,0		
	2:1	12,8	9,3	-27,3	-29,7	2
	2:2	10,3	7,0	-32,0		
	2:3	6,2	6,0	-3,2	-3,0	3
	2:4	7,4	7,2	-2,7		
Total nitrogen	1:1	4070	4127	+1,4	-2,8	1
	1:2	4800	4466	-7,0		
	2:1	1960	2321	+1,8	+4,4	2
	2:2	1501	1606	+7,0		
	2:3	1159	1455	+25,6	+30,9	3
	2:4	1071	1459	+36,2		
Total phosphorus	1:1	109,1	98,8	-9,4	-8,7	1
	1:2	107,4	98,8	-8,0		
	2:1	67,7	64,3	-5,0	-21,9	2
	2:2	64,5	39,5	-38,8		
	2:3	43,6	33,7	-22,7	-27,7	3
	2:4	52,1	35,1	-32,6		

[a] Community number

[b] Site number

dual peaks in biological activity in late spring and early autumn. After these mineralization flushes, a release of inorganic N and P may occur, as was found for P in Sites 2 and 3. It is difficult to account for the dissimilarity in Bray no. 2 P peaks between the mountain fynbos in this study and coastal fynbos at Pella (Mitchell et al. 1984) although microbial mineralization flushes may be operative at different seasons. Further, increases in soluble P may be due to an alteration in form of P within the soil. (C Piggott pers. comm.) rather than an indication of absolute levels present in the soil.

Finally, linear regressions were performed on organic matter vs total N and total P, and Bray no. 2 P, and total P vs Bray no. 2 P, for combined 0-450mm depths at each site and over five seasons (Figs. 10.1 to 10.12 and Table D.1 in Appendix D). In organic matter vs total N and organic matter vs total P there was strong correlation ($P = < 0,001$) whereas this was not evident for organic matter vs Bray no. 2 P (Sites 1, 2 and 3 : $P = < 0,05$; $P = < 0,10$ and NS respectively). Total vs Bray no. 2 P correlations were significant ($P = < 0,001$) for Sites 1 and 2 but not for Site 3.

High correlations between total N and P, and organic matter usually exist when examining data from soils of

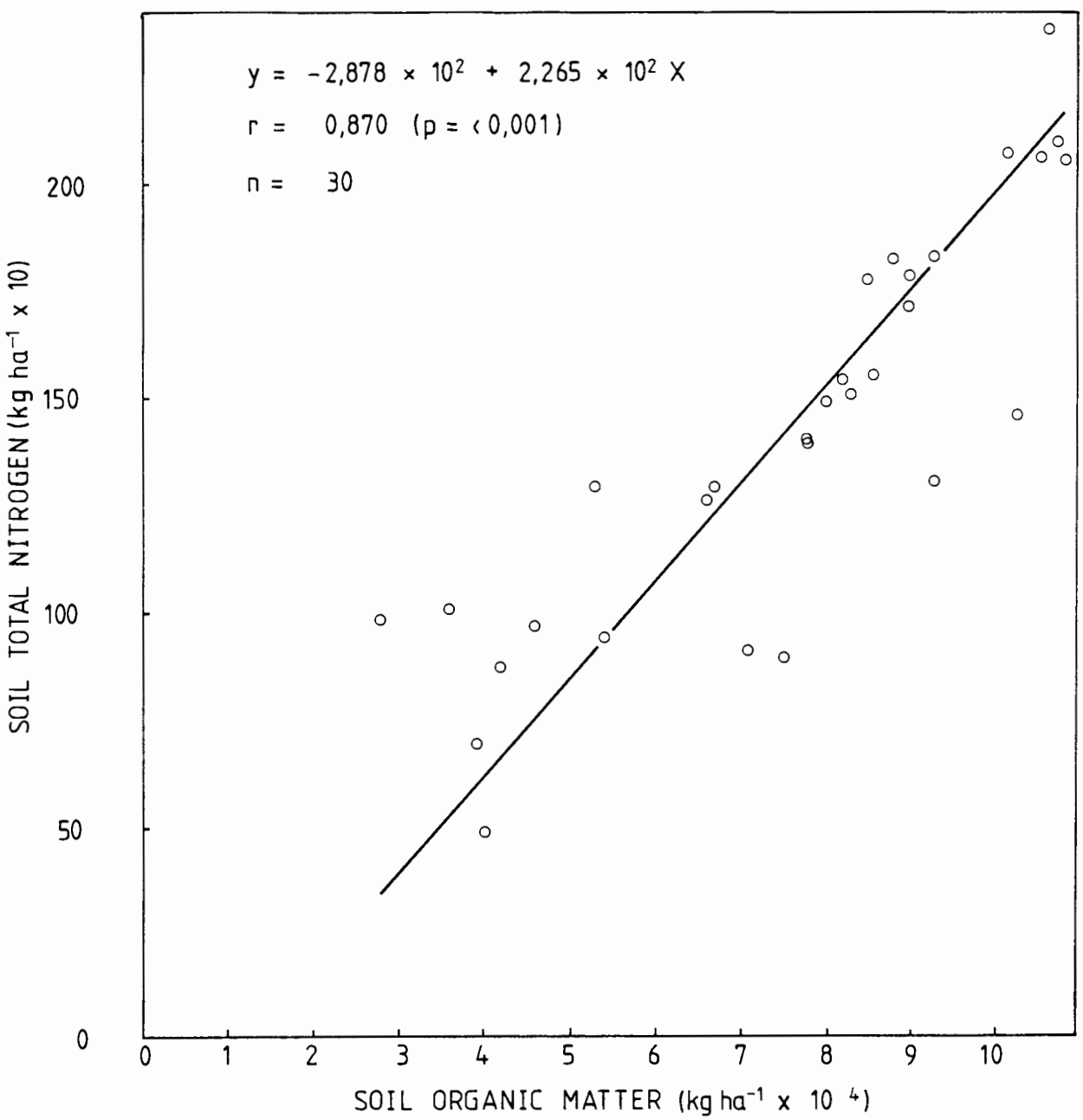


Fig.10.1 Correlation between soil organic matter and total nitrogen for Communities 1:1 and 1:2 (Site 1). Data combined from 0 –150, 150 – 300 and 300 – 450 mm depths and five seasons (Winter 1976 to Winter 1977).

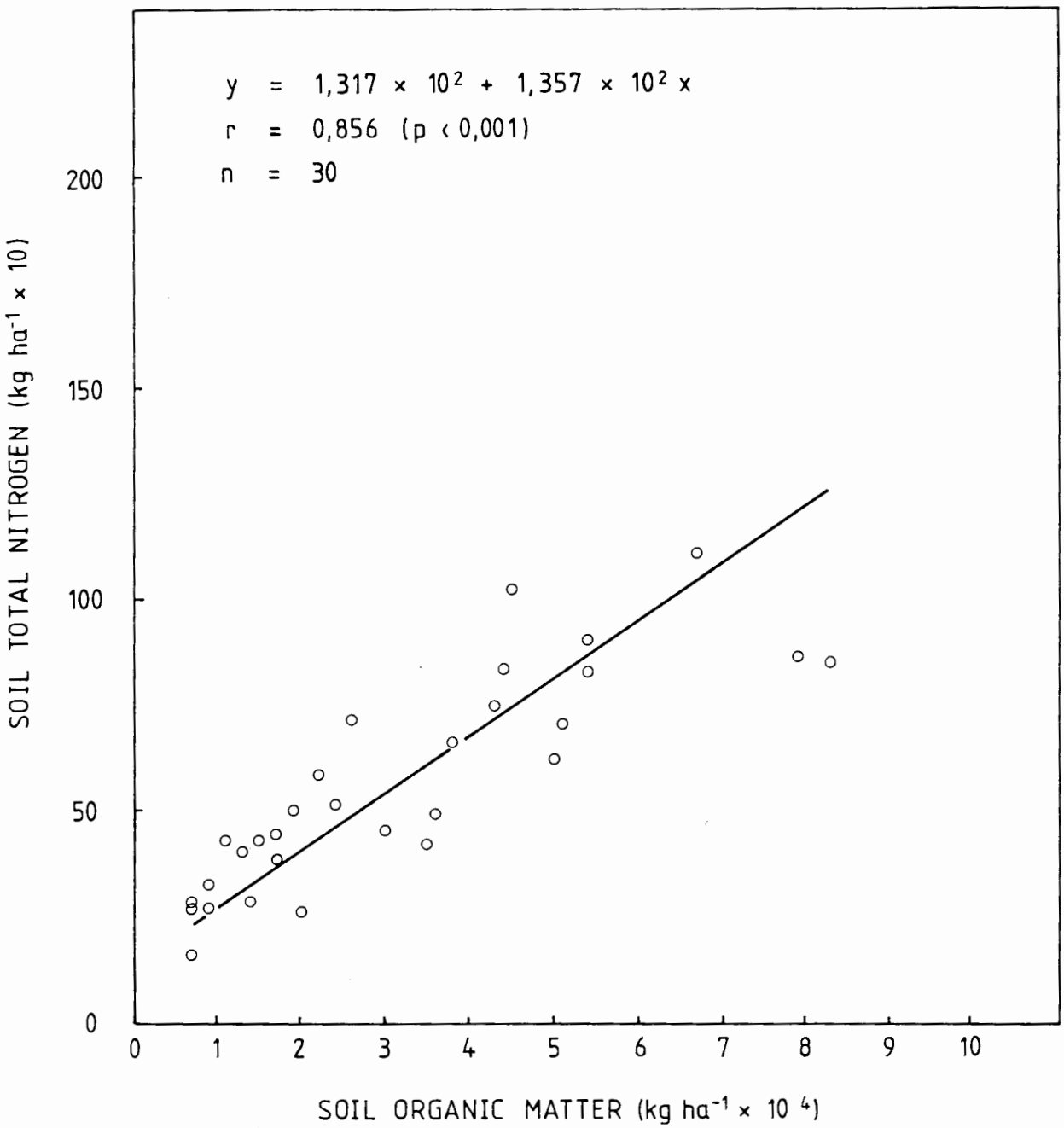


Fig.10.2 Correlation between soil organic matter and total nitrogen for Communities 2:1 and 2:2 (Site 2). Data combined from 0 – 150, 150 – 300 and 300 – 450 mm depths and five seasons (Winter 1976 to Winter 1977).

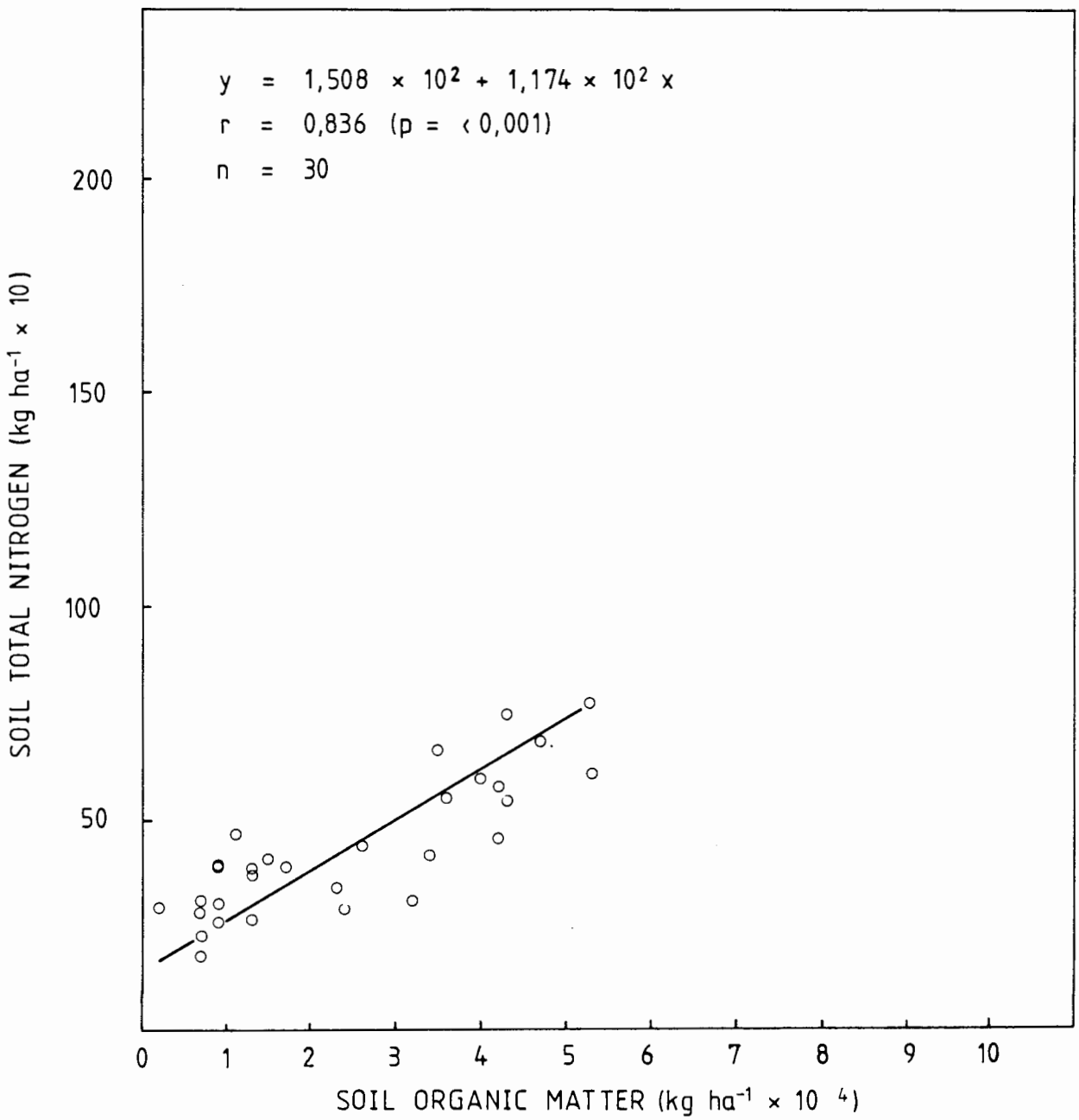


Fig.10.3 Correlation between soil organic matter and total nitrogen for Communities 2:3 and 2:4 (Site 3). Data combined from 0 – 150, 150 – 300 and 300 – 450 mm depths and five seasons (Winter 1976 to Winter 1977).

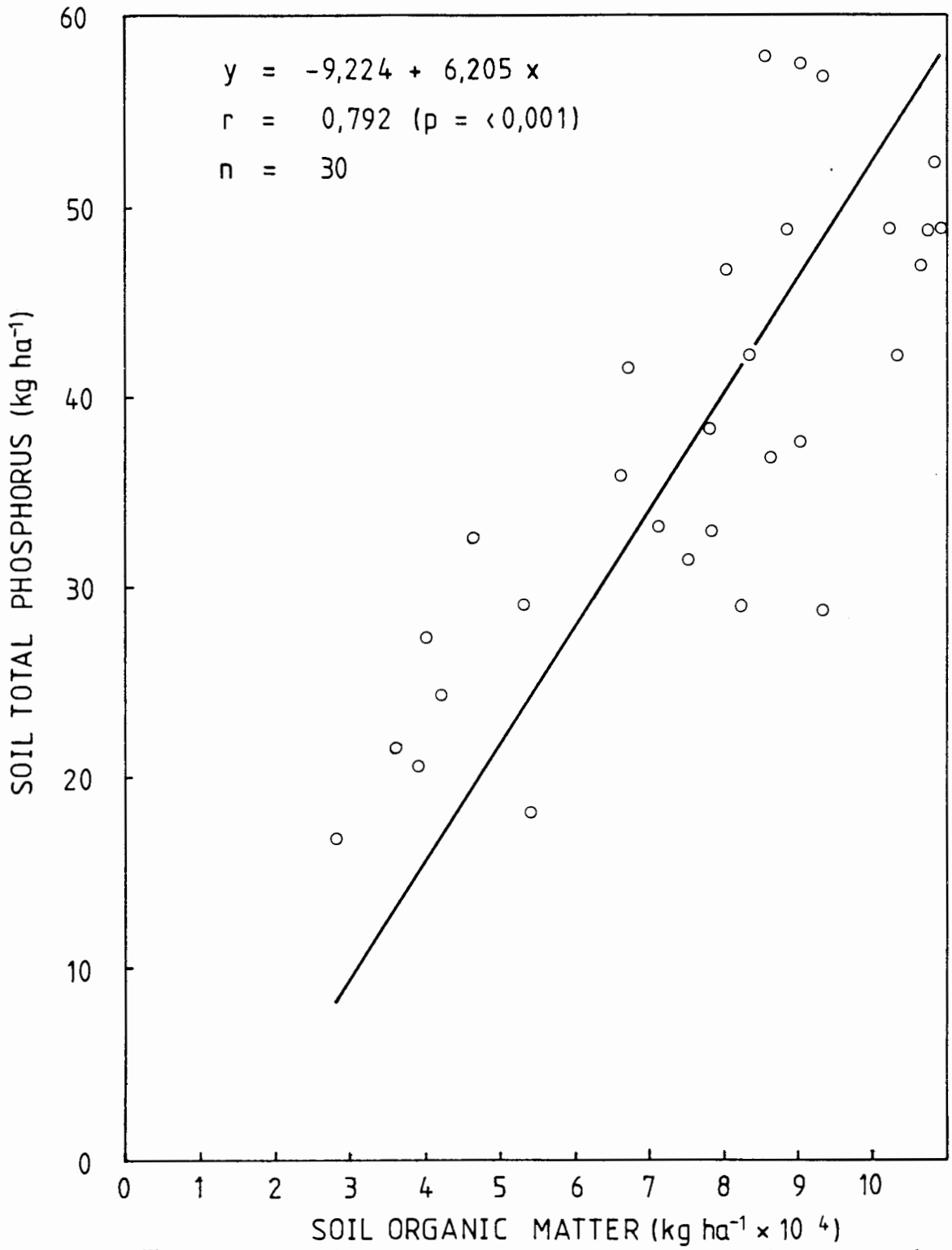


Fig.10.4 Correlation between soil organic matter and total phosphorus for Communities 1:1 and 1:2 (Site 1). Data combined from 0 – 150, 150 – 300 and 300 – 450 mm depths and five seasons (winter 1976 to winter 1977).

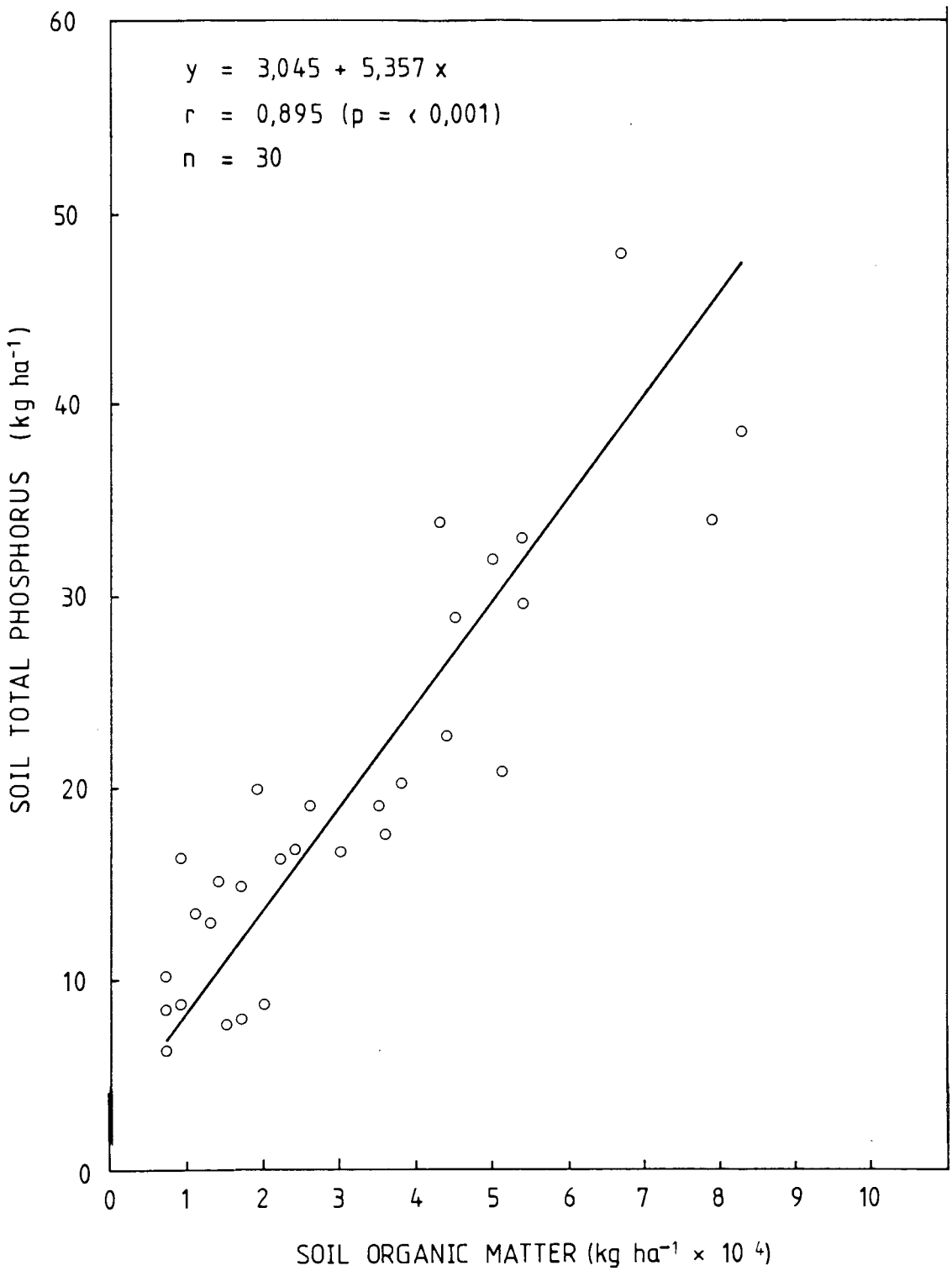


Fig.10.5 Correlation between soil organic matter and total phosphorus for Communities 2:1 and 2:2 (Site 2). Data combined from 0 –150, 150 – 300 and 300 – 450 mm depths and five seasons (winter 1976 to winter 1977).

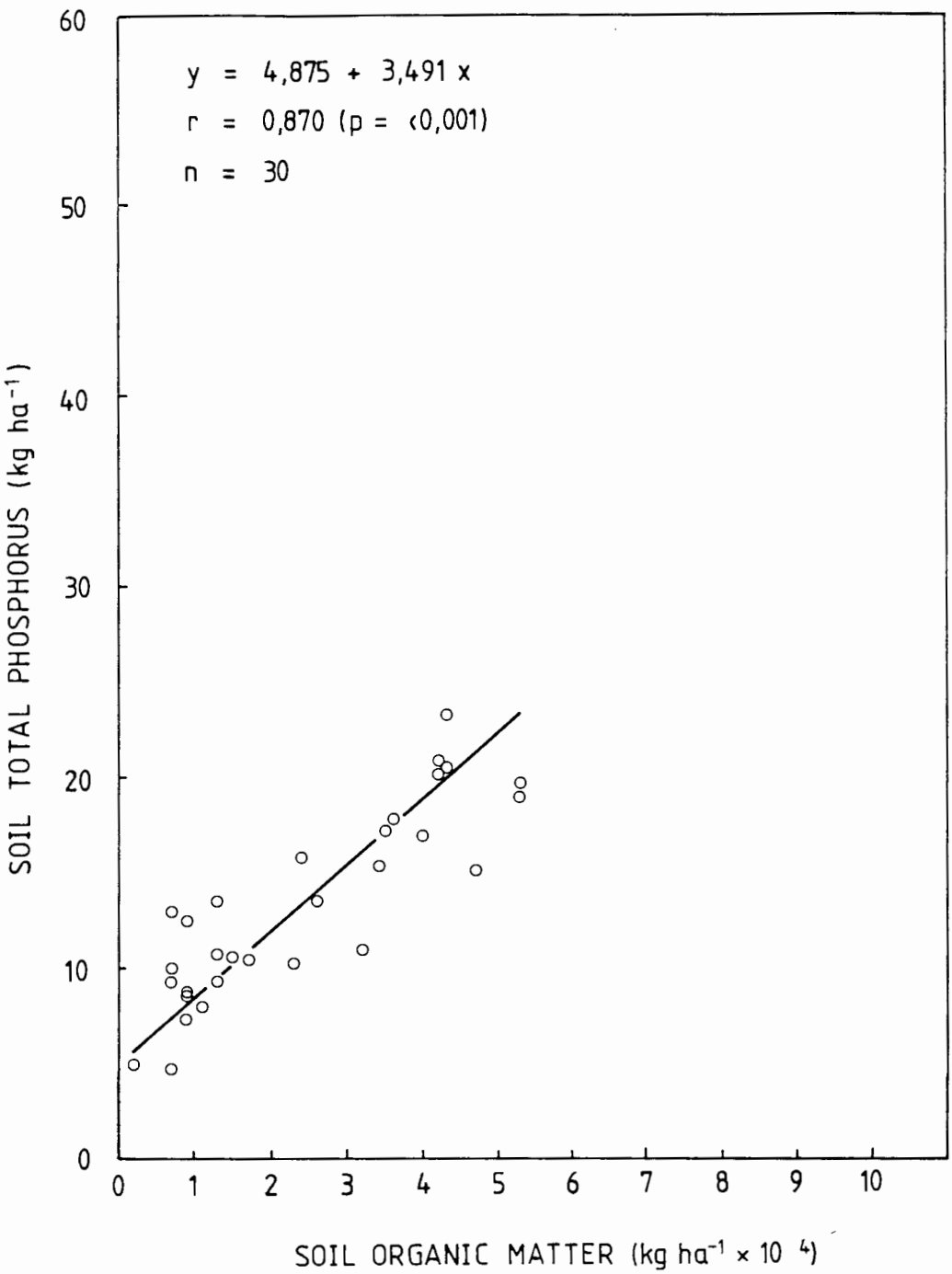


Fig.10.6 Correlation between soil organic matter and total phosphorus for Communities 2:3 and 2:4 (Site 3). Data combined from 0 – 150, 150 – 300 and 300 – 450 mm depths and five seasons (winter 1976 to winter 1977).

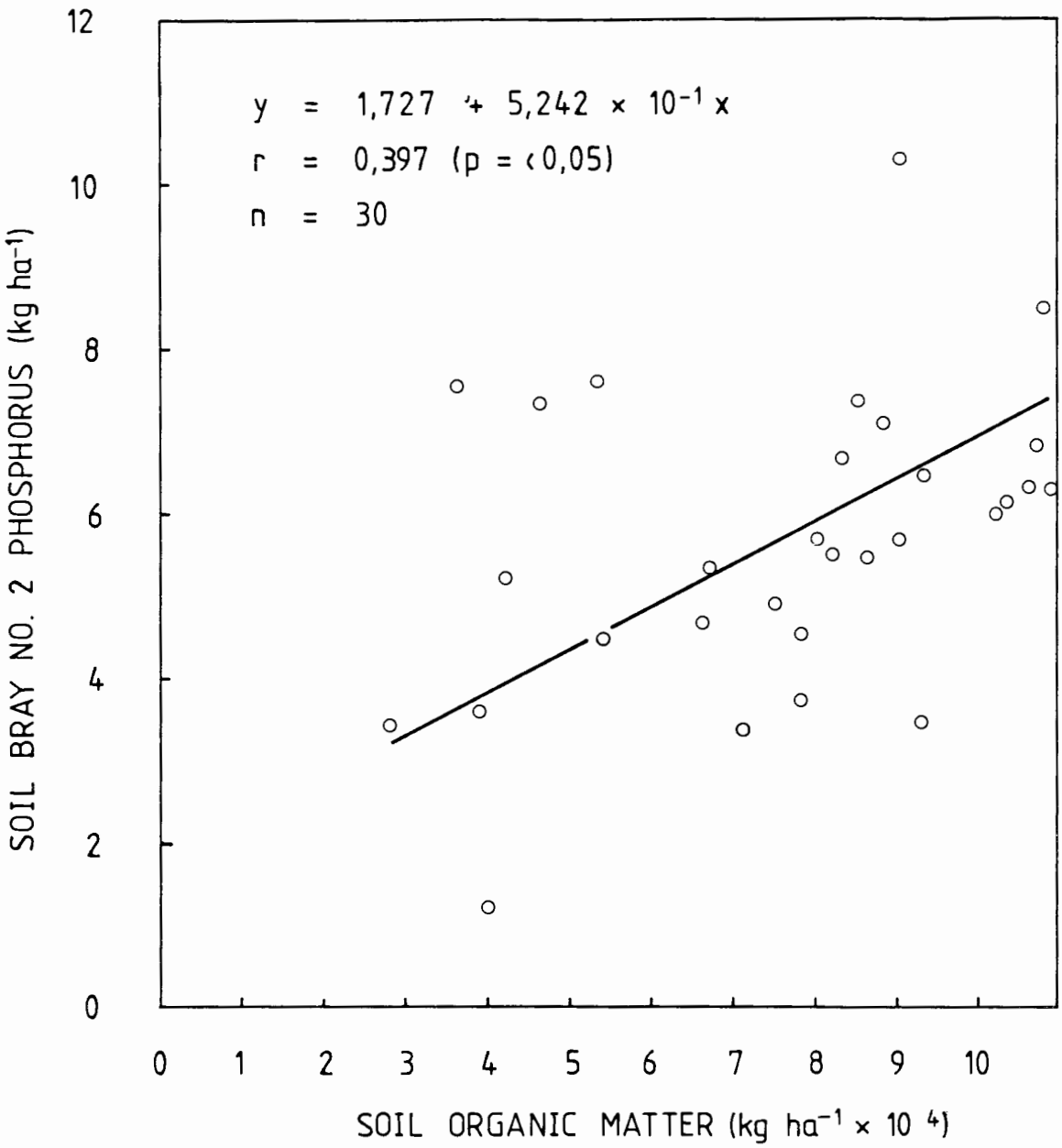


Fig.10.7 Correlation between soil organic matter and Bray no.2 P for Communities 1:1 and 1:2(Site 1). Data combined from 0 – 150, 150 – 300 and 300 – 450 mm depths and five seasons (winter 1976 to winter 1977).

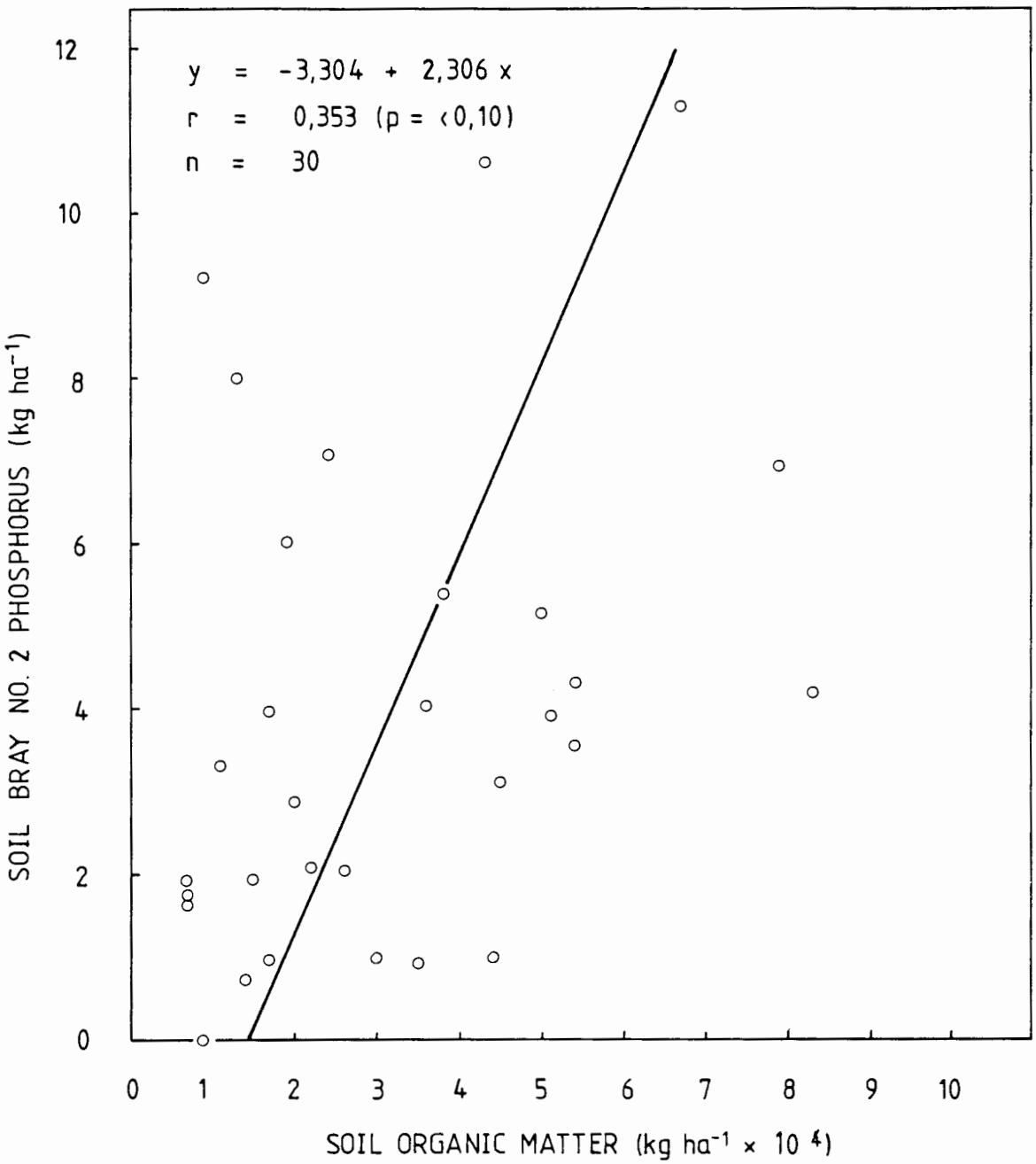


Fig.10.8 Correlation between soil organic matter and Bray no.2 P for Communities 2:1 and 2:2 (Site 2). Data combined from 0 – 150, 150 – 300 and 300 – 450 mm depths and five seasons (winter 1976 to winter 1977).

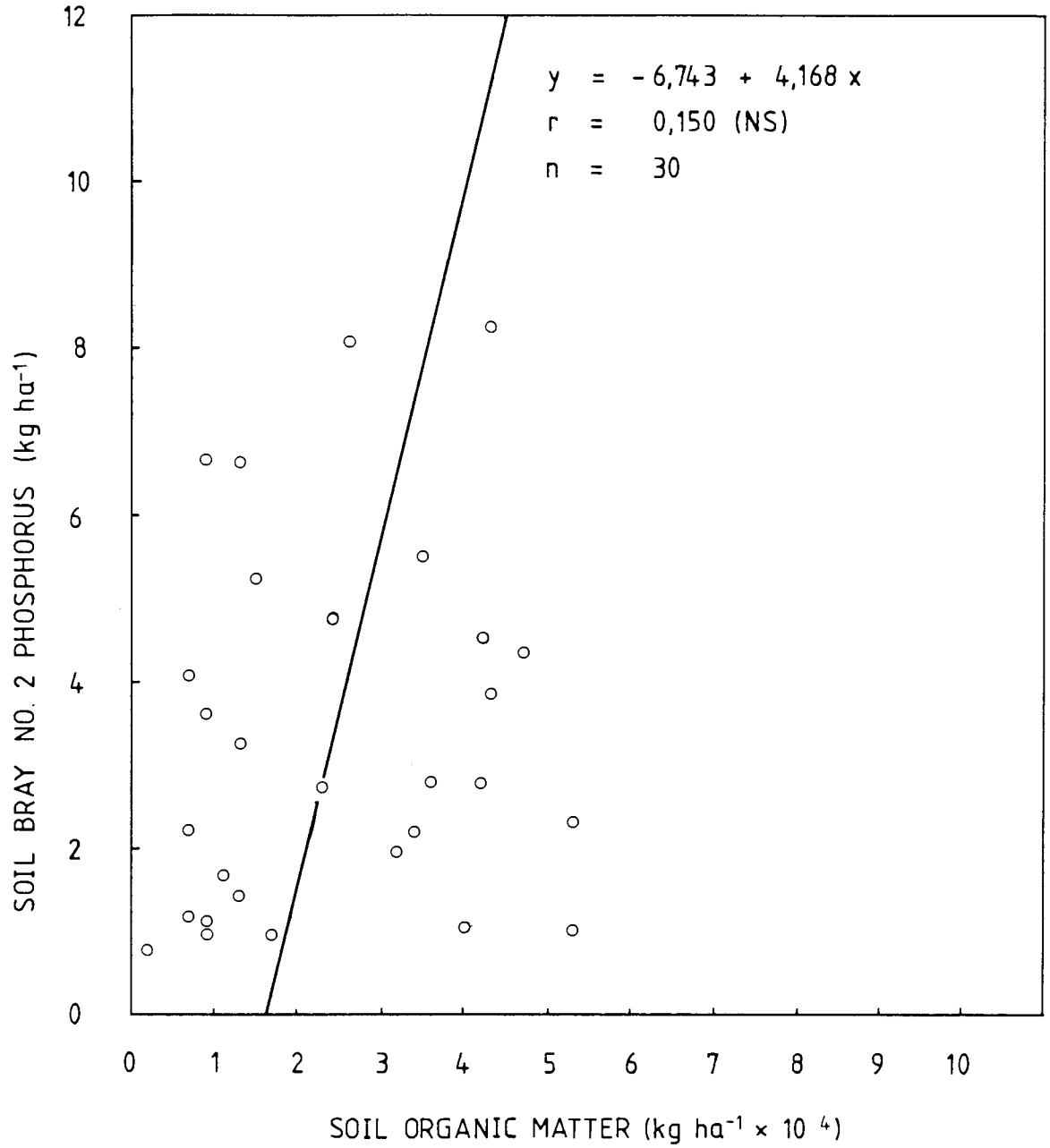


Fig.10.9 Correlation between soil organic matter and Bray no.2 phosphorus for Communities 2:3 and 2:4 (Site 3). Data combined from 0 – 150, 150 – 300 and 300 – 450 mm depths and five seasons(Winter 1976 to winter 1977).

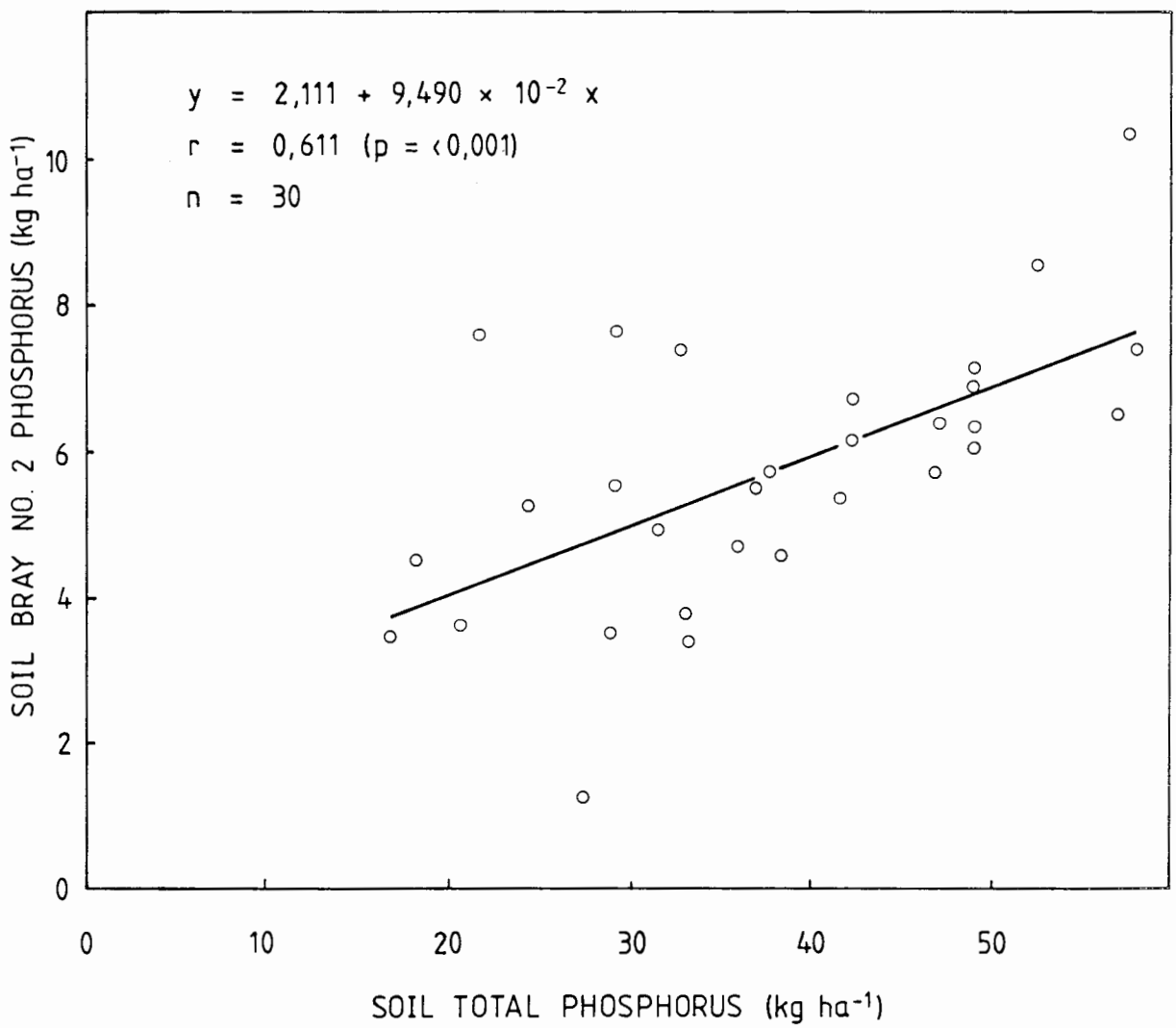


Fig.10.10 Correlation between soil total phosphorus and Bray no.2 phosphorus for Communities 1:1 and 1:2 (Site 1). Data combined from 0 – 150, 150 –300 and 300 – 450 mm depths and five seasons (winter 1976 to winter 1977).

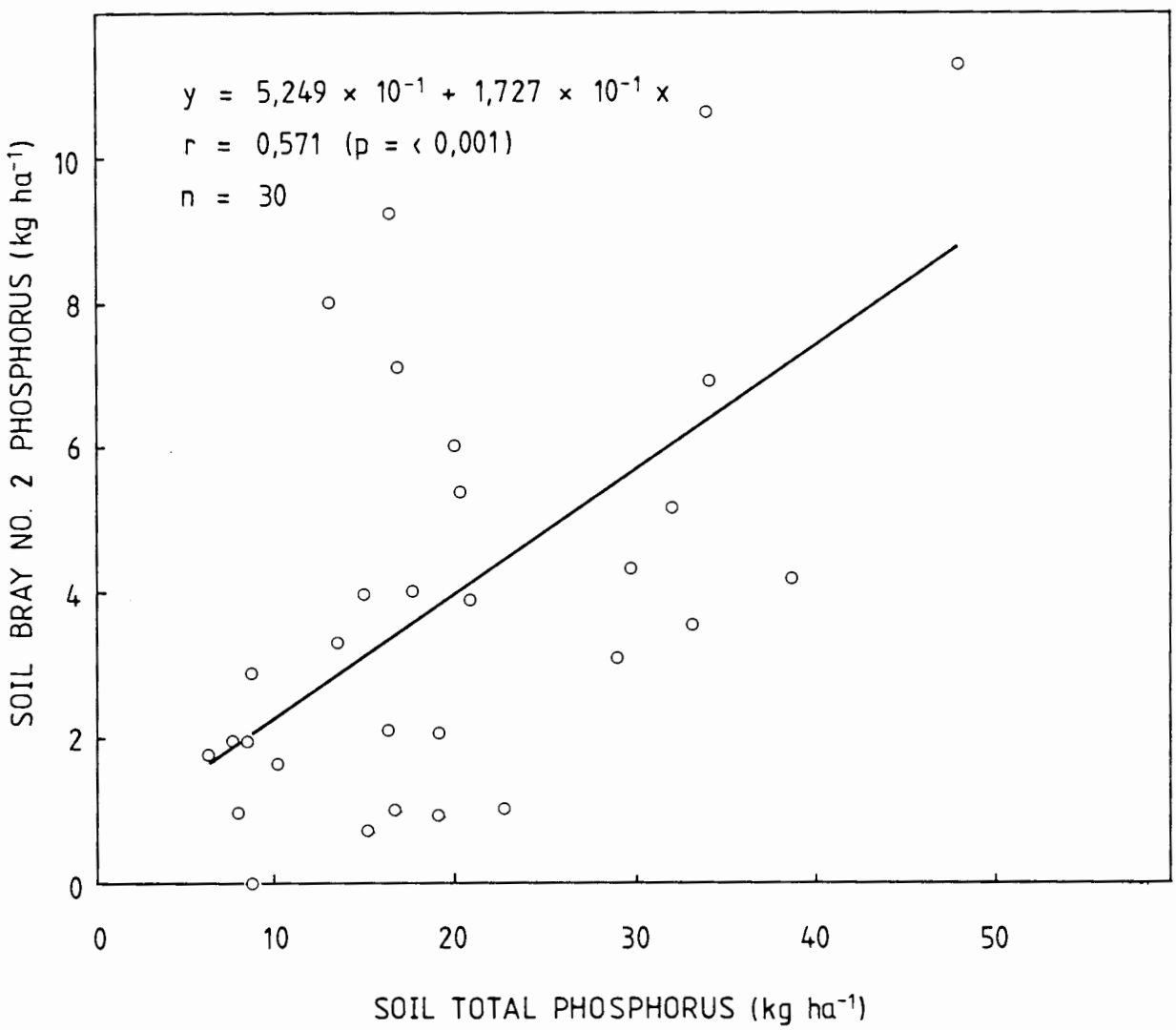


Fig.10.11 Correlation between soil organic matter and total phosphorus for Communities 2:1 and 2:2 (Site 2). Data combined from 0 – 150, 150 – 300 and 300 – 450 mm depths and five seasons (winter 1976 to winter 1977).

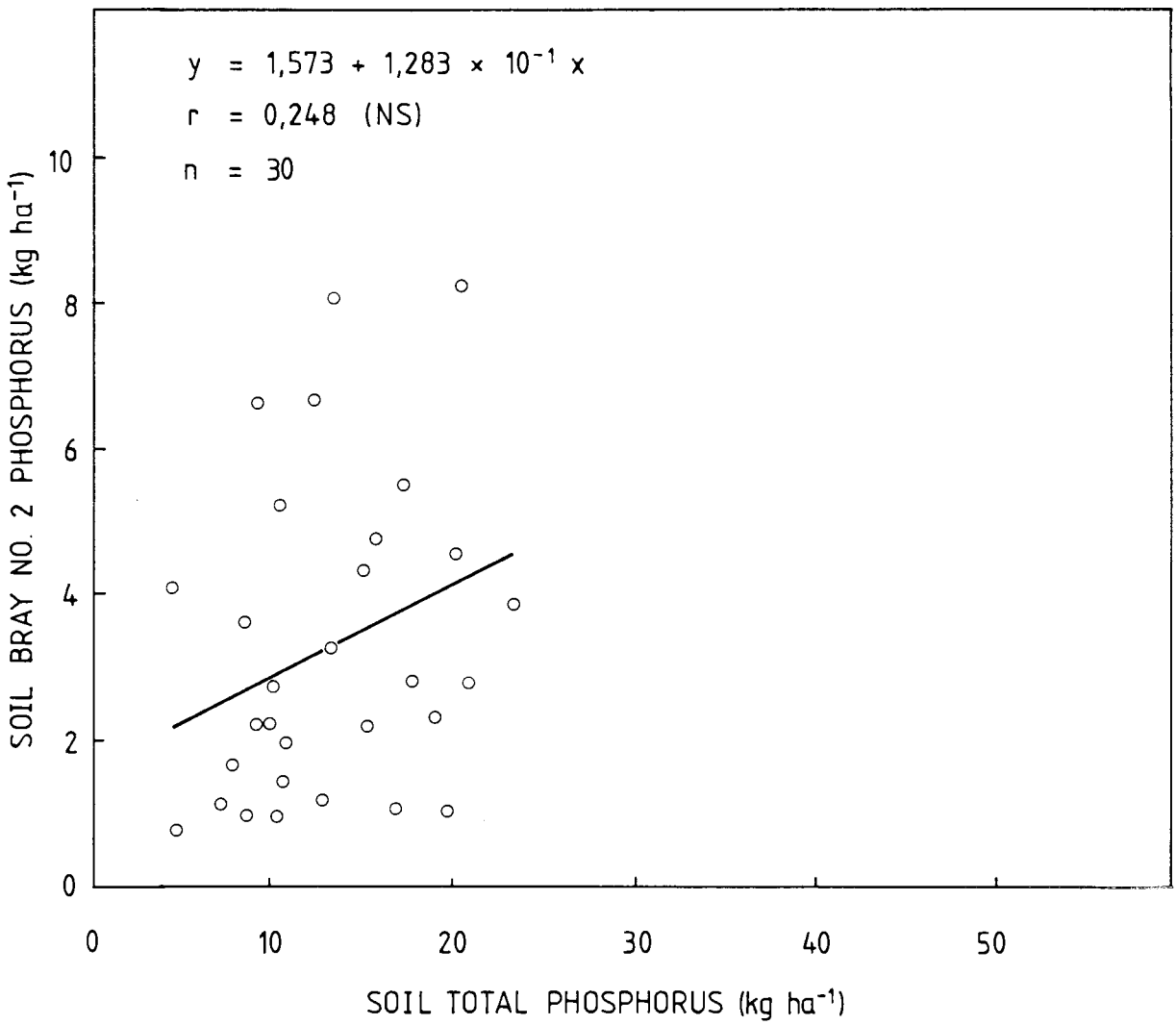


Fig.10.12 Correlation between soil total phosphorus and Bray no.2 phosphorus for Communities 2:3 and 2:4 (Site 3). Data combined from 0 – 150, 150 – 300 and 300 – 450 mm depths and five seasons (winter 1976 to winter 1977).

low nutrient status. In these systems the bulk of the available and potentially available nutrients tend to be bound up in the organic fraction of the soil, after being cycled in the plant litter. In coastal fynbos soils for example, Mitchell et al. (1984) found most of the soil P to be organically bound. These good correlations are evident in other mountain (Kruger 1974, Low 1981) and coastal (Low unpub. data) fynbos communities. Clay levels in TMS soils are negligible (Lambrechts 1979); (alternative) exchange sites such as on humic compounds exist in the soil (Brady 1974) and this may explain the slight correlation between organic matter and Bray no. 2 P. The strong correlation between total and Bray no. 2 P probably indicates a relationship between the mineralization of P compounds (predominately in organic form (Mitchell et al.1984)) and production of soluble P.

Leaf and photosynthetic stem N and P content from plants at the Cape of Good Hope Nature Reserve are similar to those from other mountain fynbos sites in the western Cape (Table 10.7). Nutrient levels were low for natural ecosystems (Loveless 1962) and also agree with the findings of Monk (1966) and Thomas (1976) for evergreen sclerophylls. Mediterranean shrubland species contain higher leaf N and P levels in the range of 0,58-1,61% N (mean = 1,01%) and 0,04-0,09% P (mean = 0,06%) for

TABLE 10.7 Leaf or photosynthetic stem nitrogen and phosphorus concentrations (mg g^{-1} dry mass) in selected mountain fynbos species.

PROTEACEAE	N	P
Leucadendron arcuatum [a]	3,50	0,344
Leucadendron salignum	3,26	0,271
Protea laurifolia	4,12	0,763
Protea nitida	3,85	0,377
Leucadendron laureolum [b] (1)	6,5	0,5
" " (2)	6,0	0,5
" " (3)	4,9	0,2
Leucospermum conocarpodendron [c]	4,52	0,186
Mimetes fimbrifolius	4,95	0,211
Leucospermum hypophyllocarpodendron [d] (Community 1.1)	5,13	0,384
Serruria furcellata (Community 1.2)	6,68	0,555
ERICACEAE		
Erica daphniflora [a]	10,45	0,510
Erica mammosa	8,87	0,513
Erica calycina [b]	7,2	0,3
Erica pulchella	6,2	0,2
Sympieza articulata	6,2	0,2
Erica clavisepala [d] (Community 2.1)	6,80	0,404
Simocheilus depressus (Community 2.3)	5,32	0,328

RESTIONACEAE	N	P
Cannamois virgata [a]	3,08	0,307
Elegia capensis (main stems)	4,76	0,173
Restio gaudichaudianus	5,60	0,308
Staberoha cernua	4,81	0,258
Elegia vaginulata [b] (1)	4,5	0,3
" " (2)	6,6	0,2
Restio egregius (1)	5,5	0,1
" " (2)	4,4	0,1
Elegia parviflora [d] (Community 2.2)	2,98	0,155
" " (Community 2.4)	4,17	0,167

a Groot Winterhoek area (Low, unpub. data)

b Kogelberg (Durand 1981)

c Cape of Good Hope Nature Reserve (Low and Von Kaschke unpub. data)

d Cape of Good Hope Nature Reserve (this study)

California, and 0,05-0,12% P (mean = 0,08%) for Chile (Mooney et al. 1977).

Elegia parviflora displayed the lowest levels of both elements and this is undoubtedly due to its growing on a highly leached, seasonally waterlogged soil. The Restionaceae appear to occupy the widest range of habitats in mountain fynbos, generally in the understorey of climax (proteoid) vegetation, in association with ericoid elements or in stands on their own (Low 1981, Taylor 1978). The latter include seasonal wet to waterlogged sandy plains and in particular mountain peaks (Low 1981, Taylor 1978) which are exposed to high rainfall and have high runoff and low infiltration rates. Low (1978) has suggested that the restioid life form is suitably adapted to a wide range of substrate nutrient concentrations which may be one explanation for its wide habitat distribution in mountain fynbos. Other advantages of this form are long retention of photosynthetic stems (Kruger 1981, Low unpub. data) (evergreeness is considered an important strategy in nutrient conservation - Thomas and Grigal (1976)). a stout rhizomatous rooting system and an ability to resprout immediately after fire.

Although seasonal plant N and P data were gathered primarily to determine annual "means" for the respective species, the data obtained revealed that concentrations of these two elements varied with the season (Fig. 6.1). This

variation probably coincides with the production of new shoots (Specht et al. 1983) although growth was not documented in these species. Nevertheless the five species investigated do show disparate flowering times (Table 10.8). Erica clavisepala exhibited a summer peak in leaf N and P which appeared to coincide with a flowering peak late in the same season, but any relation between these and growth and nutrient changes in new shoots would be highly speculative. It is of interest however that Site 1 has a different flowering rhythm from that of Sites 2 and 3 (Fig. 10.13) and this may reflect seasonal changes in for instance the availability of certain nutrients such as P.

The two major rooting forms occurring in the five species investigated were well represented in Specht and Rayson's (1957) account of the rooting systems of an Australian heath community. Species of Leucospermum and Serruria, Erica and Elegia are deep (permanent) tap-rooted, shallow tap-rooted and rhizomatous, fibrous-rooted respectively. Both the tap and fibrous systems display advantages to the plant in coping with seasonally dry topsoils and low nutrient statuses. The tap root, apart from providing mechanical support, enables the plant to search for available water at depth. Laterals radiating out from the tap root were particularly well defined in the surface layers, and lateral exploitation of these

TABLE 10.8 Flowering times of the five species investigated for plant nutrient status. Data from Adamson and Salter (1950).

Community No.	Species	Month J	F	M	A	M	J	J	A	S	O	N	D
1.1	Leucospermum hypophyllocarpodendron								+	+	+	+	+
1.2	Serruria vallaris			+	+	+	+	+	+				
2.1	Erica clavisepala		+	+	+								
2.2 & 2.4	Elegia parviflora	+	+	+									
2.3	Simocheilus depressus			+	+	+							

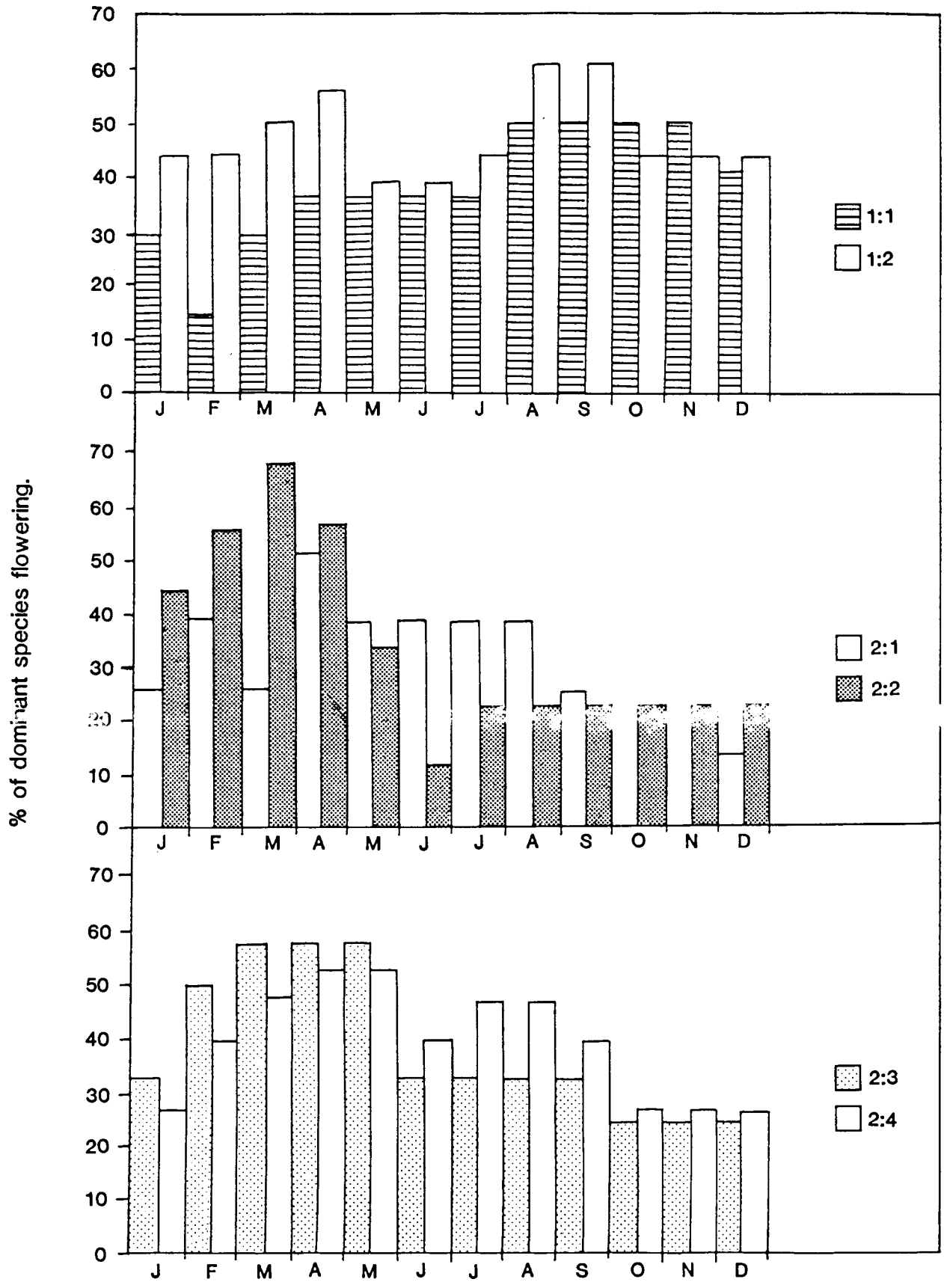


Fig. 10.13 Flowering in dominant species occurring at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Flowering times from Adamson and Salter (1950).

layers can therefore take place. Fibrous (feeding) roots arising from these laterals tend to dominate the upper soil layers in coastal fynbos at Mamre and Kraaifontein where the soil nutrient concentrations are highest (Low unpub. data).

The roots of the ericaceous species examined did not appear to be moribound when the soils were waterlogged during winter. Due to the smaller volume of the soil their roots occupied relative to Leucospermum and Serruria, their vertical and lateral root exploratory potential was not as great.

Suberization of tap and lateral roots was particularly evident in Leucospermum and Serruria and may be important in preventing water loss during the dry summer conditions. Magistad and Breazale (1929) found that unprotected root systems may lose water under extreme conditions of drought. Although Elegia lacked a tap root system it was nevertheless firmly embedded in the sandy soil. Its exceedingly dense mat of fibrous roots provided an excellent strategy for trapping water and nutrients. This system of course prevents access to moisture and nutrients deeper in the soil.

At the finer level of root structure, Elegia possessed a profusion of root hairs in localized, dense clusters which have the advantage of enhancing the total root surface area available for absorption. Known as capillaroid roots (Lamont 1983), the matted restioid root system may hold fifteen times its dry mass in water (Campbell 1981).

Proteoid roots are ubiquitous in the Proteaceae (Lamont 1983) and occur elsewhere in mountain fynbos (Low 1980). They appear to be implicit in the nutrition of this family and their production is stimulated by low P availability (Groves 1964). Jeffrey (1967) and Malajczuk and Bowen (1974) demonstrated an enhanced ability of Banksia proteoid roots to take up inorganic phosphorus but the subsequent "benefits" to plant growth are still not firmly established (Lamont 1981). Possession of these specialized rooting structures by Leucospermum and Serruria does not therefore indicate any specific advantage to these plants although they most certainly increase the area of root absorption (Lamont 1983).

Proteoid roots are confined to the surface layers of coastal fynbos (Low unpub. data) and Australian heath (Lamont 1976). It may be speculated therefore that the major zone of nutrient cycling in heaths is in the top soils, ie. in close proximity to decomposing litter and organic material in the soil. Proteoid root densities

are in fact highest where concentrations of litter and humus are greatest in the soil (Lamont 1983). This may parallel the situation for "tight" nutrient cycling in Amazonian forests where there appears to be almost direct transfer of nutrients from decomposing litter to the roots (Stark and Jordan 1978).

The endotrophic mycorrhizal associations demonstrated in Erica and Simocheilus in this study are essential to the survival of the Ericaceae (Malajczuk and Lamont 1981) particularly as the order Ericales does not possess root hairs (Brook 1952, Malajczuk and Lamont 1981). Most, if not all Ericaceae are mycorrhizal (Baylis 1967, Malajczuk and Lamont 1981, Pearson and Read 1973) and members of this group are prominent if not locally dominant in mountain and coastal fynbos (Taylor 1978). Robinson (1973) found all Erica spp. he examined in southern Africa to possess endophytes while Low (1980) found 80% of plants investigated in mountain fynbos, renosterveld, coastal fynbos and karoo vegetation to be mycorrhizal. This preliminary work indicates that the symbiosis is present if not common in other plant groups in the western Cape.

Pearson and Read (1973) maintain that mycorrhizal infections must enhance the release (due to external phosphatase activity), absorption and translocation of P from low P soils. This is of great importance as P

mineralising bacteria are impeded in acid soils (Jackson 1967). Apart from N (Read and Stribley (1974), mycorrhiza may also enhance the ability of the plant to take up Ca^{2+} and Mg^{2+} (Harley 1969). Levels of exchangeable calcium in particular are extremely low in heath soils (Gimingham 1972).

Initial observations on fynbos rooting systems and specialized structures or symbioses would seem to indicate that they are instrumental in ensuring plant survival in soils which are low in nutrients and display low moisture regimes in summer.

Turning to the soil microbiological aspects of the study, the number of 41 taxonomic entities isolated compares with the 52 species (soil plate method) found in a 760mm podzolic profile under Calluna heath in Britain (Sewell 1959a). 15 of these were Penicillium spp. (13 reported from the present study) and no Aspergillus spp. were recorded. In a further investigation, Sewell (1959b) found 185 species to occur in the soil of a Calluna community. McLennan and Ducker (1954) working in an Australian sand heath at Frankston isolated 107 species from various intervals to about 900mm depth. Mortierella ramanniana was the dominant species whereas Penicillium was the dominant genus (37 species). Unlike the study at the Cape of Good Hope Nature Reserve, Aspergillus was fairly conspicuous and, according to Mc Lennan and

Ducker (1954), "....provided forms which characterized this particular soil." Thrower (1954) in his work on a Victorian heath, demonstrated the presence of some 52 species from the free soil and the rhizospheres of the plants investigated.

Each of the above studies reflected its own particular soil microfungal population, a characteristic also evident in non-heath ecosystems. Wicklow et al. (1974) for example found there was a strong correlation between soil fungal species composition and the dominant vascular vegetation. This probably explains the major mycofloral differences between Sites 1, and Sites 2 and 3 (Table 8.2, Fig 8.1) and possibly those between Sites 2 and 3, despite overall structural similarities in the vegetation. Gimingham (1972) claims that fungal populations in heath soils are richer than those of bacteria and this has been confirmed by Low (unpub. data) in a separate investigation at the study sites (Table 10.9). In the latter, fungal colony numbers were always greater than those of the bacteria and actinomycetes and this demonstrates the supressive influence acid soils tend to have on these two groups of microorganisms. According to Gray and Williams (1971), high C/N ratios in the soil (Table 10.5) prevent many species from developing thick walled chlamydospheres and hence species numbers are low

TABLE 10.9 Numbers (per g dry soil) of fungal and bacterial/actinomycete colonies at different depths in the six communities studied. Isolation by dilution plate (x 10^{-3}). Numbers represent means of 5 replicates per each depth (Low unpub. data).

Community no.	Depth (mm)	Fungi	Bacteria/actinomycetes
1.1	75	47500	4250
	225	32000	5600
	375	27200	3200
1.2	75	41600	5600
	225	28000	4400
	375	23200	4600
2.1	75	21500	800
	225	9500	1200
	375	4800	2200
2.2	75	11600	1000
	225	2800	600
	375	1200	200
2.3	75	18500	1400
	225	12000	2600
	375	8200	2200
2.4	75	5000	600
	225	3400	600
	375	6000	600

relative to other more fertile ecosystems. Borut (1960) isolated 80 species from arid soils in Israel and noted that most of these were of world-wide occurrence. Low species numbers (70) were also recorded for an Indiana sand dune (Wohlrab et al. 1963), while Widden and Parkinson (1973) found some 76 species occurring in a sandy conifer system. Where soil variability or fertility was higher, species numbers were much greater such as in an acid and alkaline dune system (200 species - Brown 1958) and in northern Wisconsin conifer hardwood forests (476 species - Christensen 1969).

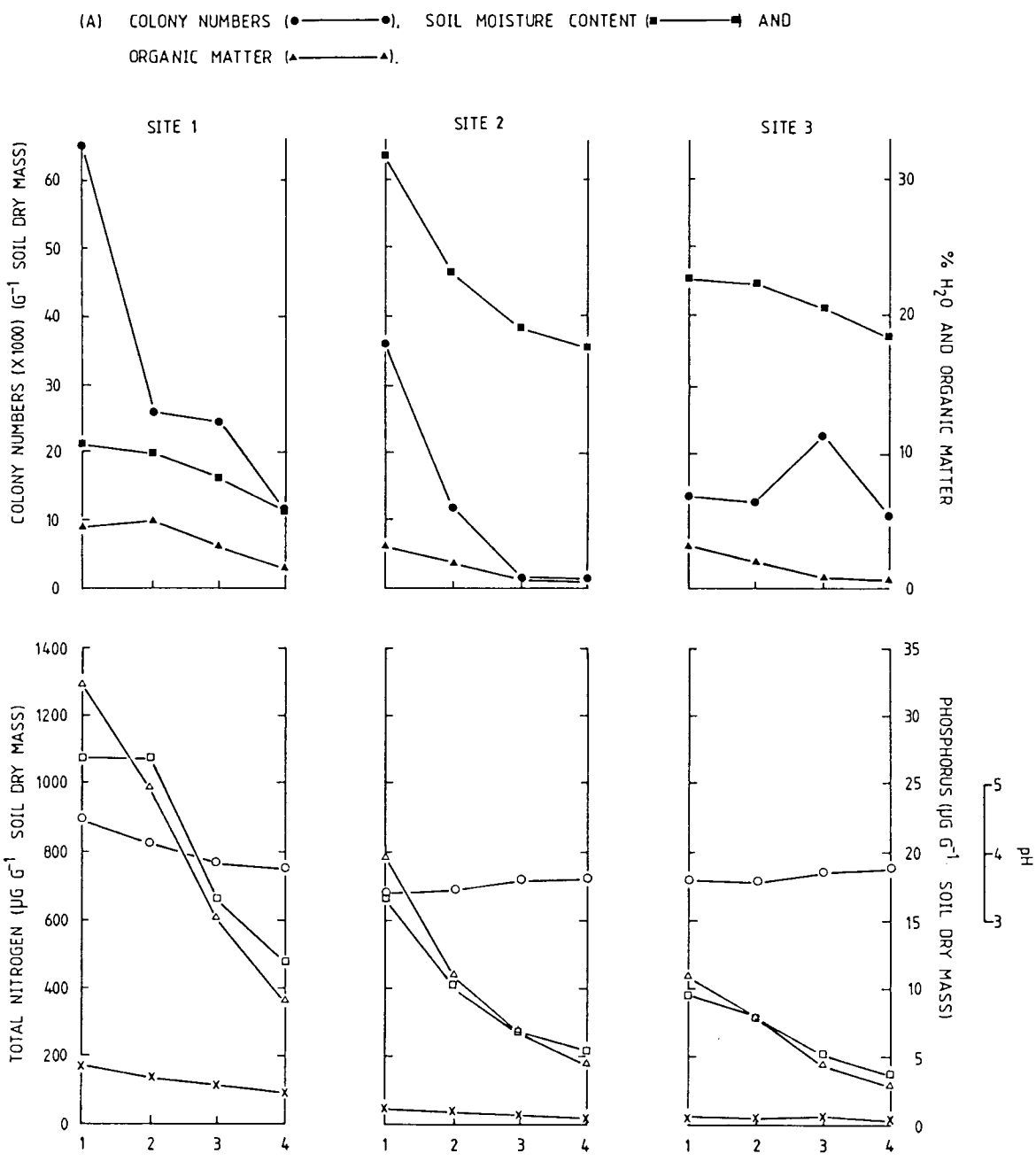
A further prerequisite for fungal survival in the sandy soils of this study, is the ability to endure summer moisture deficits, particularly in drier habitats (see for example Site 1 soil moisture contents in Fig. 5.1(a)). Penicillium spp. are renowned for their tolerance of very negative water potentials (Gray and Williams 1971) and this may explain their general ubiquitous occurrence and high species diversity under heath vegetation of seasonally dry soils.

Whatever the species composition in the various heath sites discussed above, it does appear to be characterized by genera such as Mucor, Mortierella and Trichoderma which tend to predominate at low pH's in podzols (Williams and

Parkinson 1964). Penicillium, Mucor, Trichoderma and Absidia which all occurred in this study, are also primary colonizers in acid conditions (Gray and Williams 1971) due to rapid spore germination and mycelial growth (Garrett 1951).

It is important to note Griffin's (1972) statement that ".... the basic data of fungal ecology are only as good as the techniques used to produce a description of the pattern of fungal activity in time and space." Other studies such as that of McLennan and Ducker (1954) used far greater replication and this would also increase the chance of isolating additional species.

Total numbers for Site 1 compared with those obtained by McLennan and Ducker (1954), who used the direct observational method of Jones and Mollison (1948). There was a dramatic decrease in numbers with depth in Site 1. This phenomenon has been observed by workers such as Burges (1939), Timonin (1938) and Waksman (1944), and organic matter appears to be the most important factor governing colony numbers. Meiklejohn (1957) and Warcup (1957) stated that distribution of fungal numbers was also dependent on the availability of nutrients. Fig. 10.14 presents the relationship between colony numbers and various soil factors. Soil analyses are taken from the winter 1977 sample (fungi isolated at the end of June 1977)



Numbers 1 to 4 along the horizontal axes refer to specific depths (fungi - 25; 100; 225 and 375 mm) (soil analytical parameters - 0-50; 50-150; 150-300 and 300-450 mm).

Fig. 10.14 **Variations in fungal colony number and soil analytical parameters down respective profiles in Sites 1,2 and 3.**

when the top soil (0-150mm) was subsampled from 0-50 and 50-150mm depths. Regressions of fungal numbers with organic matter, N and both forms of P were highly significant ($P \leq 0,001$).

In the nitrogen-fixation aspect of the study presence of Azotobacteriaceae was not confirmed, but members of this family have been isolated from other soils in South Africa. Saubert and Grobbelaar (1962) isolated Azotobacter and Beijerinckia from a farm soil near Naboomspruit, Transvaal and both species were shown to fix gaseous nitrogen. Strijdom (1965) isolated Beijerinckia from 90% of 73 non-lateritic soils near Rustenberg, Transvaal. Azotobacter was also present in many of the samples. In his study on the Azotobacteriaceae in South African soils, Becking (1959) could not isolate either of these genera from natural soils at Jonkershoek and Hout Bay, although both were found in a garden soil at Tokai. Similarly Strijdom and Steenkamp (1967) failed to isolate Beijerinckia from soils in the vicinity of Stellenbosch. Low (1975) however found Azotobacter and Beijerinckia to occur respectively in 13 and 12 out of 29 coastal and inland soils around Cape Town which chiefly supported indigenous vegetation. Members of the Microbiology Department, University of Cape Town, have also isolated genera of the Azotobacteriaceae in garden soils on the University of Cape Town campus (J. Lomberg pers. comm.).

Detection of both these genera thus seems to be erratic and additional methodology such as the use of agar plates with a similar chemical composition to the liquid media used, might be necessary. However, isolation of a certain group of non-symbiotic nitrogen-fixing bacteria does not necessarily imply any role in this process. Ideally other potential free-living nitrogen-fixing bacteria should be examined and their nitrogen-fixing ability investigated under conditions approximating the soils from which they are isolated. It should be emphasized that genera such as Azotobacter do not compete successfully with other microorganisms in the absence of sufficient available inorganic ions for example, P and K (Katznelson 1940). Presence of Azotobacter is also dependent on soil pH as acid soils tend to exclude it (Jurgensen and Davy 1970). Although Beijerinckia grows well under acid conditions (Jurgensen and Davy 1970) it is negatively affected by extremely dry soil conditions which would occur in the study sites in summer, and is the case for acid European soils (Becking 1961a).

There are conflicting reports on the contribution of non-symbiotic nitrogen-fixing bacteria to natural soil systems. Tribe (1964) maintained that this group probably fix little nitrogen. Jurgensen (1973) concurred, stating that it is uncertain whether their contribution is significant or not. He added that it is generally

conceded that nitrogen additions in arable soils are small. Steyn and Delwiche (1970) however claimed that free-living bacteria contribute significantly to N input in infertile soils. Moore (1963) found that non-symbiotic nitrogen-fixers were the major cause of N increases in grassland on a latosolic soil. Free-living nitrogen-fixation does occur in acid podzols under heath vegetation (Metcalfe and Chayen 1954). Azotobacter is probably of little significance here or in other systems (Jensen 1965, Virtanen and Miettinen 1963).

Nitrogen-fixation has been demonstrated for all sites investigated using the acetylene reduction assay. A linear regression analysis of soil moisture content vs nitrogen fixed gave an R coefficient of 1,00 ($y = 2,65 + 0,10x$; $P = <0,001$ for $n = 3$), which indicates moisture is an important factor governing this process. Beijerinckia survival for example is greatly affected when soils are allowed to dry out (Becking 1961). In addition under experimental conditions, Magdoff and Bouldin (1970) found nitrogen-fixation to be greatest at the top of a waterlogged soil. Highest values for nitrogen-fixation in the present study were found at Site 2 which had the wettest soils. High levels of nitrogen-fixation are also associated with low amounts of soil N (Moore 1966). Soils in this study are characterized by low nitrogen levels and in addition would have NH_4^+ as the dominant

ion (Brady 1974). Low levels of this form of N (typical of fynbos soils - W. Stock pers. comm.) promote nitrogen-fixation (Patil et al. 1967).

Deficiencies in micronutrients such as molybdenum (essential for nitrogen-fixation - Becking 1961b) are common in TMS soils of the western Cape (C. Beyers pers. comm., Schütte 1960). Molybdenum may in fact be a limiting element in acid soils (Chapman 1965) and its availability decreases appreciably with decreasing pH (Becking 1962). Further, the low availability of P in these soils may be another limiting factor to nitrogen-fixation although available P requirements can be as low as 6 mg $100kg^{-1}$ soil(0,06 ppm) for blue-green algae (Okuda and Yamaguchi 1956). Nitrogen-fixation in marine algae species may also decrease due to low availability of P (Vanderhoef et al. 1972), while Walker (1965) reported that free-living nitrogen-fixation in soils is restricted for the same reason.

Rates of nitrogen-fixation at the Cape Point Nature Reserve, at least in Site 3, are comparable with those of other ecosystems (Table 10.10). However care must be taken in drawing conclusions for estimates of annual rates of nitrogen-fixation based upon acetylene reduction assays carried out over a short period of the year. Assuming that the nitrogen-fixation tests were carried out during a period of optimal soil moisture content and temperature

TABLE 10.10 Amounts of nitrogen fixed by non-symbiotic soil bacteria in various natural systems.

Reference	System	Nitrogen fixed
Tjepkema and Evans (1976)	Juncus wetland, Oregon	0,8 kg ha^{-1} yr^{-1} (N_2 incubation) 0,5 kg ha^{-1} yr^{-1} (O_2 incubation)
Tjepkema and Burris (1976)	Relic prairie soil, Wisconsin	c.9 kg ha^{-1} yr^{-1}
Waughman (1972)	Dune system, Durham	(0,16 µ mol g soil dry mass $^{-1}$ h^{-1})
Koch and Oya (1974)	Hawaian pasture (unnatural)	0-0,25 kg ha^{-1} day $^{-1}$ (x365 = o-91,3 kg ha^{-1} yr^{-1})
Line and Loutit (1973)	Tussock grassland, Rock and Pillar Range	0-5,9 kg ha^{-1} yr^{-1}
Lockyer and Cowling (1977)	Oak wood and natural grassland, Britain	0-3,0 kg^{-1} ha^{-1} yr^{-1}
Steyn and Delwiche (1970)	Grassland, California	2,0 kg ha^{-1} yr^{-1} (max. fixation)
Low, this study	Site 1	0,1 g ha^{-1} day^{-1} (x365 = 0,04 kg ha^{-1} yr^{-1})
	Site 2	153,8 g ha^{-1} day^{-1} (x365 = 56,14 kg ha^{-1} yr^{-1})
	Site 3	8,6 g ha^{-1} day^{-1} (x365 = 3,14 kg ha^{-1} yr^{-1})

(ie. during spring), it is reasonable to speculate that this period may only reflect 3 or at best 4 months of the year. Nitrogen-fixation rates might thus only be in the region of 14 or 19 kg ha^{-1} yr^{-1} for Site 2 (1,6 or 2,2% of topsoil total N) and 0,75 or 1,05 kg ha^{-1} yr^{-1} for Site 3 (0,1 or 0,2% of topsoil total N). A seasonal study would be necessary to confirm monthly changes; nitrogen does decrease as soils dry out and the process is temperature dependent during the early spring period (Vlassak et al. 1973).

Since genera from the Azotobacteriaceae were not isolated from the soils, obligate aerobes or facultative anaerobes may be chiefly responsible for free-living nitrogen-fixation. Non-photosynthetic anaerobes for example may be important in soils (Lockyer and Cowling 1977). Clostridia enjoy anaerobic conditions and produce highly resistant endospores when the soil dries out (Jurgensen and Davey 1970). Nitrogen-fixing members of the Clostridia group are also found in aerobic soils (Chang and Knowles 1965, Jensen and Swaby 1940, Rice et al. 1967). Survival of these microorganisms may depend on the anaerobic plant rhizospheres (Jurgensen 1970) and stimulate clostridial growth (Katznelson 1946) due to high O_2

utilization by the plant root or the latter's secretion of reducing substances (Rovira 1965).

Although Haxen (1978) has demonstrated a local indigenous legume (Podalyria calyptrata) to possess nodules capable of reducing acetylene and western Cape Myrica spp. have been shown to fix nitrogen (Van Ryssen and Grobbelaar 1970), the importance of legumes in mountain fynbos is small. Apart from localized stands of eg. Aspalathus, Podalyria, Psoralea and Virgilia, they tend to be infrequent. However they often are found during the earlier stages of regeneration after fire, when nitrogen-fixation might be essential in the pioneering community. On the Cape Peninsula only 145 leguminous species (5,5% of the total) are found, while on Sites 1,2 and 3 only one species (Aspalathus capensis) occurred, and this possessed low cover-abundance values and was confined to Community 1.2.

Free-living nitrogen-fixation may thus be an extremely important if not obligatory means of nitrogen input in the fynbos ecosystem.

CHAPTER 11

CONCLUSIONS

1. The results of the study indicate that the mountain fynbos communities investigated at the Cape Point Nature Reserve possess soil chemical constitutions which are similar to the oligotrophic heaths found elsewhere in the Cape, Britain and Australia.

2. Low soil N and P levels appear to be responsible for low leaf (photosynthetic stem) N and P concentrations which are typical of sclerophyllous heath vegetation.

3. The rooting morphologies and the presence of specialized structures and mycorrhizal symbioses appear to reflect an ecological situation where efficient uptake of nutrients as well as moisture is paramount to plant survival in a seasonally dry, low nutrient substrate.

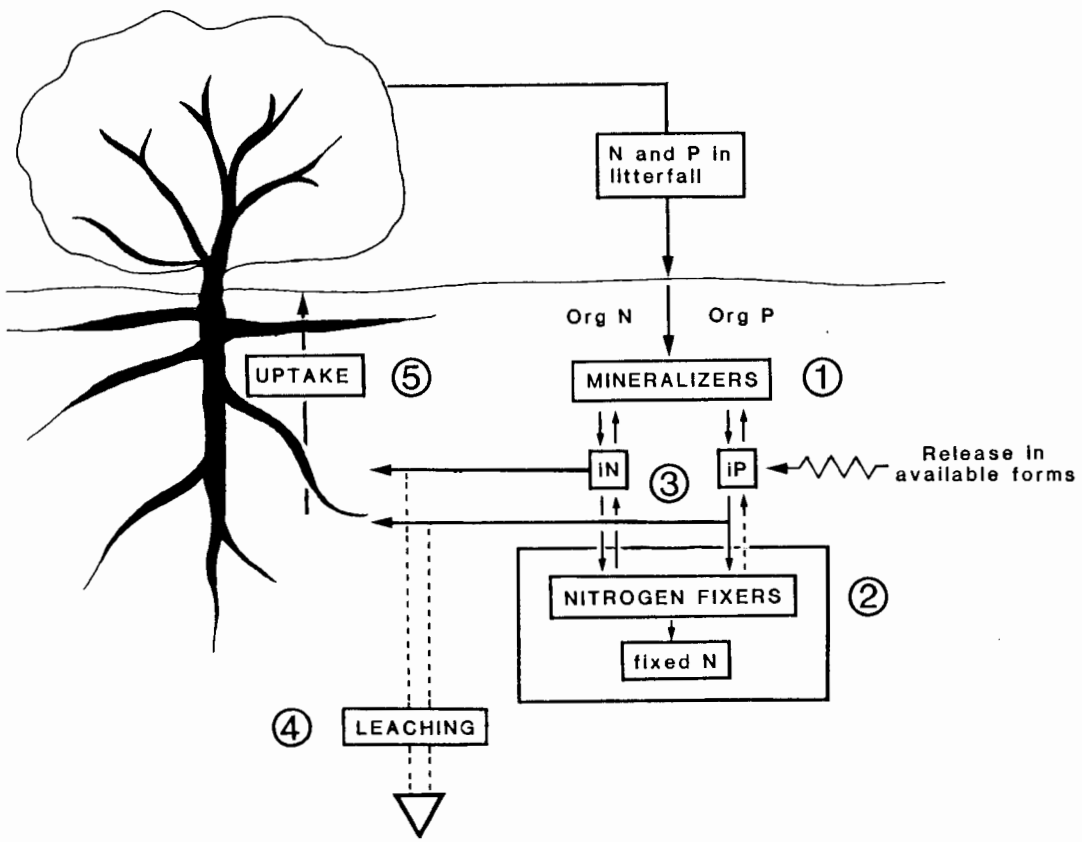
4. The soils displayed a characteristic mycoflora which appears to correspond with acid sandy heath systems elsewhere in terms of species composition, colony numbers and variation with

depth. Organic matter and nutrients played a major role in the distribution of the soil microfungi.

5. N input through free-living nitrogen-fixation maybe an essential mechanism for the maintenance of satisfactory soil N levels for plant growth.

6. Under conditions of low soil nutrient status, there must exist a delicate balance between plants and microorganisms which are competing for similar resources. This study has only touched on the soil and plant major nutrient status and the mycoflora which inevitably play a major role in cycling of these nutrients. The diagram in Fig 10.15 presents a summary of essential and probable competing steps in N and P cycling in an acid fynbos soil. It poses the following questions:

   (i) does competition between plant and micro-organisms imply that at a point in time one or the other is faced with a limiting resource(s), for example available P? Or is the balance such that heterotrophic mineralizers in the soil exist in a mutualistic relationship with the plant root, where release of energy sources ensures fair return of mineral elements for the plant to utilize.



Legend

1. High $^{C}/_{N}$ and $^{C}/_{P}$ ratios - temporary immobilation of iN and iP by micro-organisms.

2. Low soil NH_4^+, high nitrogen-fixation.

3. Major site of competition between plant roots, heterotrophic mineralizers and free-living nitrogen fixers.

4. Probable leaching due to inefficient trapping by plant/microorganisms and/or lack of soil colloids (low clay, low humus). (Loss of nitrogen through denitrification considered negligible in an acid sand).

5. Efficient uptake effected through the possession of morphologically suited rooting systems, and the invariable presence of proteoid or capillaroid type roots, or mycorrhiza.

Fig.11.1 Summary of probable major N and P cycling processes affecting the plant, heterotrophic mineralizers and free-living nitrogen fixers in an acid sandy soil under mountain fynbos (heath) vegetation. Cycle(s) effected chiefly in the rhizosphere or where energy sources, moisture and minerals adequate.

(ii) assuming that nitrogen-fixation may be of critical importance to the survival of fynbos communities, what proportion of the total available and potentially available phosphorus in the soil is utilized by the nitrogen-fixing bacteria? Once again what balance exists between the growth and function of these nitrogen-fixers and the need for the plant to take up an element which is in low supply?

(iii) heterotrophic mineralizers also compete for the same source of phosphorus. How does this affect the plant and the nitrogen-fixers?

(iv) with the soil nitrogen status being so low, does denitrification occur in these acid, sandy soils?

(v) are there sufficient biological (and physico-chemical) processes in fynbos soils which control absolute losses of essential nutrients from the system; alternately, if there is an ongoing net nutrient deficit from year to year, is fynbos resilient enough to alter its survival strategies or invoke inherent genetic abilities to meet increasingly lower soil nutrient statuses? It is only logical to predict that the high

(unnatural) fire frequencies occurring in mountain fynbos are responsible for a net depletion in soil nutrient reserves. The low geochemical content and insignificant short term weathering of TMS preclude significant elemental input from this parent material, while nutrients in precipitation form a very small fraction of the whole and probably have little effect in replenishing the system.

CHAPTER 12

RECOMMENDATIONS

A study of the nature described in this thesis has many obvious gaps. Plant ecology at the Cape of Good Hope Nature Reserve would therefore profit from further investigations involving *inter alia* nutrient and growth-linked studies, further attempts at relating the soil microflora to nutrient cycling and a more accurate determination of the annual input of N through free-living nitrogen-fixation.

Specific recommendations are:

1. The investigation of nutrient cycling processes in fynbos is still in its infancy. Commencement should begin immediately on a synthesis of existing soil, plant and other ecological material data, which would underline the weak points in this field.
2. Now that this and other recent investigations have revealed the extremely low nutrient levels present in fynbos systems, thorough studies must be made of factors causing severe nutrient losses from these systems. Of paramount importance is the effect of frequent burning cycles.
3. The three sites in this study should be monitored on a yearly or at most, three-yearly basis to determine changes in vegetation mass, structure and floristics, as well as changes in soil chemical parameters.

4. The Cape of Good Hope Nature Reserve, with its wide range of mountain fynbos and coastal communities (many of them homogeneous) should be seen as an area where ecological research into these communities should be promoted and encouraged. Further the Reserve should be considered as a future long term intensive study site; as such the existing research and overnighting facilities need drastic upgrading and expanding.

5. Projects of absolute importance at the Cape of Good Hope Nature Reserve are:

(i) The quantitative investigation of nutrient losses/gains in burns of varying frequencies, and to monitor frequently (5-10 yr) and non-frequently (20 yr +) burnt areas on a long term basis, recording net nutrient levels in each system, and changes in vegetation structure and floristics.

(ii) In hand with (i) above to establish the extent of leaching in the mountain fynbos soils and whether net losses of nutrients are occurring through this process.

(iii) To produce a leaf vs soil nutrient (N, P, Ca, Mg, K, S, Mn, Fe, Cu, Mo, Zn) index for dominant plant species in the area, and to include fibre content measurements, as well as *in situ* browse potential relative to these nutrient and fibre contents.

(iv) To establish a research nursery where growth of selected species under simulated and field conditions can be pursued, and where selected fertilization trials on both indigenous and agricultural crops can determine natural soil nutrient deficiencies.

(v) From (iv) above it would be possible to determine the suitability of introduced browsers and grazers, whether their natural plant food resources need to be supplemented, or whether their location in the Reserve is ecologically unjustifiable.

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APPENDICES

Appendix A

Definition of the mediterranean-type climate in the western Cape

Appendix A

Definition of the mediterranean-type climate in the western Cape

Köppen and Geigher (1936) define a mediterranean region as having a *Cs* climate and recognized two classes: *Csa* (hot summer) and *Csb* (cool summer). The mediterranean climate is accepted as having at least 65% of its precipitation in the winter half of the year (May to October in the southern hemisphere) and a winter mean temperature of <15°C (Aschmann 1973). In the south western Cape, Schulze and McGee (1978) also identify a *BSk* climate which signifies the arid margin of the above climatic delimitations.

The study area would have a *Csb* climate according to Schulze and McGee (1978).

B = arid zones

S = Steppe climate

k = dry hot, mean annual temperature <18°C.

C = warm temperate climate, coldest month 18°C to -3°C mean

s = summer dry season

a = warmest month >22°C mean

b = warmest month <22°C mean but at least 4 months >10°C

Appendix B

Species in the plant community classification at the three sites

Appendix B

TABLE B.1 List of species in the plant community classification at Sites 1, 2 and 3.

Asparagus capensis L.

Berzelia intermedia Schldl.

Carpobrotus acinaciformis (L.) L. Bolus

Chondropetalum nudum Rottb.

Elegia parviflora Kunth

Erica clavisepala Guthrie & Bolus

Erica pulchella Houtt.

Leucospermum hypophyllocarpodendron (L.) Druce ssp. hypophyllocarpodendron

Metalasia brevifolia (Lam.) Levyns

Pentaschistis curvifolia (Schrader) Nees

Philippia chamissomis Klotzsch

Phylica stipularis L.

Ruschia sarmentosa (Haw.) Schwantes

Serruria vallaris Knight

Simocheilus depressus (Lichenst.) Benth.

Staavia radiata Dahl

Thamnochortus fruticosus Bergius

Appendix C

Seasonal soil and leaf/photosynthetic stem analytical data from the three sites

TABLE C.1 Moisture content (kg $ha^{-1}x10^4$) of soils occurring at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:3) and 3 (2:3 and 2:4). Data recorded seasonally, between winter 1976 and winter 1977.

Community no.	Depth (mm)	Winter (1976)	Spring	Summer (1977)	Autumn	Winter
	0-150	17,9	6,0	3,3	15,1	17,9
1:1	150-300	15,4	6,0	5,1	11,8	13,9
	300-450	12,5	4,6	3,5	9,8	13,3
	0-150	20,1	5,0	4,2	17,8	18,8
1:2	150-300	17,7	6,9	5,4	12,0	16,6
	300-450	13,8	6,0	5,5	9,7	15,1
	0-150	50,6	42,7	25,5	20,8	47,4
2:1	150-300	48,2	39,2	24,5	15,7	41,7
	300-450	42,1	37,6	29,4	15,2	41,3
	0-150	53,0	27,9	6,1	16,1	52,0
2:2	150-300	49,4	29,2	8,6	12,3	42,1
	300-450	41,2	36,7	11,1	11,3	39,0
	0-150	32,1	6,0	1,9	10,8	45,9
2:3	150-300	24,1	12,7	3,0	10,4	44,0
	300-450	37,8	14,8	3,1	9,6	40,4
	0-150	18,6	7,4	3,1	12,7	47,1
2:4	150-300	18,7	13,5	3,9	11,0	43,4
	300-450	28,1	17,0	4,4	10,6	43,1

Refer to Chapter 2 for a description of the three sites

TABLE C.2 pH of soils occurring at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Data recorded seasonally, between winter 1976 and winter 1977.

Community no.	Depth (mm)	Winter (1976)	Spring	Summer (1977)	Autumn	Winter
	0-150	4,15	4,31	4,55	4,25	4,13
1:1	150-300	3,71	4,04	4,10	3,88	3,67
	300-450	3,75	4,00	4,17	3,96	3,67
	0-150	4,24	4,29	4,48	4,31	4,23
1:2	150-300	3,88	4,01	4,06	4,14	3,80
	300-450	3,80	3,98	4,10	3,87	3,70
	0-150	3,38	3,45	3,42	3,39	3,36
2:1	150-300	3,47	3,51	3,54	3,47	3,37
	300-450	3,55	3,69	3,63	3,67	3,50
	0-150	3,34	3,57	3,49	3,43	3,43
2:2	150-300	3,48	3,56	3,55	3,41	3,54
	300-450	3,61	3,76	3,66	3,53	3,66
	0-150	3,71	3,71	3,61	3,56	3,58
2:3	150-300	3,91	3,72	3,63	3,67	3,66
	300-450	4,14	3,81	3,73	3,76	3,76
	0-150	3,67	3,61	3,57	3,52	3,51
2:4	150-300	3,83	3,59	3,63	3,57	3,60
	300-450	3,92	3,68	3,72	3,67	3,75

Refer to Chapter 2 for a description of the three sites.

TABLE C.3 Organic matter content (kg $ha^{-1}x10^4$) of soils occurring at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Data recorded seasonally, between winter 1976 and winter 1977.

Community no.	Depth (mm)	Winter (1976)	Spring	Summer (1977)	Autumn	Winter
	0-150	10,8	9,0	8,5	9,3	8,8
1:1	150-300	6,6	8,3	8,0	7,5	5,3
	300-450	3,9	4,6	6,7	4,0	3,6
	0-150	10,7	10,3	10,6	10,9	10,2
1:2	150-300	8,6	9,3	9,0	8,2	7,8
	300-450	4,2	7,1	7,8	5,4	2,8
	0-150	7,9	8,3	6,7	5,4	4,5
2:1	150-300	3,8	3,5	1,9	2,0	2,6
	300-450	1,1	1,4	0,9	0,7	2,2
	0-150	5,0	5,4	4,3	5,1	4,4
2:2	150-300	3,6	3,0	2,4	1,5	1,7
	300-450	1,7	0,7	1,3	0,7	0,9
	0-150	4,2	4,2	3,5	3,6	4,0
2:3	150-300	1,3	3,2	1,5	0,7	1,1
	300-450	0,7	0,9	1,3	0,7	0,9
	0-150	4,3	5,3	4,3	4,7	5,3
2:4	150-300	2,4	3,4	2,6	2,3	1,7
	300-450	0,7	1,3	0,9	0,9	0,2

Refer to Chapter 2 for a description of the three sites.

TABLE C.4 Total nitrogen content (kg ha^{-1}) of soils occurring at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Data recorded seasonally, between winter 1976 and winter 1977.

Community no.	Depth (mm)	Winter (1976)	Spring	Summer (1977)	Autumn	Winter
	0-150	2106	1716	1782	1836	1827
1:1	150-300	1266	1510	1492	897	1294
	300-450	698	972	1294	492	1006
	0-150	2371	1467	2070	2067	2076
1:2	150-300	1557	1307	1787	1546	1407
	300-450	872	915	1397	944	983
	0-150	864	850	1107	828	1024
2:1	150-300	666	421	501	261	715
	300-450	430	288	270	161	582
	0-150	624	905	749	705	836
2:2	150-300	491	454	514	429	444
	300-450	386	268	404	284	326
	0-150	457	580	664	550	595
2:3	150-300	390	313	410	284	468
	300-450	312	308	374	183	392
	0-150	545	612	745	685	772
2:4	150-300	294	419	442	343	391
	300-450	232	270	399	262	296

Refer to Chapter 2 for a description of the three sites.

TABLE C.5 $C/_N$ ratios of soils (0-150 mm) occurring at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Data recorded seasonally, between winter 1976 and winter 1977.

Community no.	Winter (1976)	Spring	Summer (1977)	Autumn	Winter
1:1	27,3	24,7	24,1	25,2	26,5
1:2	24,7	26,9	26,6	29,2	29,3
2:1	44,3	33,0	33,7	29,8	30,0
2:2	35,3	31,6	33,8	35,3	30,5
2:3	32,7	33,3	25,5	32,7	35,0
2:4	31,3	33,0	30,8	37,0	29,0

* Refer to Chapter 2 for a description of the three sites.

TABLE C.6 Total phosphorus content (kg ha^{-1}) of soils occurring at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Data recorded seasonally, between winter 1976 and winter 1977.

Community no.	Depth (mm)	Winter (1976)	Spring	Summer (1977)	Autumn	Winter
	0-150	52,47	57,72	58,11	57,05	49,00
1:1	150-300	35,95	42,33	46,81	31,46	29,12
	300-450	20,63	32,69	41,60	27,36	21,63
	0-150	48,93	42,26	47,09	49,00	49,00
1:2	150-300	36,92	28,87	37,75	29,08	32,99
	300-450	24,37	33,22	38,39	18,20	16,85
	0-150	33,98	38,52	47,85	33,04	28,88
2:1	150-300	20,26	19,08	19,95	8,76	19,09
	300-450	13,46	15,19	16,35	8,49	16,28
	0-150	31,91	29,62	33,80	20,83	22,72
2:2	150-300	17,60	16,68	16,78	7,68	8,00
	300-450	14,95	10,20	13,01	6,36	8,76
	0-150	20,16	20,88	17,24	17,76	16,92
2:3	150-300	13,47	10,93	10,58	9,29	7,95
	300-450	9,99	7,32	9,33	4,68	8,81
	0-150	23,30	18,92	20,49	15,11	19,74
2:4	150-300	15,81	15,33	13,53	10,24	10,44
	300-450	12,94	10,76	12,46	8,61	4,96

Refer to Chapter 2 for a description of the three sites.

TABLE C.7 Bray no. 2 phosphorus content (kg ha^{-1}) of soils occurring at Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Data recorded seasonally, between winter 1976 and winter 1977.

Community no.	Depth (mm)	Winter (1976)	Spring	Summer (1977)	Autumn	Winter
	0-150	8,53	10,33	7,39	6,49	7,12
1:1	150-300	4,68	6,69	5,69	4,91	7,62
	300-450	3,60	7,36	5,34	1,25	7,56
	0-150	6,86	6,14	6,35	6,32	6,02
1:2	150-300	5,47	3,48	5,69	5,51	3,74
	300-450	5,23	3,38	4,55	4,48	3,44
	0-150	6,92	4,19	11,30	3,55	3,10
2:1	150-300	5,39	0,92	6,03	2,89	2,07
	300-450	3,31	0,72	9,22	1,94	2,09
	0-150	5,16	4,32	10,61	3,90	1,01
2:2	150-300	4,03	1,00	7,08	1,95	0,97
	300-450	3,97	1,63	7,99	1,76	0,00
	0-150	4,55	2,79	5,50	2,80	1,06
2:3	150-300	3,26	1,97	5,23	2,22	1,67
	300-450	2,23	1,12	6,62	4,09	0,98
	0-150	3,86	2,32	8,24	4,33	1,03
2:4	150-300	4,74	2,20	8,06	2,73	0,97
	300-450	1,19	1,44	6,66	3,62	0,78

Refer to Chapter 2 for a description of the three sites.

TABLE C.8 Leaf or photosynthetic stem (Elegia) nitrogen and phosphorus levels (μg g^{-1} leaf dry mass) from selected plants in Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4). Data recorded seasonally, between winter 1976 and winter 1977.

Community no.	Species		1976	1977			
			Spring	Summer	Autumn	Winter	Mean
	Site 1						
1:1	Leucospermum hypophyllocarpodendron	N	6262	4466	4457	5318	5126
		P	326	599	271	339	384
1:2	Serruria vallaris	N	7012	6690	6006	7007	6679
		P	603	579	372	665	555
	Site 2						
2:1	Erica clavisepala	N	5994	8874	6525	5805	6800
		P	328	532	434	323	404
2:2	Elegia parviflora	N	2377	3092	3087	3362	2978
		P	147	212	147	115	155
	Site 3						
2:3	Simocheilus depressus	N	3841	5071	5227	6204	5322
		P	360	366	297	290	328
2:4	Elegia parviflora	N	2163	4219	5607	4683	4168
		P	175	159	207	127	167

Refer to Chapter 2 for a description of the three sites.

Appendix D

Soil analytical linear regressions for the three sites

APPENDIX D

TABLE D.1 Soil analytical linear regressions for Sites 1 (Communities 1:1 and 1:2), 2 (2:1 and 2:2) and 3 (2:3 and 2:4) for combined depths (0-450 mm) and five seasons. n = 30.

OM vs N

1:1 and 1:2	y =	$-2,878x10^{2} + 2,265x10^{2}x$
	r =	0,870 (p = <0,001)
2:1 and 2:2	y =	$1,317x10^{2} + 1,357x10^{2}x$
	r =	0,856 (p = <0,001)
2:3 and 2:4	y =	$1,508x10^{2} + 1,174x10^{2}x$
	r =	0,836 (p = <0,001)

OM vs Pt

1:1 and 1:2	y =	-9,224 + 6,205x
	r =	0,792 (p = <0,001)
2:1 and 2:2	y =	3,045 + 5,357x
	r =	0,895 (p = <0,001)
2:3 and 2:4	y =	4,876 + 3,491x
	r =	0,870 (p = <0,001)

OM vs Pb

1:1 and 1:2	y =	$1,727 + 5,242x10^{-1}x$
	r =	0,397 (p = <0,05)
2:1 and 2:2	y =	-3,304 + 2,306x
	r =	0,353 (p = <0,10)
2:3 and 2:4	y =	-6,743 + 4,168x
	r =	0,150 (NS)

TABLE D.1 (contd.)

Pt vs Pb

1:1 and 1:2	y =	$2,111 + 9,490 \times 10^{-2} x$
	r =	0,611 (p = <0,001)
2:1 and 2:2	y =	$5,249 \times 10^{-1} + 1,727 \times 10^{-1} x$
	r =	0,571 (p = <0,001)
2:3 and 2:4	y =	$1,573 + 1,283 \times 10^{-1} x$
	r =	0,248 (NS)

OM - organic matter
N - total nitrogen
Pt - total phosphorus
Pb - Bray no. 2 phosphorus