SOIL FACTORS AND COMPETITION AS DETERMINANTS OF FYNBOS PLANT SPECIES DISTRIBUTIONS IN THE SOUTH-WESTERN CAPE, SOUTH AFRICA

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ABSTRACT

SOIL FACTORS AND COMPETITION AS DETERMINANTS OF FYNBOS PLANT SPECIES DISTRIBUTIONS IN THE SOUTH-WESTERN CAPE, SOUTH AFRICA.

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The Cape Floristic Region is one of the most species-rich regions of the world. Fynbos, the mediterranean-climate shrubland which comprises the largest part of this region, is characterized by high beta diversity and high edaphic endemism. However, very few quantitative studies of the factors controlling species turnover and community boundaries exist. I used an integrated approach of broad correlation techniques and detailed field experiments, to investigate this. The study site was a landscape on the southern slopes of the Soetanysberg hills, near Cape Agulhas. This area is exceptional in its floristic and edaphic complexity.

The first part of this work involved an investigation of the patterns of soil characteristics and the relationship between these and the vegetation patterns. This showed a strong vegetation-environment correlation, particularly with regard to communities. Community boundaries were strongly related to patterns of soil nutrients and physical factors (relating to moisture availability).

The second part consisted of detailed studies of the factors controlling the distribution of three pairs of key species (all Proteaceae). Each species is dominant in part of the landscape and, for each species pair, the replacement of one species by the other across the study site, is very distinct.

Protea susannae and P. compacta occur in deep and shallow sands respectively. Root morphology, water relations and phenology of adult (15 yr-old) plants were studied over two years in the field. Differences between these species constituted habitat-specialization for soils of different depth. A laboratory study of seedling morphology and water-use showed that species differences also exist at the seedling stage and these would be important in determining distribution patterns.

Very little is known about the importance of interspecific competition in fynbos communities. A three-year field experiment was set up to investigate its role in determining species distribution patterns across community boundaries and soil gradients. Each of the three pairs of Proteaceae species was grown from seed in cleared plots at three sites along a transect crossing a community boundary. Their growth and survival were studied in relation to site (soil factors), density and interspecific competition (monoculture/mixture). For all species, site factors had an overriding influence on survival. Average individual biomass was determined primarily by site for three species and, for the other species, by density (irrespective of monoculture or mixture). It was concluded that soil factors are a major influence on the distribution of these species and that, while competition has an important role in determining spacing patterns within communities, it has a minor role in determining species distributions.

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CONTENTS

CHAPTER 1

INTRODUCTION

1.1 THESIS RATIONALE

Species distributions and community boundaries along environmental gradients.

Patterns of plant species distributions and community boundaries have long been of interest to ecologists (Kruckeberg 1954, Odum 1971, Whittaker 1975). At the places where discontinuities in the distributions of prominent species or whole assemblages of species are observed, the ecologist is faced with the evidence that factors controlling species distributions and community composition has changed. These situations present opportunities to test the theories relating to species distributions and community composition.

Studies of factors determining vegetation boundaries have been made in a variety of ecosystems, namely, salt marshes (Snow and Vince 1984, Bertness 1991a,b), lakeshores (Wilson and Keddy 1985, Keddy 1989a), dune systems (Studer-Ehrensberger et al. 1993), grasslands (Gurevitch 1986) alpine meadows (Gigon 1971, cited in Ellenberg 1988, pp. 409-411), temperate forests (Glavac et al. 1993), and deserts (Parker 1991). However, other than the work of Lamont et al. (1989) and Mustart and Cowling (1993) in mediterranean-climate shrublands (in Australia and South Africa respectively), very few such studies have been made in species-rich ecosystems and mediterranean-climate regions in general.

The types of boundaries which have been studied include those which are associated with changes in a small number of dominant or key species (Lamont _et_ _al_. 1989, Dawson 1990, Bertness 1991a,b) changes in structurally similar communities (Barbour _et_ _al_. 1990, Mustart and Cowling 1993), and, in many cases, changes to different vegetation types (Davis and Mooney 1985, Schlesinger _et_ _al_. 1989) Wesser and Armbruster 1991, Fensham and Kirkpatric 1992).

The focus of studies of species distributions and vegetation boundaries has generally fallen into two categories:
1) environmental (abiotic) factors largely controlling distributions and 2) competition versus abiotic control of species distributions.

A variety of studies have shown how the presence and abundance of species and communities vary along environmental gradients of altitude, local topography and moisture availability (Yeaton and Cody 1978, Oberbauer and Billings 1981, Dawson 1990, Glavac _et_ _al_. 1992). In cases where environmental factors change abruptly, distinct transitions or mosaics of vegetation have been found, for example at edaphic discontinuities (Schlesinger _et_ _al_. 1989) or between north and south-facing slopes (Lipscomb and Nilson 1990). The discontinuities have been related to species tolerances to environmental factors.

In recent years community boundaries both gradual and abrupt have become the focus of field tests of theories relating to the ecological importance of interspecific competition (Snow and Vince 1984, Goldberg 1985, Gurevitch 1986, Keddy 1989a, Bertness 1991a,b). The importance of competition in producing and maintaining boundaries has been assessed in comparison to environmental factors, i.e. the balance of competitive abilities and abiotic tolerances. This has led to an extensive debate on how the importance of competition varies along productivity or resource gradients (see review, Grace 1991). Grime (1977, 1979) proposed that the intensity of competition should decrease as productivity decreases, as stress tolerant species in low-productivity habitats should be non-competitive. In Contrast Tilman (1977, 1982) argued that the intensity of competition was dependant on resource depletion and supply rates and thus need not decrease in low-productivity habitats. Recently a number of suggestions have been made towards solving this controversy. Weldon and Slauson (1986) pointed out the need to distinguish the ecological importance of competition from its intensity. Wilson and Tilman (1991) suggested that it is the nature rather than the intensity of competition that changes along productivity gradients (see also Grubb 1992 and Grace 1993).

A number of studies have inferred the importance of competition in determining species distributions without experimental testing for this (Barnes 1985, Delucia _et al_. 1988, Molony 1989, Mustart and Cowling 1993, Studer-Ehrensberger _et al_. 1993). A large number of field experiments involving the transplanting of species across boundaries have shown how abiotic environmental factors interact with interspecific competition, as well as seed predation to maintain boundaries (Goldberg 1985, Gurevitch 1986, Keddy 1989a, Bertness 1991a,b). In many of these cases the weaker competitors survived in less favourable habitats where the other species were abiotically excluded as a result of their intolerance to low soil moisture (Gurevitch 1986), high salinity (Bertness 1991a,b) or frequent disturbance (Keddy 1989a,b).

Few such studies of species distributions and community boundaries have been carried out in mediterranean-climate ecosystems. In Australian kwongan vegetation floristic patterns are complex (Hopkins and Griffin 1984), yet few experiments have considered the importance of competition in controlling floristic boundaries. One notable exception is the work of Lamont et al. (1989) which showed that the distribution of a number of species along a topographic gradient was strongly influenced by interspecific competition. In the mediterranean-climate region of South Africa, such transplant studies investigating vegetation boundaries are rare. While Manders and Richardson (1992) used transplant plots to investigate control of forest/fynbos boundaries, the only similar study within fynbos is the study of the factors controlling the distributions of calcicole and calcifuge species (Mustart and Cowling 1993). However, Mustart and Cowling (1993) only addressed the importance of soil factors in their experiment and did not assess the role of competition.

This thesis consists of a series of studies addressing control of fynbos species distributions using a range of approaches to assess the relative importance of soil factors (chemical and physical) and interspecific competition. The three main objectives of this thesis are:

To provide a quantitative assessment of the importance of soil factors in determining fynbos species distributions. Vegetation studies in fynbos have described apparent relationships between communities, soil types and high edaphic endemism (Cowling et al. 1992) as well as high species turnover between soil types (Thwaites and Cowling 1988, Cowling 1990). Despite this, no detailed assessment of the relative importance of different environmental factors has been made at the within-landscape level. Developments in direct gradient multivariate analysis (Ter Braak 1986) allow detailed testing of the relationships between vegetation patterns and a range of environmental factors.

To investigate the influence of differences in water relations at both adult and seedling stages in controlling species distributions. Many studies of the water relations of species in mediterranean-climate regions have concentrated on adult plants and the differences between growth forms and guilds often relating to possible niche separation (Miller et al. 1984, Moll and Sommerville 1985, Davis and Mooney 1986, Lamont and Bergl 1991). Recent studies have, however shown the critical importance of differences at the recruitment stage in determining community composition and distribution patterns (Frazer and Davis 1988, Lamont et al. 1989, Davis 1991, Mustart and Cowling 1993). Seedling water relations have received very little attention in fynbos, especially in comparison to adult water relations (Smith and Richardson 1991) and distribution patterns (Mustart and Cowling 1993).

To test the importance of interspecific competition in comparison to soil factors in determining species distributions across community boundaries. Competition in fynbos has not received much attention (Bond et al. 1992). Competition has been regarded as relatively unimportant (Cowling 1987) because of a moderate frequency of disturbance (fire) and low resources (nutrients and summer drought), both which have been suggested to lessen the importance of competition (Grime 1977, 1979, Huston 1979). However the conflicting views of Tilman (1977, 1982) and Wilson and Tilman (1991) suggest that the importance of competition need not decline under these conditions. As a result of the high species diversity of fynbos (Cowling and Holmes 1992), interest in competition has been from the perspective of the coexistence of many similar species within communities (Cody 1986, Cowling 1987), with little regard to community boundaries and species distributions. Evidence for the importance of abiotic factors in determining species distributions comes from a large number of phytosociological and qualitative studies (see review in Cowling _et_ _al_. 1992) and a single field study of calcicole and calcifuge species (Mustart and Cowling 1993). There remains a need for comprehensive field testing of the relative importance of abiotic factors and competition in determoning species distributions.

These issues are all considered to some extent in each of the studies presented in this thesis, but with a different focus in each case. The approach is as follows:

- a general correlative approach using direct gradient analysis to assess vegetation-environment relationships
- an examination of soil nutrient factors in more detail in relation to the associated plant communities .
- an investigation of the water relations of adult and recruitment (seedling) stages of one pair of species which were dominant in adjacent communities.
- a field experiment involving the transplanting of six key species across community boundaries to assess the influence of intra/interspecific competition versus soil factors in determining their growth, survival over three years.

1.2 THE FYNBOS

The fynbos biome comprises the sclerophyllous shrublands of the mediterranean-climate region of the south-western and southern Cape Province, South Africa (Figure 1.1) The dominant vegetation is fynbos, but patches of Afromontane forest, subtropical thicket and shrublands related to fynbos (renosterveld and strandveld) are also found (Cowling and Holmes 1992).

The main influences or driving forces of plant growth and reproduction in fynbos are the climate, nutrients and fire. The climate is of the mediterranean type, namely cool, wet winters and warm, dry summers (Tyson 1986). Precipitation is mostly frontal from mid-latitude cyclones and varies greatly with altitude, due to orographic effects. There is also a gradient of aridity towards the interior, where fynbos eventually gives way to the semi-arid karoo vegetation. Precipitation is strongly seasonal in the west (winter), but becomes less seasonal eastwards.

Fynbos is generally regarded as being associated with acid, nutrient-poor sandy soils. This is because the predominant underlying geology is quartzitic sandstone which weathers to produce nutrient-deficient sands (Deacon et al. 1992). Fynbos plant species possess a wide range of nutrient-use strategies for uptake and utilization of nutrients, such as large, nutrient-rich seeds, internal nutrient cycling and high prevalence of mycorrhizal associations (Stock and

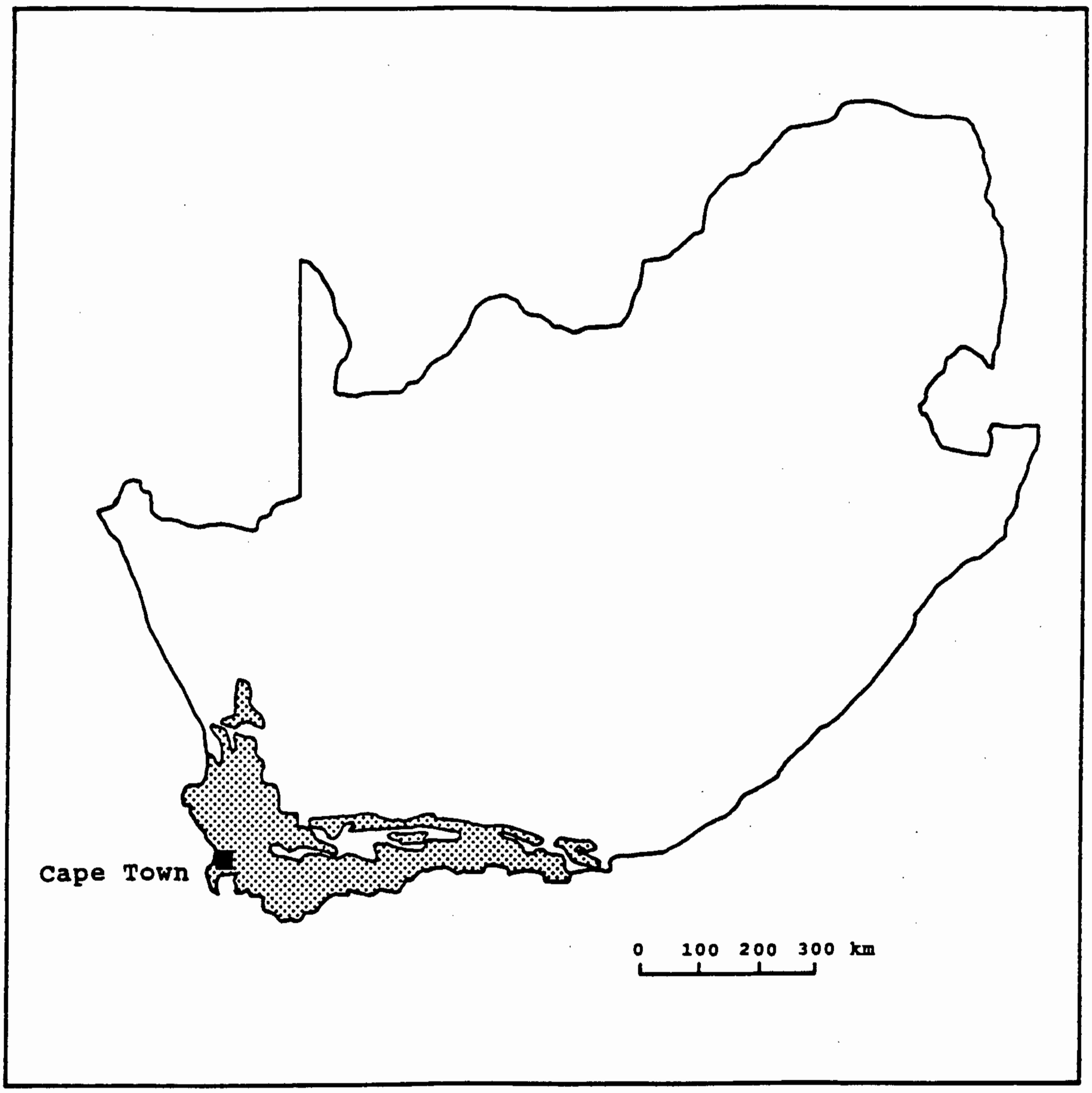

FIGURE 1.1 Map of South Africa showing the area covered by the Fynbos Biome.

Allsopp 1992). Some less common fynbos soils are, however, not so nutrient deficient, such as alkaline limestone soils and shale or granite-derived soils (Thwaites and Cowling 1988, Stock and Allsopp 1992).

Of primary importance in determining the structure of fynbos is the prevalence of fire associated with the summer-dry climate (reviewed in van Wilgen et al. 1992) Almost all recruitment is linked to fire and occurs shortly thereafter. The main recruitment strategies are soil-stored seeds, serotiny and resprouting (le Maitre and Midgley 1992). Fires vary greatly with respect to frequency (4-40 years) and season and intensity all of which have major impacts on recruitment patterns (le Maitre and Midgeley 1992).

Fynbos is characterized by extremely high species richness. the fynbos biome is roughly coincident with the Cape Floristic Region, the smallest of the worlds six floral kingdoms. This region has the highest species density and level of endemism of all temperate and tropical continental regions (Goldblatt 1978). This diversity is not reflected in the alpha diversity (which is moderate) but is most notable in extremely high beta and gamma (Cowling and Campbell 1984, Cowling 1990).

The three key families of fynbos species are Proteaceae, Ericaceae and the Restionaceae, which also characterize the three main growth forms. The large-leaved proteoid growth form is typically moderately tall shrubs (1-3 m) forming an overstorey, with small leaved or nanophyllous ericoid shrubs and leafless sedge-like restioid shrubs as the understorey. Proteoid Fynbos includes a prominent proteoid overstorey, which is lacking in Ericaceous Fynbos (Ericaceae-dominated) Restioid Fynbos (Restionaceae dominated). Classifications of fynbos types can be found in Campbell (1985) and Moll _et al_. (1984).

1.3 STUDY SITE

The site is located on the southern side of the Soetanysberg, a range of hills (to 249 m) on the southern edge of the Agulhas Plain (34^{o} 45'S; 19^{o} 15'E). This is 160 km east of Cape Town and 15 km west of Cape Agulhas (Figure 1.2). The western part of this range is composed of limestone of the Mio-Pliocene Bredasdorp Formation and the eastern part of quartzitic sandstone of the Triassic Table Mountain Group, capped in places by limestone. The hills run parallel to the coast from which they are separated by a sandy plain 1.-1.5 km wide.

Climate data (summarized in Figure 1.3) is from the weather station at Cape Agulhas (Weather Office, Dept. Environmental Affairs) which is situated 15 km to the west along the plain. The only likely discrepancy between this and the study site would be on top of the hills themselves which would experience greater precipitation from fog and orographic effects. The climate is mediterranean with 65% of the annual rainfall occurring from April (autumn) to September (spring). Average annual rainfall is 452 mm. Highest mean monthly temperature is 20.6 ^{o}C for February (absolute maximum: 38.1 ^{o}C) and lowest is 13.5 ^{o}C for July (absolute minimum: 0.8 ^{o}C).

The main study site comprises a 30 ha area (500 m X 600 m) including both limestone and sandstone parts of the Soetanysberg, as well as an adjacent part of the plain (see geology map in Figure 2.1(a)). Despite being relatively small, this site includes a range of soils representative of the range over which fynbos occurs. The fynbos vegetation formed complex vegetation patterns including both abrupt and gradual boundaries at various positions in the landscape. This combination of many different soil types, soil gradients and complex vegetation patterns made this site exceptionally well suited for detailed study of factors responsible for species distributions and community boundaries.

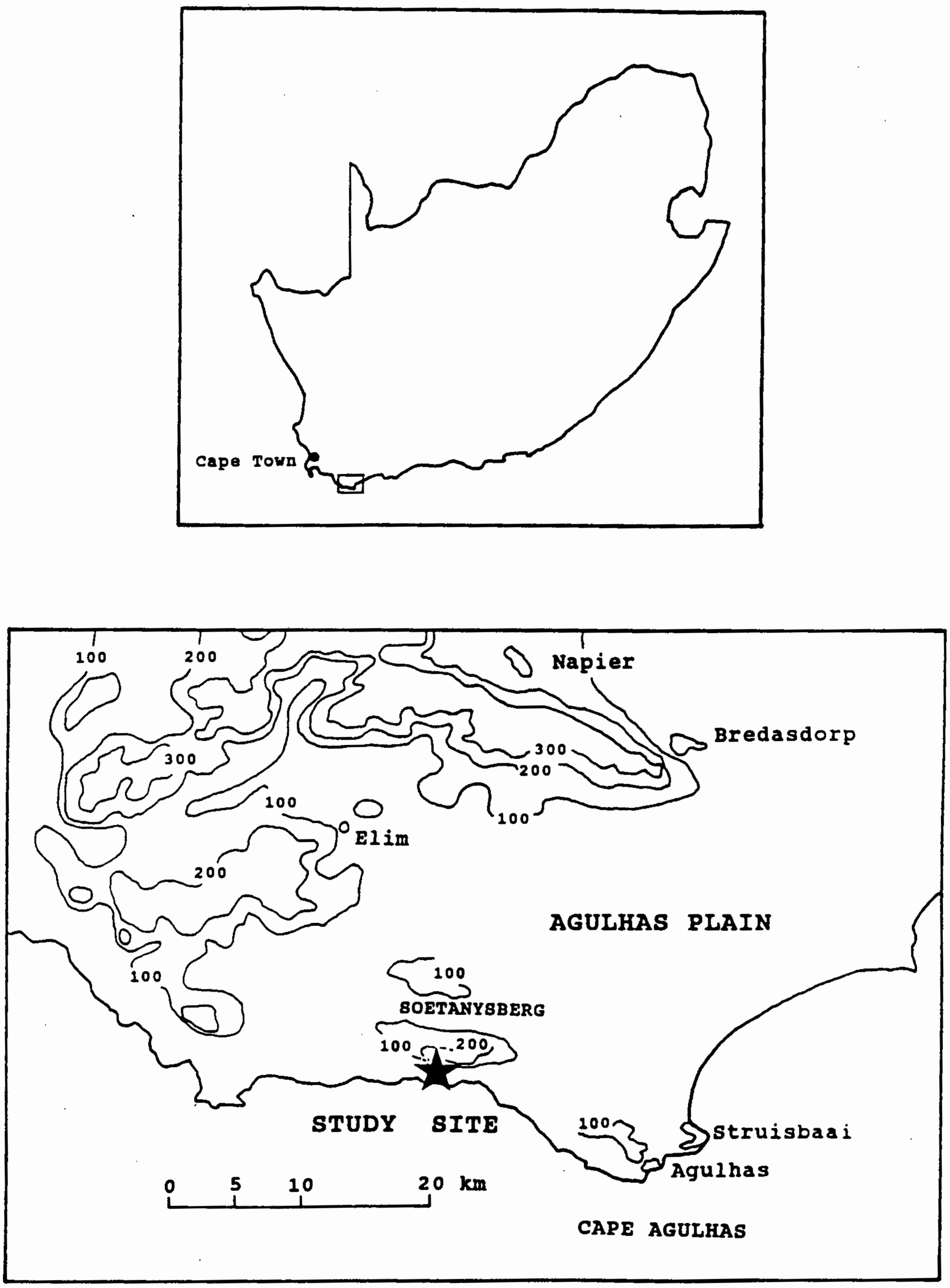

FIGURE 1.2 Map showing the location of the site in the Soetanysberg hills on the southern edge of the Agulhas Plain, South Africa. Contours are 100m intervals.

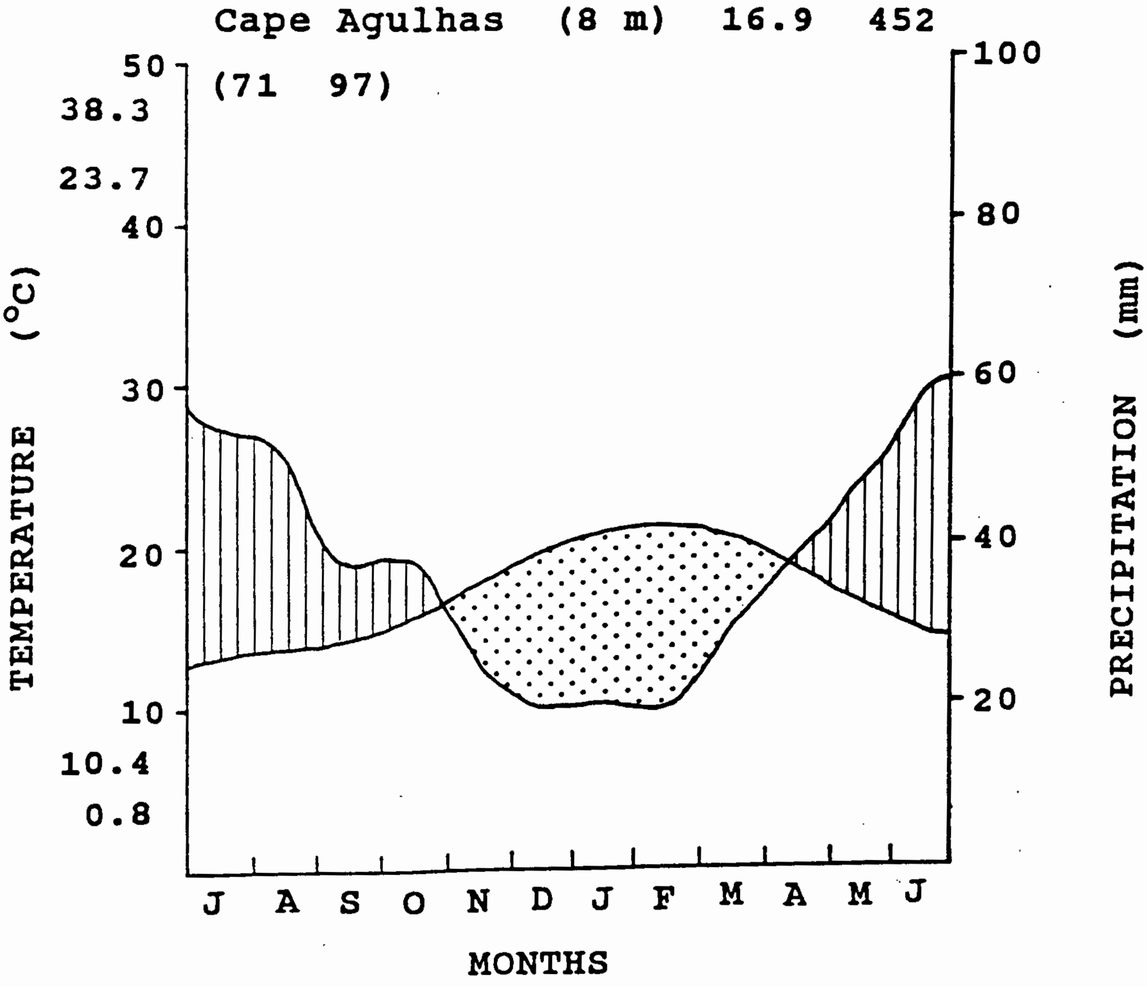

FIGURE 1.3 Walter-Leith climate diagram prepared from data collected at the meteorological station at Cape Agulhas, 15 km south-east of the Soetanysberg.

1.3.1 Photo essay

Plate 1.1 The Soetanysberg hills seen from the coast. The dark vegetation on the western part (at left) and along the top of the eastern part shows the extent of the limestone. The lighter vegetation on the eastern side is on sandstone.

Plate 1.2 View from the top of the Soetanysberg towards the south-east. The furthermost peninsula is Cape Agulhas (the southernmost point of Africa).

Plate 1.3 Part of the limestone/sandstone boundary. On the left of the ravine is limestone with the Meridianum community and on the right is sandstone with the Xanthoconus community. In the foreground is Leucadendron coniferum of the Susannae community.

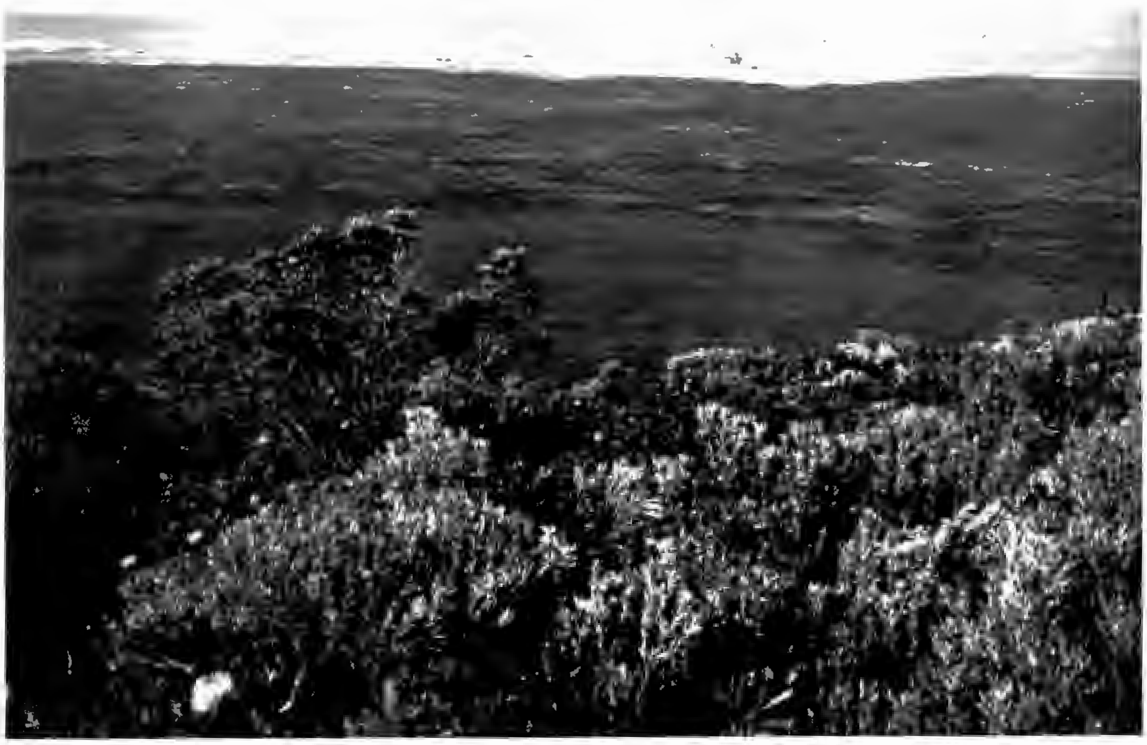

Plate 1.4 Proteoid Fynbos of the Meridianum community on limestone slopes. The dominant shrub is Leucadendron meridianum and the broad-leaved shrub in the foreground is Protea obtusifolia. The vegetation in this photograph is 1.5 - 2 m tall.

Plate 1.5 Proteoid Fynbos of the Susannae community on deep sand adjacent to limestone (just outside the left of the picture). This photograph shows the Susannae-ericoid form of this community which is adjacent to the Elegia community on the plain and includes patches of ericoid and restioid understorey shrubs with an overstorey of Protea susannae (1-2 m tall)

Plate 1.6 The Xanthoconus community on sandstone slopes, dominated by low shrub Leucadendron xanthoconus. Although generally classified as Mesic Ericaceous Fynbos (high cover of Ericaceous shrubs), the vegetation in this picture is at the lower extent of this community where low Proteaceae shrubs dominate. This vegetation is 0.3 - 0.5 m tall. Very small Protea compacta individuals are scattered throughout.

Plate 1.7 Restioid Fynbos of the Elegia community on the plain between the Soetanysberg mountain and the sea. This vegetation is 0.3 -0.5 m tall, dominated by the restioid Elegia verreauxii. Scattered large-leaved shrubs are Leucadendron laureolum (0.5 - 1.0 m tall).

Plate 1.8 Proteaceous fynbos of the Compacta community at the base of the sandstone slope. The tall shrubs (1.5 - 2.0 m) are Protea compacta. The white-flowered form in the foreground is very uncommon: the pink-flowered form (background) is typical.

Plate 1.9 Protea susannae individual age approximately 15 yrs. This shrub grows up to a height of approximately 2m and is well branched, bearing many flowers each year. This species is associated with deep sand (often 2 m or more) close to limestone).

Plate 1.10 Protea compacta, age approximately 15 years. This species grows to 2-3 m tall, but is sparsely branched, bearing relatively few flowers each year. This species occurs in acid sands of various depths, but is typical of shallow sand on sandstone hills and lower mountain slopes.

Plate 1.11 In the laboratory study of seedling growth and water relations, seedlings of Protea susannae (smaller plant at right) and Protea compacta (center) were grown in 80 cm-long PVC tubes with a reconstructed soil profile. This experiment took place over 30 weeks (7 months) in a controlled-environment room. The wires emerging from the tube at centre connect soil moisture probes to a data logger.

Plate 1.12 Field experiment to study the effects of soil factors and competition on growth and survival of three pairs of key Proteaceae species. Each pair of species was grown from seed in monoculture and mixture at cleared sites. Each of three transects consisted of three sites crossing the community boundary dividing the distributions of the species of each pair. The site in this photograph is the East Plain site and contains seedlings of Leucadendron xanthoconus and Leucadendron laureolum after 28 months of the three year experiment.

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CHAPTER 2

VEGETATION-ENVIRONMENT RELATIONSHIPS IN A SPECIES-RICH FYNBOS LANDSCAPE

2.1 ABSTRACT

The Cape Floristic Region of South Africa is an area of diverse substrata, high species diversity and complex vegetation patterns. Fynbos vegetation and soils were sampled at 75 sites in a 30 ha study area in the Soetanysberg hills in the south-western Cape Province. TWINSPAN, DCA and CCA were used to investigate vegetation patterns and vegetation-environment relationships (with emphasis on soil factors). Classification of the vegetation data, which included 251 species, identified five communities associated with distict soil types and DCA identified two main compositional gradients. These two vegetation gradients were related to 10 environmental variables, using CCA. These gradients were associated with environmental gradients of pH and soil depth. When sites associated with the three substrata, namely, limestone, sandstone and colluvial sand, were analysed by CCA separately, only sandstone and colluvial sand produced significant vegetation-environment relationships. On sandstone, the main environmental gradient consisted of the following physical factors: altitude, slope, rock cover, and soil fertility. On colluvial sand there was a strong pH and fertility gradient associated with altitude, as well as a soil depth and texture gradient. Despite the complexity of this landscape and the very large number of species, compositional gradients in the vegetation were found to be strongly related to gradients of pH and soil depth and texture. This indicates predictable structure in the

vegetation, related to various environmental factors, particularly at the community level.

Abbreviations: CCA = Canonical correspondence analysis, CFR = Cape Floristic Region, DCA = Detrended correspondence analysis, TWINSPAN = Two-way Indictator Species Analysis.

Nomenclature : Bond and Goldblatt (1984)

2.2 INTRODUCTION

The Cape Floristic Region (CFR) of South Africa ranks among the most species rich areas of the world (Goldblatt 1978, Cowling, Holmes and Rebelo 1992). Regional species richness and levels of endemism of this area are comparable to those of neotropical and Asian tropical rainforests (Gentry 1982, 1986, 1988). This diversity is not reflected at the alpha level, which is only moderate (ca. 65 spp in 0.1 ha, Bond 1983, Cowling 1983), but is most marked in the extremely high turnover between habitats, i.e. beta diversity (Cowling 1990, Cowling et al. 1992). The prevalence of edaphic endemism in the CFR (Cowling et al. 1992) suggests that much of this turnover could be related to soil factors, as has been suggested for Asian and neotropical rainforests (Ashton 1969, Gentry 1986,1988 respectively). Thus the species richness of this region can probably be attributed to a combination of high species turnover and the geological, topographic, climatic and resulting edaphic complexity (Deacon et al. 1992).

Studies investigating the floristic organisation of fynbos (the main vegetation type of the CFR) range from broad descriptions of major vegetation types (e.g. Taylor 1978, Kruger 1979, Boucher and Moll 1981, Campbell 1985), to detailed descriptions of communities (e.g., Boucher 1978, 1987, Taylor 1984, McDonald 1988). Soil factors appear to be of major importance in determining vegetation patterns at all levels (reviewed in Cowling and Holmes 1992). Many of the studies in which vegetation-soil relationships have been studied in detail, have been at the broadest level of organisation or at a large geographical scale. These include studies of transitions between major vegetation types (Taylor 1978, Kruger 1979, Campbell 1985), or of transects tens to hundreds of kilometers long (e.g., Campbell 1983, Boucher 1987, Thwaites and Cowling 1988, Cowling and Holmes 1992).

Boucher (1978) and Taylor (1984) carried out phytosociological studies in fynbos at smaller scale (24000 ha and 7750 ha, respectively). They suggested that vegetation patterns were reflected in local-scale patterns of environmental factors such as soil-type, moisture and slope. Various other studies have provided evidence that boundaries between fynbos communities are related to soil factors (Van Wilgen and Kruger 1985, Mcdonald 1988). These phytosociological studies provide qualitative descriptions of the apparent trends of community changes with environmental factors. However there is a lack of detailed, quantitative analysis of vegetation-environment relationships in fynbos.

The objective of this study was to provide a quantitative assessment of the importance of environmental factors (related to physical and chemical soil characteristics) in explaining community patterns in an edaphically complex and species-rich area. The combined use of multivariate techniques, Two-way Indicator Species Analysis (TWINSPAN, Hill 1979) and Detrended Correspondence Analysis (DCA, Hill and Gauch 1980), for such a purpose, sometimes followed by Canonical Correspondence Analysis (CCA, Ter Braak 1991) has recently become widespread in vegetation studies (e.g. Allen et al. 1991, Partridge et al. 1991, Russell-Smith 1991, Frederiksen and Lawesson 1992, Franklin and Merlin 1992, Russel-Smith et al. 1993).

I sampled vegetation in a small (30 ha) area in a landscape characterized by much edaphic and floristic complexity. Samples were classified into communities and the compositional gradients were described, using TWINSPAN and DCA. CCA was then used to relate community patterns to a range of environmental factors.

2.2.1 Study Area

The 30 ha study area is located about 15 km west of Cape Agulhas (34° 45'S ; 19° 50' E) on the southern slopes of the Soetanysberg hills (249 m). The climate is fairly typical of the south-western Cape, South Africa, namely, a mediterranean-type climate, with cool, wet winters and warm, dry summers. Mean annual rainfall at Cape Agulhas is 452 mm. Mean temperature of the warmest month (February) is 20.6 $^{\circ}$C and the coolest month (July) is 13.5 $^{\circ}$C.

The geology of the area shown in Figure 2.1 (a), using the landforms described for the Agulhas Plain by Thwaites and Cowling (1988). The eastern part of the Soetanysberg consists of Table Mountain Group sandstone and quartzite of the Bredasdorpberge Land System, capped in places by tertiary limestone of the Hagelkraal Land System (Bredasdorp Formation), while the western part of these hills consists entirely of limestone (Bredasdorp Formation). Deep colluvial sand at the foot of the limestone slope was limestone-derived and classified as part of the Hagelkraal Land System. The gradually deepening colluvial soil at the foot of the sandstone part of the hills, as well as the soil of the plain in front of the hills, was classified as part of the Bredasdorpberge Land System.

The vegetation types of the Agulhas Plain were classified by Cowling et al. (1988) using the structural-dominant species system of Campbell (1986). This system was used to provide

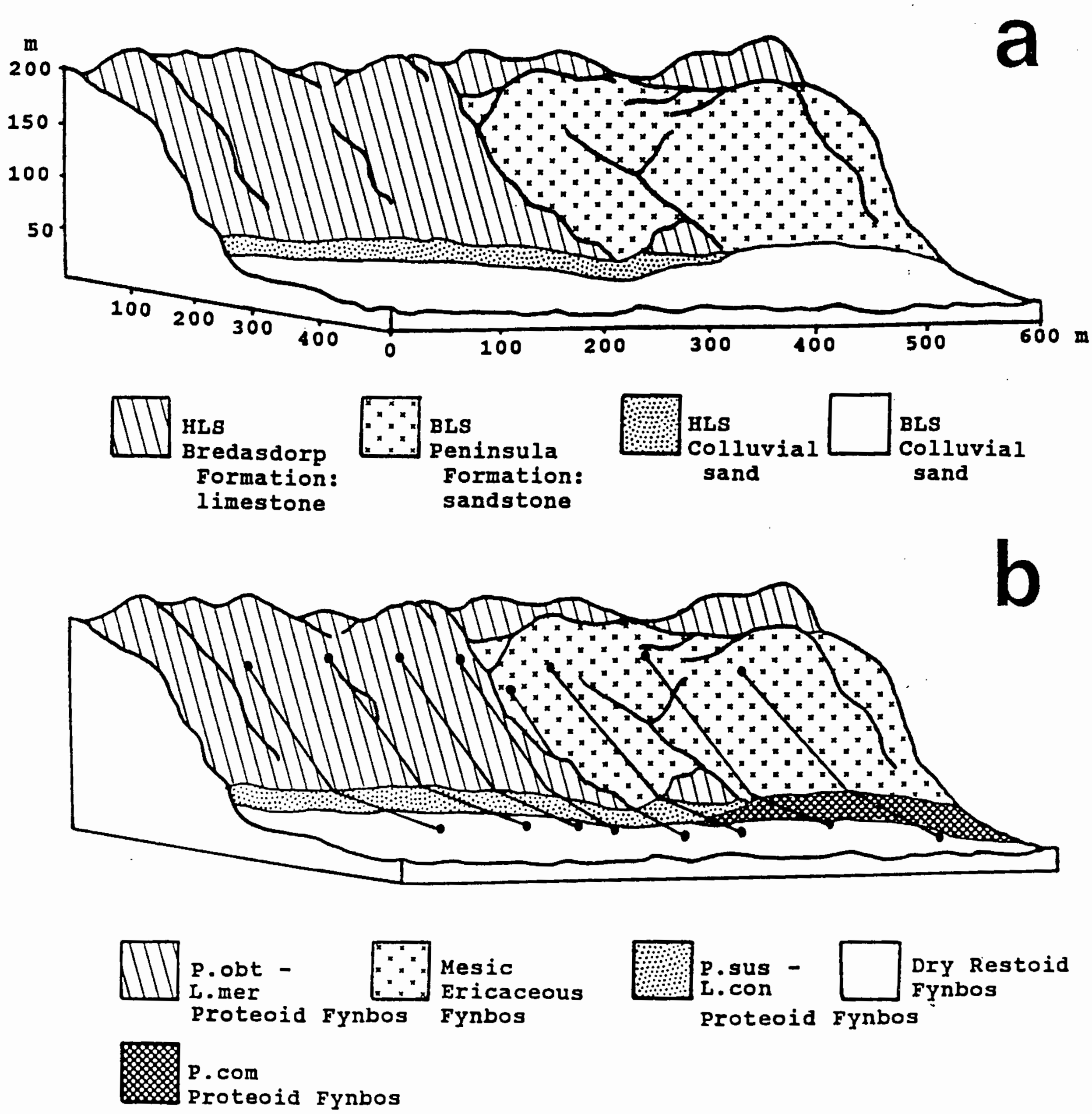

FIGURE 2.1 Diagram of the study area on the south-facing side of the Soetanysberg mountain, showing **(a)** geology, based on the classification of the Agulhas Plain by Thwaites and Cowling (1988). abbreviations: HLS = Hagelkraal Land System, BLS = Bredasdorpberge Land System. **(b)** Fynbos types, based on the classification of the vegetation of the Agulhas Plain by Cowling et al. (1988). Abbreviations: P.obt = Protea obtusifolia, L.mer = Leucadendron meridianum, P.sus = Protea susannae, L.con - Leucadendron coniferum, P.com = Protea compacta. The locations of the eight transects along which soil and vegetation were sampled are shown in (b).

an initial classification of fynbos types at this site. On both limestone and the adjacent colluvial sand the vegetation was classified as one type of Proteoid Fynbos, including the Protea obtusifolia - Leucadendron laureolum community (limestone) and the Protea susannae - Leucadendron coniferum community (colluvial sand). The vegetation on the sandstone slope was classified as Mesic Ericoid Fynbos, with Protea compacta - Proteoid Fynbos on the shallower colluvial sand at the base of the sandstone slope. The vegetation on the plain classified as Dry Restioid Fynbos.

2.3 METHODS

2.3.1 Data collection

Sampling took place along eight evenly spaced parallel transects (see Figure 2.1(b)). Ten sites, 50 m apart, were located along each transect, giving a total of 80 sites. Five of them occurred in vegetation which was at least 10 years older than the rest of the vegetation (having escaped the last fire) and so these sites were excluded, leaving 75 sites.

At each site, vegetation was sampled in a 5 m x 5 m plot by visually assessing the percentage cover of all species. This plot size was selected for its efficiency when sampling many sites in a relatively small area with dense and highly variable vegetation. The following environmental data was collected at each site: altitude, aspect, slope, percentage rock cover and soil depth (measured by knocking a steel rod into the ground at three randomly chosen locations at each site). A single soil sample was collected from 0-10 cm depth for further investigation in the laboratory. pH was measured in 0.01 M $CaCl_2$. After organic matter was removed using H_2O_2 and washing, the coarse, medium and fine sand components of the soil were determined by sequential sieving (mesh sizes: 1000 μm, 600 μm, 200 μm).

In order to integrate all soil nutrient levels and availability, a soil fertility index was determined using a bioassay of radish (Raphanus sativus L.). Seeds of approximately uniform size (about 8 mg) were selected and sown in moist soil in 9 cm diameter polystyrene pots. Because of the large number of sampling sites, only one pot with two plants was used for each site (soil sample). Three or four seeds were sown in each pot and thinned to two seedlings where necessary. Entire plants were harvested after four weeks and dried for 48 hrs at 60 ^{o}C before weighing. To correct for growth based on seed-stored nutrients, a control of 5 pots with acid-washed sand (two plants per pot) was used. Dry mass per plant was corrected using the control and used as a fertility index factor in the CCA.

2.3.2 Data Analysis

Vegetation samples were classied using TWINSPAN with default options, except that all species were included in the final output table. This was followed by ordination of sites in DCA to describe compositional gradients in the vegetation. Then these gradients were related to a range of environmental factors, using CCA.

Initially all environmental data was included in the CCA as 10 variables: altitude, slope, rock cover, soil depth, percentage coarse sand, percentage medium sand, percentage fine sand, pH and fertility index and one nominal variable, aspect, which has four classes (S-facing, W-facing, E-facing, flat). The three soil texture factors showed high inflation factors in the CCA output, indicating multicollinearity (Ter Braak 1986). This problem was avoided by removing the factor percentage fine sand from the analysis (this did not reduce the eigenvalues of the axes). Without multicollinearity, the canonical coefficients could be used to assess the relative importance of the remaining nine factors in the analysis (Ter Braak 1986). Those variables with low regression coefficients were then selectively removed so as to produce the smallest set possible with minimal reduction of the eigenvalues. The final environmental data set which was used for the output biplot consisted of six environmental variables: rock cover, soil depth, percentage coarse sand, percentage medium sand, pH and fertility index (bioassay). A Monte Carlo permutation test was used to test the significance of the eigenvalues of these axes.

To compare vegetation-environment relationships on the three substrata in the study area, sampling sites were allocated to substrata according to the following criteria: 1) limestone: any limestone rock present at the surface (18 sites), 2) sandstone: sandstone at the surface, or soil less than 50cm deep overlying sandstone (23 sites) and 3) colluvial sand: soil more than 50 cm deep (34 sites). CCA and Monte Carlo permutation tests were carried out on each data set.

2.4 RESULTS

2.4.1 Vegetation classification

Classification of the vegetation data by TWINSPAN distinguished five communities (Figure 2.2 and see summary in Table 2.1). Each of the first three divisions of TWINSPAN separated a distinct group of sites with at least 35% of the species restricted to that group. A fourth group with 9% unique species was divided into two by a fourth-level division, yielding one group with 9% unique species and another with no unique species, but with different dominant species and lacking the dominant species of the former group. The environmental factors corresponding to the sites where each of the five recognized communities were found are summarized in Table 2.2.

1. Leucadendron meridianum - Protea obtusifolia Proteoid Fynbos (referred to as the "Meridianum" community. This community included the 18 sites and 76 species on limestone. These sites were mostly on south-facing, moderately steep slopes of the limestone hills, with high rock cover and shallow soil (Table 2.2). These soils were fine-textured with high pH and the highest fertility index.

This community corresponds to the Protea obtusifolia - Leucadendron meridianum Proteoid Fynbos type described for the Agulhas Plain by Cowling et al. (1988). Forty-nine percent of these species were unique to these sites, including members of most fynbos families: L. laureolum, Mimetes saxitillus, Leucospermum pattersonii (all Proteaceae), Erica propinqua (Ericaceae), Elegia muirii (Restionaceae) and Euchaetes longibracteata (Rutaceae). Other than proteoid dominant species L. meridianum and P. obtusifolia, species with high cover or high frequency of occurrence included ericoids Erica coccinia, Erica propinqua, Erica pulvinata, restioids Ischyrolepis leptocladis and Thamnochortus fraternis, the sedge, Tetraria cuspidata and small-leaved shrub Indigofera brachystachya. The height of this vegetation varied from 0.5 m to approximately 2.5 m.

TABLE 2.1 Communities in the Soetanysberg study area, based on the TWINSPAN classification. See text for detailed descriptions

Community name	Meridianum	Susannae	Xanthoconus	Elegia	Compacta
No. sites	18	15	18	14	10
No. species	76	103	124	64	69
Dominant spp.	Leucadendron meridianum Protea obtusifolia	Protea susannae Leucadendron coniferum	Leucadendron xanthoconus Leucospermum cordifolium Aulax umbellata Tetraria thermalis	Elegia verreauxii Leucospermum pedunculatum Staavia radiata Erica imberbis	Aulax umbellata Protea compacta Calopsis hyalinus Erica imberbis Leucadendron laureolum
Character spp. include:	Leucadendron meridianum Mimetes saxitillus Leucospermum pattersonia Erica propinqua Elegia muirii Euchaetes longibracteata	Leucadendron coniferum Thamnochortus erectus Willdenowia rugosa Passerina vulgaris	Erica monadelpha Chondropetalum deustum Tetraria thermalis	Gnidia pinifolia Erica cerinthoides	
Total number Character spp. (%)	36 (47%)	36 (35%)	48 (39%)	6 (9%)	0

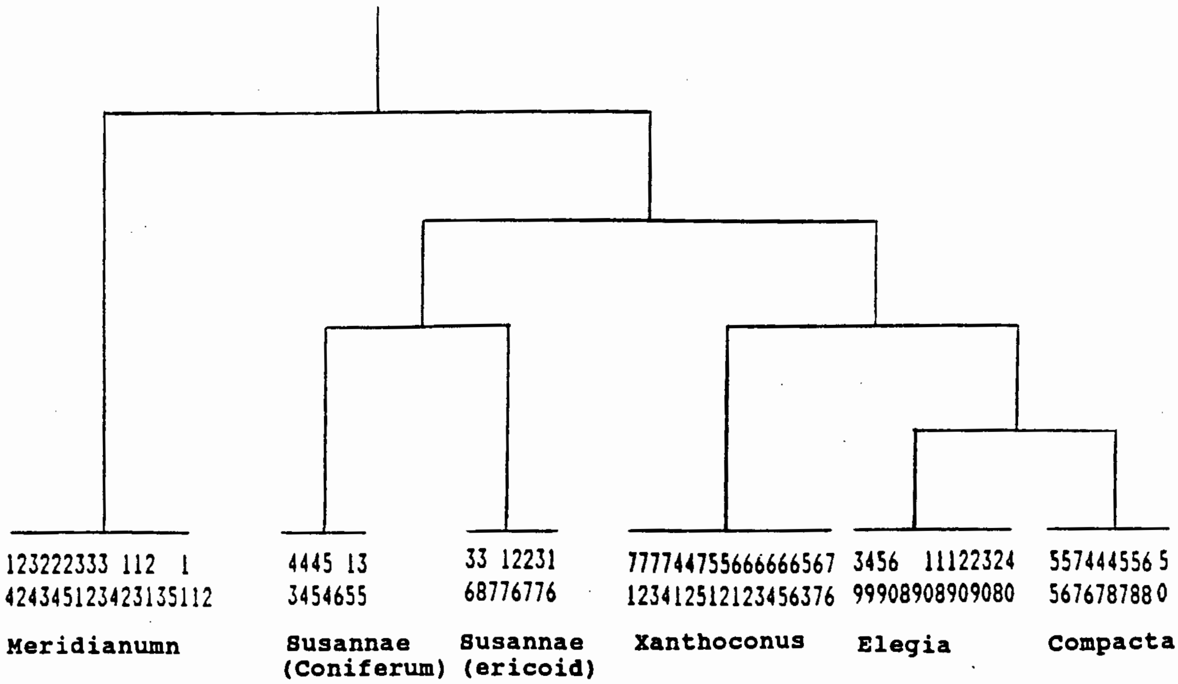

FIGURE 2.2 Two-way indicator species analysis (TWINSPAN) of 75 sites, showing the five groups recognized as communities. Lists of indicator species and full descriptions of communities are provided in the text.

TABLE 2.2 Mean values of environmental variables for the sites associated with each of the five communities. Data presented as mean ± one standard error. Analysis of variance was carried out on each factor to test for differences between sites (all factors had significant site effects). Tukey multiple range tests were used to identify significantly different sites (values with diferent superscripts are significantly different, p<0.05)

COMMUNITIES	Meridianum	Susannae	Xanthoconus	Elegia	Compacta
No. of Sites	18	15	18	14	10
Altitude (m)	80.0 ± 5.5^{b}	44.3 ± 3.0^{c}	106.9 ± 10.2^{a}	29.7 ± 1.2^{c}	41.5 ± 2.4^{c}
Slope (deg)	20.0 ± 1.8^{a}	9.4 ± 1.1^{b}	25.7 ± 2.2^{a}	1.9 ± 0.4^{b}	6.6 ± 1.0^{b}
Rock cover (%)	41.5 ± 4.3^{a}	0.0^{b}	54.5 ± 5.0^{a}	0.0^{b}	5.6 ± 3.3^{b}
Soil depth (m)	0.14 ± 0.02^{c}	1.28 ± 0.08^{a}	0.22 ± 0.07^{c}	1.39 ± 0.04^{a}	0.65 ± 0.17^{b}
% Coarse sand	2.4 ± 0.5^{c}	15.0 ± 4.2^{b}	57.9 ± 2.2^{a}	15.6 ± 4.5^{b}	43.3 ± 3.6^{a}
% Medium sand	31.2 ± 2.2^{ab}	34.9 ± 2.4^{ab}	16.2 ± 0.8^{c}	40.1 ± 2.9^{a}	25.1 ± 2.8^{bc}
% Fine sand	66.4 ± 2.2^{a}	46.2 ± 2.4^{b}	25.9 ± 2.5^{c}	44.2 ± 2.1^{b}	31.6 ± 2.6^{c}
pH	7.23 ± 0.09^{a}	5.14 ± 0.10^{b}	5.13 ± 0.06^{b}	4.29 ± 0.23^{c}	4.90 ± 0.07^{b}
Fertility index (mg dry wt.*)	46.2 ± 4.9^{a}	43.0 ± 2.9^{ab}	35.6 ± 1.5^{ab}	31.1 ± 2.1^{b}	34.1 ± 3.0^{ab}
Aspect (number of sites)					
S	17	15	13	9	10
W	0	0	5	0	0
E	1	0	0	0	0
Level	0	0	0	5	0

* Bioassay (see text for description)

2. Protea susannae - Leucadendron coniferum Proteoid Fynbos, (referred to as the "Susannae" community). This communityincluded 15 sites and 103 species on lightly sloping, very deep soil (see Table 2.2) adjacent to limestone where it formed a distinct band at the base of the limestone slope. This soil had a high percentage of fine-textured sand, but more coarse sand than the limestone soil. It was moderately acid and of similar high fertility to the limestone soil.

This community is listed as one of the types of Proteoid Fynbos on the Agulhas Plain by Cowling et al. (1988). Thirty six percent of the 103 species were unique to this community and included proteoid Leucadendron coniferum, ericoid Passerina vulgaris and restioids Thamnochortus erectus and Willdenowia rugosa. There were two distinct forms of this community. The first, referred to as Susannae-Coniferum, occurred on the sites closest to limestone and included L. coniferum as co-dominant with Protea susannae and high cover of tall ericoids Passerina vulgaris, Diosma arenicola, Erica discolor and Metalasia muricata, as well as tall restioid Thamnochortus erectus. Short ericoids and restioids were lacking and much bare ground was observed below tall shrubs. A number of typically limestone species were found at these sites, including, Protea obtusifolia, Euchaetes racemosa, Rhus lucida and Phylica dodii. This vegetation was 1.0 to 2.0 m tall.

The second form, referred to as the Susannae-ericoid group, occurred at sites further away from the limestone, towards the plain. The overstorey consisted almost entirely of Protea susannae, with a low abundance of Leucadendron coniferum. There was an understorey of low ericoid and restioid species shared with the Restioid Fynbos community on the plain. These included ericoids Erica imberbis, Euchaetis burchelii, Sympieza labialis, Salaxis sp, Staavia radiata and restioids, Elegia fenestrata and Calopsis filifolia. The height of this vegeation ranged from 0.5 m (lacking overstorey) to 1.5 m (with overstorey)

3. Leucadendron xanthoconus - Leucospermum cordifolium Ericaceous Fynbos, referred to as the Xanthoconus community. Although frequently dominated by proteoid species, this is referred to as Ericaceous Fynbos because of the high cover of Ericaceae (Cowling et al. 1988). This community consists of 124 species and is found at 18 sites at higher altitude on the middle and lower sandstone slopes. These sites were predominantly on steep south-facing slopes, where rock cover was very high and soils were shallow, coarse-textured, moderately acidic and had a moderately high fertility index (Table 2.2).

Dominant species, which varied substantially from site to site, included low proteoid shrubs, Leucadendron xanthoconus, Leucospermum cordifolium and Aulax umbellata as well as the broad-leaved sedge, Tetraria thermalis. Low ericoid shrubs, which together constituted very high cover at all sites, included Nagellocarpus serratus, Erica monadelpha, Erica cordifolia, Erica coccinia, Phaenacoma prolifera and Phylica imberbis. Common non-ericoid shrubs included Serruria elongata, Indigofera hamulosa, Penea mucronata and Bobartia indica. Restioid species, which did not occur with high cover, included Chondropetalum deustum and Hypodiscus aristatus. Besides Tetraria thermalis, another sedge Tetraria cuspidata was also common. Thirty-nine percent of species in this community were not found elsewhere, for example, Tetraria thermalis, Protea speciosa, Protea cynaroides, Erica monadelpha and Chondrapetalum deustum. Despite large differences in soil characteristics, this community shared a number of species with the Meridianum community on limestone, including Erica coccinia and Tetraria cuspidata, which were common in both communities. The height of this vegetation was 0.3 to 1.0 m.

4. Elegia verreauxxii - Leucospermum pedunculatum Restioid Fynbos, referred to as the Elegia community. This community comprised the 14 sites and 64 species on the plain in front of the mountain. Some of the sites were very slightly sloping towards the south, while the others were flat. These soils were very deep, with a low proportion of fine sand. pH and fertility were lowest at these sites (Table 2.2).

This community is classified as Dry Restioid Fynbos in Cowling et al. (1988) and is relatively uniform across the plain. It is dominated by low restioid and ericoid shrubs (30-50 cm height), especially restoid Elegia verreauxiia and ericoids Staavia radiata and Erica imbricata. Leucospermum pedunculatum, a procumbent proteoid shrub, forms dense mats and had high cover in all sites. Other common species included ericoids Erica pulchella, Erica rhophalantha, Erica filipendula, Salaxis sp. and Phylica imberbis, restioids, Staberoha cernua and Mastersiella digitata, low proteoid Mimetes cuculatus and small shrubs, Serruria nervosa, Spatalla squamata, and Gnidia imbricata. Many of these species, such as Erica imberbis, Staavia radiata and Serruria nervosa are shared with the adjacent Susannae and Compacta (Aulax umbellata - Protea compacta) communities, where they form an understorey with the dominant overstorey proteoid shrubs. Some species, such as Erica imbricata and Phylica imberbis and Serruria nervosa, are common in all communities on acid soil and are only absent from the Meridianum community on limestone. Only nine of the species in this community were unique to these sites and included Gnidia pinifolia and Erica cerinthoides.

5. Aulax umbellata - Protea compacta Proteoid Fynbos, referred to as the Compacta community. This community consists of 69 species at 10 sites. These sites were located on the gently sloping, south-facing lower slopes of the sandstone part of the mountain above the plain. Rock cover was very low and the soil was moderately deep, but much shallower than the plain soils (Table 2.2). There was a high proportion of coarse sand and the pH and fertility index were low.

This vegetation was classified by Cowling et al. (1988) as Protea compacta Proteoid Fynbos with occasional dominance of Leucadendron xanthoconus and affinity to the Ericaceous Fynbos on higher sandstone slopes, in this case the Xanthoconus community. Located between the Xanthoconus community on the higher sandstone slopes and the Elegia community on the plain, this community includes elements of both adjacent communities, but no unique species. It is, however, distinguished by the overstorey dominant species Aulax umbellata, which is also common in the Xanthoconus community and occasional in the Elegia community, and Protea compacta, which is occasional in both adjacent communities. Leucadendron laureolum is dominant at some sites, but also occurs in the Elegia community. Several other species are most prominent in, but not restricted to, this community: proteoid Leucadendron salignum, ericoids Erica filipendula and Syndesmanthus sp. and restioid Calopsis hyalinus. Widespread species which are common in this community are proteoid Mimetes cuculatus, ericoids Erica imbricata, Staavia radiata, Sympieza labialis and Euchaetis burchellii, restioids Mastersiella digitata and Staberoha cernua, small shrub Serruria nervosa and sedge Tetraria cuspidata. The height of this vegetation ranged from 0.5 m (lacking overstorey) to 2.0 m (with overstorey).

2.4.2 Detrended Correspondence Analysis (DCA)

The eigenvalues of axes 1 and 2 of the DCA for sites, were 0.86 and 0.55 respectively (Figure 2.3). Sites belonging to four communities classified by TWINSPAN (Meridianum, Xanthoconus, Elegia and Compacta) were closely grouped in the ordination. Sites belonging to the fifth community, Susannae, which had been further divided into two groups of sites, were more widely dispersed in the ordination. The 75 sites were arranged into three main groups consisting of the Meridianum community which was widely separated from the others, the Susannae community and a third group consisting of the Xanthoconus, Compacta and Elegia communities. The first two DCA axes identified two main compositional

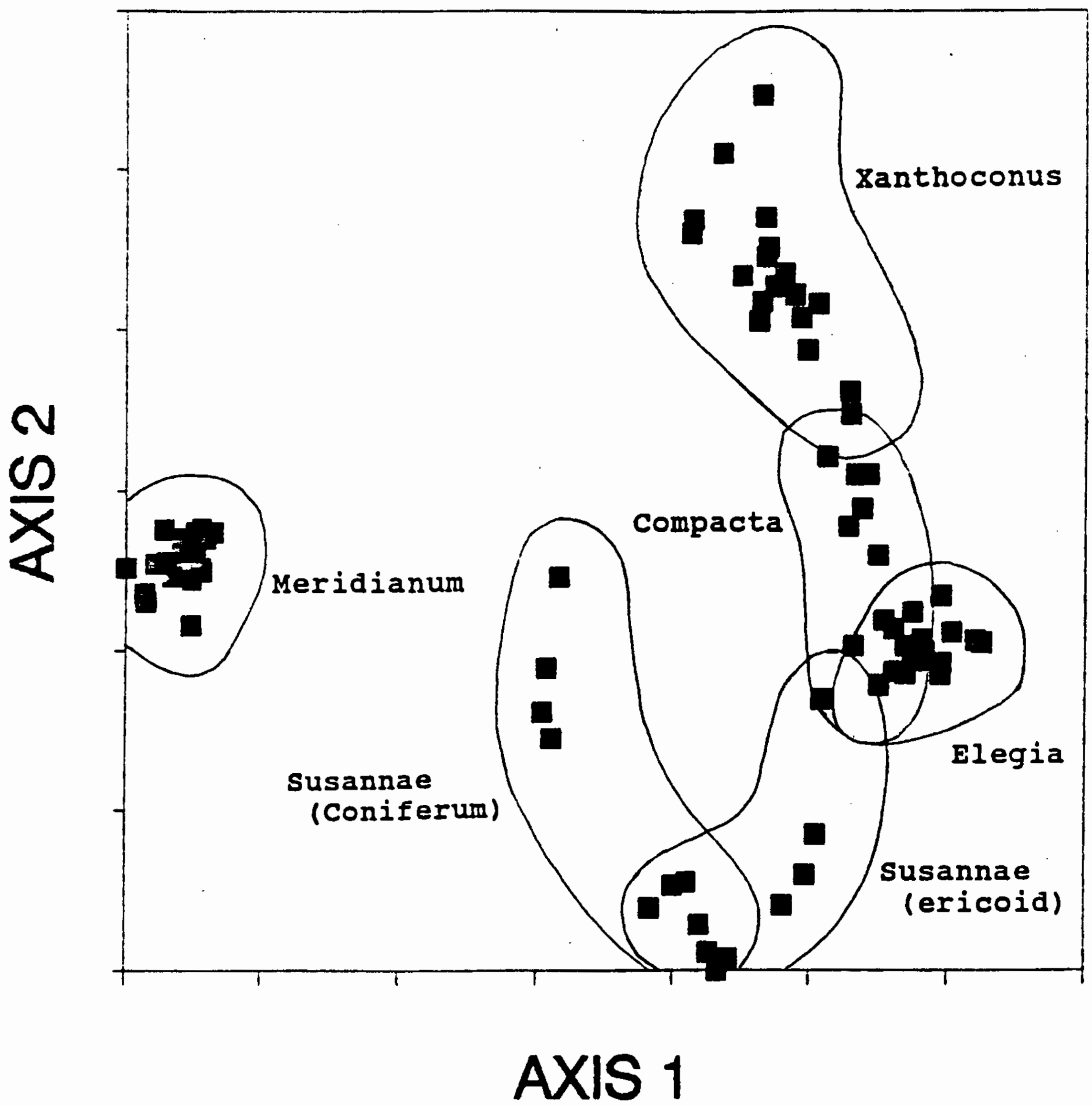

FIGURE 2.3 DCA ordination diagram for 75 sites, plotted on the first and second DCA axes. The groups of sites associated with each of the five communities are circled and labeled.

gradients in this vegetation. Along axis 1 the sequence was from the Meridianum community, to the Susannae-Coniferum group which included certain limestone species, followed by the Susannae-ericoid group and the Xanthoconus, Compacta and Elegia communities, all of which share species and were not distinguished along this axis. This sequence corresponds to a pH and fertility gradient (see soil characteristics associated with each community - Table 2.1). The Meridianum, Susannae and Elegia communities were not separated along axis 2. The main compositional gradient along axis 2 was from the Elegia and Compacta communities to the Xanthoconus community which was fairly widely dispersed along this axis. Although this sequence was not as clear as that along axis 1, it corresponds to some extent with decreasing soil depth (see table 2.1).

2.4.3 Canonical Correspondence Analysis (CCA)

2.4.3.1 Complete data set

The complete data set, incorporating all environmental factors, produced eigenvalues of the first two CCA axes of 0.82 and 0.65. Table 2.3 shows the canonical coefficients of all enviromental factors, except for fine sand which had been omitted to prevent multicollinearity). The highest coefficients indicating the main determinants of the CCA axes were for pH (axis 1) and soil depth (axis 2). Soil texture (% coarse and medium sand), % rock cover and fertility index (bioassay) had lower coefficients. Altitude

TABLE 2.3 Eigenvalues and canonical coefficients of the first and second CCA axes of the complete data set and eigenvalues and inter-set correlation coefficients for the sandstone and colluvial sand data sets. No results are shown for the limestone data set as the axes were not significant (Monte Carlo permutation test)

	Complete data set		Sandstone		Colluvial sand	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
EIGENVALUES	0.82	0.65	0.47	0.22	0.73	0.41
ENVIRONMENTAL VARIABLES: coefficients						
Altitude	0.02	0.12	-0.74	0.42	0.79	0.47
Slope	0.10	0.10	-0.81	-0.24	0.60	0.47
Rock cover	-0.02	0.17	-0.81	-0.23	-0.10	0.32
Depth	-0.14	-0.51	0.31	0.25	-0.06	-0.68
% Crs Sand	-0.36	0.11	*	*	-0.02	0.64
% Med Sand	-0.13	-0.17	0.34	-0.05	*	*
% Fine Sand	*	*	0.11	0.46	0.11	0.49
pH	0.71	-0.30	-0.03	0.34	0.79	0.07
Fertility index	0.03	-0.15	0.55	0.32	0.72	-0.29
Aspect						
S-facing	-0.02	-0.05	-0.33	0.17	-0.12	0.11
W-facing	-0.01	-0.05	0	0	+	+
E-facing	-0.03	-0.05	+	+	+	+
Flat	0	0	+	+	0	0

* Variable excluded from analysis to prevent multicollinearity (see explanation in text)

\+ These values of the nominal variable aspect are not represented in this data set.

and slope were only of minor importance, despite substantial differences between communities (see Table 2.1). The nominal variable aspect had very low influence, as the majority of sites were south-facing. Removal of factors with very low regression coefficients, namely, altitude, slope, aspect and fine sand, produced no reduction in the axis 1 eigenvalue and only reduced that of axis 2 by 0.01 to 0.64. Any further removal of factors produced more rapid decreases in the eigenvalues and so a set of six was selected as the best set. These were pH, soil depth, rock cover, % coarse sand, % medium sand and fertility index.

The biplot of 75 sites (site positions in the plot being the weighted averages of their component species) and six environmental factors is shown in Figure 2.4. The first two axes explained 16% of the variance in the species data. Despite this low value, a Monte Carlo permutation test of the F-ratios of the axis 1 eigenvalue and the trace statistic showed both to be significant ($p<0.05$). The groupings of sites of the five communities (classified by TWINSPAN) were dispersed in a manner very similar to that in DCA, although the two Susannae community groups were more closely associated, indicating similarity in environmental factors. The arrangement of these community groups among the CCA axes was also very similar to the arrangement on the DCA axes. Axis 1 separated the Meridianum community from the others along what was predominantly a gradient of increasing pH, although soil texture (decreasing percentage coarse sand) was also important. The separation of the

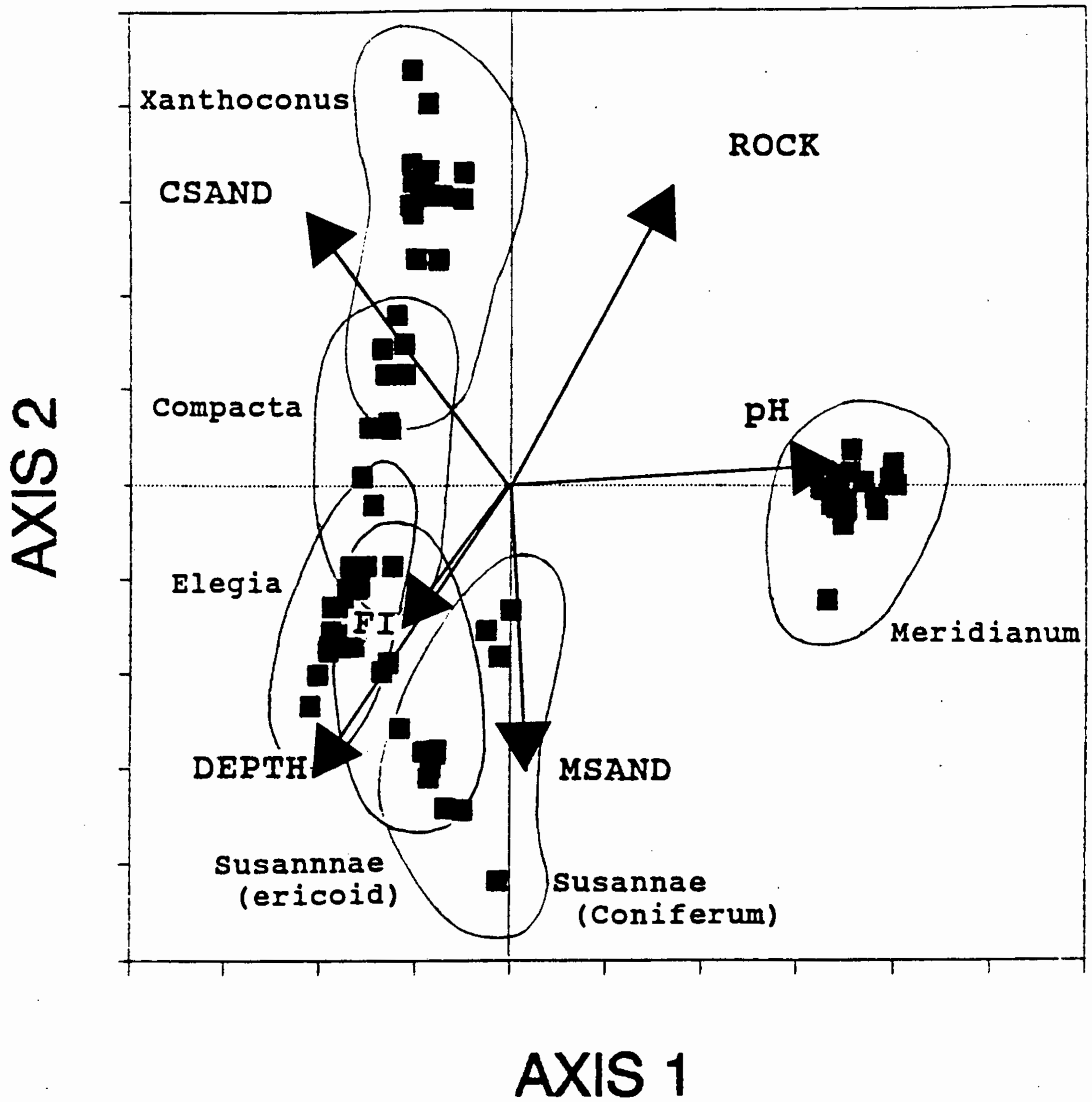

FIGURE 2.4 CCA biplot of site scores for 75 sites and the set of six most important environmental factors (vectors) on the first two CCA axes. The environmental factors were: pH, ROCK = % rock cover, CSAND = % coarse sand, FI = fertility index, DEPTH = soil depth and MSAND = % medium sand. The groups of sites associated with each of the five communities (from the TWINSPAN classification) are circled and labeled.

Meridianum community sites from all the others was more pronounced than in the DCA (resulting from major soil differences). The Susannae-Coniferum group was slightly dispersed from the Elegia and Compacta community groups along this gradient.

On axis 2, sites were dispersed along a gradient of decreasing soil depth in the sequence of Susannae and Elegia communities, followed by the Compacta community and finally the Xanthoconus community in the shallowest soil. There was also a gradient of decreasing percentage medium-textured sand and increasing coarse-textured sand.

2.4.3.2 Single Substratum Data Sets

The limestone data set consisted of 18 sites and the vegetation on all of these was classified as the Meridianum community, consisting of 76 species. These sites varied substantially in altitude, slope, rock cover and fertility index (see standard errors in Table 2.1), but no significant vegetation-environment relationship was detected (Monte Carlo permutation test).

The sandstone data set included 23 sites and 141 species. When the CCA with all environmental factors was run, it produced eigenvalues of 0.47 and 0.21 (for axes 1 and 2 respectively). Percentage coarse sand was omitted to avoid multicollinearity (the eigenvalues were not influenced by this). The effect of aspect was uncertain, as 18 sites were

S-facing (correlation coefficient: 0.33). The remaining five, which were W-facing had a coefficient of 0.0. The overall importance of aspect in the vegetation-environment relationship was apparently minor, because when this was eliminated from the CCA, the first axis eigenvalue dropped by only 0.03 and the second axis eigenvalue remained unchanged. The first two axes of the CCA with the final set of eight environmental factors (Figure 2.5(a)) explained 22% of the variation in the species data. The trace statistic (sum of all eigenvalues) was significant ($p<0.05$), but the first eigenvalue was not significant on its own. The canonical coefficients did not correspond with the biplot scores for the environmental factors and so inter-set correlation coefficients were used to determine the relative importance of each factor (Table 2.3). These are correlations of environmental variables with species axes (Ter Braak 1986) and provide an alternative means of assessing the importance of the environmental factors when the canonical coefficients cannot be used. The factors best correlated with the first axis were slope, rock cover, altitude and fertility index and, to a lesser extent, percentage medium sand and soil depth. For axis two, all correlations were much lower and the highest coefficients were for percentage fine sand and pH. The biplot (Figure 2.5 (a)), showed the sites of the Xanthoconus community to be widely dispersed along both axes, with the five Compacta community sites separated from those of the Xanthoconus community along axis 1 (lower altitude, rock cover and shallower slope).

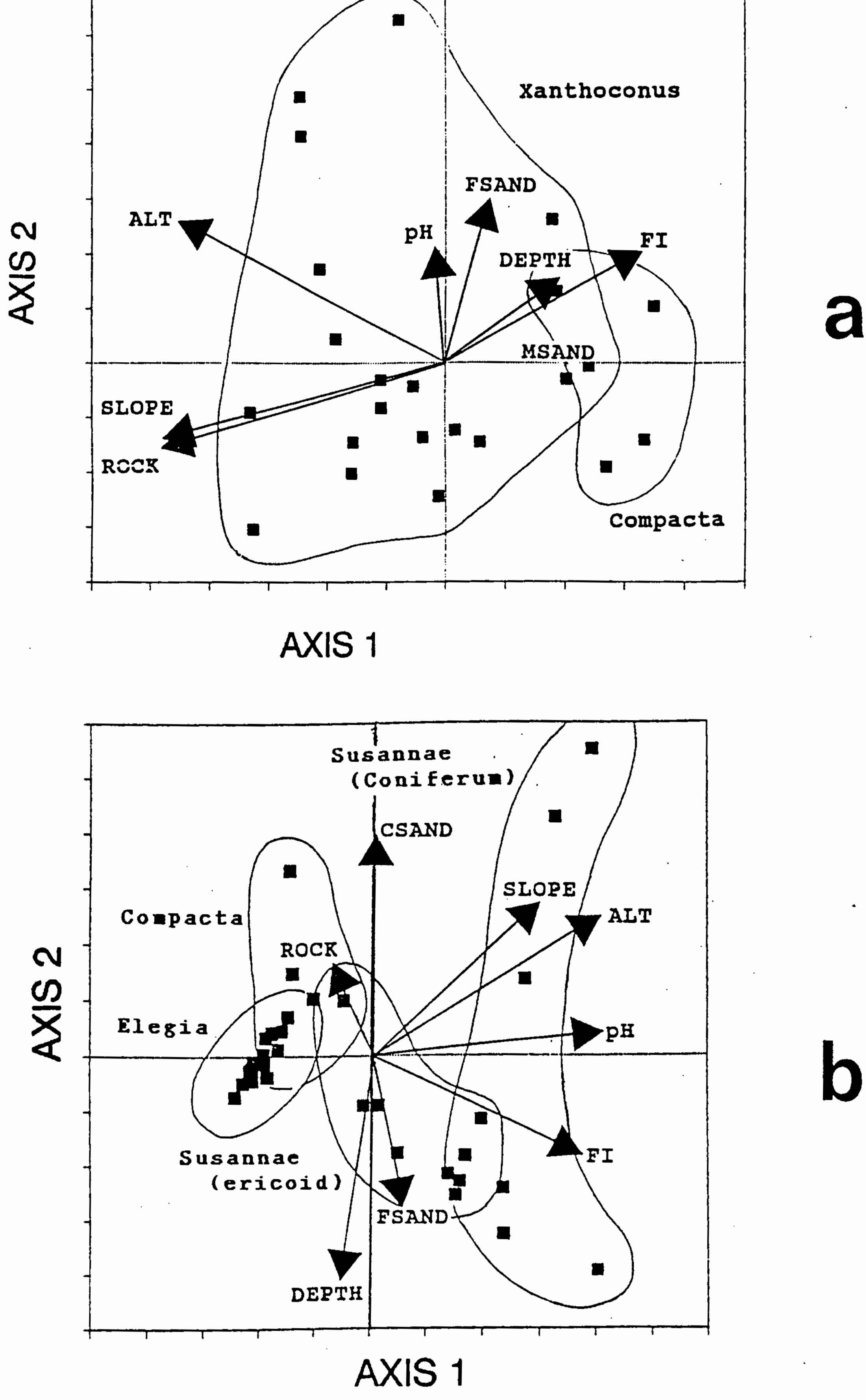

FIGURE 2.5 CCA biplots of sites on **(a)** the sandstone substratum (23 sites) and (b) the colluvial sand substratum (34 sites). Environmental factors were: ALT = altitude, SLOPE, ROCK = % rock cover, DEPTH = soil depth, FSAND % fine sand, MSAND % medium sand, CSAND = % coarse sand, pH and FI = fertility index (see text for determination). Groups of sites belonging to different communities (two on sandstone and four on colluvial sand) are circled and labeled.

The colluvial sand data setcomprised the largest of the single substratum data sets, with 34 sites and 138 spp occurring in three out of the five communities. This produced higher eigenvalues than the sandstone sites : 0.73 for axis 1 and 0.41 for axis 2, with percentage medium sand removed to prevent multicollinearity. Aspect was also removed as 29 sites were south-facing and five were on level ground. This reduced the axis 1 eigenvalue by only 0.02 and did not influence the axis 2 eigenvalue. The first two axes of this analysis explained 24% of the variation in the species data. Both the axis 1 eigenvalue and the trace statistic of the CCA with eight environmental factors were significant ($p<0.05$). As with the sandstone data set, it was necessary to assess the importance of the environmental factors on the basis of interset correlation coefficients (table 2.3) and not canonical coefficients. High coefficients were found for altitude, pH, fertility index and slope in axis 1, and depth and percentage coarse sand for axis 2.

In the biplot of sites (Figure 2.5(b)), sites representing the Elegia community, the Compacta community, and both groups of the Susannae community were arranged sequentially along axis 1. This representing what was primarily a nutrient gradient (increasing pH and fertility). This gradient was also associated with increasing altitude. Most of the dispersion of sites along axis 2 occurred with sites in the Susannae-Coniferum group, as well as the Compacta community. This is the result of a gradient of depth and soil texture (percentage coarse sand) along with altitude and slope.

2.5 DISCUSSION

The species-richness of fynbos is substantially higher than most vegetation types where multivariate analyses such as DCA and CCA have been applied. These include wetland vegetation in southern France (Grillas 1990), Bolivian savanna (Haase 1990), mountain forests in New Mexico and Colorado, USA (Allen et al. 1991), savannah and forest in Senegal and Gambia (Frederiksen and Lawesson 1992) and forest on Pacific limestone islands (Franklin and Merlin 1992). One case where more species-rich vegetation has been studied is the work of Russel-Smith (1991) and Russel-Smith et al. (1993) in Australian monsoon rainforest. Species richness was comparable to that in this fynbos study (ca. 135 species per forest patch of less than 5 ha, compared with 251 species in the 30 ha fynbos study site). Although direct gradient analysis (such as CCA) was not used, indirect gradient analysis provided strong evidence that distribution of rainforest assemblages across northern Australia was related to moisture availability and to a lesser extent, to soil fertility.

This study of vegetation-environment relationships in fynbos, took place at a much smaller scale than all the above studies, but despite this, a strong vegetation-environment relationship was shown to exist. Not only are there many species in a small area, but they were found to be grouped into distinct communities with varying degrees of spatial overlap or common species. Comparison of soil characteristics from the corresponding sites showed that each community was associated with a particular range of soil and other physical site characteristics. The CCA showed that the two main compositional gradients, in the form of community changes across the landscape, were strongly correlated with gradients of soil factors, namely pH and a physical gradient consisting of soil depth and texture. Although soil fertility did not emerge as a major factor, the importance of pH is evidence of the key role of soil chemical characteristics in this area, as suggested by Cowling (1990) for the Agulhas Plain as a whole. Distinguishing the effects of soil nutrients from physical factors relating to moisture availability has proved difficult in previous vegetation-environment studies in fynbos (Cowling and Holmes 1992), but a multivariate technique, such as CCA, was found extremely useful in this study for separating and comparing different factors. The importance of soil depth and texture relates to the importance of soil volume and texture on moisture availability and consequently on nutrient availability (Yair and Danin 1980, McConnaughay and Bazzaz 1991, Mishio 1992). Soil moisture is of particular importance during summer drought in mediterranean-climate regions such as this (Miller et al. 1983, 1984, Moll and Sommerville 1985). A study of root morphology and water relations of Protea susannae and Protea compacta at this site (Chapters 4 and 5) showed that for these species habitat specialization for soils of different depth is a major determinant of their distribution patterns.

Limestone is a relatively rare substratum in the Cape Floristic Region (Deacon et al. 1992) and has an extremely high level of endemism (Thwaites and Cowling 1988, Cowling et al. 1992). Despite the narrow overlap zone with the Susannae-Coniferum group, species turnover at the edges of the limestone in this study site was almost complete, although 37% of limestone species were recorded at sites outside the Meridianum community and the Susannae-Coniferum group. Despite this, the structure and generic composition of the limestone fynbos differs very little from the surrounding acid fynbos (Thwaites and Cowling 1988). This is an interesting contrast to the British heathlands, where acid heath is replaced by grassland on limestone, except where more acidic deposits overlie it (Etherington 1981).

It is interesting to note that in the CCA, the separation of the Meridianum sites (on limestone) from all others along the first axis occurred almost entirely on the basis of pH and was unrelated to the fertility index (which had the highest average value for these sites). This was probably because the limestone sites were extremely variable in fertility (including both the highest and lowest values). Although these soils are high in total nitrogen and phosphorus (Thwaites and Cowling 1988 and see Chapter 3), availability of these nutrients, especially phosphorus would be greatly reduced through organic and inorganic immobilization (Stewart and Tiessen 1987, Witkowski and Mitchell 1987).

The failure to detect a significant vegetation-environment relationship within the limestone substratum is not surprising since it included only one community. However, this is in spite of substantial variation in environmental factors, especially altitude, slope, rock cover and fertility. A general feature of these limestone soils is that with the very high rock cover, the soil occurs in thin sheets over rock and in pockets or fissures. Such patterns have major implications on soil moisture availability (Yair and Danin 1980) and consequently on nutrient availability (McConnaughay and Bazzaz 1991). It is thus likely that soil characteristics relating to depth and volume are important, but at a scale smaller than that detectable in the 5 m x 5 m plots used in this study.

In contrast to limestone, the sites on sandstone showed a significant vegetation-environment relationship. Altitude and slope, which did not emerge as important factors in the complete analysis, were found to be important on sandstone where they were most variable. The strongest factors were again the physical variables related to soil moisture, i.e. soil depth, texture and rock cover. Factors relating to nutrients, i.e. pH and fertility were of lesser importance and were fairly uniform across this substratum. Such overriding importance of physical factors relating to soil moisture availability has been widely supported for sandstone mountain fynbos in general (Cowling and Holmes 1992). The Xanthoconus community on the higher, steeper slopes (differentiated from the Compacta community at the base of the slope) belongs to the Mesic Ericaceous Fynbos type, dependent on this microclimate of steep, seaward-facing slopes on coastal mountains with increased orographic rainfall and exposure to fog (Campbell 1985, Cowling et al. 1988).

The colluvial sand data set was fairly complex in terms of the range of environmental factors and vegetation (although there was much overlap between the three communities) and produced the strongest vegetation-soil relationship of all three substratum types. It also included some of the most fertile sites in the landscape (adjacent to limestone), as well as the most acid and infertile sites (on the plain). This resulted in a strong correlation of the fertility index with variation in the vegetation (an effect obscured in the complete analysis) and slightly greater role for pH than on sandstone. It is interesting to note that altitude and, to a lesser degree, slope emerge as important environmental factors despite small ranges. This is probably because the most fertile soils were on the lower slopes of the hills adjacent to limestone and the most infertile on the plain. In addition, runoff may be greater near the base of the slope (Susannae and Compacta communities) compared to the plain (Elegia community) (Yair and Danin 1980). Two main compositional gradients on colluvial sand were from west to east (Susannae community to Compacta community), associated with the environmental gradients of soil depth, pH and fertility, and from north to south (Proteoid Fynbos at the base of to mountain, to Restioid Fynbos on the plain) along an environmental gradient of altitude, slope, pH and fertility.

The vegetation-environment relationships described were statistically significant correlations and explained much of the compositional pattern in the vegetation (especially as regards the communities). However, only 16% of the variance of the species data in the complete data set was explained, while 22% and 24% were explained by the first two CCA axes in the sandstone and colluvial sand data sets respectively. Ter Braak (1991) points out that low explained-variance is typical of species-abundance data in CCA analyses, resulting from the frequently high noise levels in such data. In considering additional factors to explain this "noise", it should be noted that, in this landscape, the soil factors used in this analysis were only a subset of the possible range of abiotic and biotic factors which might influence vegetation patterns. The fact that the eigenvalues of the CCA axes are similar to those in the DCA is evidence that an appropriate set of environmental factors was used (see Franklin and Merlin 1992). Nevertheless, there are certain additional explanations that should be considered:(i) additional environmental factors, (ii) fire effects on vegetation and soils and (iii) biotic interactions.

(i) Additional environmental factors, not considered here include organic carbon content of soils (this varied substantially in the landscape), individual nutrient factors (micro- and macro nutrients) and factors which vary with time. These included available nitrogen and phosphorus, levels of which vary greatly during the year, influenced by moisture, temperature, pH and Ca (Witkowski and Mitchell 1987, Stock et al. 1988). These are dealt with in a comparison of soil nutrient dynamics in the soils associated with each of the five community types in Chapter 3.

(ii) In fynbos almost all recruitment occurs after fire and, for many species, this is from seed (Kruger 1983). Fire differentially influences species distribution patterns directly, by causing local extinctions and population explosions (Bond et al. 1984, Taylor 1984, Cowling 1989). Cowling and Gxaba (1990) showed that the spatial variation in density of recruiting Leucadendron laureolum was drastically altered from that of the pre-fire population. The immediate post-fire environment may also differ from later stages in terms of fire-induced changes in nutrient availability (Stock and Allsopp 1992).

(iii) Biotic interactions, such as competition and predation, which could influence species distributions were not considered in this study. Predation of seeds and seedlings has been shown to influence vegetation boundaries (Goldberg 1985, Brown and Heske 1990). The importance of interspecific competition in influencing community composition and community boundaries is a subject of much recent ecological research (see reviews: Keddy 1989, Bond et al. 1992). However, understanding the importance of a process such as competition and its interaction with environmental factors requires manipulative field experiments involving small numbers of selected species (Keddy 1989). A detailed field study of six dominant Proteaceae species at this site is reported in Chapter 6.

In conclusion, this study area, although small is unusual in both its species richness and the fact that it includes a range of soil types representative of those on which fynbos is found. The distinct communities present in this vegetation showed compositional gradients that were strongly correlated with environmental factors. The mechanism controlling this relationship are complex and could include effects of plant physiology (Newton et al. 1991), species regeneration biology (Mustart and Cowling 1993), microsymbiont specificity (Cowling et al. 1990) and interactions of competition and environmental factors (Bond et al. 1992, and see Chapter 6). This relationship of complex patterns of vegetation and environmental factors in this fynbos landscape is convincing evidence of the crucial role that environmental factors, especially soil factors, play in determining species distributions, species turnover and ultimately the enormous species richness of the Cape Floristic Region.

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CHAPTER 3.

VARIATION IN SOIL NUTRIENT CONTENT AND THE DYNAMICS OF NITROGEN AND PHOSPHORUS ACROSS FYNBOS COMMUNITY BOUNDARIES

3.1 ABSTRACT

The relationship between changes in soil nutrient characteristics and fynbos community boundaries was investigated near Cape Agulhas. Soil characteristics relating to nutrient content (pH, total nitrogen and total phosphorus, organic carbon, and various cations) were assessed at sites along three transects crossing the boundaries between five plant communities. Dynamics of available nitrogen and phosphorus in soils of three communities were studied in the field over one year, using ion-exchange resins. There was great variation in the extent of change in soil characteristics across community boundaries. The characteristics that varied most were pH, total nitrogen, Ca^{+2} and total phosphorus. Differences in available nutrients and phosphorus among soils indicated that the communities in this landscape were associated with a mosaic of nitrogen and phosphorus avalibility. It is proposed that complex species differences in nutrient-use and soil differences in nutrient availability may be important in explaining species distributions and community composition in nutrient-poor mediterranean-climate ecosystems.

3.2 INTRODUCTION

Fynbos soils are typically acid and nutrient-poor, particularly with regard to nitrogen and phosphorus (Kruger et al. 1983). In this regard they resemble the soils of the Western Australian heathlands (kwongan), rather than other mediterranean-climate regions of the world (Groves 1983, Mitchell et al. 1984). This low nutrient status is compounded by summer drought and low winter temperatures and plants in both fynbos and kwongan possess specialised nutrient-uptake strategies (Lamont 1983) and internal nutrient cycling (Mitchell et al. 1986).

As nutrients play such an important ecological role (see review in Kruger et al. 1983), one would expect spatial variation in their availability to be a major factor in determining species distributions and community composition. Certain fynbos areas such as the Agulhas Plain have very high levels of edaphic endemism (Cowling et al. 1992). Associated with this is high species turnover across soil types that differ primarily in pH and nutrients (Thwaites and Cowling 1988, Cowling 1990).

Many studies of factors controlling species distributions and community composition (i.e. looking for niche differentiation among species) in mediterranean-climate ecosystems have concentrated on differences in water relations (Davis and Mooney 1986, Frazer and Davis 1988, Lamont et al. 1989, Lamont and Bergl 1991, Davis 1991).

Little attention has been paid to the possible importance of species differences in nutrient-use in facilitating coexistence or spatial segregation through habitat specialization. However, recent work in fire-prone woodland in Western Australia (Pate _et_ _al_. 1993, Stewart _et_ _al_. 1993) showed important differences between species in the use of nitrogen, as well as the exploitation of different nitrogen resources. This suggests that complex differences in soil nutrient availability could be important in determining the spatial distribution of species in nutrient-poor habitats such as kwongan in Australia and fynbos in South Africa. High edaphic endemism would increase the likelihood of this.

Vegetation-environment relations in fynbos were assessed using correlative techniques in the Soetanysberg, near Cape Agulhas (Chapter 2). This site included a very large number of species and a range of soil types, including deep acid sands, shallow acid sands and shallow alkaline limestone soil. Limestone soils, being alkaline and of comparatively high nutrient-status, are atypical of fynbos soils and support many calcicole endemics (Thwaites and Cowling 1988). Canonical correspondence analysis showed vegetation patterns to be strongly correlated with a range of environmental factors, especially pH and physical soil factors (depth and texture). Nutrient factors, included in the form of a fertility index (based on a bioassay), were important on colluvial sands but less so on rocky limestone and sandstone slopes.

This study is a more detailed investigation of patterns of soil nutrients and the associated different species and community distributions in this landscape, shown by the correlations in Chapter 2. Although detailed studies of the dynamics of nitrogen and phosphorus in fynbos soils have been made, almost all of this information comes from the coastal fynbos site at Pella (see review in Stock and Allsop 1992) and the nearby strandveld vegetation-type (Witkowski and Mitchell 1987). There is a need for information on the dynamics of nitrogen and phosphorus in a wider range of fynbos soils, especially with regard to their influence on spatial variation in vegetation structure.

The aim of this study was to determine whether total soil nutrient content as well as the dynamics of nitrogen and phosphorus availability vary across fynbos community boundaries within a landscape. For this purpose, the soil associated with each of the five fynbos communities in the Soetanysberg (described in Chapter 2) were sampled. Variation in the availability of nitrogen and phosphorus over one year was compared among sites in three of these communities and an area intermediate between two communities.

3.3 METHODS

The study was carried out at the Soetanysberg site, for which vegetation and soils were described in detail in Chapter 2. In order to sample the soil types associated with each of the five communities, three transects were located so as to include all of the communities and the main soil types (Figure 3.1). These transects crossed several community boundaries.

Transect A (300 m, seven sites) began in Proteoid Fynbos of the Meridianum community on shallow, rocky limestone soil (two sites). It continued down the slope to two sites in the the Susannae community (also Proteoid Fynbos) on deep colluvial sand adjacent to the limestone and ended with three sites in the Elegia community (Restioid Fynbos) on the deep colluvial sand of the plain. Dominant species at each site are listed in Table 3.1.

Transect B (300 m, seven sites) was parallel to transect A, but began on a sandstone slope. The Xanthoconus community (Ericaceous Fynbos) on shallow, rocky sandstone soil was at the top two sites, followed by the Compacta community (Proteoid Fynbos) on slightly deeper colluvial sand at the third and fourth sites and then by the Elegia community (Restioid Fynbos) at the fifth, sixth and seventh sites on the plain.

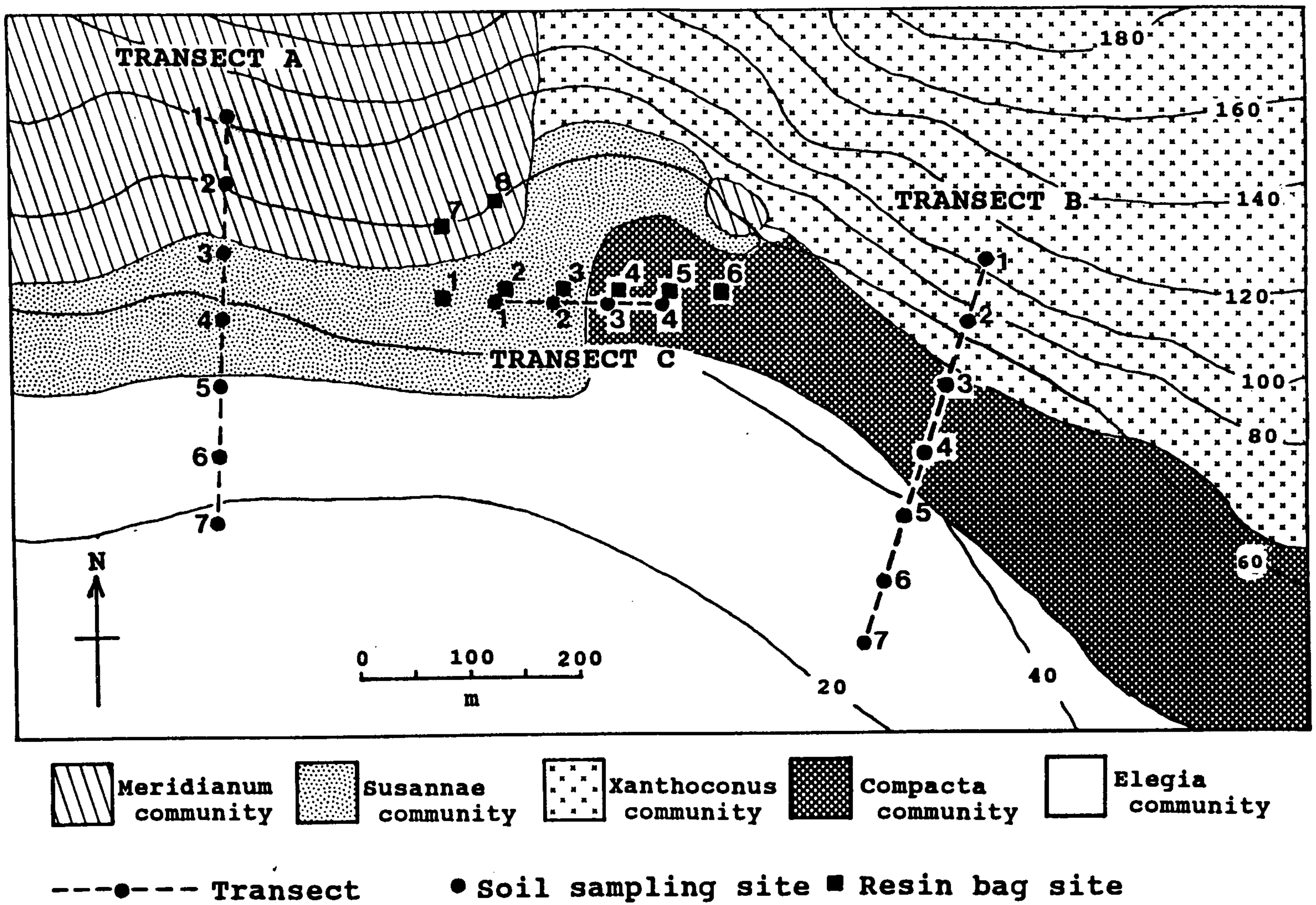

FIGURE 3.1 Map of the study site showing the locations of the soil sampling sites (transects A, B and C) and the resin-bag sites (nitrogen and phosphorus dynamics) with respect to the five fynbos communities. Community boundaries are approximate and intermediate zones are not shown. See Chapter 2 for community descriptions. Contours are at 20 m intervals.

TABLE 3.1 Substratum and vegetation information for the 18 soil-sampling sites. Full community descriptions are given in Chapter 2.

Site no.	Substratum	Fynbos Type	Community	Dominant species
Transect A				
1	Limestone	Proteoid	Meridianum	*Leucadendron meridianum* *Mimetes saxitillus* *Tetraria cuspidata*
2	Limestone	Proteoid	Meridianum	*Ischyrolepis leptocladis* *Leucadendron meridianum* *Euclea racemosa*
3	Coll. sand	Proteoid	Susannae	*Protea susannae* *Willdenowia rugosa*
4	Coll. sand	Proteoid	Susannae	*Protea susannae*
5	Coll. sand	Restioid	Elegia	*Sympieza labialis* *Serruria nervosa* *Eleiga verreauxii*
6	Coll. sand	Restioid	Elegia	*Elegia verreauxii* *Mimetes cuculatus* *Salaxis* sp.
7	Coll. sand	Restioid	Elegia	*Elegia verreauxii*
Transect B				
1	Sandstone	Ericaceous	Xanthoconus	*Leucadendron xanthoconus* *Syndesmanthus* sp.
2	Sandstone	Ericaceous	Xanthoconus	*Protea compacta* *Syndesmanthus* sp.
3	Coll. sand	Proteoid	Compacta	*Leucadendron xanthoconus* *Serruria nervosa*
4	Coll. sand	Proteoid	Compacta	*Calopsis hyalinus* *Protea compacta* *Leucadendron laureolum*
5	Coll. sand	Restioid	Elegia	*Aulax umbellata*
6	Coll. sand	Restioid	Elegia	*Sympieza labialis*
7	Coll. sand	Restioid	Elegia	*Mimetes cuculatus* *Elegia verreauxii* *Sympieza labialis*
Transect C				
1	Coll. sand	Proteoid	Susannae	*Protea susannae* *Metalasia muricata*
2	Coll. sand	Proteoid	Susannae$	*Protea susannae* *Protea compacta*
3	Coll. sand	Proteoid	Compacta$	*Protea compacta* *Erica imberbis* *Calopsis hyalinus*
4	Coll. sand	Proteoid	Compacta	*Aulax umbellata* *Calopsis hyalinus* *Serruria nervosa*

$ intermediate between Susannae/Compacta communities

Transect C (150 m, four sites) was between and perpendicular to transects A and B. This crossed the boundary between the Susannae community on the deep colluvial sands adjacent to limestone and the Compacta community on shallow colluvial sand at the bottom of the sandstone slope. While the first and fourth sites were in the Susannae and Compacta communities respectively, the second and third sites included elements of both communities.

3.3.1 Soil nutrient content

Three replicate soil samples were collected 5 m apart at each of the 18 sites. After air-drying and sieving of samples, the following analyses were carried out : pH in $CaCl_2$; total nitrogen by Kjeldahl digestion and ammonia determination by the phenyl-hypochlorite method (Allen et al. 1973); total phosphorus (Murphy and Riley 1962); total organic carbon by the Walkley-Black method (Jackson 1958) and cations, calcium, magnesium, sodium and potassium (Jackson 1958).

3.3.2 Nitrogen and phosphorus dynamics

Dynamics of plant available nitrate, ammonium and phosphorus were assessed over a one year period using ion-exchange resins as described by Sibbesen (1977) and applied for use in the field by and Lajtha (1988). Ion-exchange resins were sown into rectangular bags (4 cm x 8 cm) of fine nylon mesh. Cation-exchange bags contained 7.0 g of Amberlite IRA-120 resin and anion exchange bags, 5.0 g of Amberlite IRA-402. Bags were charged by shaking for three periods of 30 minutes each in 5% HCl (fresh solution for each wash) followed by several rinses in distilled water to remove all acid. Before placement in the soil, each bag was shaken to remove excess water. Bags were inserted vertically in the soil, with the top 1-2 cm below the surface (extending to approximately 10 cm depth). This was carried out along transect C, i.e. across the boundary between the Susannae and Compacta communities (Figure 3.1). Two additional sites were added to the transect: one 50 m from each end, resulting in two sites in each community and two sites in the intermediate zone. For comparison, two sites were located in the Meridianum community on limestone. Three anion and three cation bags were placed at each site and replaced every six weeks with a fresh set.

Sets of resin bags removed from the soil were taken back to the laboratory and washed with distilled water to remove soil and root material. Root growth through bags was very rare. Each bag was placed in a glass bottle and shaken for 30 minutes in 50 ml of 5% HCl. The resulting eluates were filtered and then stored at 4 ^{o}C for analysis. Eluates of cation resin bags were analysed for ammonium (using a sodium phenate reagent) and eluates of anion bags for nitrate, using copperized cadmium reduction followed by nitrite determination by the Griess-Ilosvay method (Stock 1983) and for phosphate (Murphy and Riley 1962).

In order to allow for effects of the resins in adsorbtion and on the later extraction of ions, standards were made up for each analysis. Resin bags were placed individually in glass bottles with 50 ml of NH_4NO_3 (cation resin bags), KH_2PO_4 or K_2NO_3 solutions (anion resin bags) of a range of known concentrations as well as distilled water (control). Bottles were shaken for 16 hrs, which was sufficient for all detectable ammonium, nitrate or phosphate to be adsorbed onto the resins. The bags were then washed with distilled water and eluted by the same procedure as bags from the field. These eluates were analysed along with those from the field resin bags and used as standards based on the quantity of ammonium, nitrate or phosphate in the 50 ml standard solution.

3.3.3 Statistical Analysis

Analysis of variance and Tukey multiple range tests (STATGRAPHICS, v 4.0, Statistical Graphics Corp. 1987) were applied to the results of all soil analyses. As the resin bag data (levels of available ammonium, nitrate and phosphate) were not normally distributed, they were either square-root transformed before analysis of variance (ammonium data) or analysed with Kruskal-Wallis analysis of variance by ranks and Nemenyi joint-rank multiple comparisons (Hollander and Wolfe 1973). The non-parametric procedures were necessary for nitrate and phosphate data, as square-root transformation did not result in normal distributions.

3.4 RESULTS

3.4.1 Soil nutrient content

Transect A showed a pH gradient down the slope, with the top two sites (Meridianum community) significantly higher than the second two (Susannae) which, in turn, were higher than the bottom three sites (Elegia) (see Table 3.2 for statistics). For all other factors (total nitrogen and phosphorus, organic carbon and cations), the two Meridianum sites had higher contents than the remaining sites, among which no significant differences were found. Total N and calcium were eight to ten times higher at the two Meridianum sites and differed significantly between them. Sodium was also significantly different between the sites 1 and 2.

Transect B showed a more or less continuous nutrient gradient. There was only a slight decrease in pH from top to bottom, but this was significantly higher at the top site, compared to all except the second site. Large decreases in total nitrogen and phosphorus, organic carbon, and cations were detected along this transect, with highest values at the top site (Xanthoconus community). Significant differences were detected among the top three sites (Xanthoconus and Compacta communities) for all factors, but not among the lower four sites (Compacta and Elegia communities).

TABLE 3.2 Soil data from 18 sites arranged in three transects in the Soetanysberg (mean ± one S.E.). Each soil characteristic was analysed separately for each transect by analysis of variance. Numbers followed by the same superscript are not significantly different (Tukey multiple comparisons, $p<0.05$).

Site	pH	Total nitrogen (μg/g)	Total phosphorus (μg/g)	Organic C (g/kg)	Ca (μg/g)	Mg (μg/g)	Na (μg/g)	K (μg/g)
Transect A								
1	7.4 ± 0.04^{a}	3687 ± 1092^{a}	82.2 ± 3.8^{a}	115.9 ± 25.1^{a}6	5062 ± 598^{a}	321.0 ± 66.1^{a}	106.3 ± 14.4^{a}	97.0 ± 12.6^{a}
2	7.3 ± 0.04^{a}	5973 ± 287^{b}	95.2 ± 3.4^{b}	148.2 ± 25.7^{a}	6203 ± 61^{b}	374.3 ± 80.0^{a}	163.7 ± 24.4^{b}	117.7 ± 6.3^{a}
3	5.4 ± 0.08^{b}	643 ± 38^{c}	66.1 ± 0.6^{c}	22.6 ± 3.6^{b}	570 ± 58^{c}	85.7 ± 5.6^{b}	15.3 ± 1.2^{c}	19.3 ± 2.0^{b}
4	4.8 ± 0.08^{c}	393 ± 64^{c}	63.9 ± 1.4^{c}	18.2 ± 2.5^{b}	326 ± 35^{c}	72.7 ± 8.9^{b}	18.7 ± 0.3^{c}	27.0 ± 2.1^{b}
5	4.4 ± 0.04^{d}	490 ± 114^{c}	61.8 ± 0.9^{c}	31.9 ± 8.3^{b}	280 ± 3^{c}	81.0 ± 1.5^{b}	37.0 ± 7.9^{c}	33.7 ± 6.2^{b}
6	4.3 ± 0.05^{d}	307 ± 7^{c}	60.5 ± 0.2^{c}	12.2 ± 1.9^{b}	138 ± 2^{c}	45.3 ± 1.9^{b}	20.7 ± 2.2^{c}	15.0 ± 1.7^{b}
7	4.3 ± 0.04^{d}	360 ± 25^{c}	60.6 ± 0.2^{c}	20.2 ± 0.9^{b}	251 ± 19^{c}	78.3 ± 3.5^{b}	42.0 ± 6.2^{c}	26.0 ± 4.7^{b}
	$F_{(6,14)}=606$ ***	F=27.3 ***	F=44.4 ***	F=15.5 ***	F=39.6 ***	F=11.8 ***	F=24.3 ***	F=44.5 ***
Transect B								
1	5.2 ± 0.06^{a}	2133 ± 168^{a}	68.6 ± 1.4^{a}	63.8 ± 4.4^{a}	1104 ± 105^{a}	307.3 ± 11.7^{a}	102.0 ± 12.2^{a}	93.3 ± 6.3^{a}
2	5.0 ± 0.06^{ab}	1280 ± 108^{b}	69.4 ± 0.3^{a}	49.8 ± 3.3^{b}	688 ± 46^{b}	165.7 ± 5.0^{b}	$51.7\pm4.3b^{c}$	58.3 ± 9.0^{b}
3	4.8 ± 0.07^{bc}	900 ± 25^{b}	65.3 ± 0.5^{b}	39.4 ± 1.7^{b}	506 ± 41^{bc}	128.3 ± 6.6^{b}	68.7 ± 8.9^{b}	50.0 ± 1.5^{bc}
4	4.8 ± 0.07^{bc}	410 ± 20^{c}	62.3 ± 0.4^{c}	20.6 ± 2.1^{c}	284 ± 45^{cd}	80.3 ± 0.4^{c}	46.7 ± 2.9^{bc}	37.7 ± 0.3^{bcd}
5	4.7 ± 0.04^{c}	290 ± 15^{c}	61.9 ± 0.2^{c}	16.9 ± 0.7^{c}	195 ± 12^{d}	62.2 ± 5.1^{c}	37.7 ± 5.0^{bc}	37.3 ± 3.0^{bcd}
6	4.8 ± 0.07^{bc}	380 ± 38^{c}	61.9 ± 0.3^{c}	19.6 ± 1.6^{c}	262 ± 41^{cd}	78.3 ± 8.3^{c}	36.0 ± 4.6^{c}	32.3 ± 5.3^{cd}
7	4.8 ± 0.04^{bc}	380 ± 65^{c}	61.3 ± 0.2^{c}	16.7 ± 1.9^{c}	217 ± 30^{d}	73.0 ± 13.7^{c}	33.7 ± 3.7^{c}	28.7 ± 3.2^{d}
	$F_{(6,14)}=9.2$ ***	F=69.5 ***	F=31.6 ***	F=56.3 ***	F=39.6 ***	F=95.2 ***	F=13.4 ***	F=20.8 ***
Transect C.								
1	5.5 ± 0.17^{a}	1047 ± 213^{a}	67.5 ± 0.7^{a}	32.6 ± 3.1^{a}	782 ± 93^{a}	149.7 ± 17.0^{a}	21.3 ± 3.9^{a}	48.3 ± 10.8^{a}
2	4.9 ± 0.09^{b}	517 ± 102^{ab}	65.2 ± 1.0^{ab}	22.1 ± 4.5^{a}	450 ± 89^{ab}	96.7 ± 15.3^{ab}	25.7 ± 0.9^{a}	37.3 ± 7.9^{a}
3	4.8 ± 0.08^{b}	420 ± 51^{b}	62.4 ± 0.1^{b}	22.2 ± 2.5^{a}	316 ± 51^{b}	80.7 ± 11.7^{b}	18.7 ± 3.2^{a}	34.7 ± 3.2^{a}
4	4.9 ± 0.03^{b}	660 ± 10^{ab}	61.5 ± 1.3^{b}	31.5 ± 4.4^{a}	473 ± 78^{ab}	118.0 ± 13.1^{ab}	27.0 ± 7.4^{a}	49.0 ± 8.5^{a}
	$F_{(3,8)}=8.8$ **	F=5.2 ***	F=9.4 **	N.S.	F=6.2 ***	F=4.3 *	N.S.	N.S.

* $p<0.05$, ** $p<0.01$, *** $p<0.001$

Transect C showed a gradient of total phosphorus which decreased from site 1 (Susannae) to 4 (Compacta). No other factors showed any continuous gradient, but pH, total nitrogen, total phosphorus, calcium and magnesium differed significantly among sites. At site 1 (Susannae community), pH was significantly higher than the other three sites (Susannae/Compacta intermediates and Compacta community). Total nitrogen, calcium and magnesium decreased from sites 1 (Susannae) to 3 (intermediate), but increased again at site 4 (Compacta). Organic carbon, sodium and potassium did not differ significantly between sites. Site 1 showed substantially higher values of total nitrogen, magnesium and potassium than sites 3 and 4 of transect A (also Susannae community). This suggests that limestone may be underlying this site (at a depth greater than 1.2 m).

3.4.2 Nitrogen and Phosphorus Dynamics

3.4.2.1 Ammonium

No distinct seasonal pattern of ammonium availability was observed (Figure 3.2(a)). Significant differences between sites were detected on only three of the nine six-week periods: those ending 14 April 1991 ($F_{(7,16)} = 2.93$, $p<0.05$), 1 June 1991 ($F_{(7,16)} = 3.42$, $p<0.05$) and 31 August 1991 ($F_{(7,16)} = 5.50$, $p<0.01$). On 14 April 1991, ammonium at site 7 (Meridianum) was significantly higher than at site 3 (Susannae/Compacta intermediate) (Tukey multiple comparison, $p<0.05$). On 1 June 1991, ammonium at Site 8

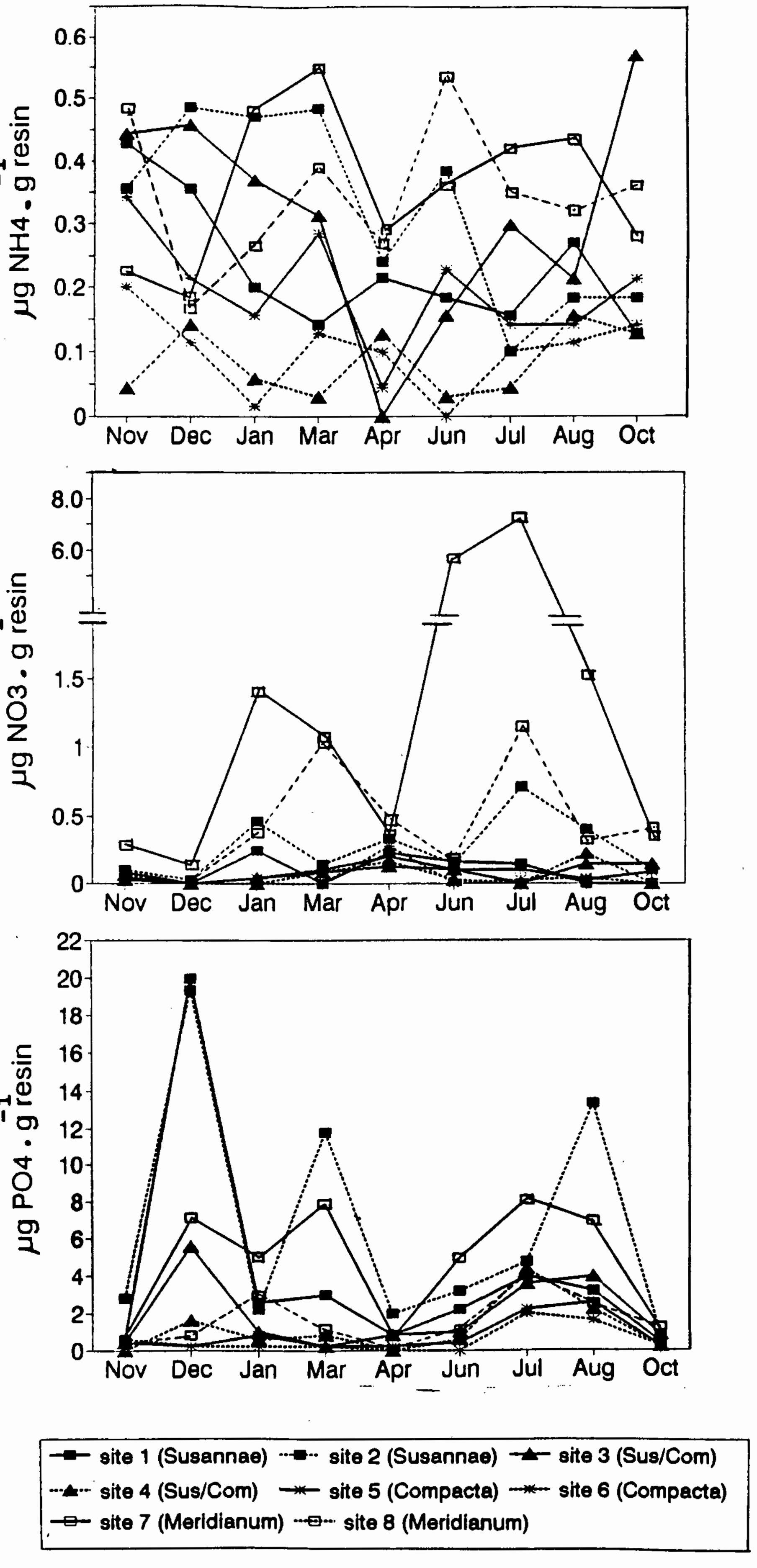

FIGURE 3.2 **(a)** ammonium, **(b)** nitrate and **(c)** phosphate extracted from soil in the field by means of ion-exchange resin bags at eight sites. Data were collected over nine six-week periods ending, 2 November and 11 December 1990, 23 January, 6 March, 14 April, 1 June, 10 July, 31 August and 5 October 1991. Each point is the average for three resin bags and bars represent one S.E.

(Meridianum) was significantly higher than site 6 (Compacta) (Tukey, $p<0.05$), while on 31 August 1991, Sites 7 and 8 were significantly higher than site 6 (Compacta) (Tukey, $p<0.05$). On the latter occasion site 7 was significantly higher than all sites except 1 (Susannae) and 3 (Susannae/Compacta intermediate).

The total amount of ammonium extracted from resin bags over the nine six-week periods (sum of the nine average values for each site) was highest at sites 7 and 8 (Meridianum) and very low sites 4 and 6 (Susannae/Compacta intermediate and Compacta respectively) (Figure 3.3(a)).

3.4.2.2 Nitrate

Resin-extractable nitrate differed significantly between sites on six out of the nine six-week periods: 11 December 1990, 23 January 1991, 6 March 1991, 10 July 1991, 31 August 1991 and 5 October 1991 (Kruskal-Wallis one-way analysis of variance, $p<0.05$ in all cases) (Figure 3.2(b)). On all of these occasions one or both of the Meridianum sites (sites 7 and 8) had significantly higher levels of nitrate than all other sites (Nemenyi Joint-Rank test, $p<0.05$). Highest values were measured on 1 June and 10 July 1991 (the rainy season) and a small peak on 23 January and 6 March (dry conditions and highest temperatures).

The total amount of nitrate (absorbed per gram of resin) over the nine six-week periods was extremely high at site 7

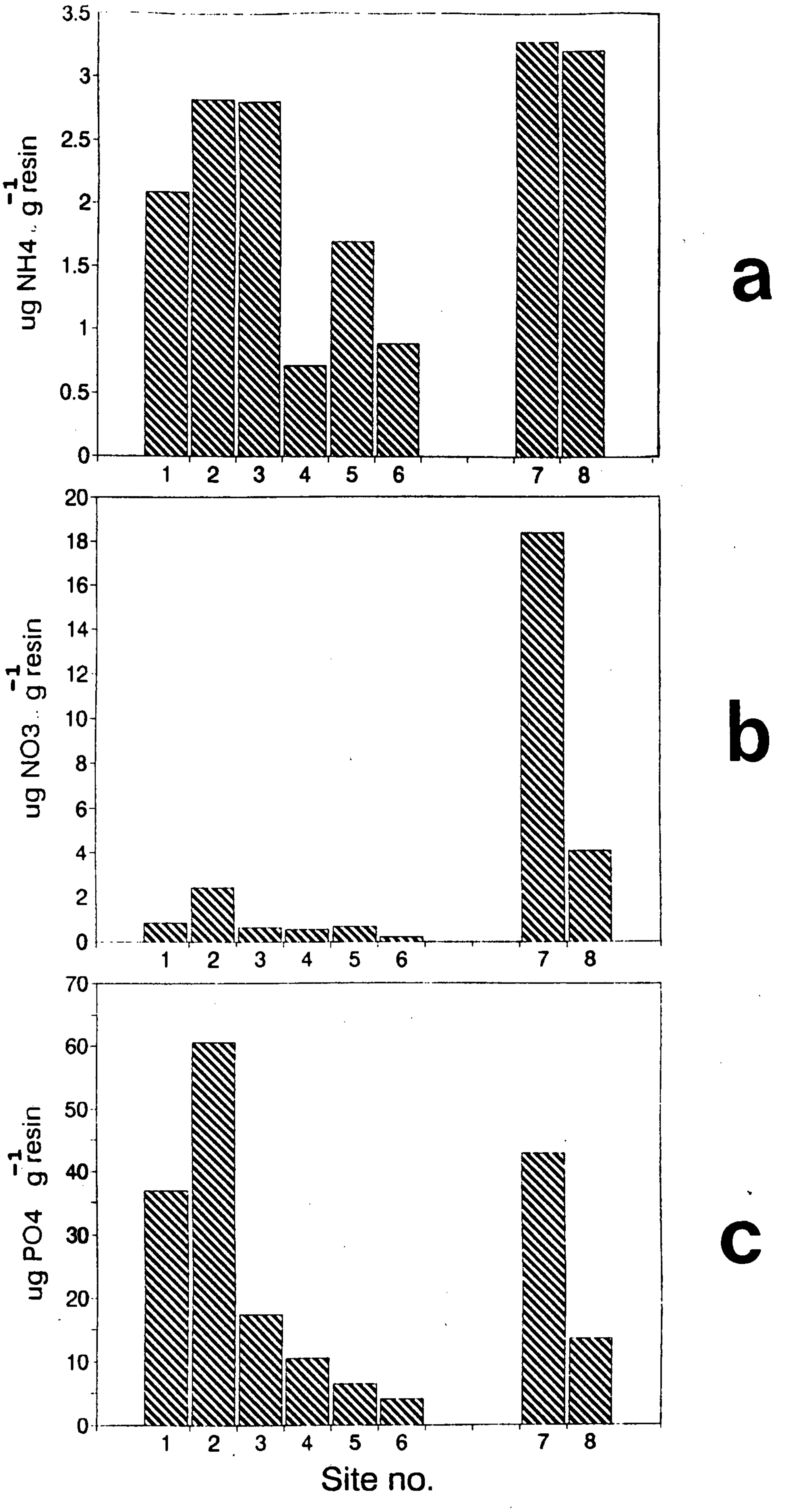

FIGURE 3.3 Accumulated 54-week totals of **(a)** ammonium **(b)** nitrate, and **(c)** phosphate extracted from soil in the field by ion-exchange resin bags. Three anion and three cation bags were buried at each of the eight sites and replaced by a new set every six weeks. Sites 1 and 2 were in the Susannae community, sites 3 and 4 in the Susannae/Compacta intermediate zone, sites 5 and 6 in the Compacta community and sites 7 and 8 in the Meridianum community.

(Meridianum) (Figure 3.3(b)). Except for sites 8 (Meridianum) and 2 (Susannae), very little nitrate was found at the other sites. At site 7, total nitrate absorbed (18.4 $\mu g/g$ resin) was much higher than the total ammonium absorbed (3.3 $\mu g/g$ resin).

3.4.2.3 Phosphate

Available phosphate showed significant differences between sites on four of the nine six-week periods: 6 March, 10 July, 31 August and 5 October 1991 (Kruskal-wallis one way analysis of variance, $p<0.05$ in all cases) (Figure 3.2(c)). The pattern across sites differed between these four periods. On 6th March site 2 (Susannae) had the highest phosphate availability and this was significantly higher than at site 5 (Compacta) (Nemenyi Joint-Rank test, $p<0.05$). Phosphate availability at site 2 was much lower for the periods ending 14 April and 1 June. On 1 June, site 7 (Meridianum) had the highest phosphate availability and was significantly higher than sites 5 and 6 (both Compacta) ($p<0.05$). Phosphate was high again at site 2 on 31 August, when sites 2 and 7 were highest, both significantly higher than site 6 (Compacta) ($p<0.05$). In the period ending 5 October all sites showed low phosphate availability, but site 8 (Meridianum) had significantly higher values than site 4 (Susannae/Compacta intermediate) ($p<0.05$). Phosphate totals (over nine six-week periods, Figure 3.3(c)) at sites 1 and 2 (Susannae) and 7 (Meridianum) were much higher than at the remaining sites.

3.5 DISCUSSION

Boundaries between the five Soetanysberg communities were associated with changes in soil pH, organic matter and nutrient content. While pH had been identified earlier as being correlated with species distributions (Chapter 2), the importance of the other factors was not clear from that study. Organic carbon and nutrient content are correlated with pH and so would account for part of its significance in the vegetation-environment correlation.

The limestone soil (Meridianum community) was the most distinctive, with the highest values of all factors, especially pH, total nitrogen and calcium. With the change to the Susannae community on deep colluvial sand adjacent to limestone, all soil factors decreased abruptly, making this the most distinct soil boundary in the study site. The soil of the Susannae community was not as clearly differentiated from those of the adjacent Elegia community (on the plain) and Compacta community (to the east) on the basis of nutrient factors. The major difference across the Susannae/Elegia boundary was decreasing pH, while decreasing total phosphorus characterised the Susannae/Compacta boundary (but see Chapter 4 for the importance of soil depth). The Xanthoconus community on sandstone was, like the Meridianum community, characterised by higher soil pH, organic carbon and nutrient content than the community at the bottom of the slope (in this case the Compacta community). The differences in the soil factors across the

Xanthoconus/Compacta boundary were much smaller than those across the Meridianum/Susannae boundary. The boundary between the Compacta community and the Elegia community on the plain was the least distinctive in this study. It was associated with small decreases in most factors but none of these differences were statistically significant. This is not surprising as these two communities were very similar in species composition (Chapter 2).

The variation in soil nutrients across community boundaries corresponds with the strong vegetation-environment relationships shown in Chapter 2. These indicate a much greater control of soil over plant species distributions than has been found in kwongan (the mediterranean-climate ecosystem of Western Australia) (Hopkins and Griffin 1984). Studies of small areas of kwongan have found floristic variation to be related to soil type, but this explains only a small proportion of the variance (Hnatiuk and Hopkins 1981, Brown and Hopkins 1983, Griffin et al. 1983, Bell and Lonergaran 1985). Many of those species found to be confined to particular soil types or microhabitats were to be found on different soil types elsewhere (Griffin et al. 1983). This is apparently an important contrast between kwongan and fynbos (the equivalent South African ecosystem) as shown by the strong assocation of many fynbos species with soil types in the Soetanysberg (see also Chapter 2) and the Agulhas Plain in general (Thwaites 1988, Cowling 1990). On a larger scale, this is supported by the high frequency of edaphic endemism of fynbos in general (Cowling et al.

1992). Hopkins and Griffin (1984) suggested that soil-vegetation relationships in kwongan may have been underestimated as a result of the use of the simplistic classification of soils into a few general types. Detailed analysis of a range of soil chemical and physical characteristics (as done here and in Chapter 2) may identify stronger vegetation-soil relationships in kwongan.

When dynamics of nitrogen and phosphorus were considered, additional soil differences across the Susannae/Compacta boundary began to emerge. Despite much lower organic matter and total nitrogen than the limestone soil, the two Susannae sites and the first of the Susannae/Compacta intermediate sites had similar annual production of ammonium to the Meridianum sites. The remaining mixed site and the two Compacta sites had lower ammonium production, despite similar organic matter and total nitrogen. In addition, pH was higher at the Susannae sites which would favour nitrification (Haynes and Goh 1978). The difference between Susannae and Compacta soils may be related to differences in the rates of decomposition of litter of the different dominant species. Litter quality influences decomposition rates (Mitchell et al. 1986). However, decomposition of sclerophyllous litter is slow (Mitchell and Coley 1987) and is seen as a relatively minor source of available nutrients, except after fire (Mitchell et al. 1986, Stock and Allsopp 1992).

With the exception of one of the Susannae sites, almost no nitrate was detected off limestone. This would be expected from the difference in pH, as the relatively low pH of the non-limestone soils would inhibit nitrification (Haynes and Goh 1978). On limestone, available nitrate showed a small summer peak and a very large winter peak indicating sensitivity of these processes to temperature and particularly to moisture (see review Haynes and Goh 1978, Stock et al. 1988). The large difference between the two limestone sites was maintained throughout the year and can probably be attributed to microsite differences as these soils occur as pockets in cracks and depressions in the rock. Such soil pockets differ in moisture characteristics (Yair and Danin 1980) which has important implications for nutrient availability (McConnaughay and Bazzaz 1991).

At various times in the year available phosphate in the Susannae soils was equivalent to or higher than in the Meridianum soil (limestone) and much higher than the Susannae/Compacta intermediate and Compacta soils. This latter difference was particularly marked when phosphorus mobilized over the whole year was considered. The difference in available phosphorus beween the Susannae and Compacta soils corresponded to the difference in total phosphorus. In contrast, available phosphorus was low with respect to total phosphorus at the Meridianum sites which was highest in these soils. The very low available phosphate in limestone soils can be attributed partly to Ca-immobilization (Stewart and Tiessen 1987, Lajtha and

Schlesinger 1988a). Lajtha and Schlesinger (1988b) showed that the presence of high $CaCO_3$ in soil can directly inhibit the uptake or availability of phosphorus to plant roots. The high organic matter could also reduce available phosphorus (Witkowski and Mitchell 1987) and together with high pH would increase microbial immobilization of phosphorus (Seeling and Zasoski 1993).

While calcium and organic/microbial factors limit phosphorus availability on limestone, low total phosphorus, together with factors such as iron and aluminium-immobilization associated with acid soils (Stewart and Tiessen 1987, Witkowski and Mitchell 1987), would be likely to limit phosphorus availability in the Compacta and probably Elegia plain soils.

When available nitrogen and phosphorus are considered together, it becomes evident that the arrangement of plant communities in the landscape was associated with a mosaic of soils with different ratios of nutrient availability. The Meridianum community (eg. <u>Leucadendron meridianum</u>) was associated with high nitrogen and moderate phosphorus availability, the Susannae community (<u>Protea susannae</u>, <u>Leucadendron coniferum</u>) with moderate nitrogen and high phosphorus availability and the Compacta community (<u>Protea compacta</u>) with low nitrogen and low phosphorus availability. Although nutrient availability was not assessed in the Elegia and Xanthoconus communities, some indication of this can be gained from total nutrient levels. Total nitrogen and phosphorus were both extremely low in the white sand of the Elegia community on the plain, while the soil on the sandstone slopes (Xanthoconus) had total nitrogen and phosphorus contents intermediate between those of the Meridianum and Susannae commumities.

This strong association of fynbos species and communities with a complex mosaic of soil nutrient availability in a landscape points to the importance of plant nutrient-use strategies in determining species distributions. A prelimnary study of δ^{-15} N in several Proteaceae species from this site (W.D. Stock, unpublished data) suggests that important differences in the use of nitrogen-resources exist among these species. Such differences in nutrient-use as described for Australian species by Pate et al. (1993) and Stewart et al. (1993) may be evidence of an important niche axis facilitating co-existence or spatial separation (habitat specialization) in mediterranean-climate ecosystems. As studies in such ecosystems have concentrated on differences in water-use (Davis 1991), the importance of differences in nutrient-use may be an important new aspect to this issue.

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CHAPTER 4

THE WATER RELATIONS AND PHENOLOGY OF TWO PROTEA SPECIES IN RELATION TO THEIR DISTRIBUTIONS ACROSS A COMMUNITY BOUNDARY

4.1 ABSTRACT

Protea susannae is associated with deep sands near limestone and Protea compacta, with shallower sands on or near sandstone hills. At a site on the lower slopes of the Soetanysberg hills, near Cape Agulhas, the boundary between a P. susannae-dominated community and a P. compacta-dominated community was found to be very distinct. This was associated with an abrupt change in soil depth. In order to find whether habitat-specialization could explain this distribution pattern of these two Protea species, I investigated their root morphology, water relations (water potential, transpiration and phenology. P. susannae (deep sand) had a very extensive root system and a "water-spending" strategy suggesting access to water throughout the year. Flowering took place during the driest time of year. P. compacta (shallow sand) had a less extensive root system and relatively conservative water use, by means of which low water potentials were avoided. Flower bud development was very prolonged and flowers only opened in winter (after the wet season had begun). Although these species appear specialized for soils of different depth, within-species comparisons of plants in deep and shallow soils showed no significant differences for either species. This suggests that if differnces in water-relations determine the distribution patterns of these species, it would have to take place at a seedling or juvenile stage.

4.2 INTRODUCTION

The study of community boundaries or changes in dominant species has provided much important information about the controls of plant species distributions (Goldberg 1985, Keddy 1989a, Dawson 1990, Studer-Ehrensnberger et al. 1993). Some boundaries result from sudden changes in abiotic environmental factors or from critical points on continuous gradients of abiotic factors and their interaction with species tolerances (Oberbauer and Billings 1981, Dawson 1990, Studer-Ehrensberger et al. 1993). Others are determined by combinations of abiotic factors and interspecific competition, with the weaker competitors surviving in those areas where the others are abiotically excluded (Snow and Vince 1984, Gurevitch 1986, Keddy 1989a, Bertness 1991a,b).

Dawson (1990) showed that adaptation of water relations to particular ranges of soil moisture availability led to separation of three Salix species along a moisture gradient in alpine vegetation. The degree of overlap of the distributions of these species depended on their degree of specialization. Similar spatial partitioning of species along gradients relating to their water relations has been shown in other alpine vegetation (Oberbauer and Billings 1981), shrubs in deciduous mountain forests (Lipscombe and Nilson 1990), and in dune grasslands (Barnes 1985).

Studies of water relations in mediterranean-climate regions have mainly concentrated on differences between species within communities rather than along gradients. Co-occurring species in the Mediterranean Basin (Lo Gullo and Salleo 1988, Rhizopoulou and Mitrakos 1990) and in chaparral (Baker _et_ _al_. 1982, Bowman and Roberts 1985, Hart and Radosevich 1987) were found to show important differences in water-use strategies and phenology, despite being otherwise similar. Such differences among species have been viewed as a form of niche separation facilitating coexistence (Davis and Mooney 1986, Hart and Radosevich 1987).

In contrast, Lamont and Bergl (1991), found that co-occurring adult shrubs of _Banksia_ species in Australian kwongan lacked any such differences in water-use. Similarly, co-occurring shrubs in fynbos (_Protea_ spp.) have been found to have very similar water-use patterns. These include _Protea_ _nitida_ and _P_. _repens_ (Richardson and Kruger 1990) and _P_. _repens_ and _P_. _nerifolia_ (Miller _et_ _al_. 1984) in wet fynbos. Excavation of the root systems of the latter species pair showed that they had similar deep root systems (Higgins _et_ _al_. 1987). The water relations of all three species were also similar when compared over a number of mountain sites with rainfall ranging from 675 to 1600 mm (Miller _et_ _al_. 1983,1984).

However, as much of the species richness of fynbos is associated with a high degree of edaphic specialization and species turnover across habitats (Cowling and Holmes 1992), differences in water-use of species from adjacent habitats could play a role in maintaining boundaries between the different communities. Miller (1985) studied the water relations of fynbos species along a 30 km (340 m altitude) fynbos-karroo gradient with a range of annual rainfall from 223 to 673 mm. He found that two Protea species confined to different portions of this gradient showed different water relations. P. laurifolia, which was associated with wetter sites, co-occurred with P. glabra at an intermediate site. At this site, P. glabra showed less water stress than P. laurifolia and it was suggested that this was because P. glabra might possess a more extensive root system, but this was not investigated further.

This study considers two Protea species that each dominate a different fynbos community (Chapter 2). These communities are adjacent in an area at the foot of the Soetanysberg mountains near Cape Agulhas. The community boundary is made particularly distinct by the abrupt replacement of the one dominant overstorey species, Protea susannae, by the other, Protea compacta. In an earlier study of vegetation-environment relationships (Chapter 2), it was shown that the P. susannae-dominated community is associated with deeper soils than the P. compacta-dominated community. It was asked whether these two Protea species differ in their root morphology, water-relations and phenology in such a way as to explain their association with soils of different depth and the boundary observed at this site.

4.3 METHODS

4.3.1 Study Site and Species

This work was carried out on the southern slopes of the Soetanysberg mountains, 15 km west of Cape Agulhas (34^{o} 45'S; 19^{o} 50'E). The climate is typical of the south-western Cape, South Africa, namely cool, wet winters and warm, dry summers. Mean annual rainfall at Cape Agulhas is 452 mm. The eastern part of the Soetanysberg consists of sandstone capped by limestone, while the western part consists entirely of limestone (see Chapter 2, Figure 2.1). Sites for studying water relations and soil moisture were chosen on the lower slopes adjacent to the region where the main limestone/ sandstone transition occurs.

Protea susannae Phill. is a 2-3 m tall, much branched woody overstorey shrub which occurs along a narrow coastal belt along the southern Cape coast, South Africa (Rourke 1980). It occurs on deep sand derived from tertiary limestone. Protea compacta R.Br. is a 2-3.5 m tall sparsely branched woody overstorey shrub which also occurs only in a narrow coastal belt on the southern Cape coast (Rourke 1980). P. compacta is found in dense stands on sandy flats and the foothills of coastal sandstone mountains. The distributions of these two species overlap in a 50 km long zone along the southern edge of the Agulhas Plain. Their local distributions at this study site are shown in Figure 4.1, with the four sampling and measuring sites indicated. At

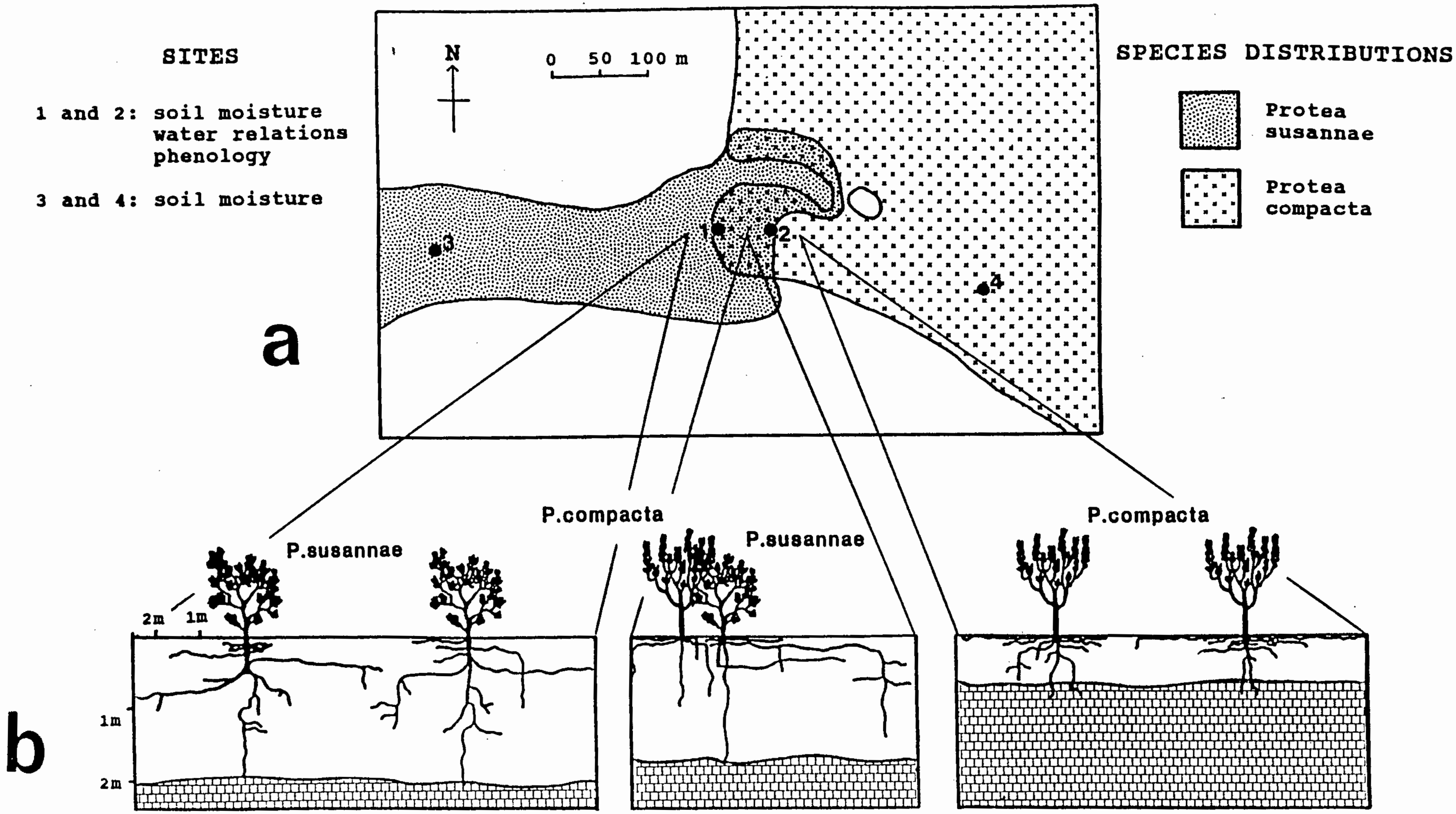

FIGURE 4.1. (a) Map of the study site on the southern side of the Soetanysberg mountains near Cape Agulhas, showing the local distributions of Protea susannae and Protea compacta and the sites at which soil moisture, plant water relations and phenology were studied. **(b)** Diagram of lateral and vertical extent of roots of P. susannae and P. compacta excavated at three locations.

site 1 (deep soil: soil depth approximately 2 m) P. susannae is dominant with respect to P. compacta (ratio of individuals, 6:1). This is the western limit of the distribution of P. compacta in the study area. At site 2 (shallow soil: soil depth 0.4-0.6 m) is the eastern limit of the local distribution of P. susannae. P. compacta is the dominant overstorey species (16:1). Soil moisture, root morphology, water relations and phenology were studied at these sites. At sites 3 (overstorey of P. susannae only, depth >1.2 m) and 4 (overstorey of P. compacta only, depth 0.4-0.6 m), only soil moisture data were collected.

4.3.2 Soil Depth.

Soil depth profiles were measured along two transects (100 m long) across the Protea susannae/Protea compacta overstorey boundary at the study site, three transects (80 m long) at a site approximately 1 km further west and one transect (80 m long) 2.5 km away on the north-facing side of the Soetanysberg (see map in Figure 4.2). At all of these sites P. susannae and P. compacta were seen to co-occur. The transects at the other two sites were shorter, as the patches of P. compacta were relatively small and completely surrounded by P. susannae. Every 4 m along each transect, soil depth was measured by driving a steel rod into the ground up to a maximum depth of 1.2 m. The presence and number of individuals of one or both Protea species were noted at each point.

4.3.3 Soil Moisture

From May 1989 to November 1990, soil moisture at sites 1 and 2 was determined every six weeks at depths of 5 cm and 20 cm. Ten samples were collected from each depth, sealed in airtight containers and transported to the laboratory for gravimetric determination of water content (percentage).

Percentage moisture data were arcsin-transformed (Zar 1984) before analysis of variance and Student-Newman-Keuls (SNK) multiple range tests were used to test for differences between sites and between depths.

From December 1990 to January 1992 soil moisture samples were collected from sites 1 to 4 at six-week intervals. They were collected at 5 cm, 20 cm and, 40-50 cm (maximum depth at sites 2 and 4) and 1 m (sites 1 and 3). Four samples were collected at each depth at each site. To estimate the total amount of water stored in the soil profile at each site, percentage moisture values were converted to depth equivalents, using the bulk density of the soil (Scholes and Savage 1989). Samples at 5 cm were taken to represent 0-10 cm of the profile; 20 cm samples as 10-30 cm; 40-50 cm samples as 30-70 cm; and 1 m samples as 70-150 cm.

4.3.4 Root Morphology

Root systems of three individuals of each species were excavated. Two Protea susannae individuals were excavated near site 1 and two P. compacta individuals near site 2. Two individuals, one of each species, growing immediately adjacent to each other were excavated halfway between sites 1 and 2. All roots more than 2 mm in diameter were exposed by hand and mapped in both the horizontal and vertical planes.

4.3.5 Water potential

From May 1989 to May 1990, predawn and midday water potentials of both Protea species at sites 1 and 2 were determined every six weeks, using a Scholander-type pressure-chamber (PMS Imstrument Company, Corvallis, Oregon, U.S.A.). Readings were taken on ten 12-15 cm long shoots per species, cut from different plants, which were randomly selected, within a circle of 10 m radius at each site. From July 1990 to June 1991, the same procedure was used, but only on the dominant species at each site. This was because of the limited number of individuals of the rarer species within the sampling area at each site.

Data from the first year were used to test for site and species effects, using analysis of variance and Student-Newman-Keuls multiple range tests (STATGRAPHICS, v4.0, Statistical graphics Corp.). The predawn water potentials of the second year were used to compare year-to-year variation.

4.3.6 Transpiration

Daily courses of transpiration were measured on 10 days selected to show transpiration on sunny days in all seasons. This was done between December 1989 and June 1991, using a LI-1600 steady-state porometer (LI-COR Inc., Lincoln, Nebraska). Measurements were taken on one recently expanded mature leaf from each of 8 individuals of Protea susannae at site 1 and P compacta at site 2. All readings at each site were taken within a circle of 10 m radius. Time constraints made it impossible to measure both species at both sites, so on each day, both species were measured at one site and only the dominant species at the other. Readings were taken every two hours from sunrise to sunset, giving 5-7 reading periods per species per site, depending on day length. Transpiration measurements were taken on the same days as predawn and midday water potential measurements and the collection of soil moisture samples. Daily transpiration rate curves were integrated, using the trapezium method, to give estimates of total daily transpiration per unit area (see Calkin and Pearcy 1984).

4.3.7 Phenology

In June 1989, 20 individuals of each species were selected along either side of the zone where they co-occur, centred on sites 1 and 2 (see Figure 4.9(a)). Three shoots, that were not bearing flowers, were randomly selected on each plant and tagged, giving a total of 60 shoots per species per site. Every six weeks from June 1989 to September 1991, shoots were measured from the apical bud to the most recent node (end of previous year's growth) to determine the growth increment. The presence and developmental stage of flower buds or flowers was noted on each occasion. A small number of shoots were lost through predation, disease or human interference and new shoots were chosen on the same plants in order to maintain sample size.

4.4 RESULTS

4.4.1 Soil Depth

Figure 4.2 shows the six transects through mixed species stands at the main site, plus two additional ones. On both transects at the main study site, the soil was more than 1.2 m deep on the western side, with an overstorey of *Protea susannae* and only occasional *P. compacta* individuals. Near the middle of these transects the soil rapidly became more shallow and varied between 0.4 and 0.8 m. The overstorey on this eastern half was *P. compacta* with occasional *P. susannae* individuals near the change in soil depth. At the three transects at the other south-facing site, as well as the one at the north-facing site, the soil was more than 1.2 m deep throughout and the overstorey consisted of more-or-less continuous *P. susannae* with occasional *P. compacta* individuals.

4.4.2 Soil Moisture

Soil moisture at sites 1 and 2 , measured from May 1989 to November 1990 (Figure 4.3), varied seasonally in accordance with rainfall patterns (see Figure 4.8). Analysis of variance of shallow soil moisture (5 and 10 cm) at sites 1 and 2 showed significant overall effects of depth ($F_{(1,414)}$ = 23.0, $p<0.001$) and site ($F_{(1,414)}$ = 4.95, $p<0.05$) and significant interactions of both with time ($F_{(11,414)}$ = 3.3, $p<0.01$ and $F_{(11,414)}$ = 4.6, p<,0.01). During winter

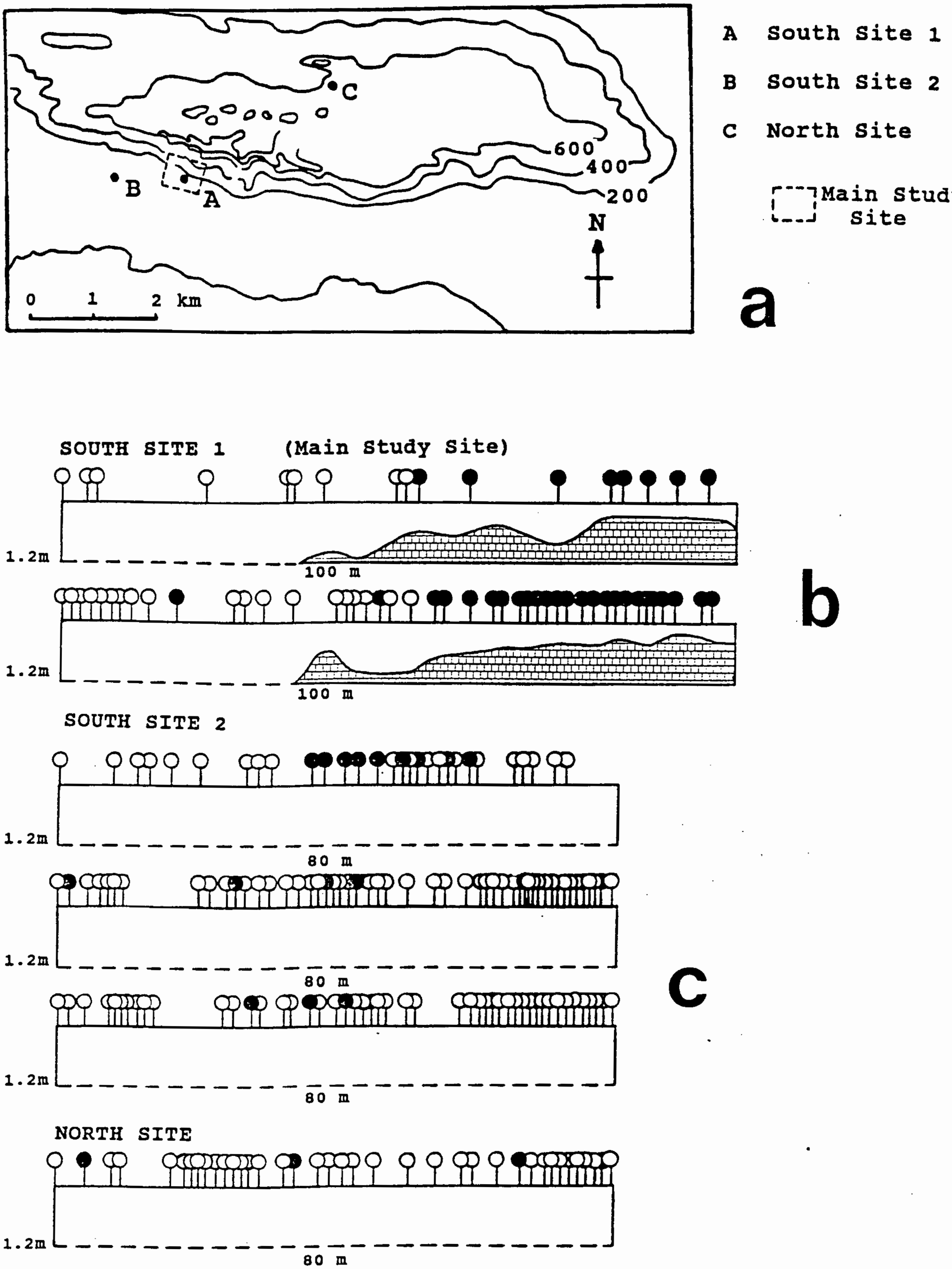

FIGURE 4.2 **(a)** Map of the central and eastern parts of the Soetanysberg mountains, showing the locations of the main study site and the three sites where transects were marked out through mixed Protea susannae/Protea compacta stands. **(b-c)** Transects at south sites 1 and 2 and the north site showing soil depth (down to a maximum of 1.2 m). Location of rock shown by hatching.

Individuals of P. susannae and P. compacta within radius of each depth-sampling point (1-8 individuals) are shown.

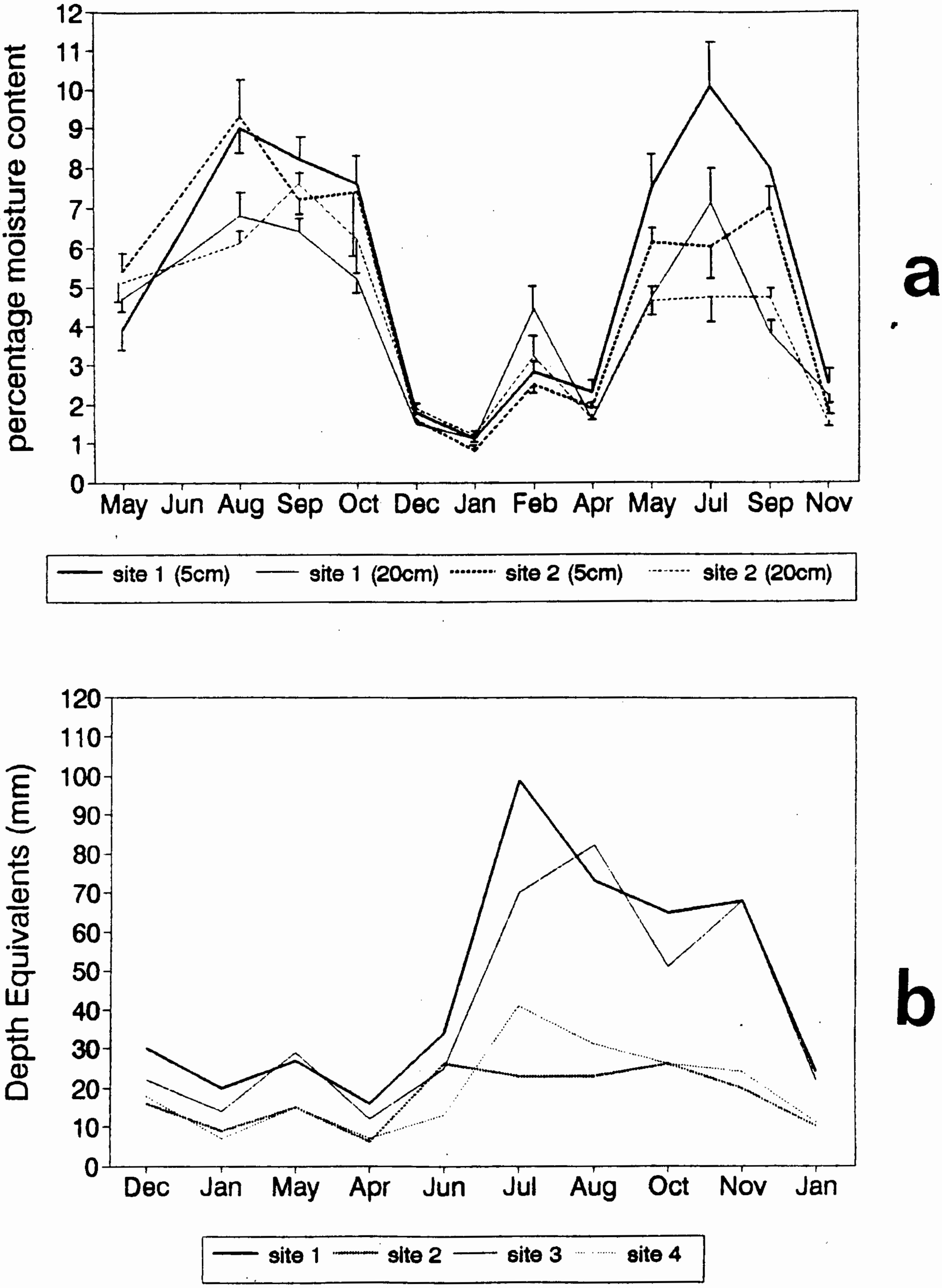

FIGURE 4.3 **(a)** Percentage soil moisture (gravimetric) at 5 cm and 20 cm, measured at sites 1 and 2 between May 1989 and November 1990. **(b)** Depth equivalents (in mm) of soil moisture down to a maximum of 1.5 m depth at sites 1 to 4, calculated from percentage moisture collected at 5 cm, 20 cm, 50 cm, and 100 cm (sites 1 and 3 only) between December 1990 and January 1992.

and spring wet periods (August and October 1989, May, July and September 1990) soil moisture content was significantly higher at 5 cm than at 20 cm (SNK test, $p<0.05$). During the summer peak in February 1990, soil moisture was significantly higher at 20 cm than at 5 cm (SNK test, $p<0.05$). The only significant difference between sites was in July 1990, when soil moisture content (regardless of depth) was significantly higher at site 1 (SNK test, $p<0.05$).

By converting the percentage soil moisture to depth equivalents, the total amount of water stored in each profile could be estimated. Figure 4.3(b) shows the depth equivalents calculated for the 4 sites for a maximum depth of 1.5 m, including the entire profile for sites 2 and 4 (both approximately 0.5 m). Throughout summer and autumn (December 1990 to April 1991), the sites with deep soil (sites 1 and 3) contained slightly more moisture, but once winter began the difference became much larger (50 to 100 mm at sites 1 and 3 compared with 20 - 40 mm at sites 2 and 4).

4.4.3. Root Morphology

Root systems and the locations of the excavated plants in the study site are illustrated in Figure 4.1. Protea compacta had a taproot that divided into two or three after about 0.3 m and extended to 0.8 - 0.9 m in the shallower soil near site 2 (the last 0.2 - 0.3 m growing through densely packed stones) and 1.0 m in the deep soil between sites 1 and 2. Thin lateral roots extended for about 2 m around the plants, mostly in the top 0.1 m of the soil. P. susannae plants had more extensive root systems, the main taproot and one or two other vertical roots extending more than 1.5 m and at least one per plant to more than 2.0 m. Lacking the extensive subsurface lateral roots of P. compacta, P. susannae had mostly small lateral roots in the top 0.2 m and thick branching lateral roots extending for 2-3 m at depths of 20-50 cm.

4.4.4. Water Potential

Seasonal patterns of predawn water potential for Protea susannae and P. compacta, at sites 1 and 2 (Figure 4.4(a),(b)) were similar over the one-year study period. Predawn water potentials were high throughout winter and spring (higher than -0.5 MPa from May to October) and then decreased with summer drought in January. The late summer increase in soil moisture resulting from rain in February 1990 was reflected in a recovery of predawn water potential. However, this was followed by a decrease to the lowest potentials in April. Recovery in autumn or early winter (May) was rapid. There was a significant overall species effect, P. susannae having significantly lower (more negative) predawn water potentials than P. compacta ($F_{(1,329)} = 6.7$, $p<0.05$). There was no significant overall effect of site (regardless of species), but there was a significant site by time interaction ($F_{(9,329)} = 6.4$, $p<0.001$) and during the driest months (January and

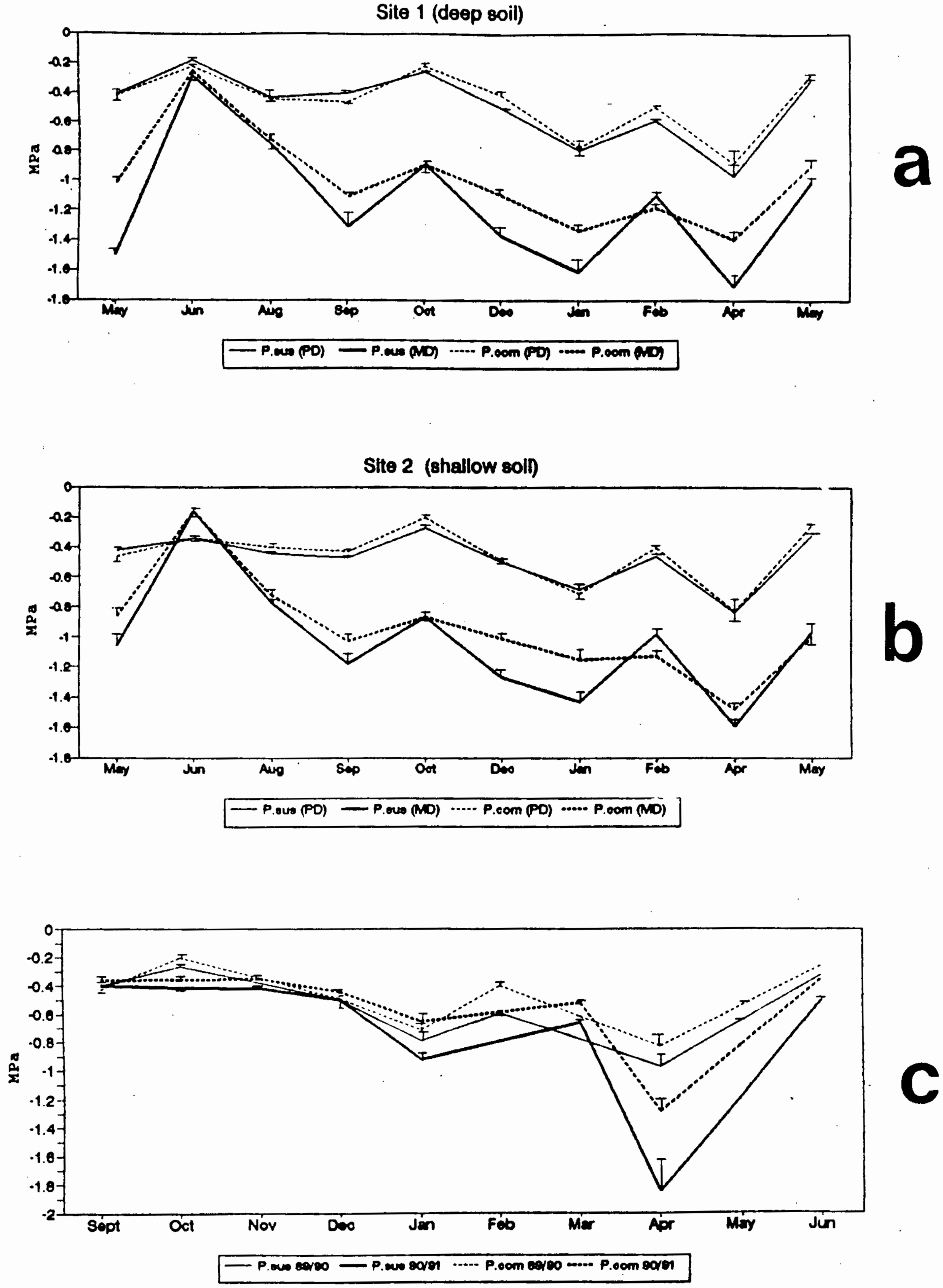

FIGURE 4.4 (a) and **(b)**. Predawn (PD) and midday (MD) water potentials of Protea susannae (P.sus) and Protea compacta (P.com) from May 1989 to May 1990 at sites 1 and 2. Each data point is a mean of 10 samples from different plants. **(c)** Predawn water potentials of P. susannae (site 1 only) and P. compacta (site 2 only) between 1 September and 1 June (spring followed by dry summer and autumn periods) in 1989/90 and 1990/91.

April 1990) predawn water potentials of both species were significantly lower at site 1 (SNK test, $p<0.01$). In June 1989 and February 1990 (relatively high soil moisture) predawn water potentials of both species were significantly lower at site 2 (SNK test $P<0.05$).

Midday water potential showed greater differences between species (Figure 4.4(a),(b)). For Protea compacta, midday water potential followed a similar pattern to predawn water potential, with winter values just around or above -1 MPa decreasing to minima around -1.4 MPa in April. P. susannae showed a more exaggerated pattern of midday water potential than P. compacta. The more rapid decreases in P. susannae midday water potential indicates larger daily ranges in water potential. Lowest midday water potential of P. susannae was recorded in April, -1.7 MPa at site 1 and -1.6 MPa at site 2. Rapid recovery of both species at both sites occurred after this and midday water potentials increased to winter values of around -1 MPa. As with predawn water potential, midday values for P. susannae were significantly lower than for P. compacta ($F_{(1,341)} = 88.4$, $p<0.001$). There was also an overall significant site effect ($F_{(1,341)} = 32.4$, $p<0.001$) and a significant site by time interaction ($F_{(9,341)} = 5.2$, $p<0.001$), as midday water potentials in May 1989 and January 1990 were significantly lower for both species at site 1 than at site 2 (SNK test, $p<0.01$). The average difference between sites (over the whole year) was much larger for P. susannae (0.13 MPa) than P. compacta (0.04 MPa). Site 1 also showed a larger average difference between species (P. susannae 0.18 MPa lower than P. compacta at site 1 and 0.09 MPa lower at site 2). There was a significant species by time effect ($F_{(9,341)} = 12.4$, $p<0.001$). P. susannae (regardless of site) had significantly lower midday water potentials in May, September and December 1989 and January and April 1990 (SNK tests, $p<0.05$).

Predawn water potentials of Protea susannae (at site 1) and P. compacta (at site 2) are compared over the spring and dry summer and autumn periods (1st September to 1st June) of 1989-1990 and 1990-1991 in Figure 4.4(c). The severity of the second period (112 mm in 1990-1991 compared to 257 mm in 1989/1990) is shown by the lower water potential of P. susannae in January 1991 and of both species, but especially P. susannae, in April 1991.

4.4.5 Transpiration

Daily patterns of transpiration of each species at its dominant site (Protea susannae at site 1 and P. compacta at site 2) for 6 of the 10 days of measurement (between December 1989 and June 1991) are shown in Figure 4.5. Neither species showed a marked difference between sites and so only data for P. susannae at site 1 and P. compacta at site 2 are referred to as these were measured on all dates except April 1991. On 31 May 1990 (after rain, cool) transpiration rates were very high throughout the day for both species, increasing rapidly at the beginning and

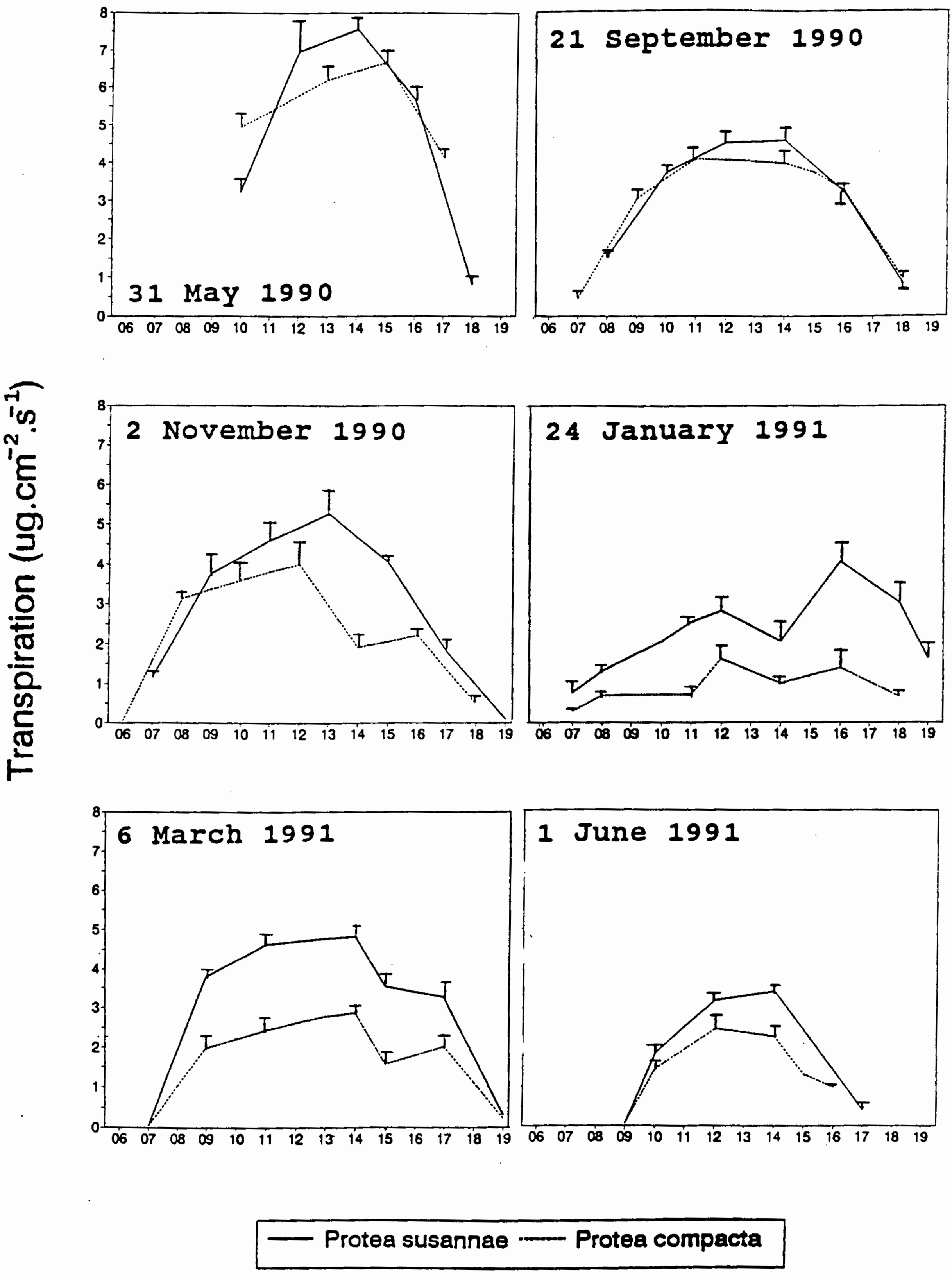

FIGURE 4.5 Daily courses of transpiration rate: Protea susannae at site 1 and Protea compacta at site 2 on 31 May 1990, 21 September 1990 and 2 November 1990, 24 January 1991, 6 March 1991 and 1 June 1991. Differences between sites were negligible.

decreasing rapidly at the end of the day. On 21 September 1990 both species showed more gradual increases and decreases, remaining fairly high through most of the day. However, on the 2nd of November, at the beginning of the dry period, P. compacta showed a reduction in transpiration rate from midday onwards, while P susannae maintained a high transpiration rate until late in the afternoon, a similar pattern to September. As the drought increased (24 January 1991) both species reduced transpiration rates, particularly P. compacta. On 6 March 1991, after rain in February and a small increase in soil moisture, both species showed increases in transpiration rate, which were maintained at relatively high level throughout the day. However, this response was much less for P. compacta. On the 1 June 1991, after winter rain had begun, transpiration rates of both species remained low and were much lower than the similar period the year before (31 May 1990).

Integration of these curves allows the estimation of the total volume of water lost per unit leaf area through transpiration during each day (see Figure 4.6). It must be noted that as most of the readings were taken on sunny days, those taken in winter may not be typical of that season. No measure of variance is possible with these daily rates, as the curves which were integrated (e.g. in Figure 4.5) were constructed from average data instead of from a range of daily curves from sequential measurements on the same

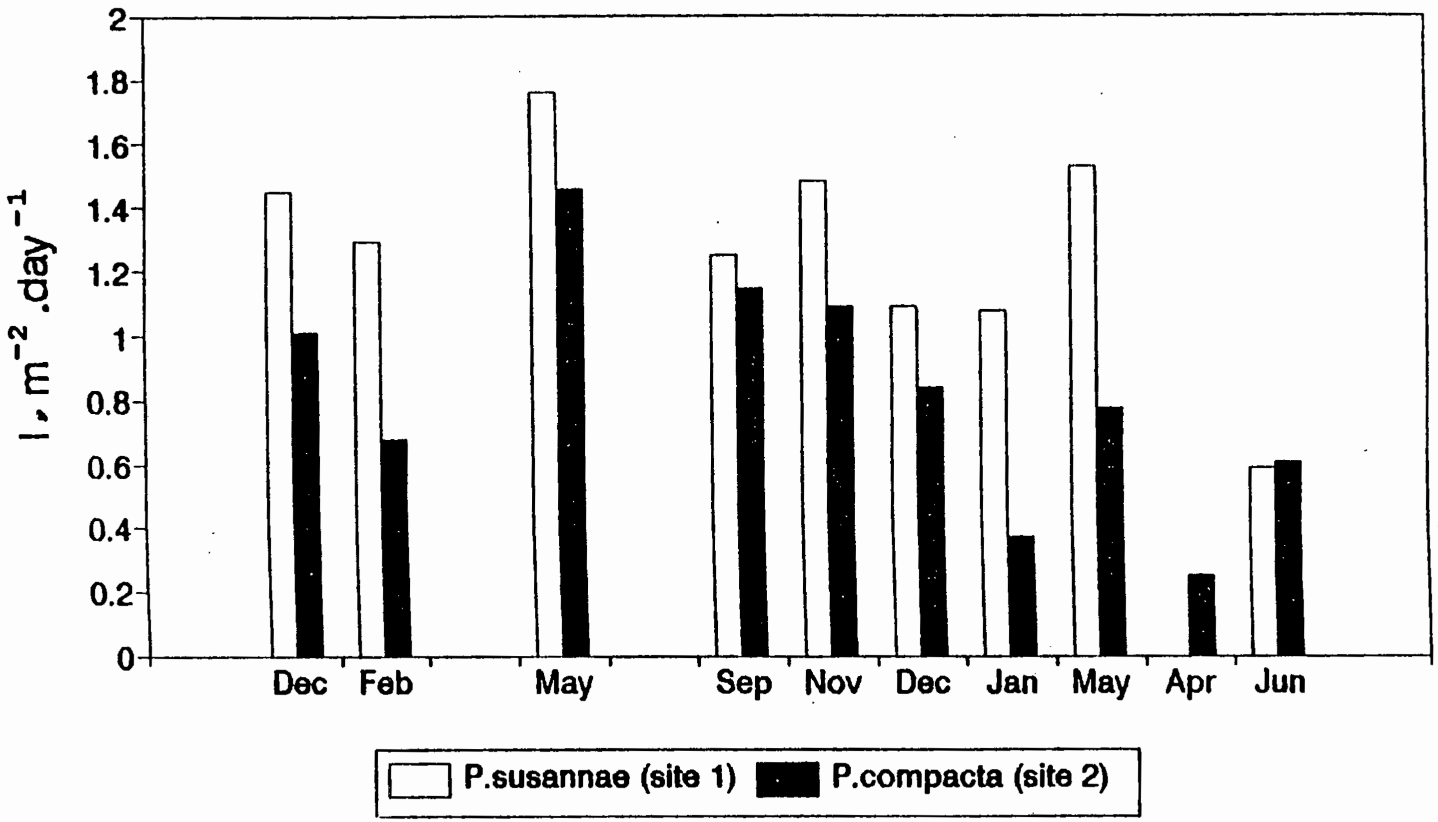

FIGURE 4.6 Daily transpiration rates per unit leaf area for Protea susannae at site 1 and Protea compacta at site 2, determined by integration of daily transpiration rate curves for 6 December 1989, 21 February 1990, 31 May 1990, 21 September 1990, 2 November 1990, 11 December 1990, 24 January 1991, 6 March 1991, 14 April 1991 (P. compacta only) and 1 June 1991. No substantial differences were found between sites for either species.

individuals (see transpiration data for seedlings in Chapter 5). On the days when transpiration rates of Protea susannae were measured at both sites (September and December 1990, March and June 1991), differences between the sites were, where present, very small.

The seasonal trend in daily transpiration was similar for P. susannae and P. compacta: decreasing through the summer (6 December 1989 to 21 February 1990) and then recovering rapidly by 31 May 1990. During those summer months, transpiration of Protea susannae was much greater than P. compacta. Transpiration of both species was slightly reduced by 21 September 1990 and as the summer progressed P. susannae maintained high daily rates. P. compacta decreased its transpiration, at first slowly, then rapidly up to 24 January 1991. With rain in late January and increasing soil moisture, transpiration of both species increased. On 14 April 1991, the period of lowest soil moisture, transpiration of P. compacta decreased rapidly (no data were collected for P. susannae at this time). P compacta showed a small recovery by 1 June 1991 to a similar level to P. susannae. P. susannae showed a drastic reduction from March to June. The transpiration of both species was substantially lower on 1 June 1991 than the similar period the previous year (31 May 1990).

4.4.6 Phenology

Figure 4.7 shows the phenological stages (shoot elongation, flower bud development and flowering) of both species at sites 1 and 2 from August 1990 to August 1992, plotted in comparison to rainfall. Almost no differences in the timing of phenological stages were distinguishable between sites for either species.

Most of the shoot elongation of both species took place from during spring and summer, with almost no growth during the cold, wet winter months (May to July). In both years the onset of shoot elongation of Protea susannae preceded that of P. compacta. Flower bud development commenced only after elongation of individual shoots was complete, but elongating and flowerng shoots could be found simultaneously on the same plant. Flower bud development took place mostly in summer (between November and March) for P. susannae, but was more prolonged for P. compacta (later in summer into winter December or February to June). Flowering of P. susannae (open flowers) took place almost entirely between February and early June, which included the driest time of the year. Flowering of P. compacta only began between March and May and continued throughout winter into spring (October) overlapping slightly in timing with the onset of the next season's shoot elongation.

To assess the impact of site differences, as well as year to year climate variation on growth and flowering, the

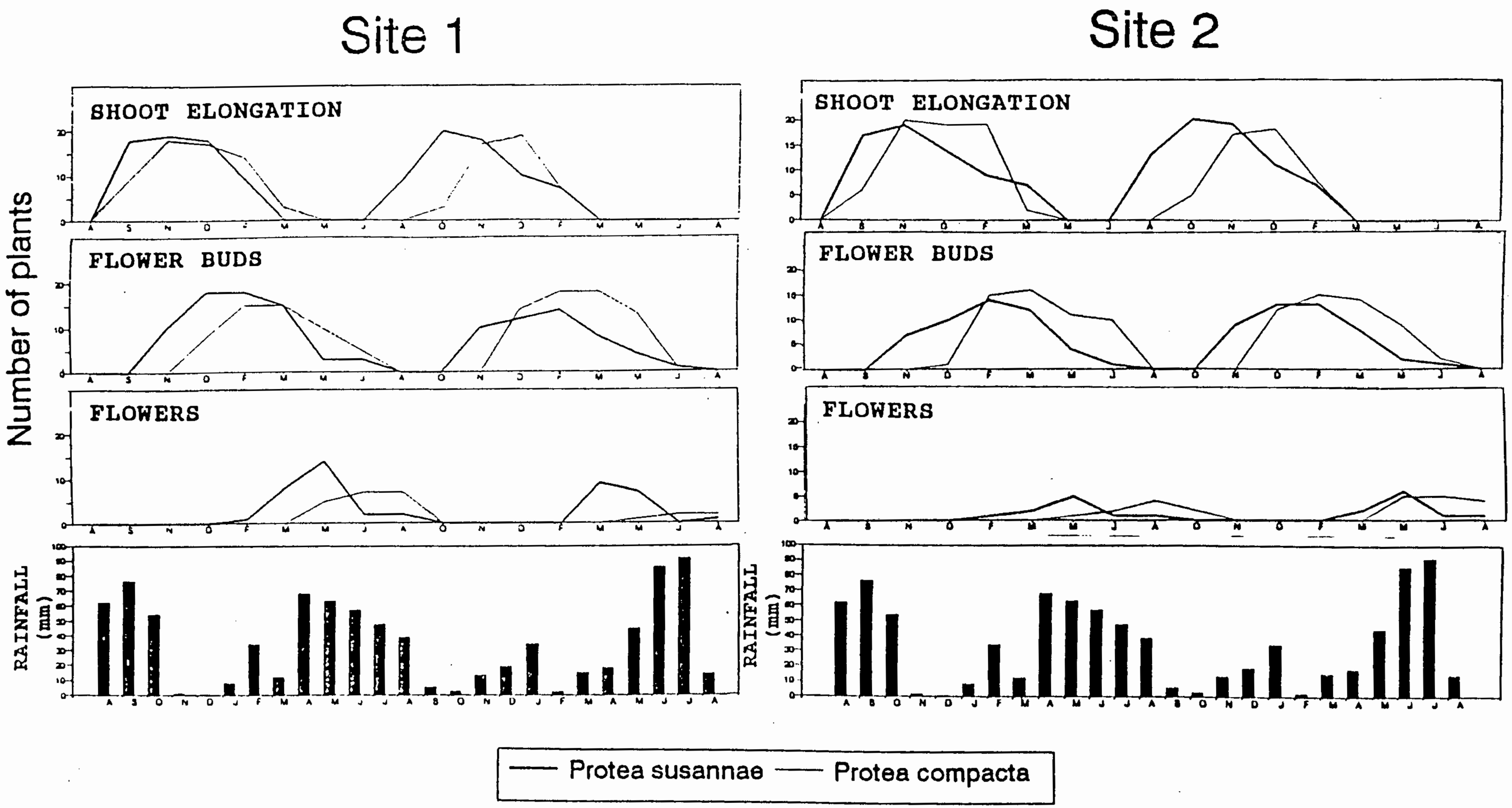

FIGURE 4.7 Phenological stages of 20 plants of each <u>Protea susannae</u> and <u>Protea compacta</u> at sites 1 and 2. Data are presented as number of plants with tagged shoots in elongation, developing flower bud or open flower stage during each six-week period between August 1989 and August 1991. Monthly rainfall totals (Cape Agulhas) for the corresponding period are shown.

proportion of tagged shoots (three shoots per individual and twenty plants per species at each site) growing and flowering each year and growth increments of all shoots were noted. Figure 4.8 shows the location of the sites where plants were tagged, as well as percentages of shoots growing, producing flowers or aborting flower buds in two successive growing seasons. In 1989-90, more than 90% of all tagged shoots grew, regardless of species or site. In the second season (1990-1991) there was a reduction in the number of shoots growing, with the exception of Protea susannae at site 2. No statistics could be applied as these proportions are of only one sample of plants per species at each site. The flowering percentage of P. susannae was much higher at site 1 than at site 2 (47% compared with 18%) in the 1989-90 season. This was reduced at both sites in the second season (22% and 12%). P. compacta showed a large reduction in flowering percentage in the 1990-91 season at site 1 (from 43% in 1989-90, to 8%), but remained fairly low at site 2 (20% in both seasons). This was associated with a large increase in the percentage of P. compacta shoots at site 1 producing flower buds, but aborting them (9% in 1989-90 and 28% in 1991), while this proportion remained low at site 2 (7% and 8%). Abortion of P. susannae flower buds was never higher than 12% and decreased from 12% 1989-90 to 3% in 1990-91 at site 1.

Average shoot increment for each species at each site in the two growth seasons is shown in Figure 4.9. These data were calculated from the average increment of the three tagged

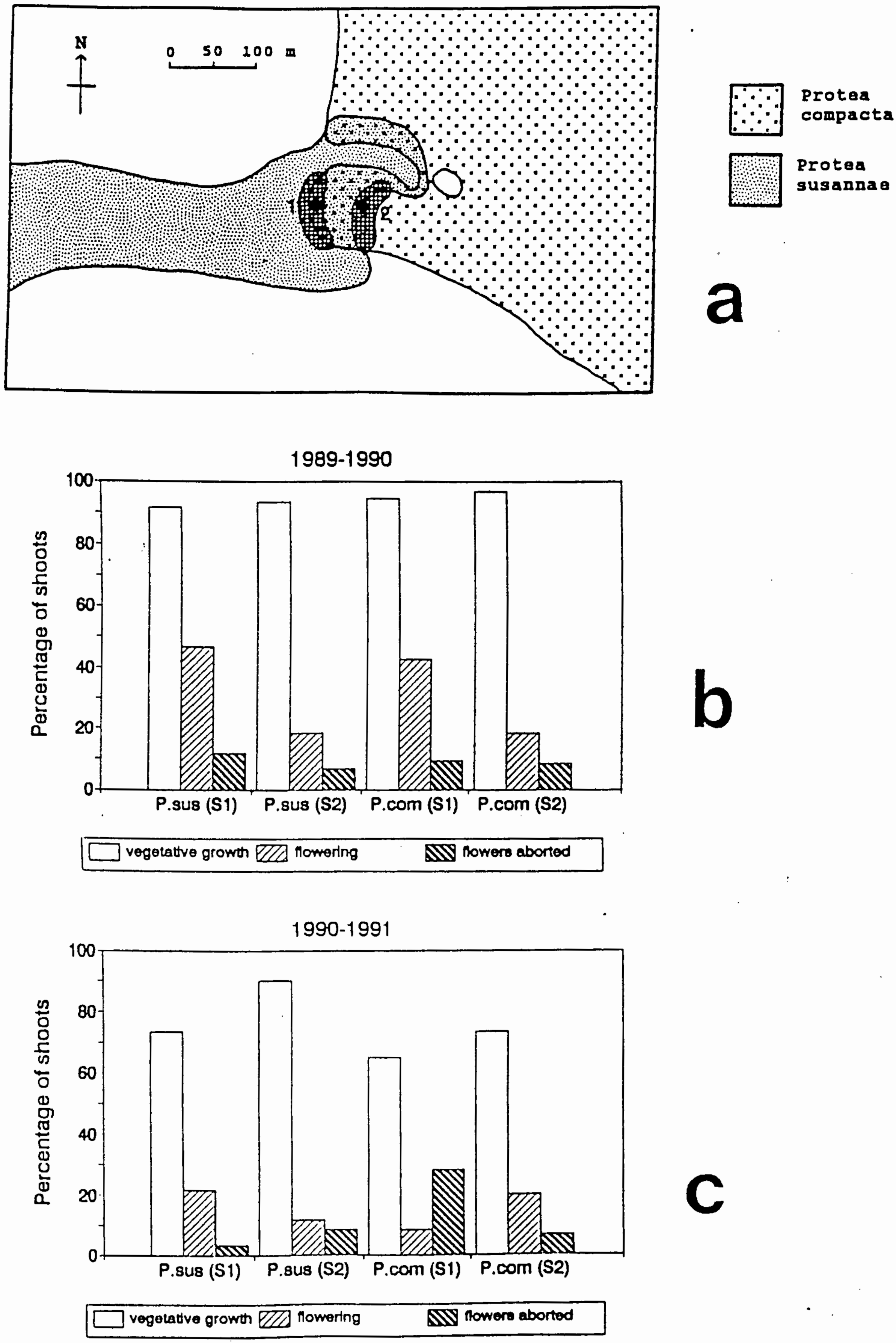

FIGURE 4.8 **(a)** Map of the study site showing the areas associated with sites 1 and 2 where three shoots on each of 20 indviduals of <u>Protea</u> <u>susannae</u> and <u>Protea</u> <u>compacta</u> were tagged to study their phenology. **(b)** and **(c)** Percentage of tagged shoots (out of 60) of <u>P</u>. <u>susannae</u> (P.sus) and <u>P</u>. <u>compacta</u> (P.com) at site 1 (S1) and site 2 (S2), producing vegetative growth, open flowers or aborting flower buds between August 1989 and August 1990 (a) and between August 1990 and August 1991 (b).

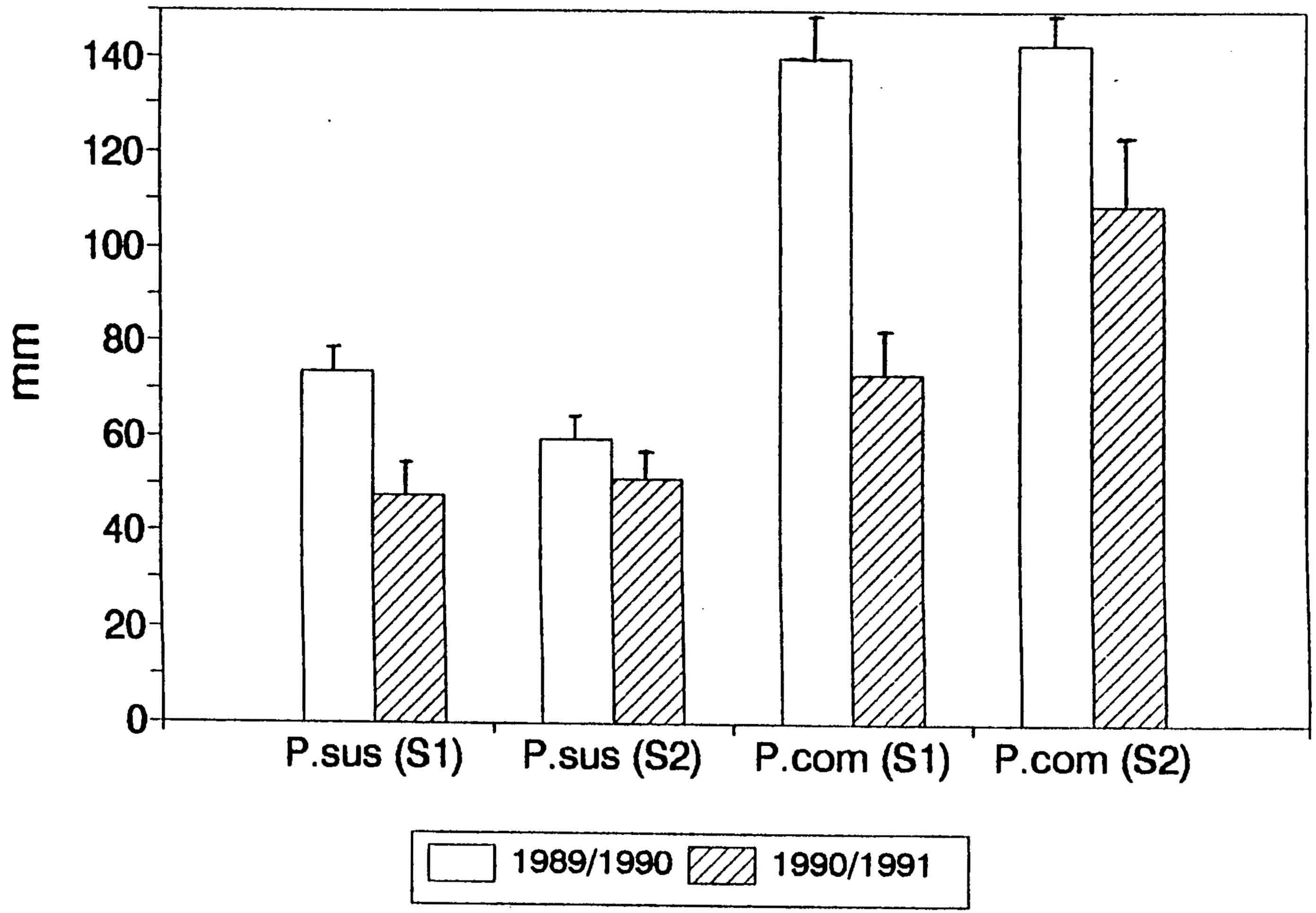

FIGURE 4.9 Average shoot increment of 60 tagged shoots of Protea susannae (P.sus) and Protea compacta (P.com) at sites 1 (S1) and 2 (S2) between August 1989-August 1990 and August 1990-August 1991. T - bars represent one standard error.

shoots. Species averages and statistics were calculated from the 20 plants per species. In 1989-90 there was a significant effect of species ($F_{(1,76)}$ = 111, p<0.001) but not site, as the average increment of P. compacta was much greater than P. susannae at both sites (140 mm compared with 73 mm at site 1 and 143 mm compared with 59 mm at site 2). The greater annual shoot growth of P. compacta was associated with a much smaller number of growing shoots per plant (pers. obs.). During the second growth season (1990-91), the species effect was still significant ($F_{(1,76)}$ = 20.6, p<0.00), but there was a significant effect of site, with both species showing significantly lower shoot increments at site 1 ($F_{(1,76)}$ = 4.57, p<0.05). Although the difference between sites was far greater for P. compacta (109 mm compared with 73 mm), than for P. susannae (51 mm compared with 48 mm), there was no significant interaction of species and site effects.

4.5 DISCUSSION

The distinct change in overstorey Protea species was associated with an abrupt change in soil depth, suggesting an abiotic explanation for the boundary (Studer-Ehrensberger et al. 1993). The correspondence of discontinuities in abiotic factors and species distributions is, however, not sufficient on its own to conclude that this pattern is caused by differences in species' physical tolerances (Dawson 1990), but requires more understanding of the physiology of the species in relation to the environmental factors.

Protea susannae root systems extended throughout the deep soil profile in which they were growing. Thus P. susannae has access to a much larger volume of water for most of the year and possibly access to water available below the 1 m depth measured (roots extend to 2 m). Deep rooted plants rely on moisture supply at depth during the dry season in other mediterranean regions (Dodd et al. 1985, Davis and Mooney 1986, Crombie et al. 1988, Lamont and Bergl 1991). The quick responses of water relations of both Protea species to a relatively small increase in soil moisture in late summer indicated their sensitivity to moisture availability near the surface. A similar response in water relations to unseasonal rain events has also been detected by Dodd et al. (1985), in Australian Banksia (Proteaceae) woodlands. As with this fynbos study, the temporary water supply was quickly depleted and the highest stress levels of the summer were detected thereafter, before winter rains began.

The higher transpiration rates and greater daily depressions of water potential of Protea susannae indicate greater water expenditure, with a complementary enhanced ability for water uptake and nighttime recovery. Despite greater access to water, P. susannae showed lower predawn and midday water potentials in the dry months. This indicates that a greater seasonal water deficit accumulates than for P. compacta. It is appears that that the lower water potential of P.susannae relative to P. compacta and the lower water potentials of both in the deep soil (site 1) are the result of different water-use strategies in addition to differences in the degree of water availability in the two soil types.

The relationship between soil moisture, water relations and phenology is not very clear for either Protea susannae or P. compacta as both species have vegetative growth taking place over the dry summer, a general trend for the genus and much of the Proteaceae family in fynbos (Pierce 1984). The ability of Australian Proteaceae species (Banksia) to carry out vegetative growth over the driest time of year has been attributed to their access to water stored deep in the profile during summer, allowing moderate stomatal closure and moderate water potentials (Lamont and Bergl 1991). This also applies to other summer-growing species in the mediterranean climate region of Australia (Specht et al. 1981). For the Banksia species studied by Lamont and Bergl

(1991), the lowest value of predawn water potential recorded, was -0.74 MPa. Although the root systems of Protea susannae were of similar depth (2 to 2,5 m), minimum predawn water potentials were much lower: -0.97 MPa at site 1 in April 1990 and -1.85 MPa, in April 1991. This species is able to maintain summer growth and flowering despite a higher degree of water stress. The summer water potentials of these fynbos species are however much higher than those recorded for chaparral species (Baker et al. 1982, Bowman and Roberts 1985). Phenology of chaparral shrubs is strongly influenced by seasonal patterns of water stress (Baker et al. 1982).

The greater access of Protea susannae to water during summer relative to P. compacta, was associated with completion of flower bud development and flowering taking place during the period of highest water stress. P. compacta showed slower flower bud development and only completed flowering in the wet season, once water potential had recovered. In addition, P.susannae maintained very high transpiration rates (both instantaneous and daily rate) throughout the year, except during very late summer, when water potentials were lowest and flower bud development was almost complete. Conversely P. compacta rapidly decreased transpiration as summer progressed, showing only a moderate response to late summer rain, and completing flower development long after rain had begun and transpiration rates were high. Baker et al. (1982) showed how chapparal shrubs possessed different phenological patterns: while two species completed vegetative growth and flowering before the worst of the drought, a third species delayed completion of flower bud development till after the end of the drought. However, the delaying strategy of the third species was not associated with a more conservative water-use strategy. Extending or delaying completion of flower bud development through the summer drought until winter has been recorded for several species of large Western Australian shrubs, including Banksia spp. (Bell and Stephens 1984).

When considering year to year differences in phenology, it is evident that in order to limit water stress, it would be advantageous to plants to be able to alter their phenology to suit variations in the climate (Baker et al. 1982, Gill and Mahall 1986). The second dry period (September 1990 to April 1991) was much more severe than the first, as only 43% of the first periods rainfall was recorded (112 mm from 1 September 1990 to 1 June 1991 compared to 257 mm from September 1989 to June 1990). This was reflected in much lower autumn (April) water potentials and daily transpiration rates at the beginning of wet season. Both species had fewer flowering shoots and in the second season in the deep soil (site 1) Protea compacta, which maintains flower bud development through the dry spell, experienced a more drastic decrease in shoots flowering and a large increase in the proportion of flower buds aborting. While P.susannae experienced a great reduction in the proportion of flowering shoots, the abortion rate was very low. This suggests that the reduction of flowering may be linked to lower flower bud initiation which occurred in spring.

Not only was the effect of the more severe drought in 1990-91 on proportions of shoots flowering much greater for both species in the deep soil (site 1), but average shoot increment was much more severely reduced in the second season on plants in the deep soil. This suggests that both species are more vulnerable to unusually severe drought when growing on the deep soil. Not surprisingly the negative effect of the deep soil was much greater for Protea compacta, the species typically associated with shallow soil.

The exclusion of Protea susannae from shallow soils is complete as out of all five transects only three P. susannae individuals were observed on soil shallower than 1 m (0.6 m, 0.6 m and 0.7 m). On the extreme edge of their range at the main study site, a large number (but not all) of P. susannae adults were observed to be stunted and the likelihood of water stress as a factor causing this was suggested by the death of one of these, late in the long summer drought of 1990-91.

The exclusion of Protea susannae from shallow soils follows from its relatively "water-spending" pattern of water-use. However, it is less easy to explain why Protea compacta, with more conservative water relations, is rare on deep soil. The roots of excavated P. compacta plants in the deep soil (the single individual excavated as well as two adjacent plants) did not extend to the bottom of the soil profile. Despite this, individuals observed in deep soil at the main site, as well as at the two additional sites showed no evidence to suggest that they had experienced water stress (e.g. stunted growth).

A number of studies of species with distributions segregated along moisture gradients have shown that certain species are competitively excluded from the more favourable sites (Barnes 1985, Gurevitch 1986, Lamont et al. 1989). However the competitive exclusion of P. compacta by P. susannae from the deep sands seems unlikely as P. compacta seedlings are much faster growing and consequently have a distinct size advantage, both above ground and in root depth (see Chapters 5 and 6).

A laboratory study of seedling root growth, shoot growth and water relations of these two Protea species (Chapter 5) showed that P. compacta seedlings had not only faster root and shoot growth, but initially, greater water use. The consequence of this was that they dried out the soil profile more rapidly than P. susannae seedlings and were very vulnerable to water stress if they lacked continuous access to the water table under hot, dry conditions. P. compacta seedlings with longer roots may survive in deep soil and this could influence the occasional presence of P. compacta adults in deep soil.

The differences in soil moisture content between the deep and shallow soils on either side of the boundary together with species differences in root morphology and water use (especially transpiration) suggest that water relations are responsible for this distribution pattern (see Oberbauer and Billings 1981, Dawson 1990, Lipscomb and Nilsen 1990). However, the lack of any major differences between sites (deep and shallow soils at sites 1 and 2) for either species indicate that those individuals in the atypical soil do not currently experience severe stress (although growth and flowering of Protea compacta was reduced in the dry soil in a severe summer and autumn). This suggests that if water-relations inflence the distributions of these species, this had already taken place and those mature (±15yr old) individuals observed now (note also the scattered P. compacta in deep soil at other sites) are the survivors. Control of species distributions by differences in water relations interacting with competition effects at the seedling stage, has been shown in Banksia species in Western Australia (Lamont et al. 1989). Davis (1991) suggested that stresses , both abiotic and competitive, would be most severe at the recruitment stage in all mediterranean-climate regions and that species differences amounting to niche differentiation are most likely to be found in the seedling or juvenile stages. While adult plants of P. susannae and P. compacta showed differences amounting to habitat differentiation, the lack of severe stress in individuals growing in atypical soils suggests that their distribution patterns are largely determined at an earlier stage.

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CHAPTER 5

THE GROWTH, MORPHOLOGY AND WATER RELATIONS OF SEEDLINGS OF TWO *PROTEA* SPECIES

5.1 ABSTRACT

Seed germination, seedling root and shoot growth and water relations of _Protea susannae_ and _Protea compacta_ were compared under controlled-environment conditions in an artificial soil profile over 30 weeks. Seeds of _P. compacta_ were larger and germinated earlier, resulting in much larger seedlings than _P. susannae_. _Protea compacta_ seedlings initially had greater root depth, but both species reached the depth of the water table (72 cm) by the end of the experiment. _Protea compacta_ seedlings initially had greater transpirational water loss, but after 30 weeks _P. susannae_ seedlings had similar rates of water loss, despite much smaller leaf area. The greater water-use of _P. compacta_ seedlings dried out the soil profile, resulting in severe water stress in those seedlings from which the water table was removed in the 23rd week, while _P. susannae_ seedlings experienced only mild water stress under these conditions. The patterns of water-use were contrary to those expected for establishment in the soil types with which these species are associated (_P. susannae_ in deep sand and _P. compacta_ in shallow sand). Despite this, seedling water-use strategies are likely to be important in determining species distributions through their effect on seedling establishment. Both species were found to experience switches in water-use strategy from seedling to adult stages: from conservative to water-spending in _P. susannae_, and from water-spending to conservative in _P. compacta_.

5.2 INTRODUCTION

Survival of summer drought is a critical factor in the establishment of seedlings in mediterranean-climate ecosystems (Cowling et al.1987, Frazer and Davis 1988). Post-fire germination usually takes place in winter, corresponding with the rainy season (Bond 1984, le maitre and Midgley 1992), and it is thus of critical importance for seedlings to develop root systems capable of maintaining access to soil moisture during the dry summer months (Kummerow et al. 1985, Rhizopoulou and Davies 1991, Enright and Lamont 1992). Deep soils may contain water at depth during the dry summer months, making them a favourable habitat for deep rooted plants (Dodd et al. 1985, Davis and Mooney 1986, Crombie et al. 1988 and see Chapter 4). However, for seedling establishment, the depth of moist soil or the water table in summer may be critical, making deeper soil less favorable (Kummerow et al. 1985, Matsuda and McBride 1986, Enright and Lamont 1992).

Mortality of seedlings as a result of water stress during the first summer after establishment is important in determining species distributions and abundances in Australian kwongan vegetation (Enright and Lamont 1989, 1992, Lamont et al. 1989, 1991) and Californian chaparral (Frazer and Davis 1988, Thomas and Davis 1989), but little is known about this with regard to fynbos. Midgeley (1988) observed very low levels of first-year mortality in several Proteaceae species and suggested that water stress over this period may not be an important cause of mortality. Similarly, Mustart and Cowling (1993) found no evidence of site-related water stress in seedlings of four Proteaceae shrub species during their second summer, but they did not examine water stress during the first year after establishment.

While water relations of mature shrubs of various Proteaceae have been studied in some detail (Miller et al. 1983, Richardson and Kruger 1990 and see Chapter 4), much less is known about the water relations of the seedlings of these species and the role that this plays in their establishment. Davis and Midgeley (1990) and Manders and Smith (1992) reported evidence for the rapid development of root systems in seedlings of large overstorey Proteaceae. These seedlings experience less water stress than other more shallow-rooted species (Davis and Midgeley 1990) as has been described for mature plants (Miller et al. 1983, Moll and Sommerville 1985). However, Smith and Richardson (1990) found that seedlings of Protea nitida were less conservative in their water-use, experiencing lower water potentials, than deep-rooted resprouting individuals of the same species. Davis and Midgeley (1990) suggested that in order to achieve faster root growth and consequently a better water supply, seedlings of deep-rooted plants maximize gas exchange at the cost of increased water loss. They did, however, provide only limited data to support this.

Protea susannae Phill. and P. compacta R.Br. both occur along a coastal band in the south western Cape Province, South Africa, associated with limestone and sandstone-derived soils respectively (Rourke 1980). A detailed study of adult plants of these species (Chapter 4) showed that the sand with which P. susannae was associated was deep with relatively high soil moisture, while P. compacta was found in predominantly shallow soil which held less soil water. The root morphology and water relations of these species were shown to be well adapted to their respective soils: P. susannae plants (deep soil), had extensive root systems, while P. compacta plants (shallow soil) possessed much less extensive root systems, but avoided severe summer water stress through relatively conservative water-use.

In this study, the germination, and subsequent growth, morphology and water relations of seedlings of Protea susannae and P. compacta over 30 weeks were examined under laboratory conditions. The objctive was to determine whether they were adapted for establishment in deep and shallow soils respectively, which would account for the strong association of adults with such soils. A second aim was to determine whether seedling water-use strategies differed from those shown for adults of these species.

5.3 METHODS

Seeds of *Protea susannae* and *Protea compacta* were collected from one year old infructescences (these species are serotinous) at a site on the lower slopes of the Soetanysberg mountains, near Cape Agulhas (34^{o} 15'S; 19^{o} 50'E). Plump, and thus potentially viable seeds were germinated on wet filter paper in Petri dishes, in a germination chamber (day/night temperatures: 20 ^{o}C/10 ^{o}C) (Mustart and Cowling 1991). After radicles reached 1 cm length, one set of seeds germinants were planted. A second set of 100 seeds per species was used for comparing germination percentage and germination rate (days to 50% of final germination). This experiment was set up using six Petri dishes as replicates, two of 16 seeds and four of 17 seeds. Germination (radicle emergence) was monitored every 2 days over 7 weeks. No germination occurred in the last 6 days.

Germinants were planted into PVC tubes, 80 cm long and 11 cm in diameter. These were filled with soil approximating the texture and drainage characteristics of a soil profile at the study site (Figure 5.1). Soil collected from the Soetanysberg site at the *Protea susannae*/*P. compacta* boundary (see map in Figure 4.1), was air-dried and sieved. Into each tube was placed 3 cm of coarse gravel (10-15 mm grain size), 2 cm of fine gravel (3-5 mm grain size), 15 cm of acid-washed river sand and 60 cm of soil. This 80 cm soil profile corresponded to the deep end of the

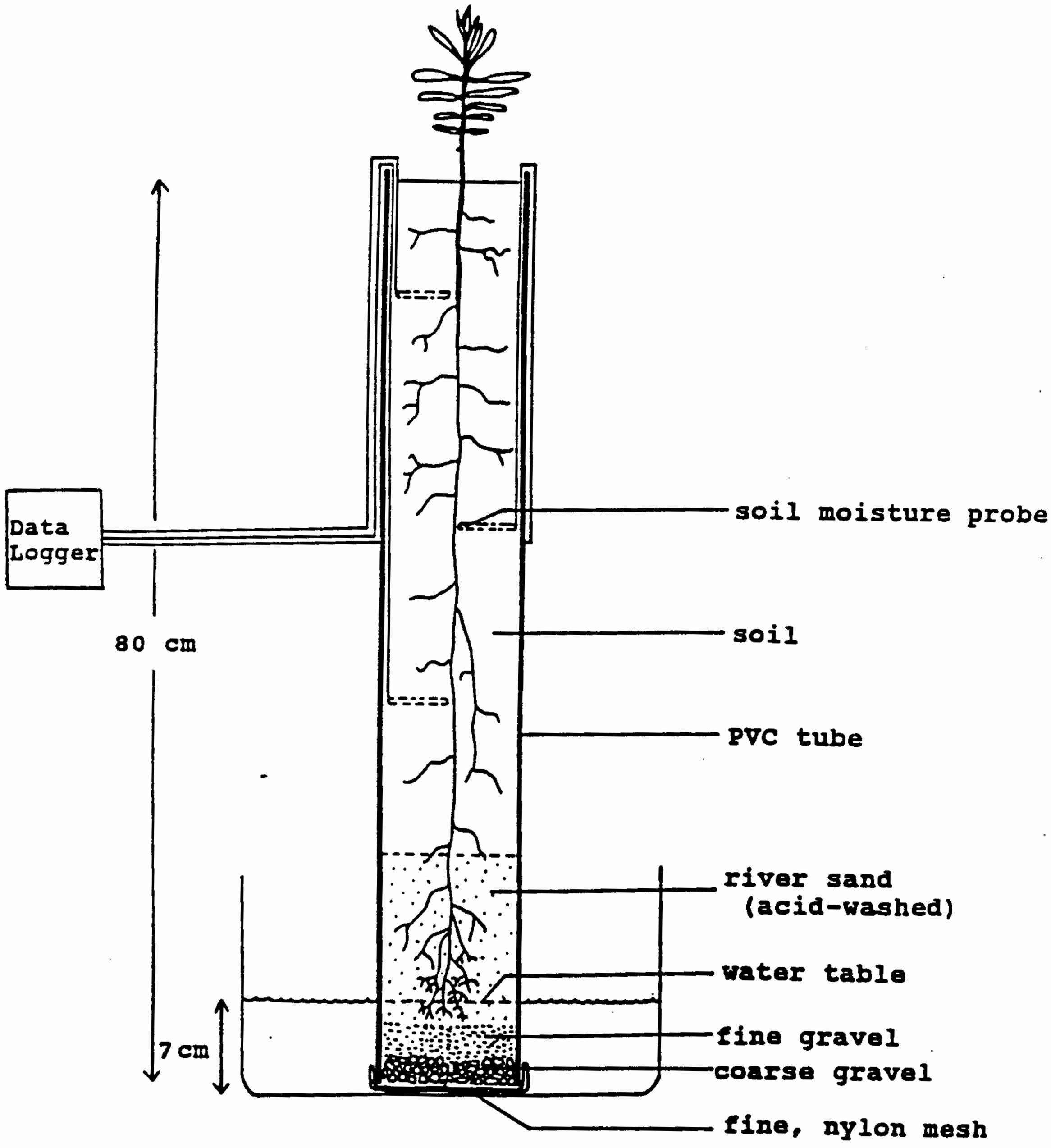

FIGURE 5.1 Experimental apparatus for studying growth and water relations of seedlings under changing conditions of water availability in an artificial soil profile. For the first 15 weeks soil was kept at field capacity. During weeks 16 to 30, the tubes were placed in basins with 7cm water to provide a constant water table. After 23 weeks, the basins of half the tubes were drained to simulate loss of the water table in severe drought. The data logger monitored the drying of the soil by means of soil moisture probes at 10, 30 and 45 cm depths during weeks 16-30.

range of soil depth where P. compacta was typically found (40-80 cm, see Chapter 4). To allow free drainage, the lower end of each tube was covered with nylon mesh. Before planting, soils were wet thoroughly to eliminate any dry patches.

During the filling of the tubes, soil moisture probes (MCS Systems, Cape Town, S.A.) were buried at various depths and connected to a MCS data logger (MCS Systems, Cape Town, S.A.) to allow monitoring of soil drying later in the experiment (see Figure 5.1). Three probes were placed in each of four tubes (10 cm, 30 cm, and 45 cm depth) and two probes only (because of limitations of the number of channels on the data logger) in each of two additional tubes (10 cm and 45 cm depth). At planting, tubes with moisture probes were allocated evenly between the species.

One germinant was planted in each tube, with sixteen tubes per species. Additional seedlings were planted in pots containing the same soil, to be used as replacements, if required. During the first two weeks after planting, seedlings which failed to establish in the tubes (ca. 10% of the total), were replaced by seedlings from the pots. No mortality of experimental plants occurred after this.

The tubes were placed in a controlled-environment room with lights of two types: mercury vapour and incandescent. Conditions were set to approximate winter : 18 ^{o}C daytime (10 hrs) and 14 ^{o}C nighttime (14 hrs), with 60% humidity and

PAR of 380 $\mu mol.m^{-2}.s^{-1}$. Soil was kept wet by watering every 3-4 days and excess water was allowed to drain out, keeping soils at, or near, field capacity.

After 15 weeks, the first set of water relations measurements were made and the first harvest was carried out. Transpiration was measured at 90 minute intervals over 12 hours (one hour before lights on to one hour after lights off), using a LI-1600 steady-state porometer (LI-COR Inc., Lincoln, Nebraska, U.S.A.). At each time, readings were taken from eight randomly selected individuals of each species. The next morning, predawn water potentials of five individuals per species were determined using a Scholander-type pressure chamber (PMS Instrument Company, Corvallis, Oregon, U.S.A.). Whole seedlings were cut off at soil level and placed in the chamber. Leaves were removed from the stem and a LI-3000 planimeter (LI-COR Inc., Lincoln, Nebraska, U.S.A.) was used to determine their area. Roots were extracted by carefully washing the soil away, noting the depth of maximum penetration. They were then separated into depth classes: 0-15 cm, 15-30 cm, 30-45 cm, 45-60 cm. >60 cm Root and shoot material was oven-dried at 70 ^{o}C until constant weight was achieved.

The second 15 weeks of the experiment was set up to approximate spring, summer and severe summer drought conditions by increasing temperature and decreasing water availability. The soil moisture probes were connected to the data logger and readings were taken once daily on all probes from this point onwards. The tubes were placed in basins in which water was kept at a constant depth of 7 cm, providing a constant water table at a depth of 72 cm below the soil surface (Figure 5.1). Watering was reduced to once a week and, after the 17th week, no further watering took place. For the first two weeks the temperature was raised to 22 ^{o}C day and 18 ^{o}C at night, with a 12 hours of light. Humidity was lowered to 50%. From week 18 onwards, the temperature was raised to 26 ^{o}C and 22 ^{o}C at night with a daylength of 14 hours and PAR of 450 $\mu mol.m^{-2}.s^{-1}$. Humidity was lowered to 40%.

In order to study the dependence of these species on a permanent water table as opposed to water remaining in the soil profile, the water table was removed from half the individuals of each species after the 23rd week. The plants were closely monitored from this time onwards and at the first sign of wilting, the experiment was terminated and the second set of water relations and morphological data was collected. This occurred in the 30th week. Determination of transpiration rates, predawn water potentials and root and shoot parameters were determined as described for 15 weeks, except that transpiration rates were measured over 15 hours. Five individuals of each species were harvested from each of the water table and dry treatments. In addition to measurements of root and shoot dry weights, leaf area, root depth and percentage root weight at each depth, ratios of root weight to shoot weight and leaf area to root weight were calculated. Water relations data consisted of predawn water potentials, daily ranges of transpiration rates and total daily transpiration for each seedling. Most data were analysed using Students t-tests and analysis of variance. Seed weight, leaf area and total transpiration per plant at week 30 which were analysed using Mann-Whitney two-sample tests and Kruskal-Wallis one-way analysis of variance. The statistical package was STATGRAPHICS (v4.0, Statistical Graphics Corp. 1987).

5.4 RESULTS

Seeds of Protea compacta were significantly larger than those of Protea susannae (156±3.6 mg cf. 35±1.1 mg) and germinated more quickly (see Figure 5.2), reaching 50% of final germination six days earlier (t-test $p<0.001$). Final germination was higher in P. compacta (100% cf. 71%), but this probably reflects a difference in the ease of detecting embryo-filled seeds.

After 15 weeks, seedlings of Protea compacta were larger than those of P. susannae . Shoot dry weight, leaf area, root dry weight and root depth were significantly higher for seedlings of P. compacta (ANOVA, Table 5.1). The root/shoot weight ratio of P. susannae seedlings was higher , although the leaf area/root weight ratios were not significantly different. Partitioning of root mass between different depths (Figure 5.3) differed significantly between species ($F_{(4,30)} = 3.25$, $p<0.05$). P. susannae seedlings had 69% of root mass in the top 15 cm, compared to 51% for P. compacta.

Despite the difference in root depth, there was no significant difference in predawn water potential between seedlings of Protea susannae and P. compacta (Table 5.2). The pattern of transpiration rate over the day at 15 weeks (Figure 5.4(a)) was similar for the species, but P. susannae maintained higher rates throughout the day. This translated into a much higher average daily transpiration rate (Table 5.2), but when this was multiplied out over leaf area and

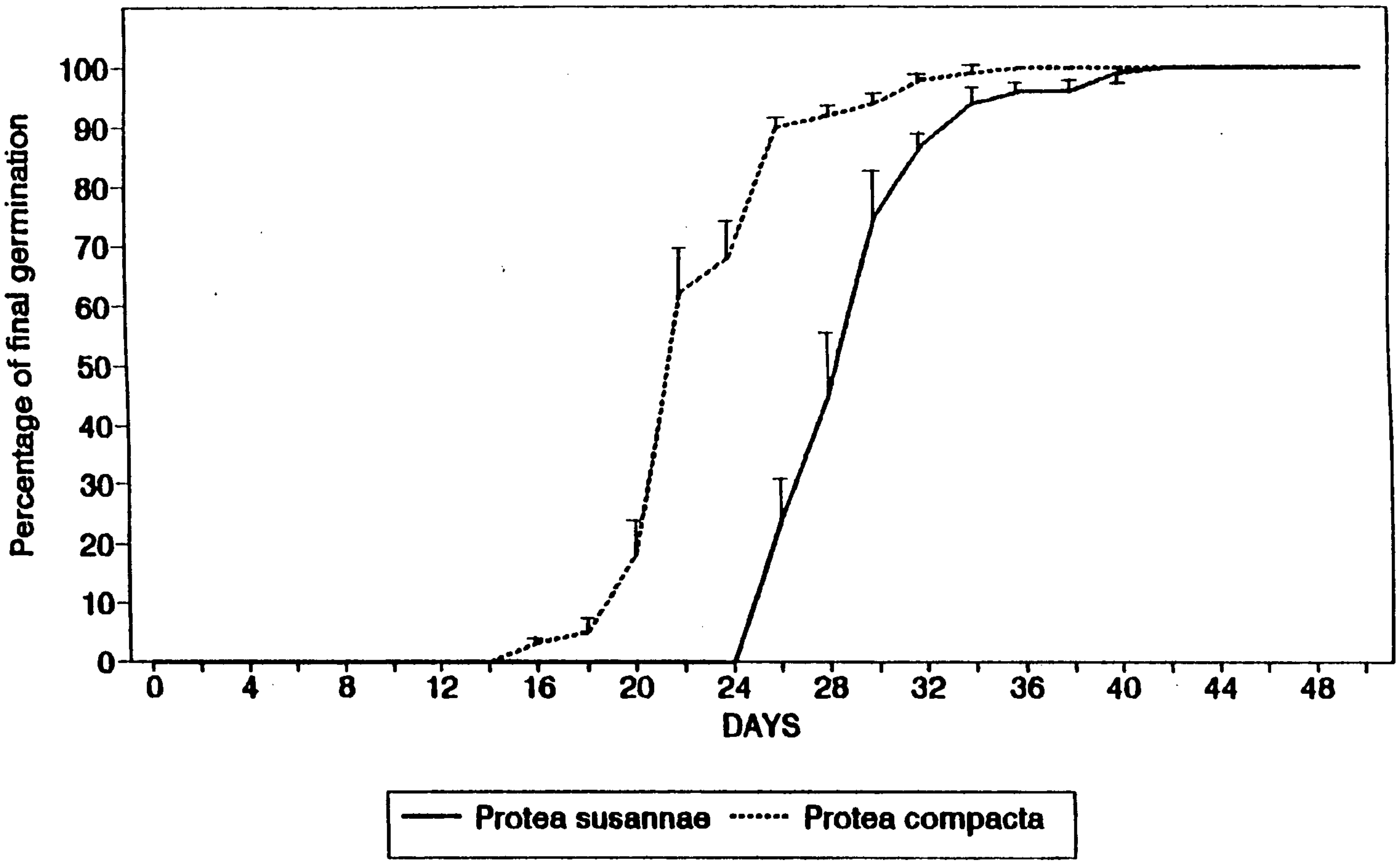

FIGURE 5.2 Percentage of final germination of seeds of *Protea susannae* and *P. compacta* in a germination chamber, with respect to time. Final germination (out of a total of 100 seeds) was 71% for *P. susannae* and 100% for *P. compacta*.

TABLE 5.1 Morphological and growth charactersitics (mean ± one SE, n = 5) of seedlings of *Protea susannae* and *P. compacta* after 15 weeks (simulated winter conditions) and 30 weeks (simulated winter followed by spring and summer with and without a water table). Values with the same superscript are not significantly different. All weights and weight ratios are dry weights.

	15 Weeks				30 Weeks					
	P. susannae	*P. compacta*			*P. susannae*		*P. compacta*			
					W/table	Dry	W/table	Dry		
Shoot wt (g)	0.28±0.01	0.97±0.06	t=11.44,	***	$2.97±0.41^{a}$	$2.64±0.23^{a}$	$7.80±0.89^{b}$	$7.77±1.43^{b}$	$F_{(1,15)}=28.8$	***
Root wt (g)	0.38±0.04	0.76±0.06	t=5.33,	***	$2.57±0.65^{a}$	$2.56±0.28^{a}$	$5.10±0.92^{b}$	$4.53±0.70^{b}$	$F_{(1,15)}=10.1$	***
Total wt (g)	0.66±0.04	1.73±0.09	t=10.40	***	$5.54±0.99^{a}$	$5.20±0.45^{a}$	$12.90±1.70^{b}$	$12.30±2.09^{b}$	$F_{(1,15)}=22.2$	***
Leaf area (cm^2)	59.4±1.7	143.2±7.3	z=-2.51	*	$183.0±21.1^{a}$	$160.2±19.9^{a}$	$401.6±46.8^{b}$	$358.6±44.5^{b}$	Kruskal-Wallis	***
Root depth (cm)	52.1±3.7	69.5±2.5	y=3.85	**	$75.4±1.1^{a}$	$73.0±1.3^{b}$	$77.4±0.4^{c}$	$75.2±0.9^{a}$	$F_{(1,16)}=4.57$	*
Root wt/shoot wt	1.34±0.15	0.79±0.06	t=-3.27	*	$0.85±0.14^{a}$	$0.98±0.11^{a}$	$0.64±0.09^{b}$	$0.60±0.03^{b}$	$F_{(1,15)}=8.1$	*
Leaf area/shoot wt	164.8±21.4	191.3±10.7	N.S.		$86.9±19.8^{a}$	$63.9±9.2^{a}$	$91.6±18.2^{a}$	$81.9±6.5^{a}$	N.S.	
RGR ($g.g^{-1}.day^{-1}$)	0.30	0.26			0.07	0.07	0.06	0.06		

*** p<0.001, ** p<0.01, ** P<0.05.

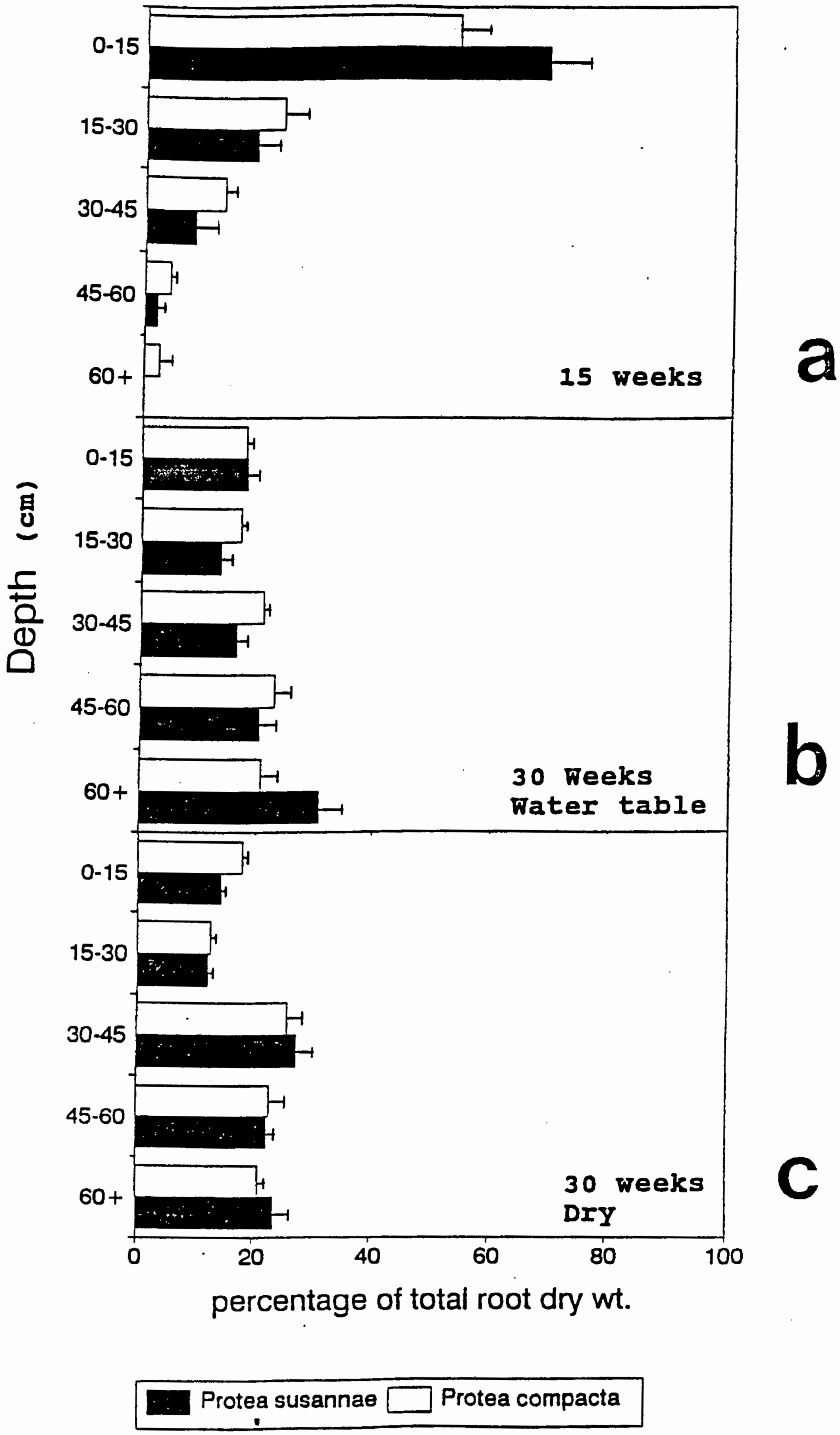

FIGURE 5.3 Percentage of total root weight of _Protea susannae_ and _P. compacta_ seedlings at different depths after **(a)** 15 weeks and 30 weeks **(b)** with a water table (weeks 16-30) and **(c)** dry treatment (water table for weeks 16-23 only). T-bars represent one SE, n = 5.

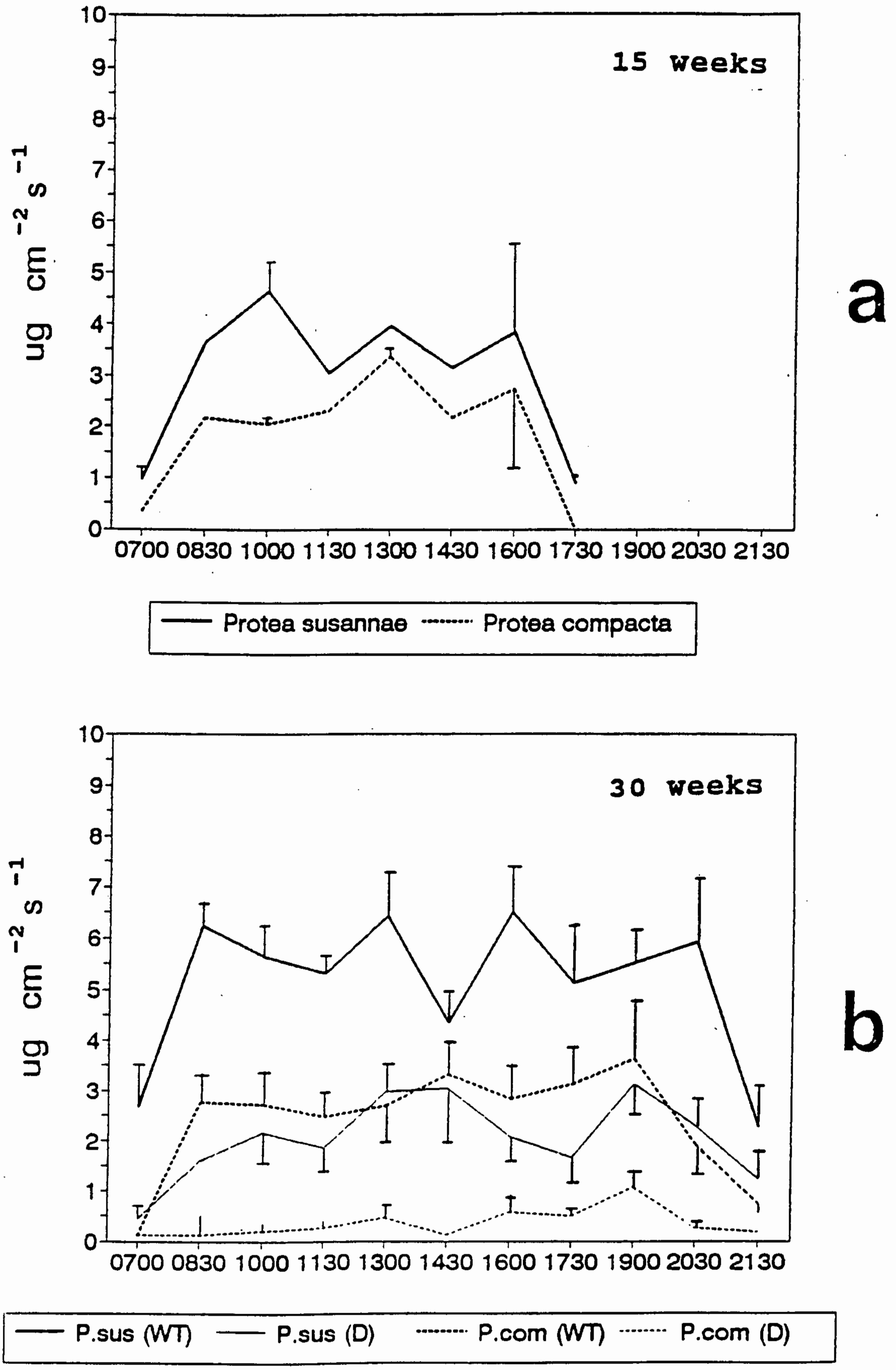

FIGURE 5.4 Transpiration rates of seedlings of Protea susannae (P.sus) and P. compacta (P.com) recorded at 90 minute intervals over the light period of one day, **(a)** at 15 weeks (12 hrs) and **(b)** at 30 weeks (15 hrs) in both the water table and dry treatments. Each point is an average of eight readings (15 weeks) or five readings (30 weeks) on different individuals. Bars represent one SE, WT = water table treatment, D = drought treatment.

TABLE 5.2 Pre-dawn water potential and transpiration (mean ± one SE n=5) of *Protea susannae* and *P. compacta* seedlings after 15 weeks (simulated Winter conditions) and 30 weeks (simulated winter followed by spring and summer conditions with or without water table). Values followed by the same subscript are not significantly different.

	15 Weeks			30 Weeks				
	P. susannae	*P. compacta*		*P. susannae*		*P. compacta*		
				W/table	Dry	W/table	Dry	
Water potential (MPa)	-0.39+0.02	-0.36+0.02	N.S.	-0.62 ± 0.03^{a}	-0.83 ± 0.07^{a}	-0.55 ± 0.13^{a}	-3.55 ± 0.31^{b}	$F_{(1,16)}=66.0$ ***
Transpiration								
Daily maximum rate ($ug/cm^2/s$)	(-)	(-)		8.45 ± 0.91^{a}	4.37 ± 0.84^{b}	4.61 ± 1.06^{b}	1.10 ± 0.33^{c}	$F_{(1,16)}=18.3$ *** $F_{(1,16)}=20.8$ ***
Daily rate ($g/cm^2/day$)	0.130$	0.079$		0.30 ± 0.03^{a}	0.12 ± 0.18^{b}	0.14 ± 0.03^{b}	0.02 ± 0.01^{c}	$F_{(1,16)}=30.2$ *** $F_{(1,16)}=41.4$ ***
Daily plant rate (g/plant/day)	7.7$	11.2$		54.3 ± 8.6^{a}	18.9 ± 4.2^{b}	60.7 ± 16.6^{a}	6.2 ± 1.2^{c}	Kruskal-Wallis *

*** $p<0.001$, ** $p<0.01$, * $p<0.05$.

(-) not determined

$ denotes mean only, no variance or statistical analysis (see text) expressed on a per plant basis, the quantity of water transpired in a day was higher for P. compacta. No statistics were applied to the per plant transpiration data at 15 weeks, as they were calculated from the average rate (for a randomly selected sample of individuals) at each 90 minute sampling time.

After 30 weeks, Protea susannae seedlings were still smaller than those of P. compacta (Table 5.1). Shoot weight, leaf area and root weight of P. susannae were significantly lower (Table 5.1), but these did not differ significantly between the water table and drought treatments for either species. Average root depth for both species in both treatments was 73 cm or more, indicating that roots of all plants had reached the depth of the water table. Root depth of P. susannae was significantly less than that of P. compacta ($F_{(1,16)} = 4.57$, $p<0.05$) and both species had significantly deeper roots in the water table treatment ($F_{(1,16)} = 5.48$, $p<0.05$). However, these differences are very small (2 cm or less).

Root mass partitioning between depths (Figure 5.3) did not differ significantly between species at 30 weeks. There were overall differences between depths, with allocation of both species to the greater depths (30-45 cm, 45-60 cm, >60 cm) significantly larger than to 0-5 cm and 15-30 cm ($F_{(4,79)} = 3.36$, $P<0.05$). This effect was not constant across treatments. The highest percentage (26.6%) was at

30-45 cm in the drought treatment, compared to >60 cm (26.5%) in the water table treatment.

Root/shoot ratios decreased over the second 15 weeks of growth (Table 5.1) and, although the decline was greater for Protea susannae seedlings, root weight/shoot weight remained significantly higher than for P. compacta ($F_{(1,15)} = 8.13$, $p<0.05$). As with the 15 week measurement, leaf area/root weight ratios did not differ significantly between species. No significant differences between treatments were detected for either ratio.

Of the 16 soil moisture probes, only 7 provided reliable data. This left data on soil drying for only two Protea susannae tubes (2 probes), one in each treatment, and one P. compacta tube in the water table treatment (3 probes). Soil drying was substantially slower in the P. susannae tubes and did not differ substantially between water table and drought treatments. Soil at 10 cm was dry after 20 weeks, while at 45 cm this occurred in the 27th week. The soil in the P. compacta tube was dry at 10 and 30 cm depths by week 18, one week after surface watering ceased, while at 45 cm this point was reached after 20 weeks (Figure 5.5).

Water potentials in the water table treatment differed little between species and were only slightly lower than at 15 weeks (Table 5.2). Water potential of Protea susannae seedlings did not differ significantly between water table and dry treatments. However, the removal of the water

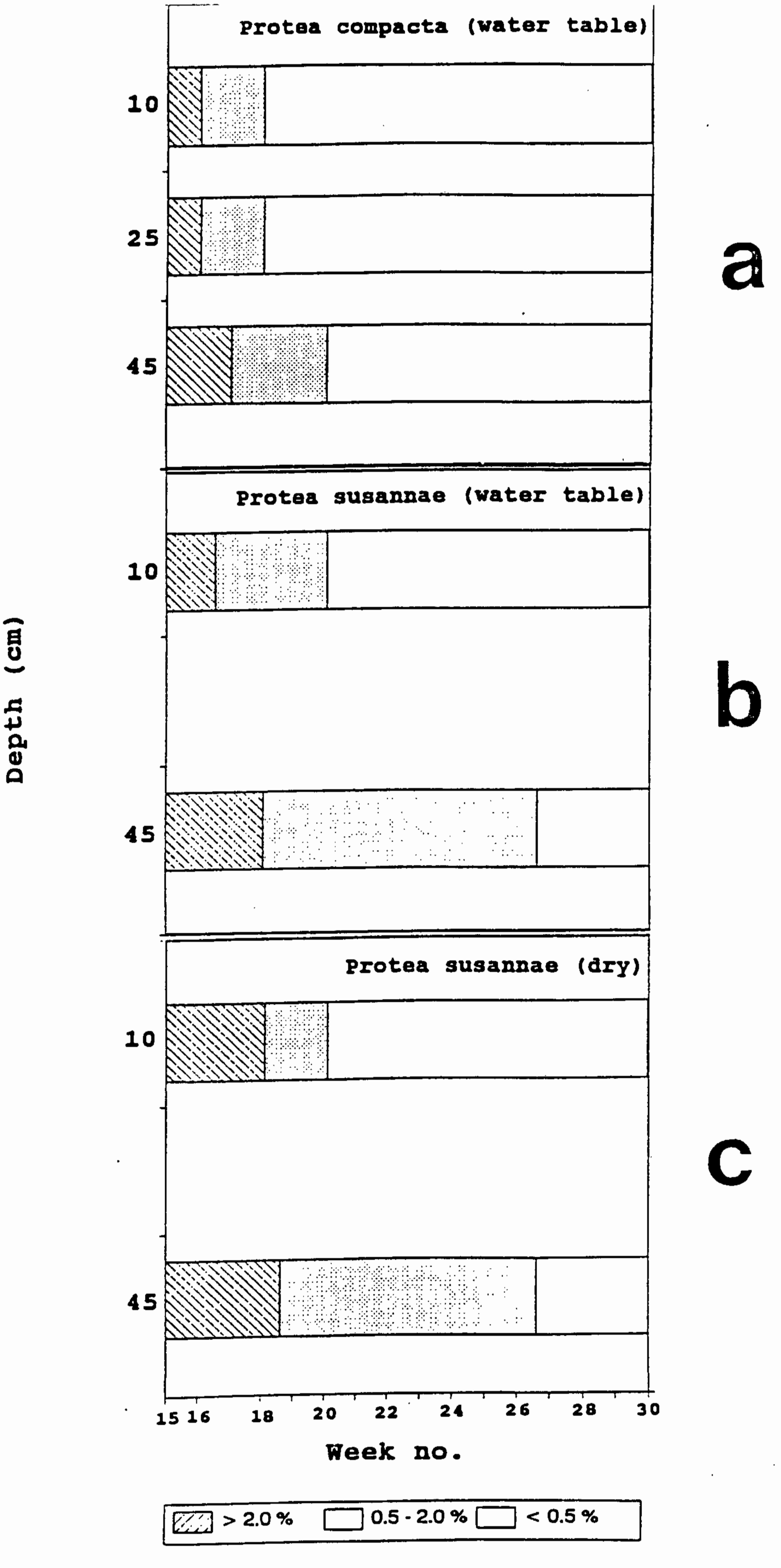

FIGURE 5.5 Percentage soil moisture content at various depths in soil-filled tubes, from the 15th to the 30th week after planting of seedlings. This was calculated from logged readings of soil moisture probes which were sensitive to soil moisture over the range of 0.5 to 2.0 % (see Figure 5.1 for arrangement). Results are shown for those probes which functioned correctly: two tubes with <u>Protea susannae</u> seedlings, **(a)** from the water table treatment and **(b)** from the drought treatment, and **(c)** one tube with a <u>P</u>. <u>compacta</u> seedling from the water table treatment.

table had a great effect on P. compacta seedlings, with water potentials 3 MPa lower and all individuals showing signs of wilting. Transpiration rates on the day preceding harvest (Figure 5.4(b)) showed that in both water table and dry treatments, P. susannae maintained much higher transpiration rates per unit area than P. compacta. Both species had greatly reduced transpiration rates in the dry treatment, and for P. compacta, transpiration under drought was close to zero. As sequential readings of transpiration rates were taken on each individual, as opposed to sampling at random from a larger group as was done at 15 weeks, daily maximum and total plant transpiration could be calculated for each individual and statistics applied. In both treatments P. susannae had significantly higher daily maximum transpiration rate ($F_{(1,16)} = 18.31$, $p<0.001$) and daily total transpiration per unit area ($F_{(1,16)} = 30.18$, $p<0.001$). However, when transpiration was calculated on a per plant per day basis (using leaf area), there was no significant difference between species in the water table treatment, while P. susannae plants had higher total transpiration in the drought treatment ($p<0.05$). In the drought treatment, transpiration (all measures) was significantly lower ($P<0.05$) for both species.

5.5 DISCUSSION

The most important difference between Protea susannae and P. compacta was seed size and the subsequent difference in seedling size. The positive correlation between seed and seedling size is well documented (Gross 1984, Fenner 1985, Stock et al. 1990), although seedling size is related primarily to the nutrient quality of the seed (Fenner 1985, Stock et al. 1990). A factor adding to the size difference was the earlier germination of the P. compacta seeds. This is in conflict with the work of Stock et al. (1990) who found that the emergence rates of five Australian and South African Proteaceae species were unrelated to seed size. Mustart and Cowling (1991) showed differences in germination rates between, but not within, Proteaceae genera. Despite later germination and smaller size, P. susannae seedlings had a similar relative growth rate (RGR) to P. compacta in both the first and second 15 week periods, confirming the work of Stock et al. 1990 who found RGR to be unrelated to seed size in the Proteaceae.

Although shoot weight, root weight, root depth and leaf area were greater for Protea compacta seedlings after 15 weeks, P. susannae seedlings had higher root/shoot weight ratios. The ratio of leaf area to root weight, characteristic of species in xeric habitats (Matsuda and McBride 1986), did not differ between the species. At this time, P. compacta seedlings were more expensive in their water-use, despite lower transpiration rate per unit area, as a result of the much higher leaf area. After a further 15 weeks (summer conditions), transpiration of both species increased in the water table treatment, especially for P. susannae, for which total plant transpiration was similar to that of P. compacta despite leaf area being less than half. The dependence of P. compacta seedlings on a continuous water supply, i.e. the water table, was clearly shown by the development of severe, and probably fatal, water stress of all plants in the dry treatment, seven weeks after the water table was removed. In contrast, although P. susannae seedlings in the dry treatment showed lower transpiration rates than those with a water table, this was still higher than at 15 weeks. Water potential of P. susannae seedlings did not differ between water table and dry treatments, indicating that more water remained in the soil profile.

The differences between these species at the regeneration stage (germination and early seedling growth) has important implications for understanding the virtual restriction of Protea susannae to deep soil and the strong association of Protea compacta with shallow soil, described in Chapter 4. The water-spending strategy of P. susannae adults and the conservative water-use of P. compacta adults (individuals of both species approximately 15 years old) were found to be well suited for deep and shallow soils respectively. However, the lack of any major within-species differences in water relations between individuals of growing in deep and shallow soils (Chapter 4) suggests that this distribution pattern was likely to be determined by processes at the regeneration (seedling) stage.

The slower root extension of Protea susannae seedlings is characteristic of species in relatively mesic sites with shallow water tables (Matsuda and McBride 1986). The low leaf area, relatively low total plant transpiration (in the first 15 weeks) and slow drying of the soil profile amounted to a conservative water-use strategy. Such a water-sue strategy is contrary to that usually associated with establishment in deep soils in mediterranean-climate regions, namely, rapid root growth at some cost of water-loss, in order to ensure a better water supply later in the season (Rhizopoulou and Davies 1991, Davies and Midgley 1992). Slow root growth in species establishing in deep soil implies a need to be resistant to water stress, at least during the first few years of establishment (Frazer and Davis 1988). This may be offset by relatively low water use in the early stages, but will depend on the ability of neighbouring plants to dry out the soil (Midgley and Moll 1993).

Protea compacta seedlings showed a drought-avoiding strategy of early germination, large seeds and seedlings and rapid root growth. This occurred at a cost of high early transpiration, corresponding with the establishment strategy suited for deep soils, as proposed by Rhizopoulou and Davies (1991) and Davis and Midgley (1992) and not the shallow soil with which this species is associated. Success of this strategy is, however, dependent on reaching a suitable water supply before the upper soil dries out, a risk increased by the high water-use of this species. Midgley and Moll (1993) showed that some shrubs from semi-arid habitats show high conductance and low water-use efficiency at moderate and high soil water content and suggested that this may be a competitive strategy of drawing resources away from neighbours. This may be a competitive advantage for P. compacta seedlings, but only if faster root growth enables them to reach moist soil. Although the shallow soil has lower water content (Chapter 4), it would be relatively easy for P. compacta seedlings to reach the bottom of this profile (40-50 cm), providing them with a competitive advantage over P. susannae seedlings. Achieving this in shallow soil would not be as dependent on mild summers, as it would be in the deep soil. If the water table in the deep soil were to drop rapidly in the first summer after germination, the more conservative water-use of P. susannae seedlings would place them at an advantage.

These distinct differences between seedlings of two Protea species associated with different habitats points to the importance of considering regenerative stages when seeking explanations for species distributions. It has recently been suggested (Lamont et al. 1989, Davis 1991) that niche differentiation explaining coexistence or restricted distribution patterns in species of mediterranean-type ecosystems is most likely to be found at the post-fire regeneration stage. Despite a general focus of ecological studies on mature plants in such habitats (Davis 1991), a number of recent studies have shown species differences at the regeneration stage responsible for community composition (Frazer and Davis 1988, Saruwatari and Davis 1989) and restricted distributions (Lamont et al. 1989, Enright and Lamont 1991 Mustart and Cowling 1993 and see Chapter 6).

Of particular interest in this study is the switch in water-use strategy that occurs between the seedling and adult stages of these Protea species, but in opposite directions. Protea susannae seedlings were conservative in their water-use during the first 15 weeks, but under warm, dry conditions and in contact with a water table, had more than doubled their transpiration rate (per unit area) after 30 weeks. By this stage they were showing the water-spending strategy characteristic of mature plants (15 yr old) studied in the field (Chapter 4). Protea compacta seedlings were large and expensive in their water-use throughout the 30 week experiment, provided that access to a water table was continuous. This conflicts with the conservative water-use of adult P. compacta plants in the field. If such a water-use strategy occurs in seedlings establishing in the field, it raises the question as to when the switch occurs. Although the state of water stress of P. compacta seedlings in the dry treatment at the end of the experiment was severe, the great reduction in transpiration compared to the water table treatment suggests that for seedlings are able to adjust to conservative water-use in dry conditions as found for certain shrubs from arid habitats (Midgley and

Moll 1993). Further study of young plants is required to investigate whether those P. compacta seedlings which survive the first summer drought remain conservative in their water-use or whether further switches occur.

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CHAPTER 6

THE IMPORTANCE OF SOIL FACTORS AND COMPETITION IN DETERMINING THE DISTRIBUTIONS OF SIX PROTEACEAE SPECIES.

6.1 ABSTRACT

The importance of competition in relation to soil factors in determining the distributions of fynbos species was assessed by means of a three-year experiment. Three pairs of Proteaceae species were selected as case studies. For each pair one species replaces the other along a transect across the landscape, crossing one or more community boundaries. These species were grown from seed in cleared plots (three plots per species pair) arranged along the corresponding transect. At each site plants were grown in monoculture and 1:1 mixture at a range of total densities. The effects of site (soil factors), density and monoculture/mixture on survival and above-ground biomass were determined after three years. Nearest-neighbour analysis was also used to determine the relative effects of intra- and interspecific competition on growth (biomass) of one species pair. Site had the greatest effect of all factors on survival of all species. For three species, average individual biomass was related primarily to site effects and, for the other three, to density effects. Although strong effects of reduced biomass with density were found for all species, no difference between intra- and interspecific competition were detected. It was concluded that the distribution of these species across this landscape is determined primarily by soil factors. While competition may be important in determining growth and the spatial arrangement of individuals within communities (as indicated by density

effects), this work suggests that it may be relatively unimportant in determining fynbos species distributions.

6.2 INTRODUCTION

It has been suggested that competition plays only a minor role in structuring plant communities in habitats with low resource levels (Grime 1977, 1979) and frequent disturbance (Huston 1979, Keddy 1989a,b). This would seemingly apply to South African fynbos, with its nutrient-poor soils and recurrent fires (Kruger 1983, Cowling 1992). According to Grime's (1977,1979) theory of the major syndromes of plant life-history traits, plants in such habitats would be adapted for nutrient and water stress ("stress tolerators"). Consequently, they would be relatively non-competitive due to slow growth rates and low reproductive effort. In contrast, the theory of Tilman (1977, 1982, 1983) holds that competitive exclusion occurs when one species is able to reduce a resource to a level below the tolerance of another, resulting in the inhibition of the growth or reproduction of the other species. The likelihood of competitive exclusion would then be dependent on resource supply and depletion rates (Tilman 1982, 1983). Although the mechanism of competition may change along resource gradients, it is not restricted to non-stressed habitats (Wilson and Tilman 1991). Grubb (1992) argued that competition may occur both where resources are abundant and where they are scarce, although different forms of competition may take place. Weldon and Slausson (1986) and Grace (1991) have pointed out that much of the controversy concerning the role of competition stems from the assumption that the importance of competition in any community is equivalent to its intensity.

They suggest that the importance of competition depends on the magnitude of its effect in comparison to other factors and thus it does not have to be intense to be ecologically important.

The subject of competition and its importance in structuring plant communities has not received a great deal of attention in fynbos (see review in Bond et al. 1992). Species diversity in fynbos is high (Cowling and Holmes 1992) and the co-occurrence of many morphologically similar species is a characteristic feature (Bond et al. 1992). Not surprisingly, the small number of studies considering competition have done so from the perspective of coexistence, i.e. seeking to find out how all these species manage to avoid competitive exclusion. Of particular interest has been the relevance of classical niche theory (Gause 1934). The most frequently cited case where niche differentiation has been reported for fynbos species, is the work of Cody (1986), who proposed that various Proteaceae species showed niche differentiation in terms of leaf shape. This work, however, has a number of flaws, most notably in the lack of a null model and in the lack of a known physiological link between leaf shape and competition in the species studied (Bond et al. 1992).

It has been argued that in a fire-prone (disturbance-dominated) ecosystem such as fynbos fire , equilibrium-based classical niche theory cannot be applied, as the process of competitive exclusion rarely continues to completion without being interrupted (Huston 1979). Cowling (1987) argued that the spatial and temporal variation associated with the disturbance regime in fynbos is itself sufficient to explain the coexistence of so many similar species. One particular case where the combination of disturbance and dispersal differences was shown to prevent competitive exclusion of one fynbos species by another, was reported by Yeaton and Bond (1991), but this is an unusual species pair (Bond *et al*. 1991).

Evidence for competition playing a role in structuring fynbos communities comes from studies of pattern, but these are few. Midgley and Watson (1992) studied the spacing of individuals of a variety of Proteaceae species in several stands. They found that spacing changed from clumped in seedling stands to regular or random in adult stands and suggested that competitive interactions were responsible for this. Average distance between intraspecific pairs was greater than between interspecific pairs, implying that intraspecific competition was more intense than interspecific competition. In contrast Witkowski (unpublished data) examined nearest-neighbour relationships in two *Leucadendron* species at two sites and found that interspecific competition had a major influence on spacing of individuals. Although patterns such as those examined in these studies suggest competition to be structuring these communities, more direct experimental evidence of the process of competition is required, as it is potentially misleading to make inferences about processes from studies of the patterns they are thought to create (Cale et al. 1989).

The debate concerning the ecological importance of competition, both internationally and with respect to fynbos, together with the paucity of experimental evidence, indicates a need for comprehensive field experiments with fynbos species. A large number of field experiments investigating plant competition have been carried out in relatively species-poor ecosystems, such as salt marshes (Snow and Vince 1984, Bertness 1991a,b), lakeshores (Keddy 1989a,b), oldfields (Goldberg 1987, Gurevitch et al. 1990) or arid and semi-arid regions (Fowler 1986, Gurevitch 1986 and see reviews in Connell 1983 and Schoener 1983). It is thus of great interest to investigate the importance of competition in species-rich vegetation such as fynbos.

In this study an approach was taken which differs fundamentally from those typical of earlier fynbos competition studies. Instead of seeking ways in which co-occurring species avoid competition (i.e. niche separation), I considered species with adjacent distributions that overlap very slightly or not at all and investigated the causes of their different distributions. A large number of recent studies of the importance of competition have used transplant or removal experiments along natural resource and disturbance gradients to compare the effects of competition and abiotic factors in controlling species distributions (Snow and Vince 1984, Gurevitch 1986, Keddy 1989a,b, Bertness 1991a,b, Lamont _et_ _al_. 1991). Investigating the importance of competition versus soil factors, I was also able to test the traditional view in fynbos ecology that species distributions are controlled mainly by abiotic environmental factors (Bond _et_ _al_. 1992, Cowling and Holmes 1992).

Three pairs of Proteaceae species whose distributions include a wide variety of soil types were selected. A field experiment was set up to investigate the factors controlling their distributions across community boundaries or changes in dominant overstory species. The survival and growth of seedlings of these species at a variety of sites was monitored over a three-year period to assess the influence of soil factors. Within each site survival and growth was compared across monoculture, two-species mixture and range of total densities to determine the relative effects of intra- and interspecific competition (Connel 1983, Firbank and Watkinson 1985). To distinguish experimental plants (which, with a few exceptions, did not reach reproductive maturity during the experiment) from the surrounding mature vegetation, they will be referred to as seedlings and the mature plants as adults.

In this study the following questions were posed: **1)** do patterns of seedling survival and growth across sites, regardless of competition, correspond with the present distribution of the adults, indicating control of distribution by soil factors at the seedling stage, and **2)** does the effect of interspecific competition at any site exceed that of intraspecific competition and thus influence the distribution of the seedlings by means of one species competitively excluding the other from part of its range?

6.3 STUDY SITE

The study site was located on the southern slopes of the Soetanysberg mountains, about 15 km west of Cape Agulhas (34^{o} 45' S; 19^{o} 50' E). The climate is of a mediterranean type, with warm, dry summers and cool, wet winters. Mean annual rainfall at Cape Agulhas is 452 mm. The geology of the area is described in Thwaites and Cowling (1987). The eastern part of the mountain consists of Triassic quartzitic sandstone (Table Mountain Group), capped with Mio-Pliocene limestone (Bredasdorp formation), while the eastern part consists entirely of limestone (see Figure 6.1).

The vegetation and soils at this site have been described in detail Chapters 2 and 3. In association with the variety of soil patterns in this area, the vegetation forms complex patterns with considerable species turnover across the site. This is made particularly obvious by distinct patterns of various overstorey Proteaceae species. Three pairs of these species were selected for detailed study. All are large, serotinous overstorey shrubs, killed by fire. Each is dominant or co-dominant, in part of the study site. They are <u>Leucadendron</u> <u>meridianum</u> Williams and <u>Leucadendron</u> <u>coniferum</u> (L.Meisn.), <u>Leucadendron</u> <u>xanthoconus</u> (O.Knutze) K.Schum and <u>Leucadendron</u> <u>laureolum</u> (Lam.) Fourc. and <u>Protea</u> <u>susannae</u> Phill. and <u>Protea</u> <u>compacta</u> R.Br. All have more or less discrete distributions at this site, with the distinct replacement of one species by the other of the pair across the site. For each pair, three sites were located along a

FIGURE 6.1. a) The south-facing side of the Soetanysberg hills, showing the location of the three transects with respect to the main soil types. limestone, sandstone, deep colluvial sand adjacent to limetstone, acid colluvial sand.
b-d) Diagrammatic representation of transects A, B and C, showing locations of the sites along each transect relative to topography and the dominant species or growth forms.

LEGEND

M <u>Leucadendron</u> <u>meridianum</u>

C <u>Leucadendron</u> <u>coniferum</u>

X <u>Leucadendron</u> <u>xanthoconus</u>

L <u>Leucadendron</u> <u>laureolum</u>

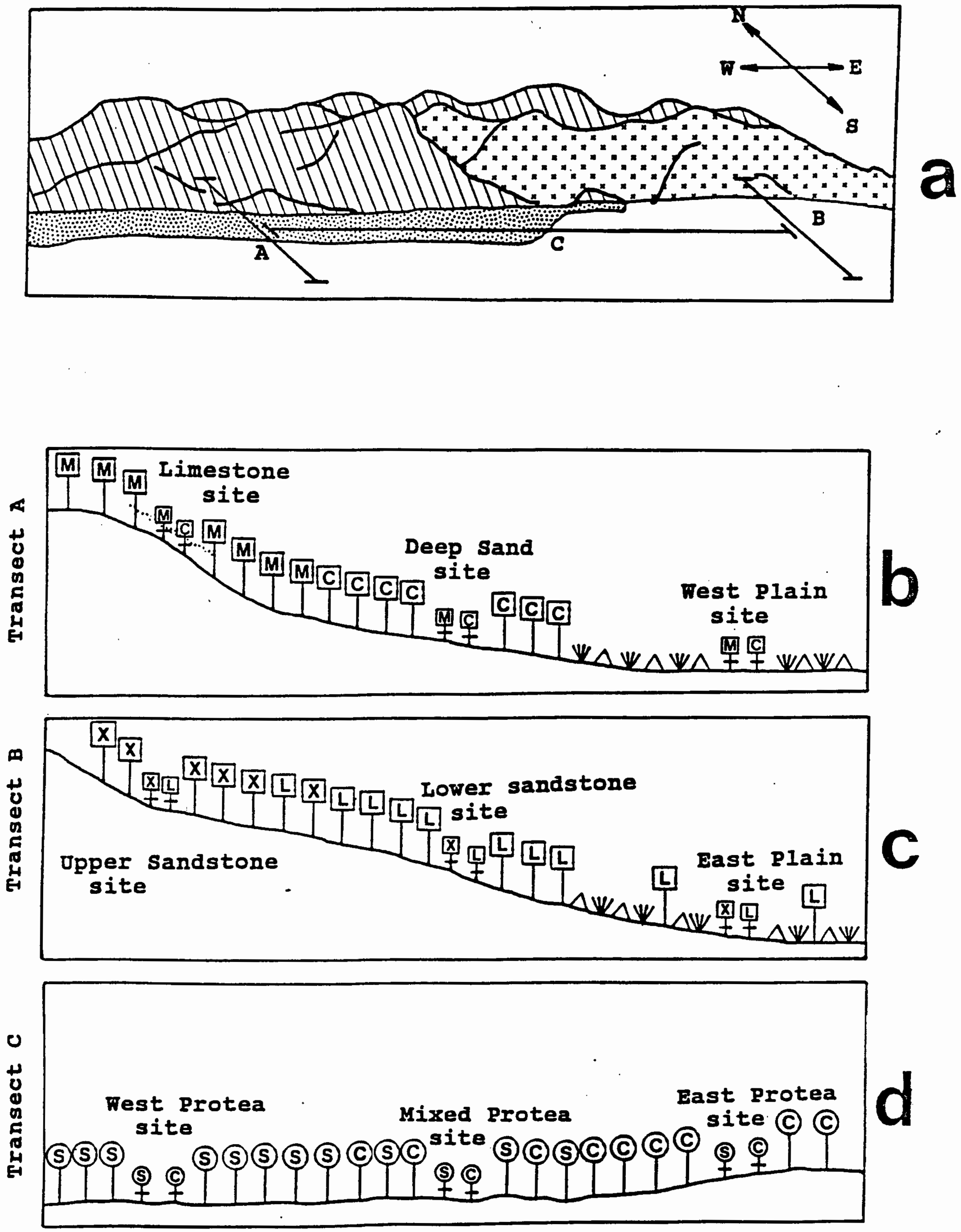
S <u>Protea</u> <u>susannae</u>

C <u>Protea</u> <u>compacta</u>

ericoid shrubs

restioid shrubs

S C planted seedlings showing location of experimental site



N
W
E
S
a
A
B
C
Transect A
Limestone site
Deep Sand site
West Plain site
b
Transect B
Lower sandstone site
Upper Sandstone site
East Plain site
c
Transect C
West Protea site
Mixed Protea site
East Protea site
d

transect crossing the boundary where one species replaces the other (see Figure 6.1).

6.3.1 Leucadendron meridianum and Leucadendron coniferum (Transect A)

This transect included the most distinct soil differences (Table 6.1). At the Limestone site, soil was in pockets and cracks in the rock or in shallow sheets over rock surfaces. Organic material and nutrients were relatively high and soil was slightly alkaline This soil had a very high proportion of fine sand. Ths site was dominated by L. meridianum and L. coniferum was absent (Figure 6.1). The Deep Sand site was on very deep moderately acid sand with much lower organic content and nutrient levels. This site was dominated by Protea susannae and L. coniferum. L. meridianum was absent. The West Plain site was on deep, very acid sand with very low organic material and nutrient levels. Both the Deep Sand and West Plain sites had a high proportion of medium-textured sand. The West Plain site was dominated by dominated by low shrubs (Restionaceae and Ericaceae). Both L. meridianum and L. coniferum were absent. P. susannae was only present at the deep sand site

6.3.2 Leucadendron xanthoconus and Leucadendron laureolum (Transect B)

The Upper Sandstone site was rocky with very shallow soil (Table 6.1). Organic carbon and nutrient levels were much

TABLE 6.1 Soil data summarised from Chapter 2 (altitude, slope, % rock cover, soil depth, % fine, medium and coarse sand and pH) and Chapter 3 (organic carbon, total nitrogen and total phosphorus). For each site soil was taken from thesoil sampling site closest to the location of the cleared experimental plot.

	Altitude (m)	Slope (deg)	Rock cov (%)	Soil Depth (m)	% Sand fine	med.	coarse	pH	Organic C (g/kg)	Total N (ug/g)	Total P (ug/g)
TRANSECT A. *Leucadendron meridianum* *Leucadendron coniferum*											
Limestone site	50	11	40	0.08	69.4	14.6	5.7	7.4	115.9	3687	82.2
Deep sand site	35	4	0	>1.2	39.2	49.8	2.4	5.4	22.6	643	66.1
West plain site	30	0	0	>1.2	20.7	53.4	21.2	4.3	12.2	307	60.5
TRANSECT B. *Leucadenrdron xanthoconus* *Leucadendron Laureolum*											
Upper sandstone site	50	18	55	0.09	34.3	16.1	42.4	5.0	49.8	1280	69.4
Lower sandstone site	40	3	0	0.75	18.8	22.1	50.5	4.8	20.6	410	62.3
East plain site	30	0	0	0.97	33.3	19.2	40.9	4.8	16.7	380	61.3
TRANSECT C. *Protea susannae* *Protea compacta*											
West protea site	35	4	0	>1.2	39.2	49.8	2.4	5.4	22.6	643	66.1
Mixed protea site	35	3	0	>1.2	46.5	15.9	30.7	4.9	22.1	517	65.2
East protea site	40	3	0	0.75	33.3	19.2	50.5	4.8	20.6	410	61.3

lower than limestone soil, but higher than the other acid soils. This site was dominated by Leucadendron xanthoconus and L. laureolum was absent (Figure 6.1). From the Upper Sandstone site to the East Plain site there was a gradient of decreasing rock cover, increasing depth and decreasing nutrient levels. All three sites on this transect had moderately low pH and a high proportion of coarse sand. The Lower Sandstone site was dominated by L. laureolum and L. xanthoconus was absent. The East Plain site was dominated by low shrubs (Restionaceae, Ericaceae) with occasional L. laureolum individuals.

6.3.3 Protea susannae and Protea compacta (Transect C)

The main difference between the three sites on this transect was that of soil depth, which was much greater in the West and Mixed Protea sites than at the East Protea site(Table 6.1). There was an increase in percentage coarse sand from west to east. All three sites were moderately acid and low in organic matter and nutrients, although total P and pH decreased slightly from west to east. The West Protea site was dominated by P. susannae and Leucadendron coniferum (Figure 6.1). P. compacta was absent. The Mixed Protea site was dominated by an even mixture of P. susanane and P. compacta, while the East Protea site was dominated by P. compacta and Leucadendron laureolum, while P. susannae was absent. L. coniferum and L. laureolum were dominant only at the West Protea and East Protea sites respectively.

6.4 METHODS

6.4.1 Experimental design

At each of the nine sites, a 5 m x 5m plot was cleared of all vegetation and planted with both species of the corresponding species pair. Each plot was divided into sixteen 1 m x 1 m subplots, with a 0.5 m wide border (Figure 6.2) The subplots at each site were allocated randomly: five monocultures of each species, five 1:1 mixtures and one empty subplot. In both the monoculture and mixture subplots, seeds were planted in 12 positions in each of three concentric rings of diameters 10, 30 and 70 cm. These rings provided a range of initial densities which was constant across monoculture and mixture treatments. Three seeds were planted in each position to allow for those failing to emerge. In the mixed subplots, the 12 positions within each ring were alternated with respect to species. Seed planting took place during May 1989 and emergence occurred during July and August of that year. Extra seedlings were thinned out by cutting at ground level in December 1989, so that only one seedling remained in each position. A wire mesh cage was secured over each subplot to prevent rodent predation. It was necessary to remove these after one year, as seedlings had reached the wire which was began to interfere with their growth. Throughout the experiment, plots were cleared of other seedlings.

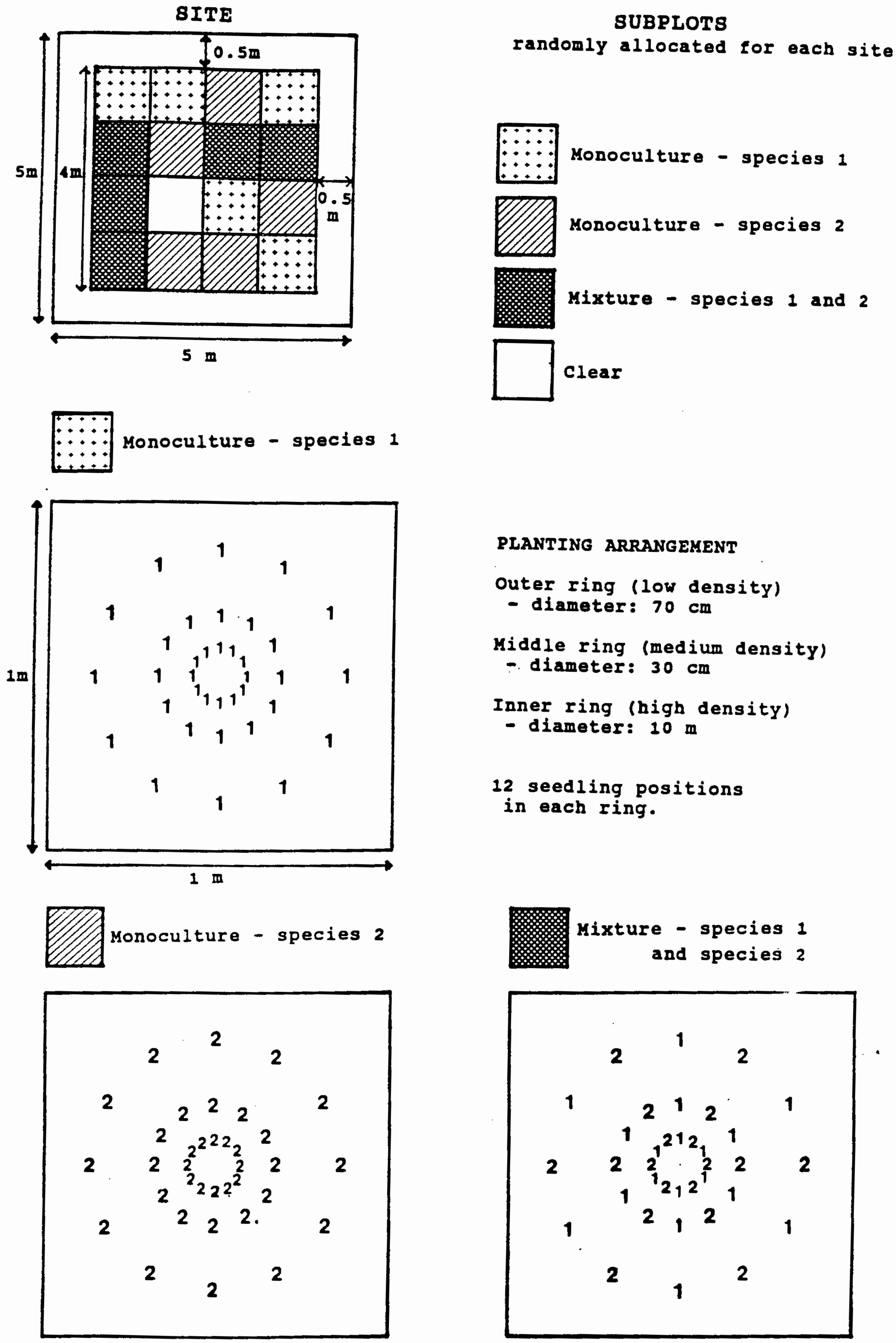


FIGURE 6.2. Field experimental design, showing the arrangement of subplots within a site and the planting arrangement for monoculture and mixture subplots. Three seeds were planted in each position and, after emergence, seedlings were thinned out to one per position.

6.4.2 Survival and average individual biomass

Percentage survival was determined in July 1992, three years after seedling emergence. The unit of measurement was the proportion of seedlings surviving in each ring (initially of 12 seedlings in monoculture and 6 per species in mixture). Initial numbers were corrected for the small number of missing positions (where none of the three planted seeds emerged). Percentage survival data were binomially distributed and with unequal variances. Arcsin transformation (appropriate for percentage data (Zar 1984)) was insufficient to correct this and so nonparametric Kruskal-Wallis one-way analysis of variance by ranks was used (STATGRAPHICS, v4.0 Statistical Graphics Corporation). Data were analysed for the effect of site (soil factors), then within each site, for density (differences between 3 ring sizes) in monoculture and in mixture, and, finally for competitive effects by comparing monoculture and mixture survival for each density class (ring size).

Individual size was determined in July 1991 and July 1992, two and three years after seedling emergence. Basal diameter, height, greatest canopy diameter and diameter perpendicular to that were measured. Data from July 1991 were used for calculating growth increments for the third year for use in estimation of nearest-neighbour relationships. Data from July 1992 were used for determining experimental effects on final biomass. Fifty individuals of each species, representing the complete size range, were then harvested by cutting at ground level and dried to constant weight in ovens at 70 °C. Basal diameter and volume (cylindrical) were regressed against dry mass to obtain the best formula to predict the biomass of individuals. These regressions showed volume to be the best predictor of biomass for Leucadendron meridianum, L. coniferum, L. xanthoconus, L. laureolum and Protea susannae (r^2 = 0.82 - 0.93). Basal diameter was the best predictor for P. compacta (r^2 = 0.80). It was necessary to use above-ground biomass and not whole-plant biomass, as the proximity of the seedlings and the rockiness of the soil at some sites made excavation of individual root systems impossible. Using these regression equations, final above-ground biomass of each individual seedlings (g dry weight) was estimated. Highly skewed frequency distributions of the data, as well as unequal variances, made it necessary to use non-parametric statistics. These data were analysed using Kruskal-Wallis one-way analysis of variance by ranks, in the same way as the percentage survival data, for the effects of site (soil factors), density and monoculture/mixture competition.

6.4.3 Size-distance relationships

An additional test for the effects of intra- and interspecific competition was carried out for Leucadendron xanthoconus and L. laureolum. As mortality of both species was extremely low, it was possible to obtain sufficient replication to use size-distance regressions to test for competition effects at the level of the individual, instead of looking at average effects on a group. Much higher mortality of the other four species made this impossible. In July 1991, 30 monoculture and 30 mixture seedlings of each species were randomly selected at each site and the distance to the nearest neighbour measured. In the mixture treatments, the nearest neighbour was always the other species. No seedling was used as both target and neighbour. A small number of these pairs were lost as a result of the death of one of the individuals in the following year. Where possible, additional pairs were randomly selected to replace them. As basal diameters and cylindrical volumes had been determined for all individuals in July 1991 and July 1992, it was possible to determine individual increments of basal diameter and volume during the third year. The relationships between distance and final volume, final basal diameter, volume increment and basal diameter increment were determined using linear and exponential regressions (STATGRAPHICS v4.0, Statistical Graphics Corporation, 1987). Taking the slope of such a regression to be a measure of the intensity of competition (Silander and Pacala 1985), differences between slopes of the regression lines were tested using the procedure described in Zar (1984).

6.4.4 Water Stress

In February 1991, seedling water stress was investigated. Predawn water potential was selected as a good overall indicator of plant stress and access to soil water (Crombie et al. 1988) As this is a destructive method (killing small seedlings), it was only possible to take a small number of samples, in order to limit the extent of interference with the main experiment. An additional limitation was that of time available for predawn measurements on any one day. As it was, time constraints made it necessary to measure the four Leucadendron species on one day and the two Protea species on the next. This study addressed site and species differences only and so samples were only taken from low density rings of monoculture subplots, one per subplot. This provided five replicates per species per site. Data was analysed using two-way analysis of variance (STATGRAPHICS, v4.0) and the Tukey multiple comparison procedure (Zar 1984). To provide a measure of relative seedling size at the time of water potential measurement, heights of low density seedlings were measured.

6.5 RESULTS

6.5.1 Survival and Biomass

6.5.1.1 Leucadendron meridianum and Leucadendron coniferum (Transect A)

The pattern of L. meridianum survival across sites (Figure 6.3) strongly matches the present adult distribution. At the Limestone site, survival was 87% which was significantly higher than the Deep Sand (41%) and West Plain sites (28%) (Kruskal-Wallis one-way analysis of variance, $p<0.001$). With the exception of significantly lower survival in monoculture than in mixture at low density at the Limestone site (Kruskal-wallis, $p<0.05$), no significant effects of density or competition treatment on survival were detected.

Average biomass of Leucadendron meridianum corresponded with survival across sites, being six times higher at the Limestone site (14.9 g) than the lower two sites (2.5 and 2.3 g respectively) (Kruskal-Wallis, $p<0.001$, see Figure 6.3). Despite the overall size difference among sites, a significant reduction of biomass with increasing density was recorded in monoculture and mixture at both the Limestone site (reduced by 70% and 64% for monoculture and mixture respectively) (Kruskal-wallis, $p<0.05$) and the Deep Sand site (15% and 19%) (Kruskal-wallis, $p<0.01$) and in monoculture at the west plain site (16%, $p<0.05$). At medium

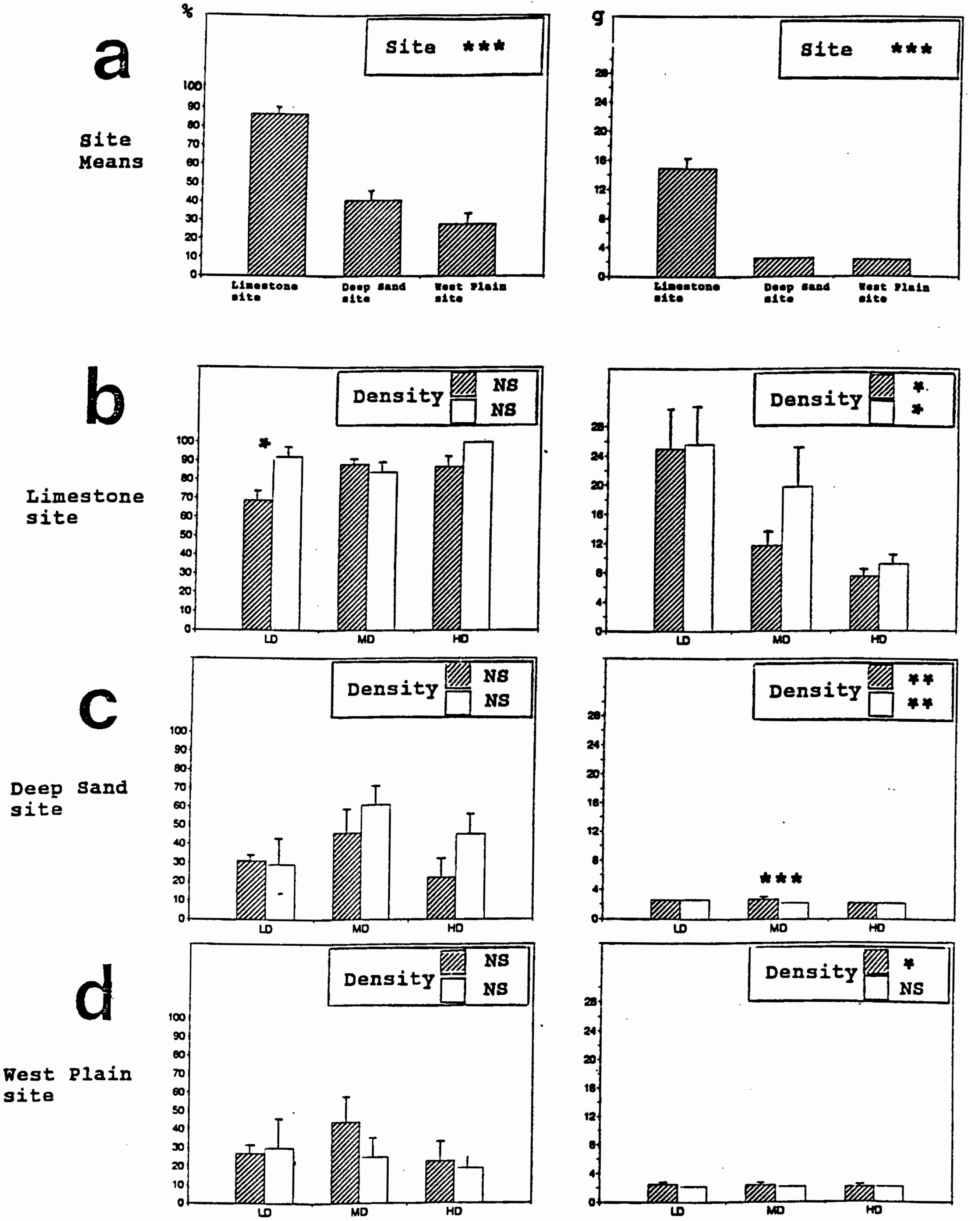


FIGURE 6.3. Results of the field experiment for Leucadendron meridianum. Mean percentage survival and mean individual above-ground biomass after three years are shown (a) across sites (inset: level of significance of site effect), (b) across densities for monoculture (▨) and mixture (□) at the Limestone site (inset significance of density effect in monoculture and mixture), (c) the Deep Sand site and (d) the west plain site. T-bars = one SE. * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

density in the deep sand site, biomass in mixture was significantly lower than in monoculture (Kruskal-Wallis, $p<0.001$).

Significantly higher survival Leucadendron coniferum occurred at the Deep Sand site than at the Limestone and West Plain sites (Kruskal-Wallis, $p<0.001$) (Figure 6.4). The Deep Sand site was the one site where adults were found. A high percentage of seedlings (82%) survived at this site, compared to 16% at the Limestone site and 24% at the West Plain site. No significant effects of density or monoculture/mixture treatment were found, other than the lower survival in mixture compared to monoculture at medium density at the West Plain site (Kruskal-Wallis, $p<0.05$).

Average biomass at the Deep Sand site was approximately double that at the other sites (6.4 g, compared to 2.9 g and 2.8 g at the Limestone and West Plain sites respectively) (Kruskal-Wallis, $p<0.001$). No density effects were detected at the Limestone and West Plain sites, but at the Deep Sand site, biomass was significantly lower at high density compared to low density in both monoculture (79% lower) (Kruskal-Wallis, $p<0.001$) and mixture (79% lower) (Kruskal-Wallis, $p<0.05$). The only significant effect of monoculture/mixture treatment was found at low density at the Limestone site, where biomass was significantly higher in mixture than in monoculture (Kruskal-Wallis, $p<0.05$).

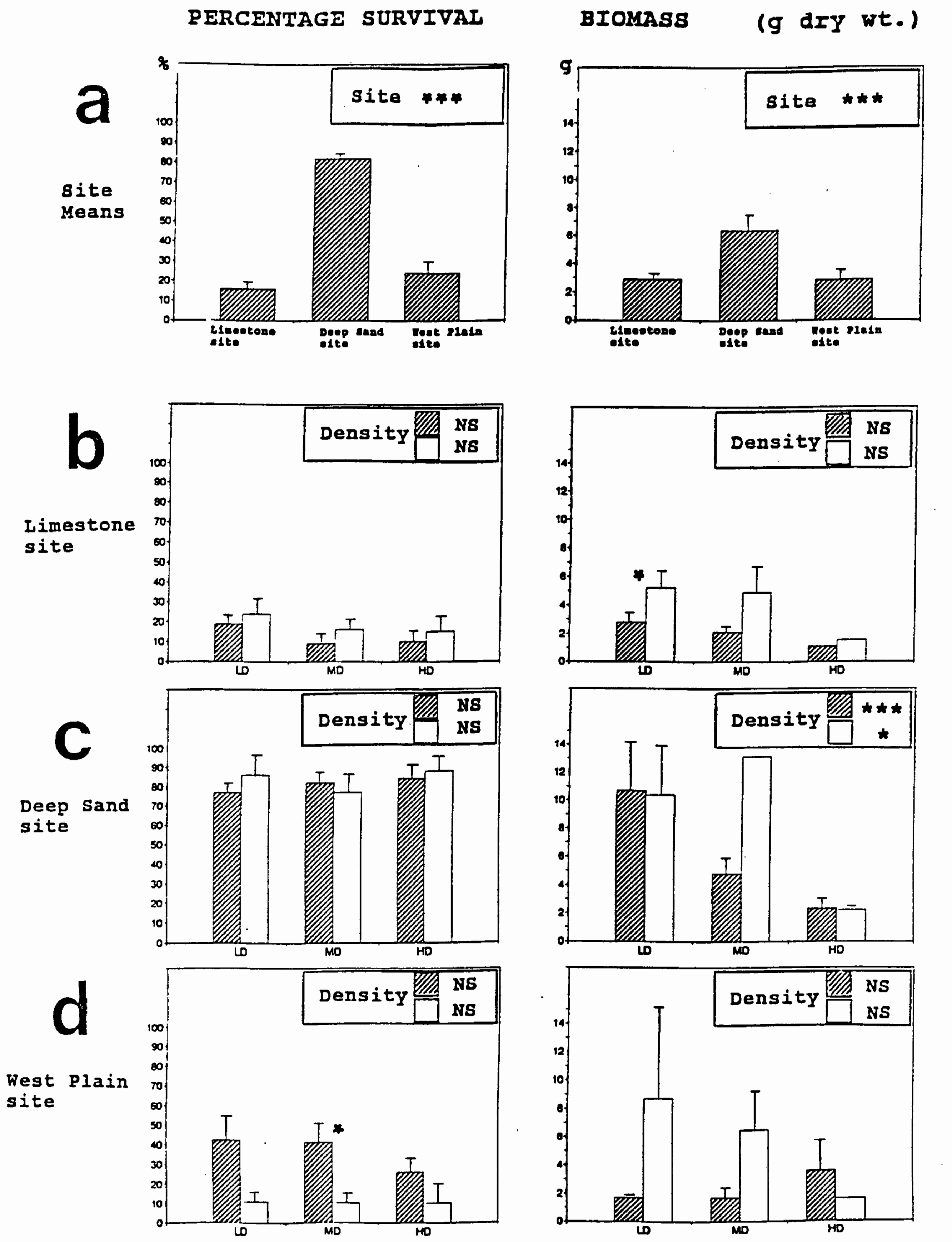


FIGURE 6.4. Results of the field experiment for Leucadendron coniferum. Mean percentage survival and mean individual above-ground biomass after three years are shown (a) across sites, (b-d) at each site. See caption of Figure 6.3 for full description. ▨ Monoculture ☐ Mixture.

6.5.1.2 <u>Leucadendron xanthoconus</u> and <u>Leucadendron laureolum</u> (Transect B)

Survival of <u>Leucadendron xanthoconus</u> was extremely high at all three sites (Figure 6.5), but showed a significant increasing trend (from 80% to 96%, p<0.001) from the Upper Sandstone site (<u>L</u>. <u>xanthoconus</u> only) to the Lower Sandstone and East Plain sites (where <u>L</u>. <u>laureolum</u>, but no <u>L</u>. <u>xanthoconus</u> occurred). At the Upper Sandstone site, survival was significantly lower in monoculture than in mixture at low density (Kruskal-Walls, p<0.01). No other significant effects of density or competition treatment on survival were detected.

Average biomass of <u>Leucadendron</u> <u>xanthoconus</u> differed significantly between sites (Kruskal-Wallis, p<0.001) and was low at the East Plain site (3.6 g) compared with the Upper (4.4 g) and Lower Sandstone sites (5.0 g). There were no significant differences between competition treatments at any density at any site. There was, however, a significant reduction of biomass with increasing density in both monoculture and mixture at all three sites (Kruskal-Wallis, p<0.001). This reduction from low to high density was 72% in both monoculture and mixture at the Upper Sandstone site, 78% (monoculture) and 75% (mixture) at the Lower Sandstone site and 67% (monoculture) and 58% (mixture) at the East Plain site.

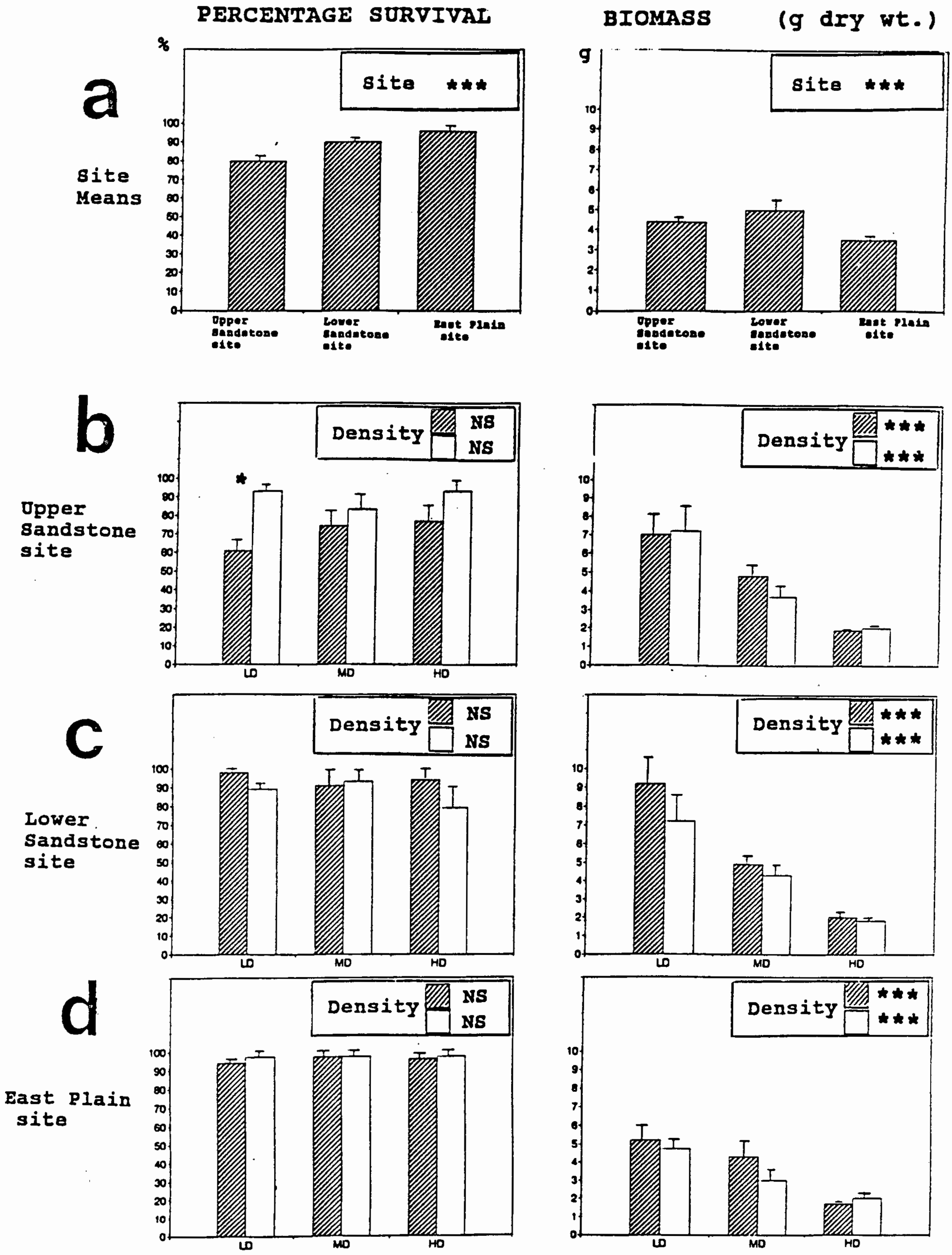


FIGURE 6.5. Results of the field experiment for Leucadendron xanthoconus. Mean percentage survival and mean individual above-grou8nd biomass after three years are shown (a) across sites, (b-d) at each site. See caption of Figure 6.3 for full description. ▨ Monoculture ☐ Mixture.

The pattern of survival of Leucadendron laureolum across sites (Figure 6.6) was very similar to that of L. xanthoconus, increasing from 83% at the Upper Sandstone site to 98% at the East Plain site (Kruskal-Wallis, $p<0.001$). No significant differences were found for survival with respect to density or competition treatments.

Average biomass of Leucadendron laureolum across sites resembled that of L. xanthoconus, but with larger site differences. It was significantly higher at the lower sandstone site (16.7 g compared to 9.2 and 9.0 g at the upper sandstone and east plain sites respectively) (Kruskal-Wallis, $p<0.001$). At the Upper Sandstone site there was a significant reduction in biomass with density in mixture (55%) (Kruskal-Wallis, $p<0.01$), but not in monoculture. Mixture biomass at this site was almost double that of monoculture at low density (Kruskal-wallis, $p<0.01$). At the Lower Sandstone site, strong density effects were detected (Kruskal-wallis, $p<0.001$): 89% reduction in monoculture and 69% in mixture from low to high density. At middle and high densities biomass in mixture was significantly higher than in monoculture (Kruskal-Wallis, $p<0.05$ and $p<0.01$ for middle and low densities respectively). At the East Plain site the density effect was very strong in monoculture (85% reduction) (Kruskal-Wallis, $p<0.01$), but was not significant in mixture. Mixture biomass was significantly lower than monoculture at low (Kruskal-wallis, $p<0.001$) and medium density (Kruskal-Wallis, $p<0.05$), but not at high density.

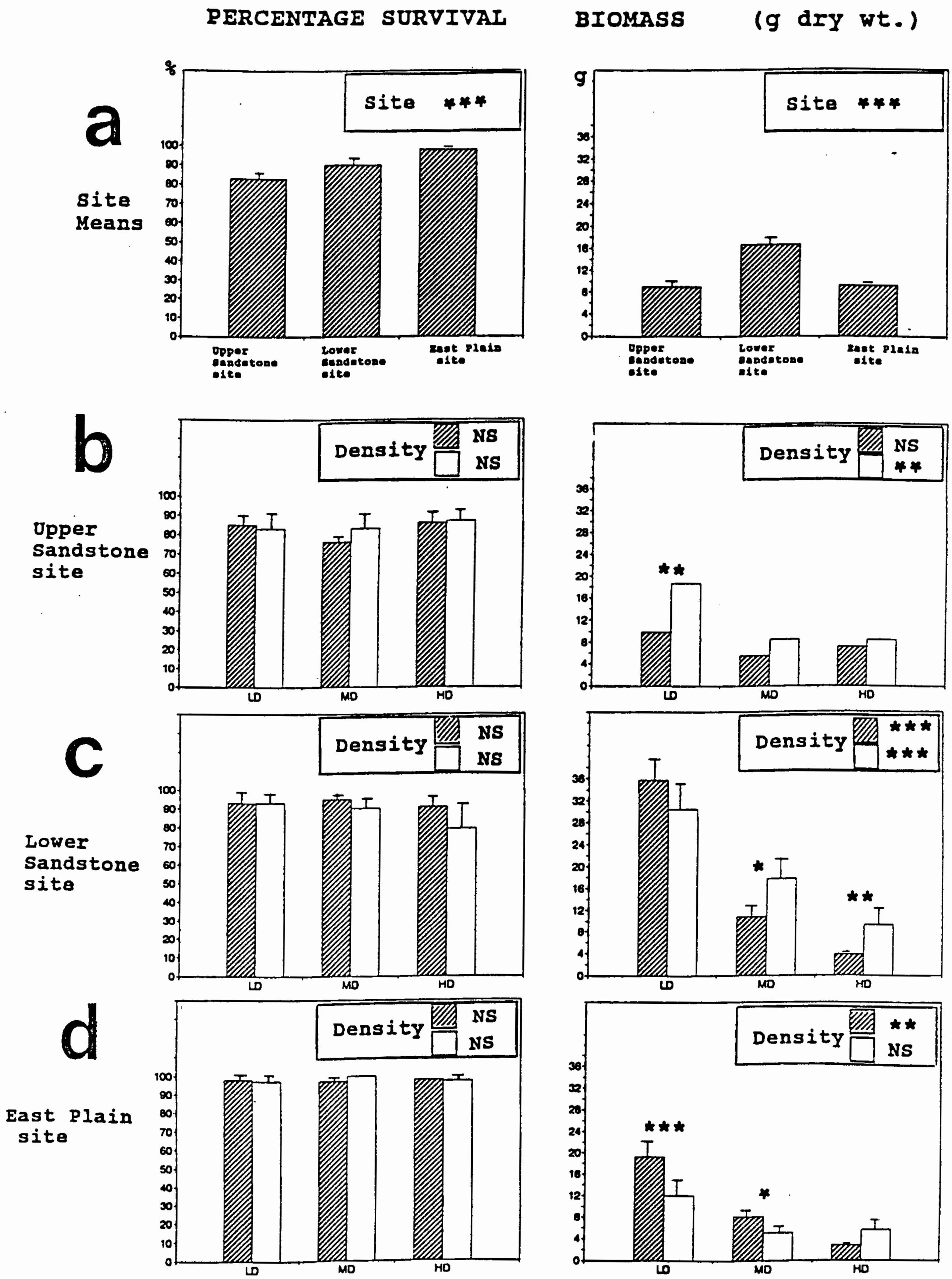


FIGURE 6.6. Results of the field experiment for Leucadendron laureolum. Mean percentage survival and mean individual above-ground biomass after three years are shown (a) across sites, (b-d) at each site. See caption of Figure 6.3 for full description. ▨ Monoculture ☐ Mixture.

6.5.1.3 Protea susannae and Protea compacta (Transect C)

Survival of Protea susannae was highest at the mixed protea site (57%), where adults co-occurred with P. compacta. (Figure 6.7). There was significantly lower survival at both the West Protea site (Kruskal-wallis, $p<0.05$) where P. susannae adults occurred in the absence of P. compacta (43% survival) and the East Protea site where P. susannae was absent (44% survival. At the West Protea site, survival in monoculture at high density (20%) was significantly lower than the other monoculture densities (Kruskal-wallis, $p<0.05$) and the mixture treatment at high density (Kruskal-Wallis, $p<0.05$). No other significant difference in survival between density or competition treatments was detected.

Average biomass of Protea susannae was three times higher at the Mixed Protea site than at either of the other sites (7.2 g compared to 2.5 g and 1.5 g at the West and East Protea sites respectively (Kruskal-wallis, $p<0.001$). While no significant effects of density or monoculture/mixture treatment were detected at the West Protea site, there was a stong reduction of biomass with increasing density in monoculture and mixture (Kruskal-Wallis, $p<0.001$ and $p<0.01$ respectively) at the Mixed Protea site. There was no significant difference observed between monoculture and mixture at any density at this site. In monoculture, average biomass decreased from low to high density by 60%, and in mixture, by 73%. At the East Protea site, biomass was generally very low, regardless of density or competition

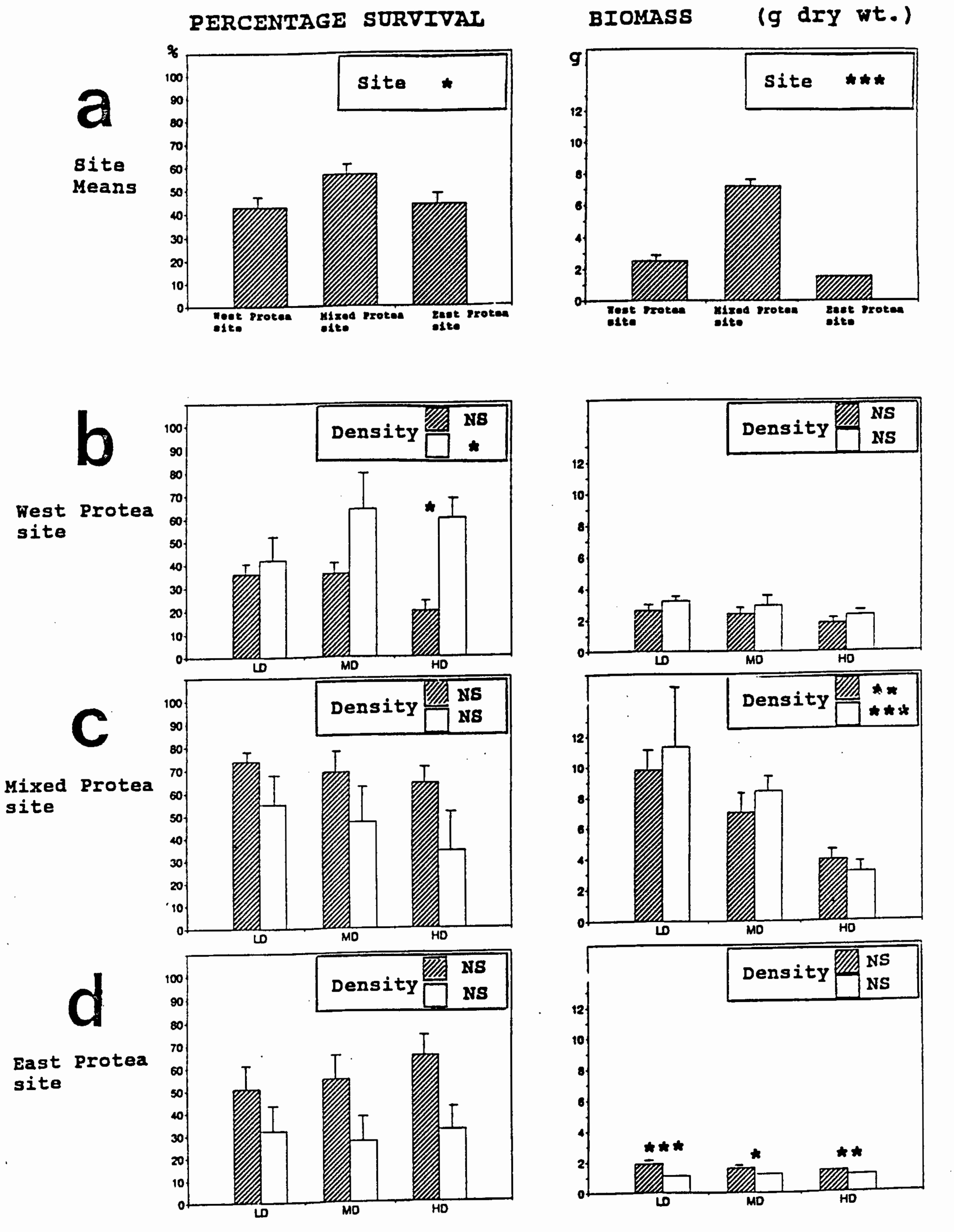


FIGURE 6.7. Results of the field experiment for Protea susannae. Mean percentage survival and mean individual above-ground biomass after three years are shown **(a)** across sites, **(b-d)** at each site. See caption of Figure 6.3 for full description. ▨ Monoculture ☐ Mixture

treatment and no significant effect of density was detected. Monoculture biomass was significantly lower than mixture biomass at all densities (Kruskal-wallis, $p< 0.05$).

Survival of Protea compacta. was extremely high (86%) at the East Protea site (where P. compacta adults occurred in the absence of P. susannae) and significantly lower (Kruskal-wallis, $p<0.001$) in the mixed (53%) and West Protea sites (44%, Figure 6.8). No significant differences in survival were detected between density and competition treatments at any site.

The pattern of average Protea compacta biomass across sites was very similar to that of P. susannae, with biomass at the Mixed Protea site significantly higher than at either of the other sites (12.6 g compared to 3.6 g and 5.6 g at the West and East Protea sites respectively) (Kruskal-Wallis, $p<0.001$). No significant effects of density or competition treatments were detected at the West Protea site but at the Mixed Protea site, there was a significant reduction of biomass from low to high density in monoculture (43%) (Kruskal-wallis, $p<0.01$). There was no significant reduction in mixture. Biomass at high density was significantly lower in monoculture than in mixture (Kruskal-wallis, $p<0.05$). At the East Protea site density effects were similar for monoculture and mixture (48% and 53% reduction respectively) (Kruskal-Wallis, $p<0.001$). At middle and high density, biomass was significanlty higher in mixture than in monoculture (Kruskal-wallis, $p<0.05$, 0.01).

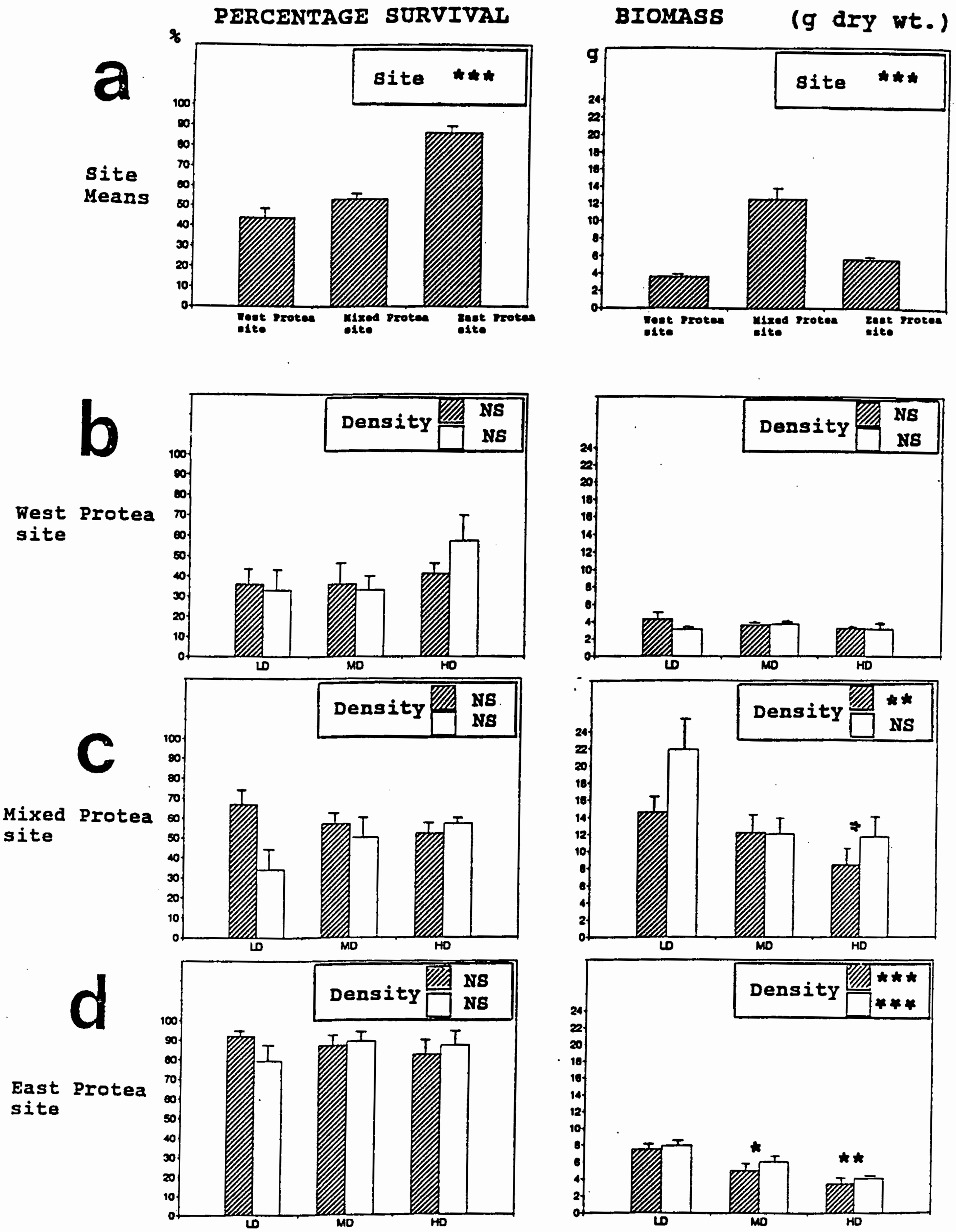


FIGURE 6.8. Results of the field experiment for <u>Protea compacta</u>. Mean percentage survival and mean individual above-ground biomass after three years are shown (a) across sites, (b-d) at each site. See caption of Figure 6.3 for full description. ▨ Monoculture ☐ Mixture.

6.5.2 Size-distance regressions

The regression slopes and coefficients of total basal diameter vs. distance for Leucadendron xanthoconus and L. laureolum are shown in Table 6.2. Final basal diameter (after three years) was selected as the best measure of size as it produced the highest r^2 values in 11 out of 12 cases (two species, two competition treatments, three sites). The exception was L. laureolum in monoculture at the Lower Sandstone site, where volume and volume increment produced higher r^2 values than basal diameter.

Leucadendron xanthoconus produced very strong regressions (high r^2 values) of basal diameter versus distance in monoculture (r^2 = 0.74) and mixture (r^2 = 0.59) at the Upper Sandstone site as well as at the Lower Sandstone site (r^2 = 0.59 and 0.54 for monoculture and mixture respectively). At the East Plain site, the monoculture regression was relatively weak (r^2 = 0.19) and no significant regression was found in mixture. This is in conflict with the biomass data where significant density effects were shown in both monoculture and mixture at all three sites. The only significant difference between regression slopes for L. xanthoconus was found at the Upper Sandstone site where the slope for mixture (0.049) was steeper than that for monoculture (0.033, $p<0.001$).

At the Upper Sandstone site, Leucadendron laureolum showed a stronger regression in mixture (r^2 = 0.30) than in

TABLE 6.2 Coefficients and slopes of nearest neighbour regressions (basal diameter after three years vs. distance) for Leucadendron xanthoconus and Leucadendron laureolum in monoculture at three sites.

	Monoculture			Mixture			Between[1] slopes
	n	r^2	slope	n	r^2	slope	
Upper Sandstone site							
L. xanthoconus	25	0.74	0.033	29	0.59	0.049	p<0.05
L. laureolum	33	0.16	0.024	25	0.30	0.039	N.S
Lower Sandstone site							
L. xanthoconus	30	0.59	0.043	19	0.54	0.041	N.S
L. laureolum	30	0.34	0.047	25	0.33	0.029	N.S
East Plain site							
L. xanthoconus	30	0.19	0.023	29	0.01	0.004	no test[2]
L. laureolum	29	0.30	0.033	30	0.29	0.023	N.S

[1] procedure from Zar 1984. There were no significant differences between sites.

[2] No test was made between monoculture and mixture slopes for L. xanthoconus at the east plain site, as no significant regression was obtained in mixture.

monoculture (r^2 = 0.16), and both were significant ($p<0.05$). The stronger regression for monoculture corresponds with average biomass data, where a siginificant density effect was detected in mixture but not in monoculture. At the Lower Sandstone site, regression coefficients were fairly high in monoculture and mixture (r^2 = 0.34 and 0.33 respectively). However, at the East Plain site, monoculture and mixture regressions were also similar (r^2 = 0.30 and 0.29 respctively), unlike the result for average biomass where only the monoculture treatment showed a significant density effect. No significant differences in regression slope between sites or between monoculture and mixture were detected for _L. laureolum_.

6.5.3 Predawn water potentials.

6.5.3.1 _Leucadendron meridianum_ and _Leucedendron xanthonus_ (Transect A)

Leucadendron meridianum showed significantly lower water potential at the Limestone site (-0.94 MPa $F_{(2,23)}$ = 33.1, $p<0.001$), compared to the Deep Sand site (-0.39 MPa) and the West Plain site (-0.46 MPa) (see Table 6.3). For _L. coniferum_ there was no significant difference between water potential at the Limestone and Deep Sand sites (-0.87 and -0.65 MPa respectively) but this was significantly higher at the West Plain site (-0.33 MPa). While no differences between species were detected at the Limestone and West Plain sites, water potential of _L. coniferum_ was

TABLE 6.3. Predawn water potentials and average height (mean ± one SE) of three pairs of Proteaceae species in monoculture at low density at three sites per species pair, 19 months after emergence.

Site	Predawn water potential (Mpa)		Average Height (mm)	
TRANSECT A.				
	Leucadendron meridianum	*Leucadendron coniferum*	*Leucadendron meridianum*	*Leucadendron coniferum*
Limestone	-0.94 ± 0.07^{a}	-0.87 ± 0.06^{a}	205±17	130±9
Deep sand	-0.39 ± 0.06^{b}	-0.65 ± 0.14^{ab}	65±5	115±7
West plain	-0.46 ± 0.01^{b}	-0.33 ± 0.03^{b}	42±3	59±3

Predawn water potential:
species effect: N.S., site effect: $p < 0.001$
site x species interaction: $p < 0.05$

Site	Predawn water potential (Mpa)		Average Height (mm)	
TRANSECT B.				
	Leucadendron xanthoconus	*Leucadendron laureolum*	*Leucadendron xanthoconus*	*Leucadendron laureolum*
Upper sandstone	-0.34±0.02	-0.47±0.05	149±6	166±4
Lower sandstone	-0.57±0.03	-0.62±0.04	142±6	211±8
East plain	-0.45±0.07	-0.43±0.03	110±5	171±6

Predawn water potential:
species effect: N.S., site effect: $p < 0.001$
site x species interaction: N.S.

Site	Predawn water potential (Mpa)		Average Height (mm)	
TRANSECT C.				
	Protea susannae	*Protea compacta*	*Protea susannae*	*Protea compacta*
West protea	-0.65±0.02	-0.54±0.05	87±5	35±7
Mixed protea	-1.61±0.28	-1.81±0.21	184±8	216±9
East protea	-0.73±0.06	-1.14±0.02	84±5	193±4

Predawn water potential:
species effect: N.S., site effect: $p < 0.001$
site x species interaction: N.S.

significantly lower than that of *L. meridianum* at the Deep Sand site ($F^{(2,23)} = 4.18$, $p<0.05$). Both species were tallest at the limestone site (205 mm and 130 mm for *L. meridianum* and *L. coniferum* respectively), followed by the deep sand site (65 mm and 115 mm) and the west plain site (42 mm and 59 mm).

6.5.3.2 *Leucadendron xanthoconus* and *Leucadendron laureolum* (Transect B)

Water potentials of *Leucadendron xanthoconus* and *L. laureolum* did not differ significantly from each other at any site (Table 6.3). However, both had significantly lower water potentials at the Lower Sandstone site (-0.57 and -0.62 MPa respectively) compared to the Upper Sandstone site (-0.34 and -0.47 MPa) and the East Plain site (-0.45 and -0.43 MPa) ($F_{(2,23)} = 10.3$, $p<0.001$). *L. xanthoconus* was of similar height at the Upper and Lower sandstone sites (149 mm and 142 mm respectively) and much shorter at the East Plain site (110 mm), while *L. laureolum* was tallest at the Lower Sandstone site (211 mm), compared to the the Upper Sandstone site (166 mm) and the East Plain site (171 mm).

6.5.3.3 *Protea susannae* and *Protea compacta* (Transect C)

Both *Protea susannae* and *P compacta* showed significantly lower water potential (Table 6.3) at the Mixed Protea site (-1.61 and -1.81 MPa respectively), than at the West Protea site (-0.65 and -0.54 MPa) and the East Protea site (-0.73

and -1.14 MPa) ($F_{(2,24)}$ = 24.4, $p<0.001$). No significant difference in water potential between species was found at any site. Both species were tallest at the Mixed Protea site (184 mm and 216 mm for _P. susannae_ and _P. compacta_ respectively) compared to the West Protea site (87mm and 95 mm) and the East Protea site (84 mm and 193 mm).

6.6 DISCUSSION

Growth and survival of seedlings of four of the six species (Leucadendron meridianum, L. coniferum, Protea susannae and P. compacta) showed marked differences between sites. Smaller site differences were found for L. xanthoconus and L. laureolum. Without considering any biotic factors, much of the present distribution of adults of these species can thus be explained on the basis of soil factors acting at the seedling stage. The lack of conclusive evidence (i.e. some seedlings survived at all sites) and the fact that much of the evidence of site effects comes from average biomass data (as opposed to survival data) suggests that the site factors were relatively slow-acting.

In contrast, interspecific competition was not shown to influence the distribution of any of the six species, other than as a small additional effects of reducing biomass in sites where it was already very low. It cannot, however, be dismissed entirely as one of the factors structuring these communities. Strong density effects were recorded for all species (at least at some sites). Stand density has an influence on reproductive output and consequently on recruitment after the next fire Bond et al. 1984, le Maitre 1988). The fact that average biomass produced such clear density effects (outweighing the overall site effect for some species) and gave such strong nearest neighbour regressions, is evidence that the range of densities used (which are similar to those observed in natural post-fire environments) was appropriate for testing competitive effects. Thus, as has been shown in other studies in fynbos (Beukman 1988, Midgley and Watson 1992, Witkowski, unpublished data), competition strongly influences the spacing of individuals within communities, but for these species it does not restrict their distribution across the landscape.

6.6.1 *Leucadendron meridianum* and *Leucadendron coniferum* (Transect A)

Mustart and Cowling (1993) investigated the soil factors controlling the distribution of these species as part of a study of calcicole and calcifuge Proteaceae species. The site was similar to the one in the present study, about 40km to the west. They grew seedlings in plots on limestone and the adjacent deep sands, but as they were only considering site effects, all plots were monocultures and density was not varied. They found that *Leucadendron meridianum* was clearly restricted by soil factors, with no seedlings surviving off limestone after the 20 months of the experiment and 57% survival on limestone. *L. coniferum* showed only 17% survival in its typical soil deep sand and 53% survival on limestone (where adults were absent). Although no test of interspecific competition was made, they invoked this as the probable cause of *L. coniferum*'s eventual exclusion from limestone.

In the present study, which is of a substantially longer duration (36 months cf. 20 months), somewhat conflicting results were found. Survival patterns (regardless of competition treatment) corresponded strongly with adult distributions. For Leucadendron meridianum the trend across sites was similar to that in Mustart and Cowling's (1993) study, although percentage survival was much higher (87% on limestone and 41% on deep sand). The result of this experiment for L. coniferum was in sharp contrast to the earlier work, with very high survival on its typical soil, deep sand (82% compared with 17% in Mustart and Cowling 1993), and very low survival on limestone (16% compared with 53%). There is some evidence that the lower limestone survival of L. coniferum is the result of the longer duration of this experiment, as survival after the corresponding 20 months was 69% (cf. 53% in Mustart and Cowling 1993). The cause of the extensive mortality in the third year is uncertain. Although water potentials were lowest at the Limestone site, seedlings of both species were also largest at that site. This would suggest that the low water potential was more likely a consequence of plant size rather than lower soil moisture availability (see Chapter 5). This suggests that soil moisture stress would be unlikely to cause mortality.

The role of herbivory by beetles (Chirodica sp, fam. Chrysomelidae, subfam. Alticinae) is likely to have played a role as of the 53% of all L. coniferum seedlings which died during the last 14 months, approximately one in three experienced very heavy herbivory and all experienced some damage. It is not, however, clear whether similar levels of herbivory would be experienced and have such an effect in normal post-fire seedling establishment and survival.

Survival of both species at the West Plain site was very low. This is not surprising, since the soil on the plain was very acid and nutrient poor, and usually lacks a proteaceous overstorey (Chapter 2). Average biomass was extremely low at this site. Seedlings of both species were so small at this site that if they established naturally on the plain after a fire, it would be unlikely that they would survive competition from the rapidly regenerating ericoid and restioud shrubs (Kruger 1983).

No evidence comes from this study to support Mustart and Cowling's (1993) suggestion of an important role for competition in determining the distribution of Leucadendron coniferum. No significant effects of density or competition treatment on survival were found at the Limestone site. However, average biomass showed strong density effects for both species at the sites where they are largest (L. meridianum at the limestone site and L. coniferum at the Deep Sand site). Significantly lower biomass of L. meridianum in mixture at medium density at the deep sand site suggests that interspecific competition could be more intense than intraspecific competition, but biomass of this species at this site, is already greatly reduced by site factors, making any effect of competition relatively unimportant. The only difference between monoculture and mixture treatment recorded for L. coniferum was lower biomass in monoculture at low density (the outside ring) at the top site. As L. coniferum appeared to be preferred over L. meridianum by herbivores (Chirodica sp.), mixed stands may provide a refuge from herbivory for L. coniferum.

6.6.2 Leucadendron xanthoconus and Leucadendron laureolum (Transect B)

In the light of the distinct transition from Leucadendron xanthoconus on the upper sandstone slopes to L. laureolum on the lower slopes, it is surprising that neither survival or average biomass of the seedlings reflected this pattern. The patterns of survival and biomass across sites was very similar for these two species. Survival of L. laureolum at the upper sandstone site, where adults do not occur, was significantly lower than at the other sites, but was still very high (83%). Despite its complete absence (as adults) from the east plain site, L. xanthoconus seedlings showed 96% survival there after 3 yrs. Both species showed largest average biomass at the lower sandstone site, but L. laureolum seedlings were significantly larger than L. xanthoconus at all sites.

There are a number of factors which could act to produce these site effects. The upper sandstone slopes have higher total nutrient levels than the lower slopes and the plain (Chapter 2). However, survival of both species was lowest at the Upper Sandstone site and biomass was highest at the Lower Sandstone site. A possible limitation on growth at the Upper Sandstone site is the low soil volume (shallow, very rocky soil) which has consequent limitations on moisture and nutrient availability (McConnaughay and Bazzaz 1991). This factor would increase in importance with plant age and size. In addition to the low nutrient levels on the plain, the much greater depth of plain soil, could make it difficult for seedlings to obtain sufficient moisture during summer drought (Enright and Lamont 1992 and see Chapter 5). However, both species showed lowest summer predawn water potentials at the lower sandstone site, where seedlings were largest. This suggests that the lower water potential was a consequence of greater water expenditure, as with the Leucadendron meridianum and L. coniferum seedlings, but this was not sufficient to limit growth.

The similar site effects on survival and biomass for both species suggests that they responded similarly to the same environmental factors. The case in this study where two species have completely overlapping potential distributions, but no (or limited) overlap in actual distributions, suggests that competitive displacement has occurred (Snow and Vince 1984, Gurevitch 1986, Bertnesss, 1991a,b, Lamont et al 1991). However no effects of competition on survival were detected. With the exception of lower survival in monoculture of Leucadendron xanthoconus at low density at the Upper Sandstone site, no significant differences in survival between monoculture and mixture were found. If one species had been competitively excluded by the other from part of its potential range, interspecific competition would be expected to be more intense than intraspecific competition at that site (Connel 1983).

Although competition had no detectable effect on survival in the three years of this study, its long term influence cannot be discounted. Density had a very strong effect on biomass in monoculture and mixture for both species at all three sites (except for Leucadendron laureolum in monoculture at the upper sandstone site and mixture at the east plain site). Post-fire recruitment of L. laureolum has been shown to be reduced when taking place from dense pre-fire parent stands (le Maitre 1988). This corresponds with the work of Bond et al. (1986) who showed that individuals of various Proteaceae species are smaller and have reduced reproductive output when growing in dense stands. For L. laureolum, biomass was significantly higher in mixture than in monoculture at low density at the top site and medium and high density at the middle site. This suggests that intraspecific competition is more intense than interspecific competition for this species and follows from the larger above-ground size of L. laureolum (average biomass two to three times greater than L. xanthoconus). At the East Plain site, however, L. laureolum showed significantly reduced biomass in mixture at low and middle density. As the above ground size of L. laureolum at this site is approximately 3 times that of L. xanthoconus, the possibility of root competition with L. xanthoconus could be suggested. This experiment does not, however, address the mechanisms of the competitive effects. It is interesting to note that the average biomass of L. xanthoconus is not influenced by competition type (monoculture or mixture) at any site, despite strong density effects in both treatments at all sites. Equivalent intra-and interspecific competitive effects at all three sites suggests that these species are similar enough to coexist (Agren and Fagerstrom 1984, Keddy 1989, Keddy and Shipley 1989) and that competition does not influence distribution (certainly of L. xanthoconus) across the sites.

Another test of the intensity of competition is provided by the slopes of size-distance regression lines (Pielou 1961, Wiener 1984). The only site where this method indicated interspecific competition to be more intense (i.e. producing a significantly steeper regression slope) than intraspecific competition, was for Leucadendron xanthoconus at the upper sandstone site, where it is the dominant species. This result is in conflict with the average biomass result for this species, where there were no significant differences between monoculture and mixture at any density. This suggests that an individual-based approach such as the use of size-distance regressions may be more sensitive in detecting density effects than techniques measuring average effects on groups of individuals (Silander and Pacala 1985).

As neither interspecific competition nor site factors were found to play a major role in controlling the distribution of these species in the three years of this experiment, more long-term effects should be considered. While Leucadendron laureolum is found on a relatively wide range of soil types, L. xanthoconus is a more specialist species associated with on rocky sandstone soils on foothills and lower mountain slopes (Williams 1972). In the absence of L. laureolum, L. xanthoconus does occur on lower slopes on the north-facing side of the Soetanysberg (pers. obs.). The absence of the larger L. laureolum from upper slopes at this site could be related to intolerance of the low soil volume (McConnaughay and Bazzaz 1991). Such a factor would increase in influence with plant age and size and thus may not yet be detectable in an experiment of three years duration. L. xanthoconus exclusion from lower slopes and the plain on the southern side of the Soetanysberg is unexplained by this work.

6.6.3 Protea susannae and Protea compacta (Transect C)

For Protea susannae, the decrease in survival and biomass from the Mixed Protea site to the East Protea site was in accordance with adult distributions, as adults were not found at the East Protea site. The difference in biomass was much more pronounced than that of survival, suggesting that the exclusion of P. susannae from the shallow soils is a gradual process, more prolonged than would be covered by this three-year experiment. A possible cause of the site effect is that of differences in available nutrients. A year-long field study of resin-extractable ammonium, nitrate and phosphorus (Chapter 3) showed that the deep soil, close to limestone where P. susannae is found, contained higher levels of available phosphorus, than the shallow soils where P. compacta occurs.

A number of field studies of species distributions along natural resource gradients have found that the species occupying the more favourable sites are usually the stronger competitors, with the weaker competitors surviving in less favourable sites where the others are abiotically excluded (Snow and Vince 1984, Goldberg 1985, Gurevitch 1986, Keddy 1989a, Lamont et al. 1989). However, instead of escaping competition in an abiotically less favourable site (eg. Gurevitch 1986), Protea susannae experiences a reduction of growth as a result of interspecific competition at the site which is least favourable and not at the more favourable site. The stronger competitor in this case, P. compacta also showed a large reduction in biomass (50%) from the Mixed to the East Protea site, presumably in accordance with the difference in nutrient availability between these sites. In the light of work showing competition to be most intense where productivity or biomass are highest (del Moral 1982, Wilson and Keddy 1986, Bertness 1991a,b), it is surprising that a distinct effect of interspecific competition was detected in the East Protea site and not at the other sites. This contradicts the idea that competition is constrained in low resource habitats (Grime 1979, Reader 1990). However, the effect of competition in reducing P. susannae biomass in mixture relative to monoculture is extremely small in comparison to the site effect, making the additional effect of interspecific competition of minor ecological importance (Weldon and Slauson 1986).

The reciprocal exclusion of Protea compacta adults from the west site is more difficult to explain. A laboratory study of growth and seedling water relations of P. susannae and P. compacta (Chapter 5) showed that P. compacta has faster root and shoot growth, but because of its larger size dries out the soil profile more rapidly and is vulnerable to severe water stress if it does not have a continuous water supply. The significantly lower survival of P. compacta at the mixed and east sites, which have much deeper soils, could be the result of difficulty of maintaining water supply during the first few summers (Saruwatari and Davis 1989, Lamont and Witkowski 1993). Water potentials measured during the second summer were significantly lower at the Mixed Protea site where seedlings were largest (see Chapter 5). However, this did not have any long-term deleterious effect, as it was not followed by any sudden increase in mortality and 18 months later, average individual biomass at the Mixed Protea site was double that at both the other sites.

At the West Protea site, survival and biomass of both species were relatively low, despite this being the site where Protea susannae adults are dominant. There is some evidence that this site effect is possibly the result of heavy herbivory (a biotic factor not included in this experimental design) which was particularly high at this site. Herbivore damage took the form of cutting of the stem, usually just below the apical bud. The nature of this damage together with the fact that it began immediately after the exclosures (mesh size 12 mm) were removed, suggests rodent herbivory. While herbivory of P. compacta seedlings began immediately and included most seedlings at this site, extensive herbivory of P. susannae was only observed at the end of the next summer, about nine months later. This suggests that there was an apparent herbivore preference for P. compacta seedlings. Leaves of P. susannae are known to give off a strong sulphurous odour when broken (Rourke 1980) which may reduce herbivory. Although planting seedlings in clearings may result in enhanced levels of herbivory (recruitment normally takes place in a post-fire environment, Kruger 1983) the species preference and higher herbivory at the West Protea site suggests that this may play a role in excluding P. compacta from this site. Rodent herbivory has been shown to play a key role in maintaining certain vegetation boundaries (Davis and Mooney 1985). Although the boundary between these two species is very distinct at this site, the exclusion of P. compacta from the deep sands where P. susannae occurs is not absolute as scattered P. compacta individuals at low densities have been observed in P. susannae stands at a number of other sites around the study area (see Chapter 4).

6.7 GENERAL CONCLUSIONS

The overall minor importance of competition in relation to soil factors appears to support the work of Grime (1977, 1979) that in low-resource habitats, abiotic factors outweigh competitive effects. However strong trends of decreasing size with increasing density (or decreasing nearest-neighbour distance) were shown in a wide range of fynbos soils, from limestone to extremely nutrient-poor acid sand on the plain. These soils also differ in physical factors relating to soil moisture availability (Chapters 2 and 4). While three of the species showed density effects only at the site where average biomass was highest, the other three showed density effects at two or three sites. This is in agreement with the argument of Tilman (1988, also Wilson and Tilman 1991) that competition need not be restricted to the high end of a productivity gradient. The extent of the density effects also indicates that growth rates are fast enough to allow competition to influence community structure, despite a regular disturbance regime (4-40 yr fire intervals, le Maitre and Midgeley 1992). Yet, in spite of this interspecific competition had almost no impact on the distribution of these six species. For some species, however, much of the adult distribution remained unexplained by seedling patterns after three years. Nevertheless, soil factors emerged as critical determinants of seedling growth and survival.

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CHAPTER 7

GENERAL DISCUSSION

In this chapter the contribution of this thesis to the understanding of the control of species distributions and community boundaries in fynbos and other Mediterranean-climate shrublands is assessed. Attention is focused on the three main aspects of this subject as set out in Chapter 1.

7.1 Soil Factors

The use of direct gradient analysis confirmed the relationship between fynbos species and communities and soil factors suggested by many phytosociological studies (reviewed in Cowling and Holmes 1992). These techniques allowed the most important factors (pH and soil depth) to be distinguished and showed that their relative importance varied among substrata (sandstone, limestone and colluvial sand). A further advantage was the quantitative assessment of vegetation-environment relationships that was provided. Despite a significant vegetation-environment correlation and the strong association of communities with soil factors, much unexplained variance remained in the species data. This could be attributed to temporal variations in nutrient dynamics (not included in the vegetation-environment correlation), fire effects on recruitment patterns (van Wilgen et al. 1992) or biotic factors such as competition (Keddy 1989) and herbivory (Hogenbirk and Reader 1989).

The set of environment factors considered in this study was comprehensive and despite the size of the study area, soils were fairly representative of fynbos soil types with regard to pH and nutrient status. The range of altitude was, however, small and no north-aspect sites were included. Altitude and slope are known to be extremely important environmental factors influencing the distribution of fynbos communities in mountainous regions (see McDonald 1993 a,b), particularly in the more arid regions of the Fynbos Biome.

The boundaries between communities identified in the landscape studied all corresponded to changes in soil factors, although some boundaries were more distinct than others. Of particular interest is the mosaic of nitrogen and phosphorus availability across the landscape with which the communities appeared strongly associated. This association suggests that species differences in nutrient-use, as shown by Pate et al. (1993) for an Australian mediterranean-climate woodland, may be an important, and yet little considered, cause of habitat specialization or niche differentiation. Soil nutrients and plant nutrient-use strategies should thus be considered along with the more widely studied differences in plant water relations in mediterranean-climate ecosystems.

7.2 Water Relations

The two Protea species studied showed differences in root morphology, water relations and phenology (to a lesser extent) corresponding with the soils of different depth with which each was associated. Such habitat partitioning of species on the basis of water relations differences has been shown in alpine plants (Oberbauer and Billings 1981, Dawson 1990) and in dune grasslands (Barnes 1985) and scrub vegetation on subtropical islands (Mishio 1992). However, the small number of individuals in the atypical soil did not show any alterations in their water-use or exhibit signs of water stress. This suggests that if the adult distribution pattern was related to differences in water relations then the exclusion of species from certain soils (as a result of water stress) must take place at an earlier stage (i.e. in seedling or juvenile plants). Lamont *et al*. (1989) found that seedling differences in water relations were important in determining the distributions of a number of Australian *Banksia* species (Proteaceae) which, as adults, showed no such differences (Lamont and Bergl 1991). Davis (1991) suggested that such species differences, at the recruitment stage may be critical in determining community composition in mediterranean-climate regions in general.

The laboratory study of seedling growth and water relations showed a surprising reversal of the "spending" and conservative water-use strategies of *Protea susannae* and *Protea compacta* adults, respectively. The switch for *P. susannae* from relatively conservative water-use at the seedling stage to a water-spending strategy in the adult stage is in direct contrast to that proposed for large proteoid shrubs in fynbos (Davis and Midgley 1990, Smith and Richardson 1990). This implies that assumptions and generalizations about seedling water-use strategies based on adult patterns or those of congeneric species may be incorrect. Seedling growth and water-use strategies were also contrary to those expected for their typical soil types (Davis and Midgley 1990, Rhizopoulou and Davies 1991). The differences between species did, however, provide a partial explanation of distribution pattern. These results point to the importance of studying recruitment stages in addition to adult plants (Davis 1991).

Although this study was fairly detailed, it was, however, limited to one site (except for soil depth study). There is thus a need to expand this work to other areas and species. Further work (possibly long-term studies) of plants from seedlings to adults stages in atypical soils, may help to explain how the species distribution patterns develop. Such field studies of establishing seedlings and juvenile plants could show whether switches in water-use strategies are present in other Proteaceae species as well as at determining the point at which the physiological properties of plants switch.

7.3 Competition vs soil factors

Soil factors were found to be the overriding determinants of growth and survival of these six key species and thus of their distribution across community boundaries (Chapter 6). Interspecific competition was of only minor importance in this regard. A substantial reduction in above-ground growth with density was measured at sites where plants were largest. Despite this, interspecific competition almost never resulted in greater density effect than intraspecific competition (monocultures). Thus while competition (inter- and intraspecific) could be important in determining spacing within communities (Midgley and Watson 1992), no evidence was found for competitive exclusion of one species by another at any of the site. The fact that the trends were observed in terms of growth and not survival implies that effects producing the distribution patterns are slow-acting.

The mediterranean-climate region of South Africa, with summer drought and relatively low soil nutrients, could be regarded as a resource-constrained environment. The minor importance of competition in determining species distributions across vegetation boundaries suggests, in low-resource habitats, stress tolerance is more important than competition (Grime 1977, 1979) . However, the reason for the low importance of competition is not the slow growth rate associated with stress-tolerant species (Grime 1979). The a strong reduction of growth with increasing density at certain sites showed that plants grow fast enough to compete. Rather it was the similarity of intra and interspecific competition intensity which limited the effect of interspecific competition on species distributions. It should be noted that interspecific competition with species other than those considered in this study (eg. Restionaceae on the plain) could influence species distributions.

This experiment avoided several of the weaknesses limiting the general applicability of many competition experiments

(Keddy 1989): it was carried out over a moderate time scale (three years), more than two species were compared (six in total) and it included a number of very different soil gradients. In addition monoculture and mixture comparisons were made within each of three levels of total density allowing the effects of interspecific competition to be distinguished from density effects (Rejmanek et al. 1989). This was a problem with the study of Lamont, et al. (1989) where initial mixture densities were much higher than monoculture densities. Consequently, in this study the effect of interspecific competition could not be distinguished from the effect of higher mixture density.

Field manipulative experiments, however, are always subject to logistical limitations, especially if the ranges of factors (such as species, site, density and species ratio) are to be maximized. In this case, in order to avoid being limited to a single case study (i.e. two species) across a single vegetation boundary and soil gradient, a compromise was made in terms of the replication of sites (soil types). Instead of having a number of replicate sites in each soil type, a single site was used per soil type (three soil types for each of the three case studies) and the randomly located subplots were treated as replicates in testing the importance of soil factors (site differences). The emphasis of this study was on distribution across soil gradients and community boundaries. In an intensive study of competitive interactions of species within a single soil type it would be feasible to carry out an experiment with a complex, fully replicated design (eg. Riegel et al. 1992, Shainsky and Radosevich 1992).

While this experiment pointed to soil factors as the overriding influence on species distributions it also provided an indication that seedling herbivory may be an important biotic factor in this regard. Very little is known about the ecological importance of herbivory in fynbos (Johnson 1992), but evidence of species and site specific herbivory in this study suggests that this subject should be investigated. Vertebrate and invertebrate herbivory have been shown to influence species distributions (Hogenbirk and Reader 1989) and to be crucial in maintaining vegetation boundaries (Davis and Mooney 1985).

This thesis has provided an integrated approach to the understanding of the controls of fynbos species distributions. Both abiotic and biotic factors were considered. Techniques ranged from broad correlative studies to detailed experiments. In addition both adult plants and their recruitment stages were examined. This approach has gone a long way in explaining control of distributions and community boundaries, not only for the six main species, but for fynbos in general. Such understanding of the controls of vegetation pattern is becoming increasingly important to ecologists with the prospect of climate change and the need to predict its impact on ecosystems.

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