

**THE ROLE OF NURSE PLANTS IN THE VEGETATION
DYNAMICS OF THE SUCCULENT KAROO**

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For my Parents - Jackie and Edie

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ABSTRACT

Little is known about the vegetation dynamics of the Karoo region of South Africa. The aim of this study was to focus on the role of the "availability of suitable space" in the regeneration of Succulent Karoo vegetation.

By undertaking a series of manipulative experimental transplants and pattern analyses, it was shown not only that shrubs in the Karoo facilitate other species by provision of 'suitable space' beneath their canopies, but also that certain shrub species are more effective "nurses" than others. The plants dependent on nurse plants are referred to as "patient" plants. Not only did the main patient species Tylecodon wallichii require nurse plants generally for successful establishment, but this species was also most successful (in terms of reaching maturity) beneath a specific nurse Pteronia pallens. Thus the patient was "nurse specific". In time however, the initial commensal relationship between the nurse and the patient (whereby the patient benefits and the nurse is unaffected) changes to a competitive one, since nurse vigour declines as the patient grows larger. Despite this area being arid, a manipulative experimental investigation revealed that competition between the nurse and the patient was not for water. An examination of the rooting patterns of the two species showed that their root systems were separated in vertical and horizontal space.

Though the mechanism of competition between Pteronia and Tylecodon was not resolved in this study, the patient Tylecodon did appear to reduce nurse vigour and ultimately replace the nurse Pteronia pallens.

Since specific species associations do exist (i.e. some patient species are nurse specific), the replacement of one species by another (the nurse by its patient) is predictable and so 'succession' at the scale of the individual plant can be said to occur in the Karoo.

THE ROLE OF NURSE PLANTS IN THE VEGETATION DYNAMICS OF THE
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INTRODUCTORY CHAPTER

The Karoo : (Size, Climate and Vegetation and Geology)

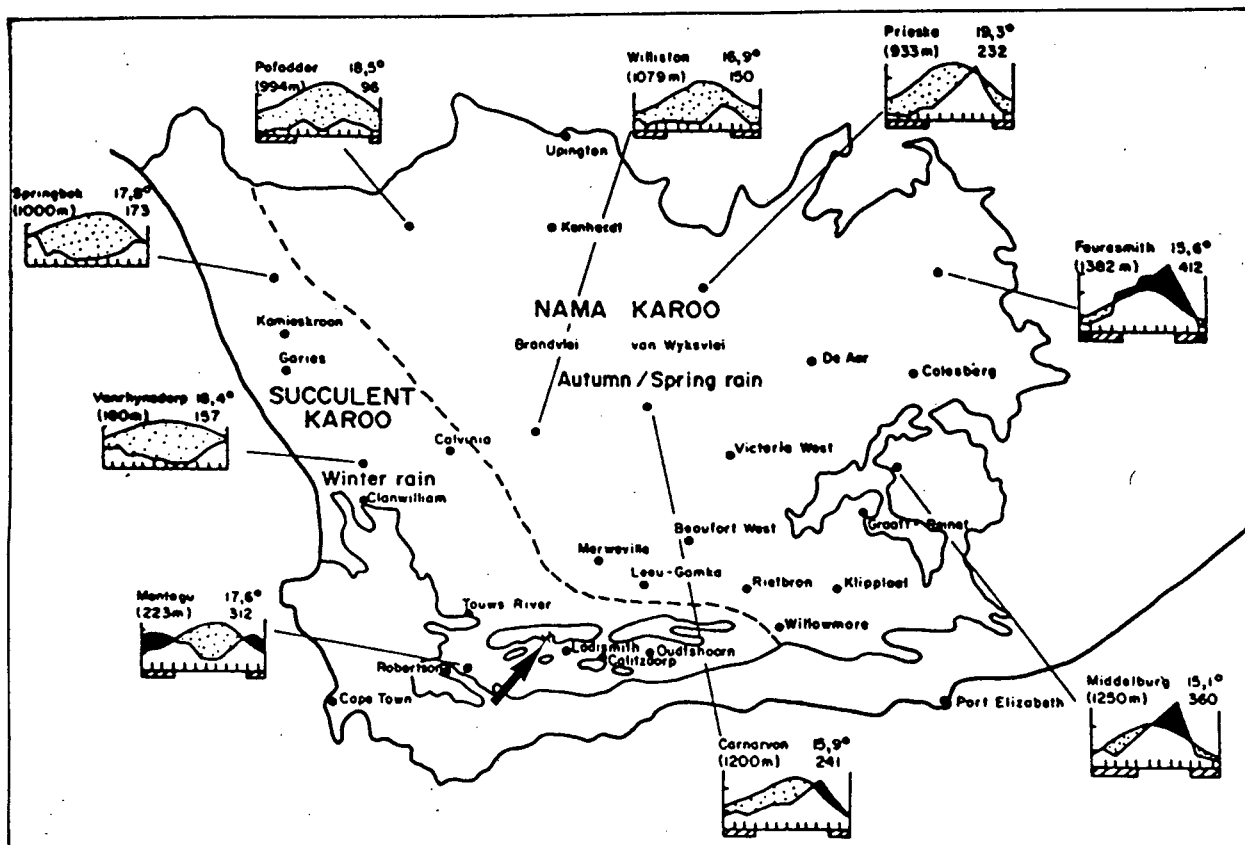
The Karoo biome (sensu Huntley 1984) occupies 427000km² (35.1%) of South Africa (Cowling 1986). This biome has been divided into two smaller biomes, the Nama Karoo and the Succulent Karoo, based on climatic, edaphic and floristic characteristics (Rutherford and Westfall 1986) (see Map 1). This region comprises the arid and semi-arid areas of the south western part of Southern Africa, and incorporates a number of climatic types depending on rainfall seasonality (Schumann 1949 cited by Cowling 1986). The Winter rainfall area in the western part of the biome (see Map 1) receives 60% of its rain from cyclonic fronts in Winter (May to July). The Succulent karoo biome falls within this region, and the predictability of the winter rain has profound influences on vegetation structure and functioning (Cowling 1986). Rain may fall at any time of the year in the Nama karoo but the peak rainfall is recorded in Autumn (including the period from August to September).

The rainfall is generally less reliable in the Nama karoo than the Succulent karoo (Hoffman and Cowling 1987). The greatest probability therefore of a significant rainfall (>10mm) occurring in the Succulent karoo is in the winter months and in spring and autumn in the Nama karoo, but within the Nama karoo region the coefficient of variation (for rainfall) is higher than in the Succulent karoo.

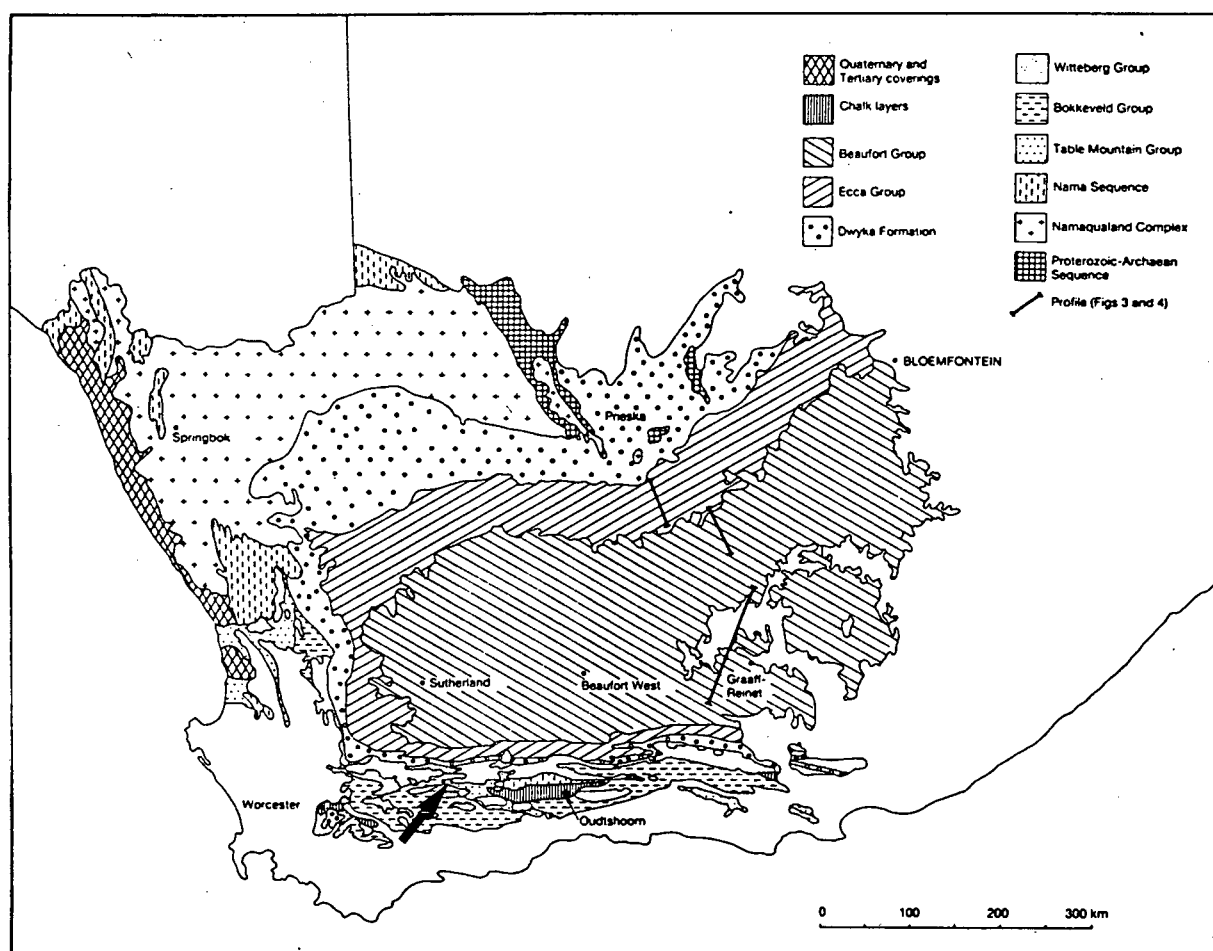
In general then, the climate varies from extremely arid in the west and far north-west to semi-arid in the east. Despite the low rainfall in the western Succulent karoo it is still more predictable than the Nama karoo, which is subject to the variable precipitation characteristic of arid and semi arid regions (Cowling 1986).

The typical vegetation of the Karoo covers a large variety of rock types, which because of their extent, provide various geomorphological characteristics (Visser 1986). To the extreme south and west, isolated strips of Quaternary and Recent sands are underlain by Nama, Table Mountain, Bokkeveld, Witteberg, Dwyka, Cretaceous and Cenozoic beds (see Map 2) (Visser 1986).

The vegetation of the Karoo biome is characterised by dwarf and low open shrublands in which xerophytic, fine leaved and succulent shrubs predominate (Huntley 1984).



MAP 1: Climate regions and biomes (sensu Rutherford and Westfall 1986) of the Karoo). (Arrow indicates study area)



MAP 2: Generalised geological map of the Karoo biome (Visser 1986) (arrow indicates study area).

In the winter rainfall region dwarf and low succulent shrubs dominate, comprising of 1500 species of the Mesembryanthemaceae and many species of the genera Aloe, Anacampseros, Crassula, Cotyledon, Euphorbia and many others. Geophytes and annuals are also very common in the west. Eastwards in the Great and Upper Karoo, succulents become less conspicuous and dwarf shrubs (deciduous and evergreen) belonging to the Asteraceae (Eriocephalus, Pentzia, Pteronia) predominate (Cowling 1986). Grasses increase from west to east and are correlated with an increasing rainfall and a decrease in winter rain (Hoffman and Cowling 1987). It is believed that prior to european settlement, grasses were more common in the Succulent karoo region (Hilton-Taylor and Moll 1986). Taller shrubs and low trees occur in varying quantities depending on topography and substrate (Huntley 1984). Common examples are Acacia karoo, Rhigozum species, Rhus species, and Lycium species (Vorster and Roux 1983).

Importance of the Karoo region (Farming and Conservation)

The Karoo biome is used almost exclusively for extensive pastoralism and supports a profitable small stock industry (Cowling 1986). South Africa also earns a substantial amount of foreign exchange in terms of animal products (wool, mutton, mohair and pelts) from farming in the karoo region (Vorster and Roux 1983). Of the total national income derived from small stock, 36% of the wool, 48% of the mutton, 60% of mohair and 60% of goat meat incomes are produced in the Karoo region (Roux et al 1981 cited by Cowling 1986). The considerable contribution of the area to the gross domestic product of South Africa is dependent on veld as a primary source of fodder for small stock, making the Karoo a very important area to the agricultural economy of South Africa.

The western and southern regions of the biome contain a rich and endemic succulent flora of which a high proportion of taxa have very narrow distributions (Hilton-Taylor 1986). At present only very small areas of succulent karroid types are conserved (0.5% of the Succulent biome) (Rutherford and Westfall 1986). The conservation status of the biome is very poor and needs to be improved.

Not only do areas in the karoo need to be conserved for ethical reasons but also for trying to rehabilitate the veld (vegetation) which has deteriorated rapidly since the establishment of the livestock industry in colonial times.

Given the importance of the Karoo biome to South Africa's economic and conservation needs, a sound, predictive understanding of the karoo vegetation dynamics is essential. This is lacking at present. Current rangeland policies are based on Clementsian successional concepts and for a number of reasons shown to be 'inadequate' for the purposes of managing and understanding the Karoo veld.

Problems with rangeland policies in arid lands (Succession)

In the arid rangelands of North America, Australia and the Nama Karoo, managers and researchers have applied rangeland policies based on the understanding that arid system dynamics are consistent with Clementsian succession (Westoby 1980, Hoffman and Cowling 1987). Incorporated in these policies is the assumption that in arid plant communities there is a predictable and deterministic developmental sequence towards a climax community which is permanent if undisturbed.

According to the Clementsian succession scheme, grazing is considered a 'disturbance' which may retard the successional sequence. Depending on the degree of disturbance (grazing intensity) and the annual rainfall the successional clock may be altered and the vegetation may be maintained in an optimum state for grazers (Hoffman 1988, Hoffman and Cowling 1987, Westoby 1980). The rangeland policies of the Nama karoo have been referred to as 'theoretically unsound' (Hoffman and Cowling 1987) and Westoby (1980) has also criticised the policies used in Australia and other regions. Rainfall, herbivory and fire vary in space and time, particularly in respect of their seasonal timing, intensity and spatial extent. The effect of such events depends on the current state of the system (the phenophase of the plants or the size and composition of the seed banks (Mentis et al 1989). In addition to the above factors, management action may change rangelands in ways which are not simply reversible and are not consistent with the classical range succession model (Westoby et al 1989). Arid and semi-arid rangelands might be viewed as event driven systems (Mentis et al 1989) and because of the variability of a factor such as rainfall, vegetation changes are not predictable. Disregard for rare episodic events in arid plant community dynamics presents serious problems for veld (vegetation) management.

There is a severe lack of data on Karoo plant dynamics and there is little factual basis for comparing 'alternatives'. Thus blindly adopting a Clementsian type rangeland policy is obviously problematic, but perhaps complete disregard for the possibility of 'predictable changes in species replacement over time' occurring at all in arid plant communities may also not be without short comings.

The "state and transition" model proposed by Westoby et al (1989) is adapted to cope with episodic events, influences of grazing and intrinsic vegetation change. The principle of this model is that rangelands would be catalogued in terms of 'alternative states' and 'transitions', the transitions being brought about by a combination of climatic events and management action. In this model the research emphasis is on the causes of transition and the onus on managers would be manipulating the brief transition periods to improve range quality.

It is crucial then to try and identify the types of dynamics that exist in arid plant communities and the mechanisms responsible for these dynamics.

A further necessity is to state clearly at which scale the dynamics of the arid vegetation is to be examined and to what extent (if at all) this can be extrapolated to other scales.

Research approach for this study

Noy-Meir (1980) discussed the 'Ecosystem' versus the 'Autecological' hypotheses in studying desert structure and function. The Ecosystem hypothesis emphasizes the interrelations between species populations and the environment - as a whole. Thus, the biological feedbacks which tie the system together and cause it to behave as a recognizable integrated system are studied in favour over the study of a collection of independent sub-systems (Noy-Meir 1980).

The Autecological hypothesis applied to desert environments considers species population reactions to the overriding factor of water availability to be of the utmost importance i.e. reactions to the environment outweigh the interactions between species and the effect of desert plants and animals on the environment (Noy-Meir 1980).

To manage the karoo vegetation effectively, a sound predictive understanding of the plant community dynamics is required (Hoffman and Cowling 1987). Ideally an holistic, ecosystem approach should be adopted to understand how the Karoo ecosystem works. However to study in sufficient detail all the biological feedbacks within the vast and variable integrated system of the Karoo seems an impossible task in so far as time, manpower and funding for plant ecological research goes in South Africa.

A more realistic approach would be to follow generally the 'reductionist', 'autecological' hypothesis whereby each population and its reaction to the environment is studied. The danger with this approach ofcourse is the assumption that "the sum of autecologies of all species gives us virtually the whole story of desert ecology" (Noy-Meir 1980). I believe this assumption is untrue if the species interactions and species effects on the environment are disregarded. Apart from this basic problem, it is also unlikely that all the studies that will be and have been undertaken would be consolidated i.e. "summed" and put in a form that would give us a broader understanding of how the Karoo works, let alone a form that is directly applicable to management.

Theoretical and organizational difficulties aside however, in my view there are sound approaches to studying the vegetation dynamics of the karoo. In brief, the autecological hypothesis may be followed but with the incorporation of some ecosystem hypothesis ideas i.e. species interactions and feedbacks on each other and the environment.

It is this approach that I have tried to follow by considering one species in particular, its reaction to the physical environment and its varying relationships with different plant species. The latter includes the dependence on some shrubs and not on others and also how dependence on one species initially may lead to competition and species replacements later on.

The Nurse Plant phenomenon in context of Arid system
vegetation dynamics

It is thought that the variable driving vegetation dynamics in arid and semi-arid ecosystems is rainfall, whose timing, magnitude and spatial patterns are not only discontinuous but highly stochastic (Noy-Meir 1973). Though considered the major factor influencing arid plant community structure and dynamics, it should not be viewed in isolation. There are also other determining factors important in this regard and these should be considered in conjunction with the low and unpredictable rainfall regime typical of these areas. These include plant species phenologies (flowering, seed set), germination, seedling recruitment and survival, plant-plant interactions and plant-animal interactions. This study concerns mainly plant-plant interactions.

Deserts provide classic examples of space pre-emption where intense competition for water among established plants prevents any further recruitment of seedlings (reviewed by Fowler 1986). A number of studies in North American and Mexican desert communities have shown both intraspecific and interspecific competition to be important in the determination of community structure (Yeaton and Cody 1976, Yeaton et al 1977, Cody 1986). Establishment, survival and physiological responses of many desert plants are strongly affected by the proximity of the same and different species and the resulting intensity of competition (Fonteyn and Mahall 1981).

Plants in deserts may however influence their neighbours in ways other than direct negative interference.

Plants in arid regions have to cope with a harsh physical environment, but some avoid these conditions by establishing in favourable microclimates such as those near rocks, in crevices and beneath other plants. Shrubs are prominent in vegetation of many deserts and though they usually cover only a small proportion of the surface, and their effects on the edaphic and atmospheric conditions on the desert surface small, they do create strongly modified microenvironments for other organisms (Noy-Meir 1985). The mosaic of shrub canopies and open areas presents physical microhabitats that differ considerably with respect to factors influencing seed distribution, germination and post-germination survival (McAuliffe 1988). The larger trees and shrubs therefore serve to provide small areas in which the conditions are more favourable than they are in the wide open spaces between desert perennials (Shreve 1931). The effect of shade in merely prolonging the favourable conditions and shortening the duration of the adverse ones was noted to be of great importance by Shreve (1931).

Trees and shrubs providing this shelter are referred to as "Nurse Plants" and have been widely studied in North American deserts.

Nurse plants have been shown to provide favourable conditions of moisture and temperature (Nobel 1980, Shreve 1931 and Steenbergh and Lowe 1969), solar radiation (Turner et al 1966) and soil nutrients (Franco and Nobel 1988, Nobel 1989, Garcia-Moya and M^CKell 1970). Protection against herbivores has also been investigated as a probable advantage provided by the nurse (Shreve 1931, Steenbergh and Lowe 1969 and M^CAuliffe 1984).

Though seed germination requirements may well play a decisive role in structuring some plant communities, I have chosen to rather emphasize post-germination survival with a view to highlighting nurse plants. The assumption that germination is less important than establishment and survival of seedlings in determining community structure is based on descriptive and experimental studies in other arid regions of the world, especially North America. Shreve (1931) wrote, "The shade is no more favourable than the open for germination of the seeds of the larger perennials, but is far more favorable for these plants during the very critical rainless periods in their early history". Went (1948) also referred to this topic and claimed that for desert shrubs, the main factor controlling their abundance and distribution was the growing conditions rather than germination and wrote, "For though many seedlings come forth in a rainy season, few survive long enough to become established".

Many experimental studies focussing on desert plant communities and the maintenance of species populations have concentrated on seedling establishment and how difficult this may be (Jordan and Nobel 1979,1981,1982 and Sherbrooke 1977). I therefore concentrated on this life-history stage in determining the structure and dynamics of arid plant communities rather than viable seed banks and germination.

It has already been mentioned that the timing and amount of rainfall is considered the most critical factor affecting seedling establishment. This precipitation however is not often strictly related to the duration of moist and drought periods of the soil (Jordan and Nobel 1982). This is because the length of time that the soil is moist depends on local run off and shading, which can change the period when soil moisture is available (Jordan and Nobel 1982).

So, even though the driving variable of the Karoo may be the timing and amount of rainfall, the conditions beneath nurse plants must also be considered since the 'open' desert environmental conditions may be quite different to the "phytosphere" of the nurse shrub.

Nurse plants therefore play a major role in the facilitation of seedling establishment by the provision of favourable microsites in an otherwise harsh environment. What then are the implications for a community of the the Nurse Plant phenomenon? Since chances of survival are greater beneath the canopy of plants in arid environments, do all the plants behave as nurses and in this way maximize chances of seedling survival? If not, and only certain plants act as nurses, what are the possible consequences for the nurse plants and the plants that require their protection (referred to in this study as "Patient Plants") ?. As the seedling beneath the nurse grows larger and resource requirements increase, will not the proximity of the nurse and the patient plants result in some form of negative interference? How would this affect the nurse plant population in the community? In so far as the nurse plant phenomenon goes, do sequential species replacements occur? If so, are these predictable?

Given that seedling establishment may depend on rare heavy rainfalls, what role do plant species interactions play in the subsequent establishment and survival of Karoo plant species? Should predictions about rainfall for regeneration and drought conditions for mortality be 'predicted', how accurately could we predict vegetation change without considering intricate biotic plant species interactions such as 'facilitation' and 'competition'? This study focusses on these interactions with the aim of revealing their importance in arid system vegetation dynamics.

M^CAuliffe (1988) stated that the establishment of certain perennials beneath the canopies of others was one of the principal components of the dynamics of desert plant communities. I hope to substantiate this claim by revealing experimentally and descriptively the role of these nurse plants in the Karoo vegetation dynamics.

The Study Area

All intensive studies were undertaken in the Anysberg Nature Reserve (33°30'S, 20°30'W). This 34000 hectare reserve falls within the winter rainfall, Succulent Karoo region as depicted by Rutherford and Westfall (1986) (see map 1).

The study sites were located in the flats below the Anysberg mountain (see Plate 1). The altitude here was approximately (900m) and the annual average rainfall 250mm. The peak rainfall period is between April and June (see Table A).

The study area occurs in a region where approximately 90 days in the year experience maximum temperatures greater than 30 °C. The mean daily maximum temperature (January) in the Laingsburg-Ladismith area is 32°C (Venter, Mocke and de Jager 1986). The area is subject to occasional frost in June and July (pers.obs.) but is generally not a frost prone area, (a frequency of only 10 days in the year where temperatures are below 0°C (Venter, Mocke and de Jager 1986)).

The general geology of the Ladismith-Anysberg region is that of the Table Mountain group (Map 2, Visser 1986).

The vegetation at the study sites is low, woody, evergreen and deciduous shrubs consisting of mainly Pteronia pallens L.f., Galenia africana L., Elytropappus rhinocerotis (L.f.)Less and Lycium species, (probably L.cinereum Thunb. but the genus is being revised, thus referred to as Lycium sp. only). These plants rarely reach a height greater than 1.5m. The shorter plants (<1m high) are mainly the leaf succulent dwarf shrubs of the Mesembryanthemaceae; Eberlanzia ferox* (L.Bol.)L.Bol., Ruschia pungens (A.Berger) H.J.Jacobsen and Drosanthemum lique (N.E.Br.)Schwantes dominating. In the understory, numerous dwarf succulents are found beneath the canopies of the larger shrubs. Common succulent genera are Tylecodon, Cotyledon, Senecio, Andromischus, Haworthia, Stapelia, some creeping species of the Mesembryanthemaceae and numerous species of Crassula. The veld is dominated though by Pteronia pallens, Eberlanzia ferox and Tylecodon wallichi (Harvey) Tolken .

*There is some confusion as regards the classification of Eberlanzia ferox. It has been referred to as Eberlanzia c.f.vulnerans (Yeaton and Esler 1990) and more recently Ruschia vulnerans (pers.comm. Nicky Phillips). For simplicity, I will use the original name Eberlanzia ferox.



PLATE 1: The main study site on the flats beneath the Anysberg mountain. The plant community is dominated by Pteronia, Tylecodon and Eberlanzia.

Table A: Monthly average rainfall (mm) at Anysberg (1955-1977)

MONTH	AVERAGE RAINFALL (+SD)	NO. OF YEARS USED TO CALCULATE AVERAGE (n)
January	9.6 (13.2)	19
February	16.2 (18.4)	18
March	14.3 (13.8)	18
April	19.5 (16.2)	18
May	21.6 (17.4)	18
June	13.3 (9.6)	19
July	11.3 (16.7)	21
August	19.3 (24.7)	19
September	9.0 (12.9)	19
October	20.4 (17.3)	20
November	12.5 (12.9)	19
December	9.6 (15.9)	20

ANNUAL TOTAL 176.6
 ANNUAL MONTHLY AVERAGE 14.72(4.57)

(Data supplied by National Botanical Institute, Cape Town)

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CHAPTER ONE

The existence of the Nurse plant phenomenon in the Karoo

Introduction

It has been noted by many that small plants are more often associated with large perennial shrubs and bushes in arid areas than in the open spaces between (Shreve 1931). Young perennials frequently occur beneath the canopies of other plants, with high mortality rates and therefore low recruitment occurring in the open (Steenbergh and Lowe 1969, M^CAuliffe 1988). The larger trees and shrubs serve to provide small areas in which conditions are more favourable than those in the open (Shreve 1931). Shreve (1931) also noted the importance of the effect of shade in prolonging the favourable conditions and shortening the duration of the adverse ones.

The successful establishment of seedlings beneath other shrubs has been well documented in the Sonoran Desert (Turner, Alcorn, Olin and Booth 1966, Steenbergh and Lowe 1977), the Mojave Desert (Wallace and Romney 1980) and the Chihuahuan Desert (Yeaton 1978). Whilst some of these studies included manipulative, experimental work in the field the only one undertaken in South Africa (Compton 1929) was descriptive.

In the initial part of this chapter I first demonstrate the existence of nurse plants in the Anysberg region of the Karoo. The first part of the study was two-fold, descriptive followed by manipulative experiments in the field.

The microenvironmental conditions beneath nurse plants compared to those in the open have been examined by several North American authors (Shreve 1931, Jordan and Nobel 1979, Franco and Nobel 1988). The environmental variables investigated include soil and air temperatures, soil moisture and nutrient availability and also Photosynthetically Active Radiation (PAR).

It has been shown in other studies that the microenvironmental conditions beneath nurse plants are more favourable for regeneration than in the open. I believe that these conditions also vary beneath the different nurse species. Since chapter one is introductory to nurse plants in the Karoo, the examination of certain microenvironmental variables beneath different shrub species and in the open are included here. This has been done to characterise the different microhabitats and to try and determine which microenvironmental conditions are more favourable.

It is apparent in the Anysberg region that not all perennial shrubs act as nurse plants. Many in fact do but casual observation lends thought to the possibility that some shrubs are "better" nurses than others.

In this first chapter therefore I,

a) address the question as to whether there are plants in the Karoo that require nurse plants for successful establishment

b) investigate whether all established shrubs are adequate nurse plants or whether some are more suitable than others and

c) ask whether microclimates differ beneath different nurses and whether (if any) these differences, might influence patient specificity.

d) determine whether the rooting patterns of the patient Tylecodon differ in relation to the different nurse plants in such a way that might affect patient specificity.

METHODS

It was first necessary to establish whether the nurse plant phenomenon exists in the Anysberg region of the Karoo. This was undertaken in two ways.

1) Open versus nursed

Firstly I compared the abundance of Tylecodon wallichii (see Plate 2), a succulent plant in open excluded areas and beneath shrubs.

(i) QUADRATS

Eight, 5.00m x 5.00m quadrats were laid out in the Pteronia-Eberlanzia dominated plant community.

The occurrence of Tylecodon wallichii plants in the open and under any nurse plant was noted in each quadrat. All plants were measured for crown cover. This was to assess total plant cover in each quadrat. This value was subtracted from 25.00m² (5.00m x 5.00m) to attain a value for the open space area in each quadrat.

A Chi-square analysis was used to determine whether the frequency of occurrence of Tylecodon wallichii beneath nurse plants was significantly different to its occurrence in the open.

To determine whether nurse plants facilitate Tylecodon growth and survival, I transplanted the patient into the open and beneath nurses.

Transplant experiments were necessary to resolve the question of whether the distribution of patient plants beneath shrubs could merely be a result of wind blown seeds getting caught beneath the canopies of other plants, rather than subsequent seedling growth and survival.

(ii) TRANSPLANTS

Fifty similar sized (juvenile) Tylecodon plants were collected in the field, in February 1990 (when dormant).

Plants were measured for height, two diameters and maximum leaf length. The number of leaves were also counted.

Twenty-five plants were transplanted in polystyrene cups (to partially control for soil differences between the two microsites, cups were were 6cm in diameter and 6cm deep once the bottom was removed), beneath twenty-five Pteronia pallens nurse plants. The remaining twenty-five plants were transplanted in a similar way except that they were placed in open sites, not beneath nurse plants. Each plant was tagged. The transplant experiment therefore consisted of twenty-five pairs of Tylecodon wallichii plants, each pair consisting of one transplant in the open versus one transplant beneath the nurse. Transplants were monitored every second month, for ten months, from February 1990 to December 1990. Monitoring included plant diameter and leaf measurements.

Leaves were also collected in the field, their lengths and area calculated to establish a relationship between leaf area and leaf length using a linear regression. Leaf lengths were measured for the entire monitoring period but an area estimate was preferred in the analysis. Twenty two Tylecodon wallichii leaf lengths were measured and their areas calculated using the formula for the area of a cylinder - $2\pi rl$, since this species has cylindrical leaves. Leaf length was regressed against leaf area. The resulting equation of the straight line was then used to find out the leaf areas of the plants where only leaf length was recorded. The increase or decrease in leaf area could then be calculated and compared for plants in the open and plants beneath nurse plants.

An estimate of the percentage dead of the canopy of each plant was calculated based on the number of leaves that were turgid and green in comparison to how many were totally shrivelled.

Where no leaves were completely shrivelled, the length of the leaf tips that were shrivelled was measured and compared with the maximum leaf length measurements.

2) Nurse Specificity

As mentioned in the introduction, Karoo patient plants appear to be more concentrated under certain shrubs. These seem to be the more "popular" nurse plants. This investigation aimed at determining whether some nurse plants are more effective than others and if this were so, why?

(i) PATIENT SPECIES RICHNESS BENEATH NINE NURSE SPECIES.

Fifty individuals per nurse species were sampled at random, using the Wandering Quarter method (Catana 1963). The number of patient plant species beneath each of the nine nurse plants was counted. A total of four hundred and fifty nurse plants were sampled. The nine species were Lycium sp. (genus under revision), Pteronia pallens, Pteronia paniculata Thunb. Elytropappus rhinocerotis, Eberlanzia ferox, Galenia africana, Ruschia pungens, Drosanthemum lique and Helichrysum excisum (Thunb.)Less.

An Analysis of Variance was used to determine whether the distribution of patient species beneath the nine nurses was significantly different among the nurses.

Assuming that not all nurse plants were equally effective, this next section aims at determining whether the microclimates beneath the different nurse species are important in establishing what determines how effective a nurse is.

(ii) MICROENVIRONMENTAL CONDITIONS BENEATH DIFFERENT NURSE PLANTS AND IN THE OPEN

It was evident from the previous introductory section that not all nurse plants were equally effective. The microenvironmental conditions were therefore investigated as possibilities for the differences in occurrence of patient plants beneath different nurses. The nurse plants examined were Lycium, Pteronia pallens (two of the "preferred" nurses) and Eberlanzia ferox (less common as a nurse), (see Plate 3,4 and 5).

The microenvironmental variables examined were daily soil temperatures, air temperatures and Photosynthetically Active Radiation (PAR). An MC 120S data logger was used to record temperatures for two days at four times in the year (both solstices and equinoxes). Daily PAR was recorded using a PAR meter. Data were collected for open sites as well.

Soil collection was undertaken once, in the wet season (May) at Anysberg. Ten centimeter soil cores were used to collect soil samples from the four different microsites. Ten samples from ten individual nurse plants per species and ten samples from sites in the open were collected. Each sample was divided into two, 0 - 5cm and 5 - 10cm so that total soil nitrogen could be analysed at two depths. The Kjeldahl analysis was used to determine total soil nitrogen.

The diameters of all the nurses were also measured to investigate the possible influence of size on the number of patient plants a nurse could support. An Analysis of Variance (ANOVA) was carried out on the average diameters of ten individuals of each of the nine nurse species. A regression analysis of nurse diameter versus the number of patient plants was also done to check if there was a significant relationship. The latter investigation was undertaken for the nurse Pteronia pallens only since this was the main study species.

This last section investigates the possible influences the different nurse species rooting patterns might have on the subordinate patient plants.

(iii) ROOT STUDY

The roots of Tylecodon were examined in relation to the rooting patterns of Pteronia, Lycium and Eberlanzia.

Two Tylecodon adults, two Pteronia adults, one Eberlanzia and one Lycium were excavated. The method of root excavation was one using water delivered under pressure (Higgins, Lamb and van Wilgen 1987), (see Chapter 3 root study methods).

The percentage of roots at two soil depths were determined for three nurse species and the one patient species Tylecodon wallichii.



PLATE 2: The main "patient" species Tylecodon wallichi
(4 juveniles)



PLATE 3: The Lycium species



PLATE 4: A common Karoo shrub Pteronia pallens
(beneath its canopy are many Tylecodon patients)



PLATE 5: Eberlanzia ferox (c.f. vulnerans or Ruschia vulnerans)

RESULTS

1) Exposed versus nursed

(i) QUADRATS

In the eight, 5.00m x 5.00m quadrats laid out, the patient plant Tylecodon walichi only occurred beneath the canopy of various shrubs and not once did it occur in the open, exposed sites. Establishment therefore appears to be limited to those areas beneath the canopies of other plants. Despite there being large open space areas (see Table 1.1) in all the quadrats no patient plants were found there.

(ii) TRANSPLANTS

All plants were transplanted when they were dormant and therefore did not have any leaves. Those patients transplanted into the exposed, open sites did not grow any new leaves during the 8 month monitoring period. In contrast patients transplanted beneath nurse plants showed evidence of new growth (see Table 1.2).

Table 1.1 : Total Plant Cover and Open Space Area in each quadrat (areas in m²)

QUADRAT	PLANT COVER	OPEN SPACE AREA
1	9.005	14.343
2	12.395	9.494
3	12.296	12.258
4	14.459	9.592
5	13.154	11.845
6	10.761	14.238
7	8.952	16.047
8	12.167	12.832

Table 1.2 : Summarised results of exposed versus nursed transplant experiment (n=22, each).

MONTH	NO.OF LEAVES		TOTAL LEAF	
	(+SE)		AREA(+SE)	
	EXPOSED	NURSED	EXPOSED	NURSED
February	0	0	0	0
May	0	4.41(0.84)	0	47.8mm ² (9.24)*
September	0	4.68(0.66)	0	51.2mm ² (7.77)**

* = z=4.39 (z statistic for Mann Whitney U Test) p<0.0001
(comparing leaf areas of Exposed and Nursed plants in May)

** = z=5.56 (z statistic for Mann Whitney U Test) p<0.0001
(comparing leaf areas of Exposed and Nursed plants in September)

The results of this transplant experiment are very clear in that not a single Tylecodon patient transplanted into the open grew a leaf. Most of those patients transplanted beneath the Pteronia nurses survived and showed evidence of new growth (see Table 1.2 above).

2) Nurse Specificity

(i) PATIENT SPECIES RICHNESS BENEATH NINE NURSE SPECIES

The observed number of patient plant species beneath the nine nurse species was compared using a one-way Analysis of Variance (see Table 1.3).

Table 1.3: Results of the ANOVA showing the distribution of patient species beneath the nine nurse species. n=50 plants for each nurse species. Comparison of means = Confidence Interval

NURSE SPECIES	AVERAGE	HOMOGENEOUS GROUPS
Drosanthemum	0.5	*
Eberlanzia	0.52	**
Pteronia pan.	0.9	***
Ruschia	1.16	****
Galenia	1.36	****
Helichrysum	1.4	****
Pteronia pal.	1.74	****
Elytropappus.	2.08	****
Lycium	2.68	****

KEY:

(ANOVA results F-ratio=18.54 p<0.0001 df=8, 441)

Pteronia pal.= Pteronia pallens

Pteronia pan.= Pteronia paniculata

The number of patient species occurring beneath the nine nurse species differ significantly. It is evident that Lycium, Elytropappus and Pteronia pallens have significantly more patients beneath their canopies, while the leaf succulent dwarf shrubs Eberlanzia and Drosanthemum tend to have significantly fewer patients beneath them.

The number of patient plants beneath Pteronia paniculata, Galenia, Helichrysum and Ruschia are intermediate in terms of number of patients nursed.

2 (ii) MICROENVIRONMENTAL CONDITIONS BENEATH DIFFERENT NURSES AND IN THE OPEN

MARCH: Daily Air and Soil temperatures

The air temperatures recorded beneath the different nurse canopies in March (late Summer) were all similar. This is evident from the hourly averages and the hourly maxima (see Figures 1.1 and 1.2).

For the two days that data were collected, soil temperature trends differed for day one and day two. On the first day (see Figure 1.3) soil temperatures beneath Eberlanzia peaked after temperatures beneath Lycium and in the open. The temperatures beneath Lycium and in the open were also the highest recorded during this first day (see Figure 1.3). Soil temperatures beneath Pteronia remained the lowest.

Since it is late Summer in the Karoo in the month of March, maximum temperatures were noted.

Midday maximum soil temperatures (Figure 1.4) were highest beneath Eberlanzia and Lycium which followed temperatures in the open.

MARCH: Photosynthetically Active Radiation (PAR)

A comparison of the daily PAR beneath Lycium, Pteronia and Eberlanzia shows that PAR is the highest under Lycium. PAR beneath the Eberlanzia canopy was the lowest throughout the day (see Figure 1.5). At midday when PAR levels as high as $2000\text{umol/m}^2/\text{s}$ in the open, greater than $1000\text{umol/m}^2/\text{s}$ for Lycium and Pteronia, a reading of less than $500\text{umol/m}^2/\text{s}$ was recorded for Eberlanzia.

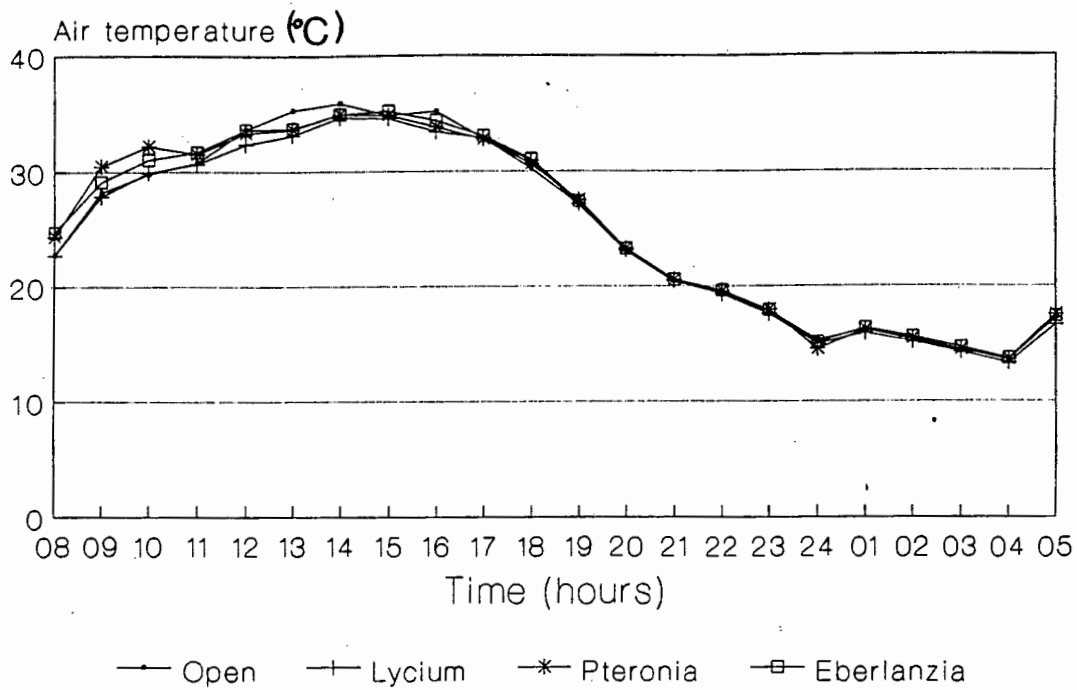


FIGURE 1.1: March hourly average Air temperatures in the open and beneath three nurse plants (SUMMER)

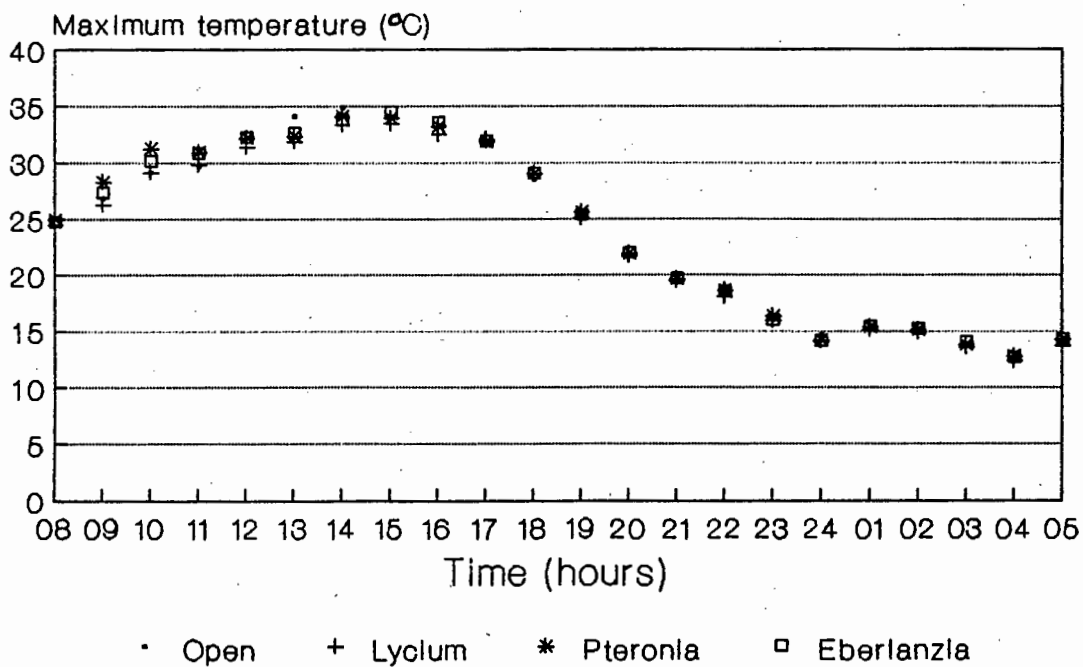


FIGURE 1.2: March hourly Maximum Air temperatures in the open and beneath three nurse plants.

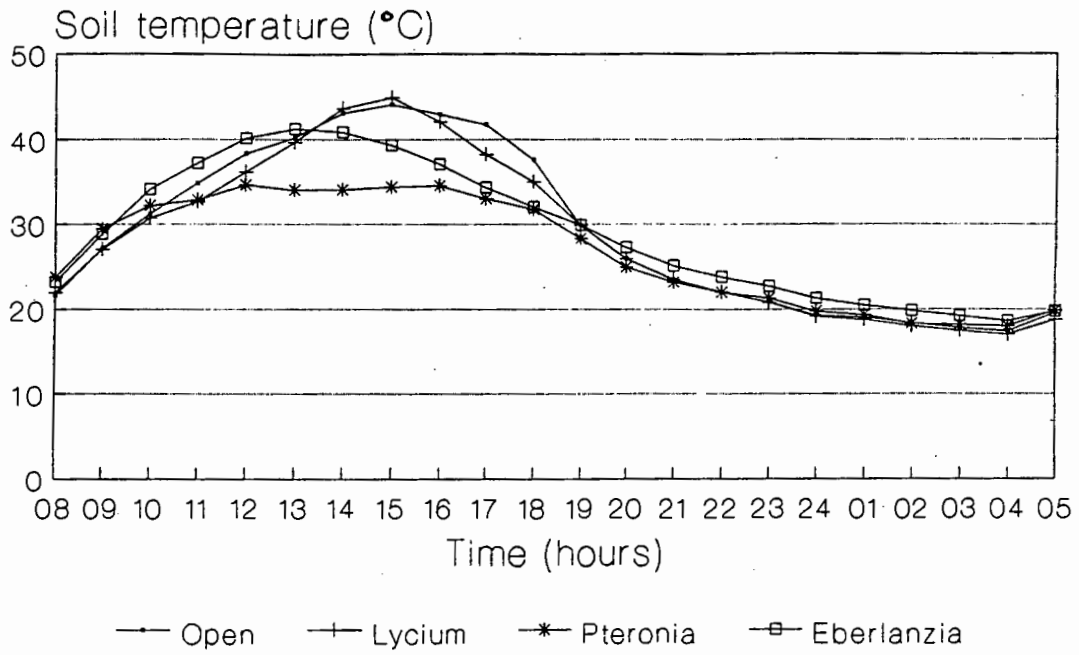


FIGURE 1.3: March hourly Soil temperatures in the open and beneath three nurse plants. (1cm below soil surface)

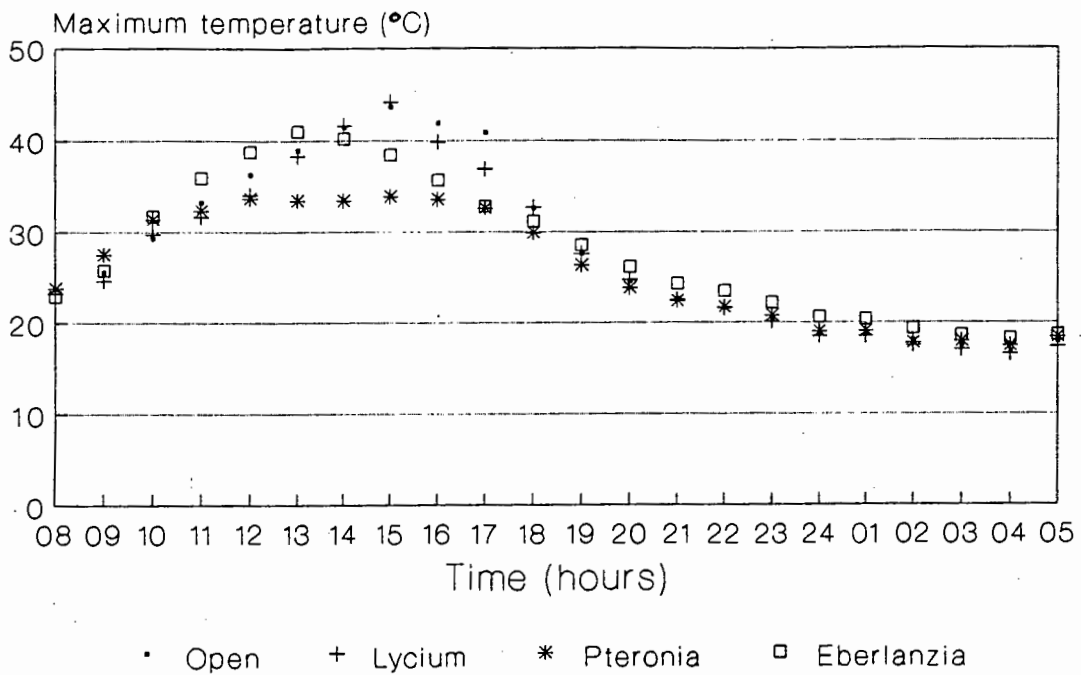


FIGURE 1.4: March hourly Maximum Soil temperatures in the open and beneath three nurse plants. (1cm below soil surface)

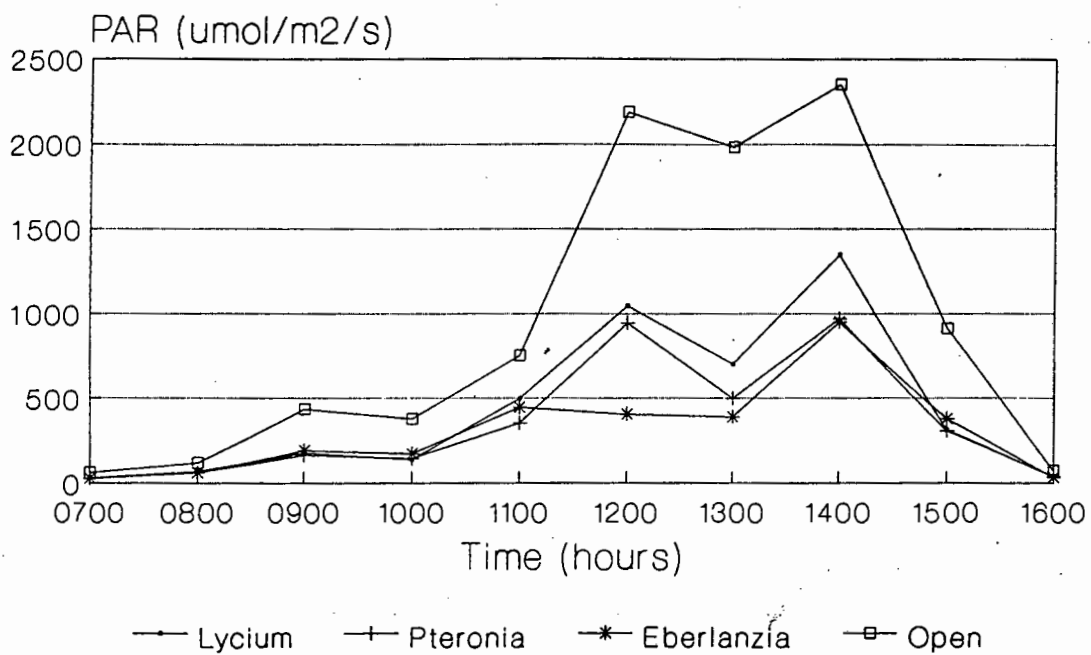


FIGURE 1.5: March hourly PAR in the open and beneath the canopies of three nurse plants.

JUNE: Daily Air and Soil temperatures

Similar air temperatures were found in the open and beneath the various nurses. Temperatures peaked at midday then declined quite rapidly. After 16:00 hours temperature decline appeared gradual until 23:00 hours when the daily minimum was reached. A surprisingly rapid increase in air temperature was evident after midnight in all the microsites (see figure 1.6).

Daily soil temperatures showed a similar trend to the air temperatures but unlike the latter differences were evident between the nurse plants and in the open. At midday the temperatures in the open and beneath Lycium were much higher than beneath Pteronia and Eberlanzia (see figure 1.7)

The minimum soil temperatures were found in the open, from 18:00 hours onwards. Temperatures beneath the canopies of Lycium and Eberlanzia were similar, whilst the Pteronia nurse had the highest minima. After sunset therefore, warmer temperatures were evident beneath Pteronia (see figure 1.8). Minimum temperatures were examined because it is Winter in the month of June in the Karoo.

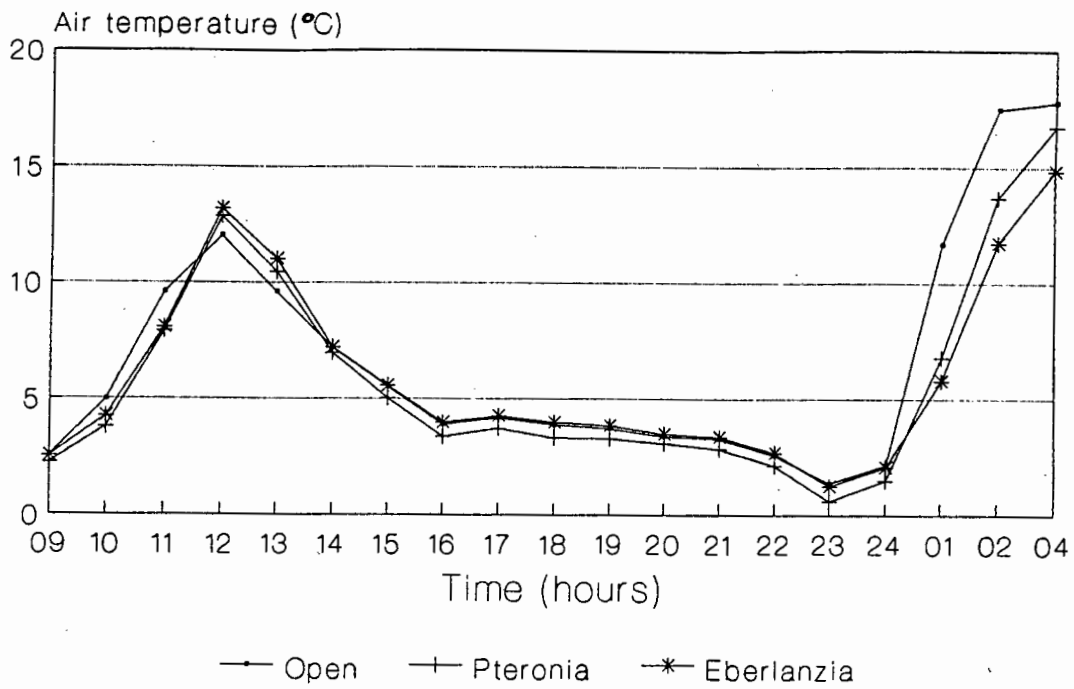


FIGURE 1.6: June hourly average Air temperatures in the open and beneath three nurse plants (WINTER)

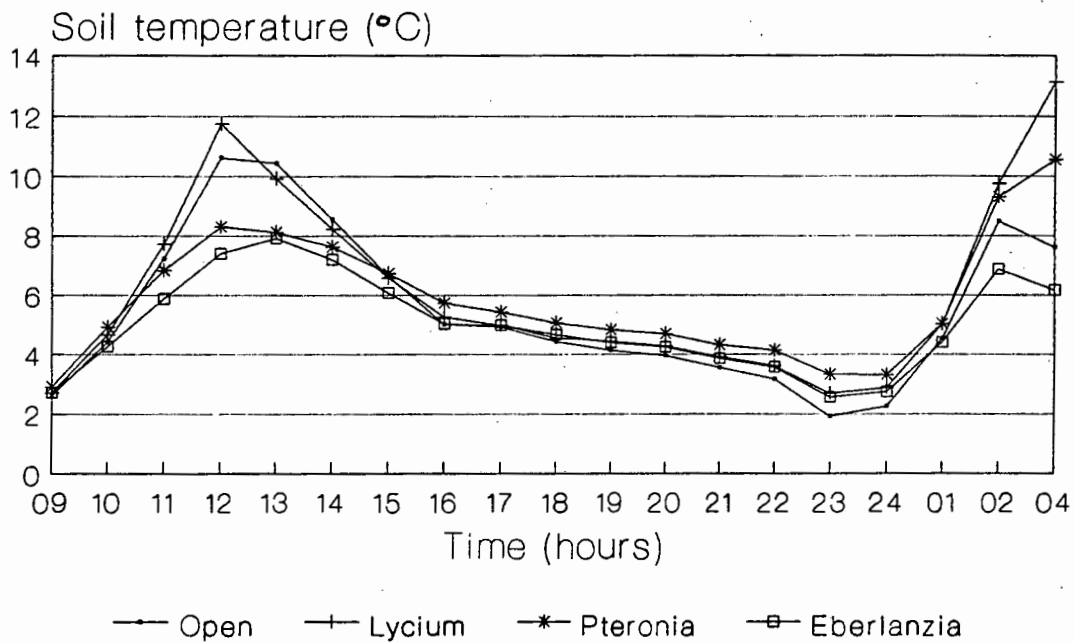


FIGURE 1.7: June hourly average Soil temperatures in the open and beneath three nurse plants (1cm below soil surface)

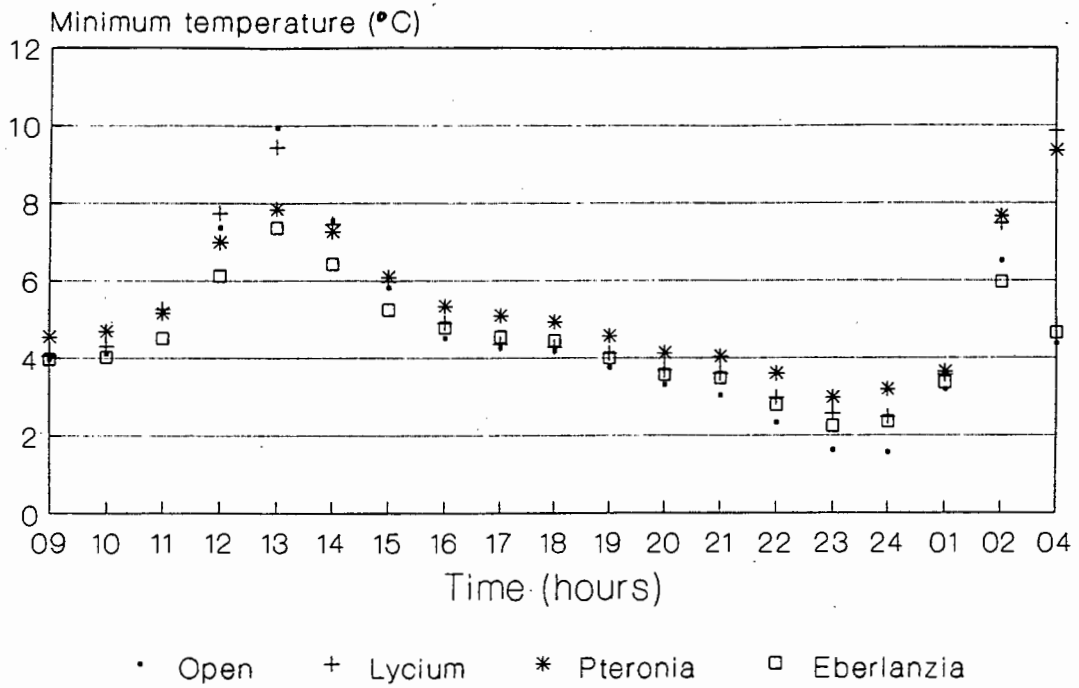


FIGURE 1.8: June hourly Minimum Soil temperatures in the open and beneath three nurse plants (WINTER) (1cm below soil surface)

SEPTEMBER: Daily Air and Soil temperatures

Daily air temperatures for both days in September were similar for the open sites as well as those beneath the different nurse species. Slight variations in air temperature occurred around midday (see Figure 1.9). On both days Lycium and Pteronia air temperatures were the highest. Except for the 11.00hr to 17.00hr period daily trends were all similar.

Soil temperatures in the open sites were the highest throughout the day. Soil temperatures beneath the Lycium nurse were the next highest. These temperatures appeared to follow closely those in the open (see Figure 1.10). Soil temperatures beneath Pteronia and Eberlanzia were lower, their maxima not greater than 40⁰ whereas the maxima for the open and Lycium went beyond this. Minimum soil temperatures for all the microsites were similar.

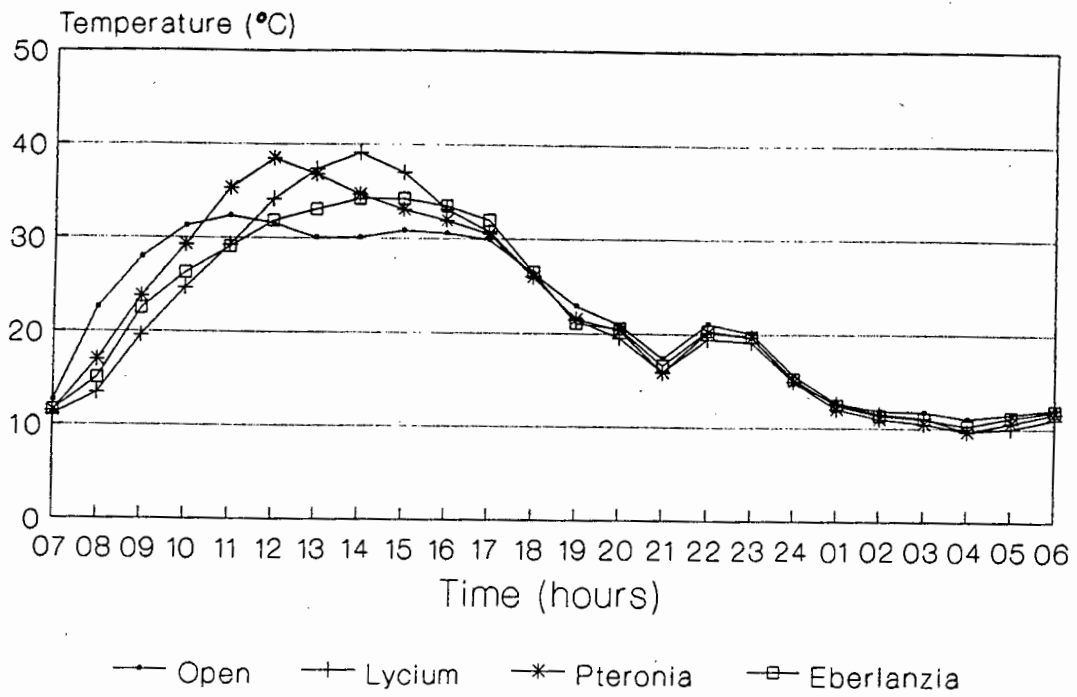


FIGURE 1.9: September hourly average Air temperatures in the open and beneath three nurse plants (SPRING)

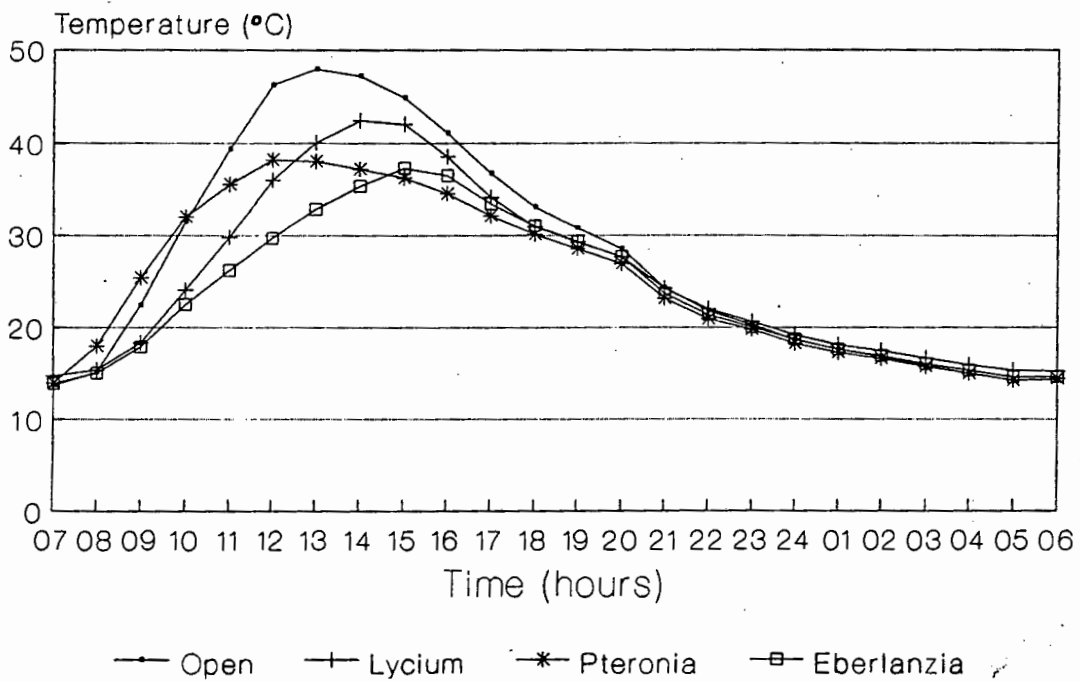


FIGURE 1.10: September hourly average Soil temperatures in the open and beneath three nurse plants (1cm below soil surface)

SEPTEMBER: Photosynthetically Active Radiation (PAR)

PAR recorded in the open sites was the highest, peaking at midday with a reading of $1800\text{umol/m}^2/\text{s}$ (see figure 1.11).

Great fluctuations, especially for Lycium were evident throughout the day. From 12.00hours until sunset at 18.00hours the PAR levels beneath Pteronia were highest. Except for a high reading beneath Lycium at 10.00hours, PAR levels for Lycium and Eberlanzia were similar.

These PAR results differ to those recorded in March where light levels beneath Lycium were greatest. In March however Lycium had dropped its leaves whereas in September leaves were actively growing, filling the canopy and therefore reducing the amount of incoming light.

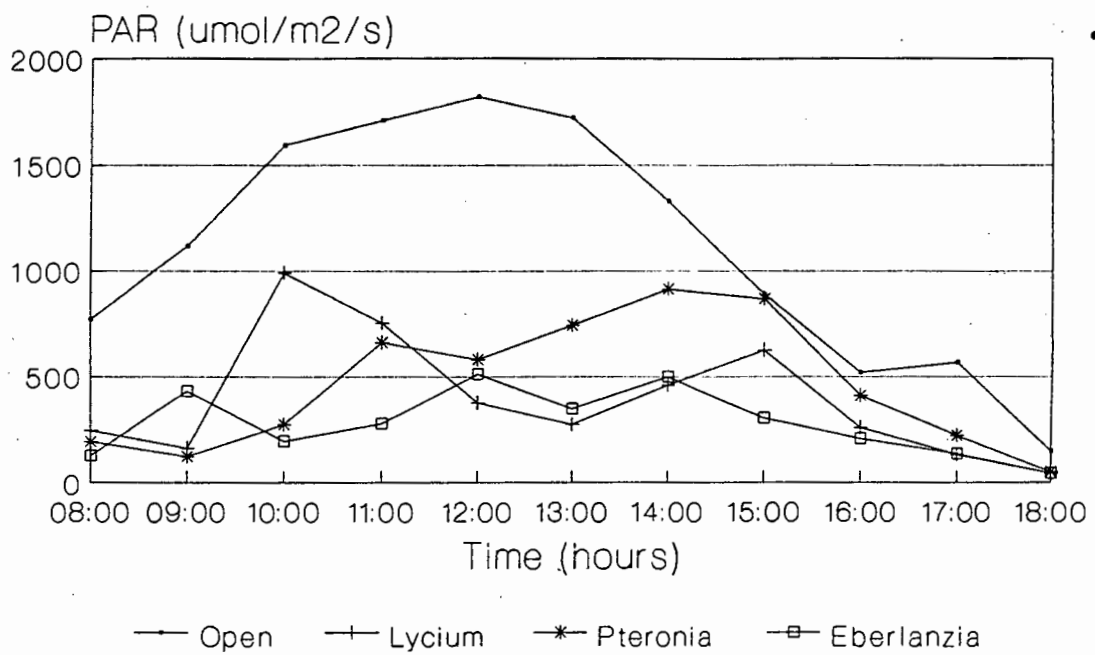


FIGURE 1.11: September hourly PAR in the open and beneath three nurse plants

DECEMBER: Daily Air and Soil temperatures

The unusually cloudy, overcast weather during the logging period was unrepresentative of the Karoo in December. The highest soil temperatures recorded were below 40° (see figure 1.12). Daily trends in soil temperature beneath all the nurse species were similar, though temperatures beneath Lycium and in the open were slightly higher.

DECEMBER : Photosynthetically Active Radiation (PAR)

PAR readings in the open were higher than beneath all three nurses throughout the day. When the PAR levels beneath the different nurses are compared, midday recordings were highest beneath Lycium. The daily trend in PAR levels beneath the three nurses though appear quite similar (see Figure 1.13).

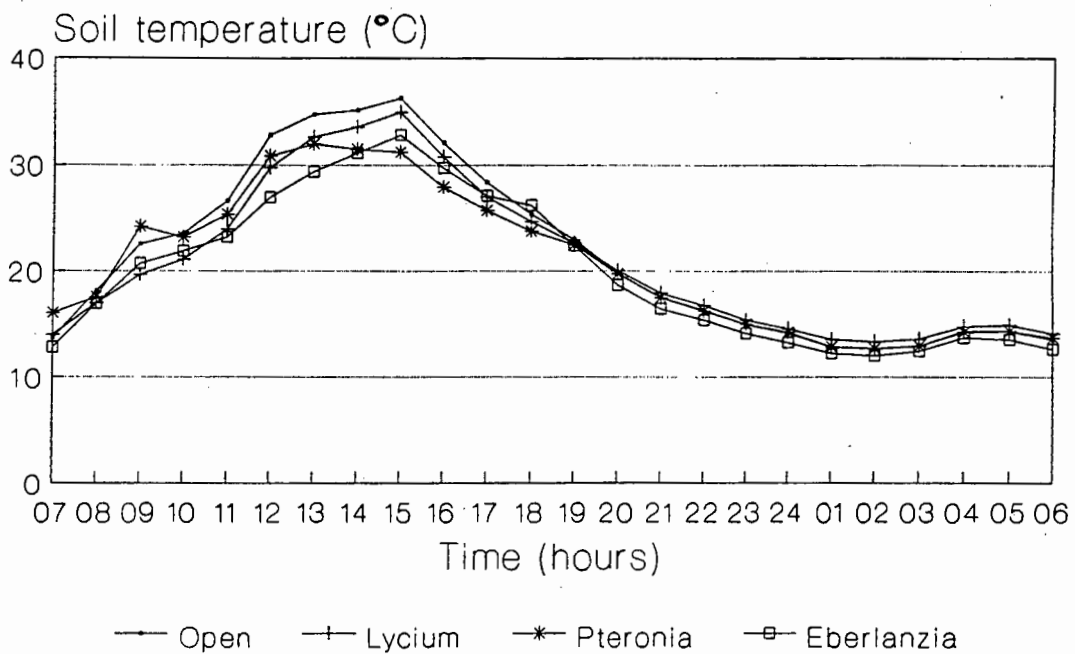


FIGURE 1.12: December hourly average Soil temperatures in the open and beneath three nurse plants (SUMMER but an unusually cool day) (1cm below soil surface)

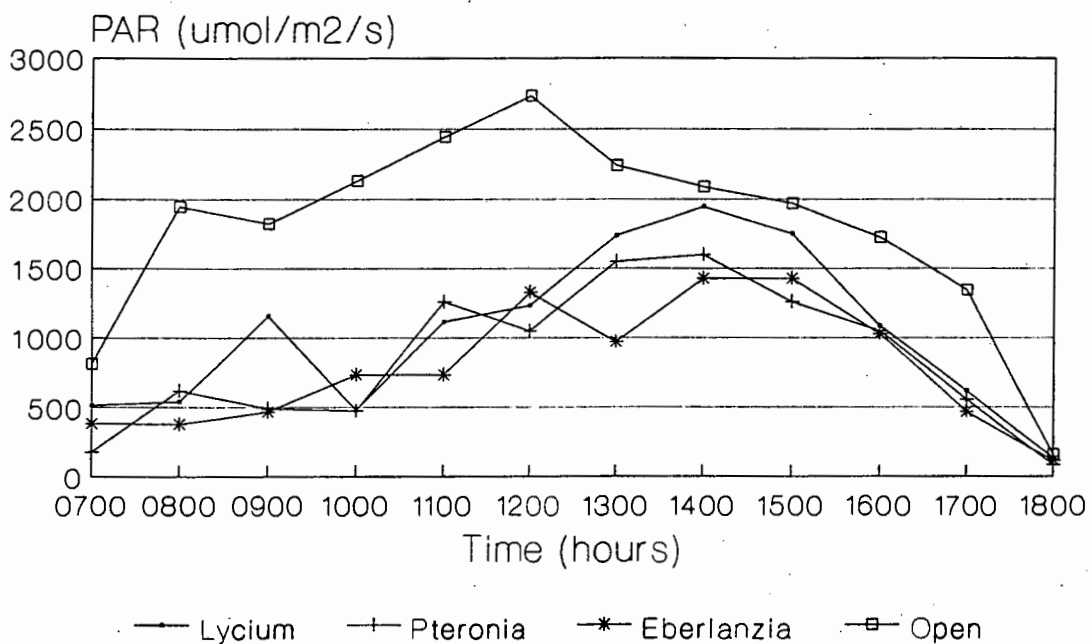


FIGURE 1.13: December hourly PAR in the open and beneath the canopies of three nurse plants

SOIL NITROGEN

The nitrogen data were analysed in two ways.

An analysis of variance was performed on nine soil replicates of each of the four microsites (open, Lycium, Pteronia and Eberlanzia), at both soil depths (0-5cm and 5-10cm).

Nitrogen levels of group 1 (open) and group 2 (Lycium) differed significantly. Nitrogen levels in the soil from beneath Pteronia and Eberlanzia did not differ from the levels in the open, beneath Lycium or each other (see Figure 1.14 and Figure 1.15). This trend was evident at both soil depths.

Four t-tests were also carried out on the data.

Nitrogen levels in the open were compared with nitrogen levels in the soil from beneath each nurse (in turn). (See Table 1.4b)

These tests yielded similar results to the ANOVAS i.e. only the nitrogen levels between the open and the nurse Lycium were significantly different.

Intervals for Factor Means

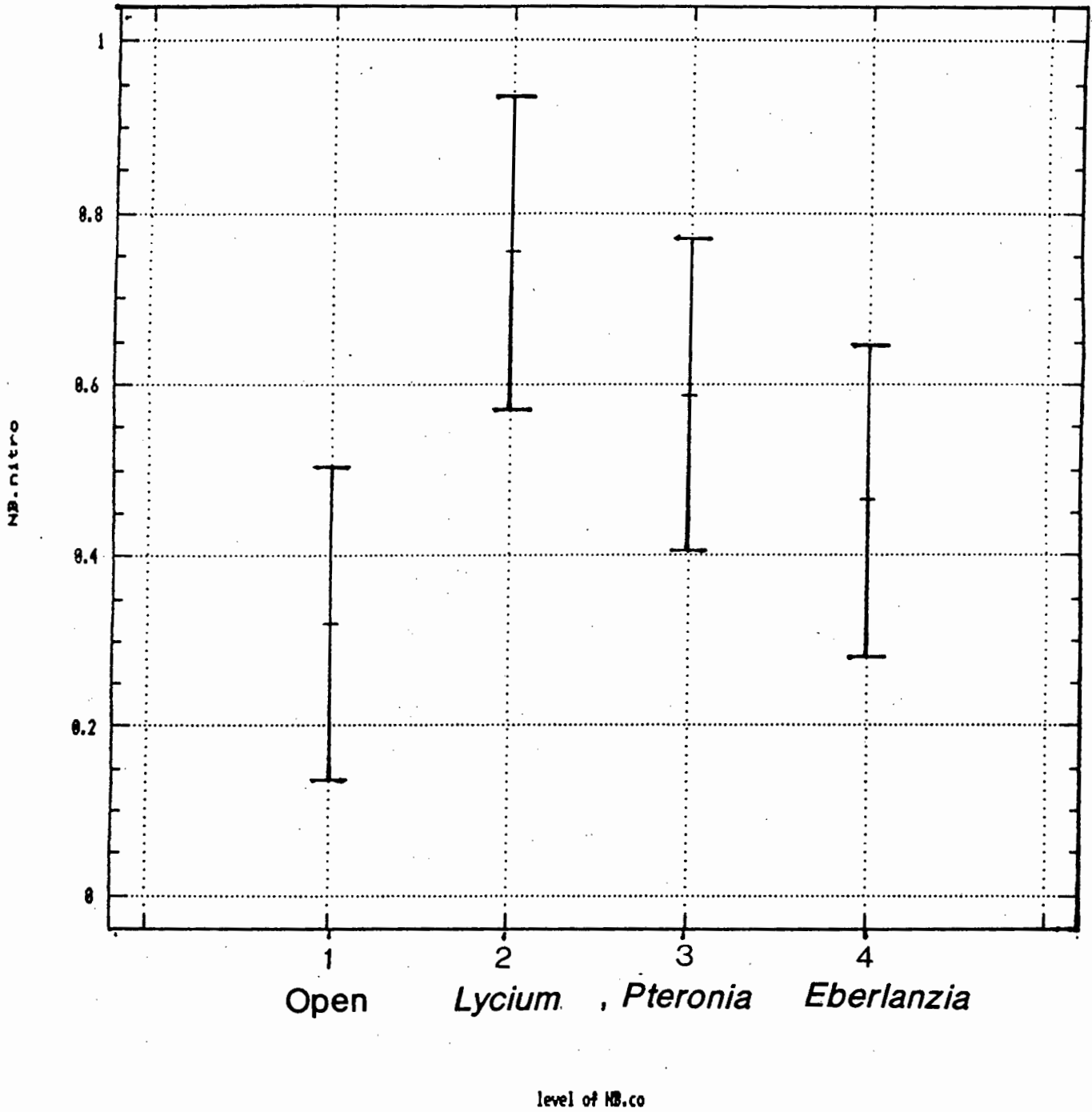


FIGURE 1.15: Means plot showing Total Soil Nitrogen levels in the open and beneath three nurse plants at the 5-10cm soil depth (n=40, 10each)

Intervals for Factor Means

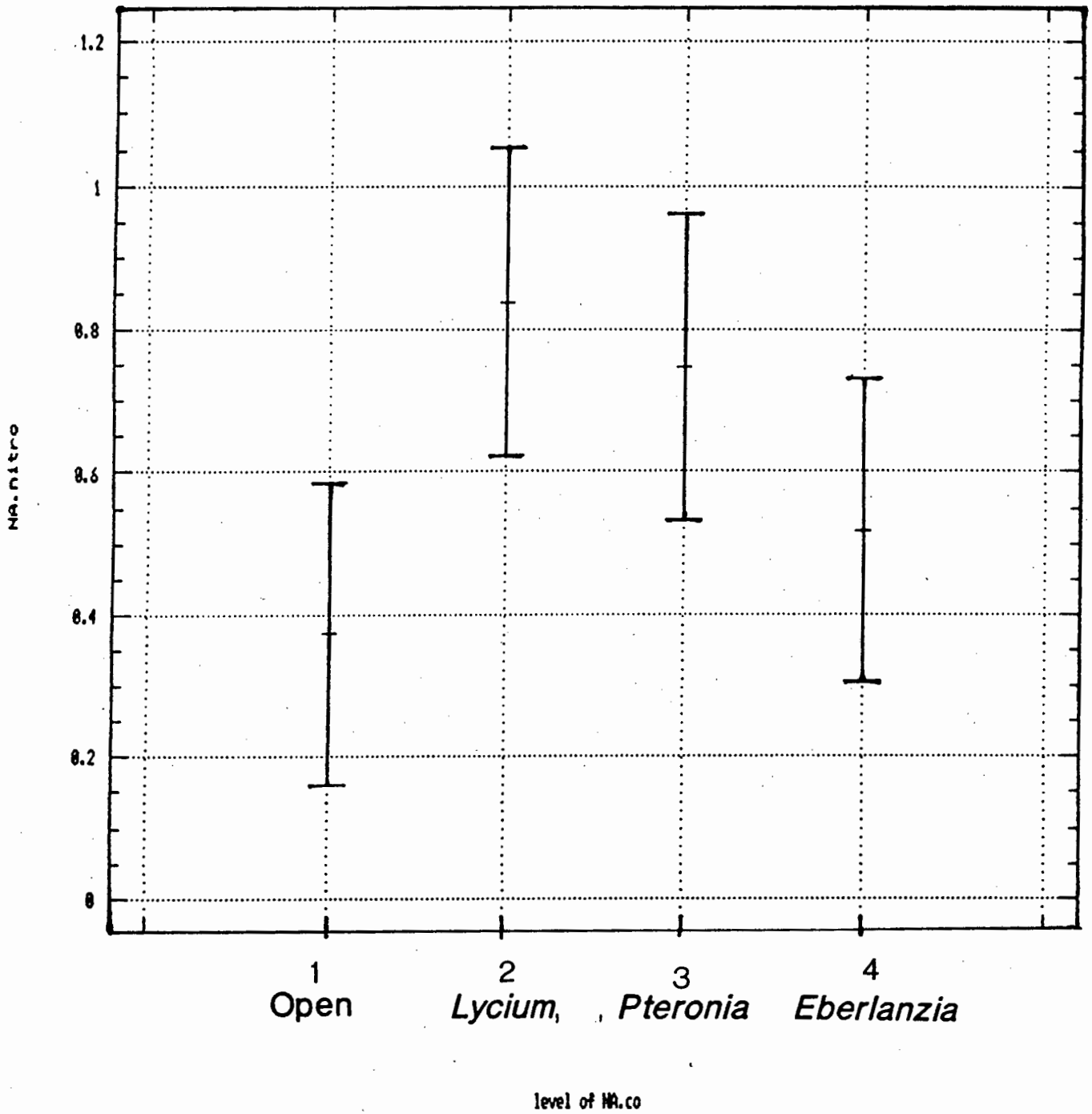


FIGURE 1.14: Means plot showing Total Soil Nitrogen levels in the open and beneath three nurse plants at the 0-5cm soil depth (n=40, 10each)

Table 1.4b: t-test results of Soil Nitrogen levels(mg/g)
 (Open vs Lycium, Pteronia and Eberlanzia)(n=10)

Microsite Pairs compared and Nitrogen level(+SE)	t	significance
1OPEN .398(.075) LYCIUM .789(.12)	2.76	0.013 *
2OPEN .398(") PTERONIA .691(.14)	1.79	0.089 ns
3OPEN .398(") EBERLANZIA .582(.07)	1.74	0.099 ns
4OPEN .349(.046) LYCIUM .708(.13)	2.63	0.016 *
5OPEN .349(") PTERONIA .546(.09)	1.97	0.064 ns
6OPEN .349(") EBERLANZIA .506(.07)	1.78	0.091 ns

* = $p < 0.05$

1-3 = Soil depth 0-5cm

4-6 = Soil depth 5-10cm

NURSE SIZE AND THE NUMBER OF PATIENT SPECIES:

The result of the ANOVA on the nurse diameters gave an insignificant result ($F = 1.236$ $p > 0.05$. Similarly there was no significant relationship between nurse diameter and the number of patient plants ($p > 0.05$, $r^2 = 0.18$, $df = 19$)

ROOT STUDY: Tylecodon versus three nurse species

100% of the root volume (per diameter class) of Tylecodon plants were found in the upper 10cm soil level. In comparison, small percentages of the root volume for each diameter size class were found at this soil level for Pteronia and Lycium. For Eberlanzia roots however in the 0.2-0.5mm category 71.8% was in the top 10cm of soil.

A clearer picture of the rooting patterns is given by disregarding the diameter size classes and examining only the percentage root volume at each soil depth (see Figure 1.16). While Lycium and Pteronia have less than 10% of their root volume in the top 10cm of soil , Eberlanzia has 41.3% in this soil level. Compared with Tylecodon then, Eberlanzia roots appear to overlap in vertical space with Tylecodon roots since 100% of its roots are in this soil level.

Lycium and Pteronia have the greatest proportion of their roots (90%) in the soil levels below the 10cm depth. It was clear that both these species have roots that extend well below 20cm but due to difficulties encountered it was not possible to excavate further.

Not only do Eberlanzia and Tylecodon roots overlap in vertical space but also tend to behave similarly in horizontal space (see Figures 1.19 and 1.17). Both these species roots are 'surface creepers' with their roots following in the directions of neighbouring shrubs.

The roots of the other plants excavated (Lycium and Pteronia) do not behave in this way. The only roots that are shallow for Lycium and Pteronia are thin, fibrous roots which do not extend much beyond the plant canopy(see Figures 1.18a and 1.20a). Figures 1.18b, (Pteronia), 1.19b (Eberlanzia) and 1.20b (Lycium) show the plans of the species roots at deeper soil levels.

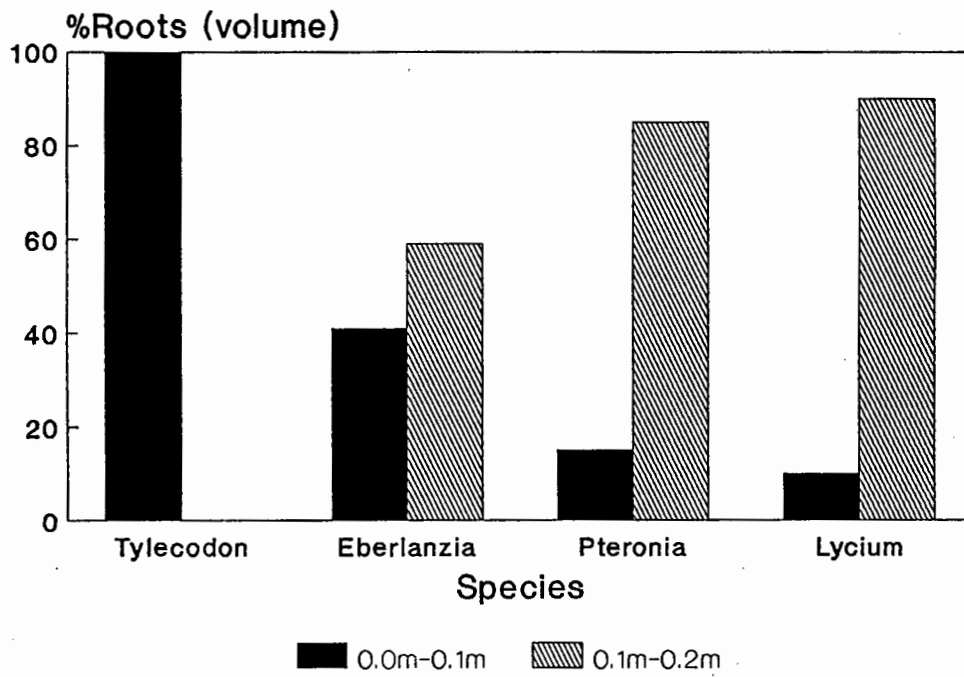
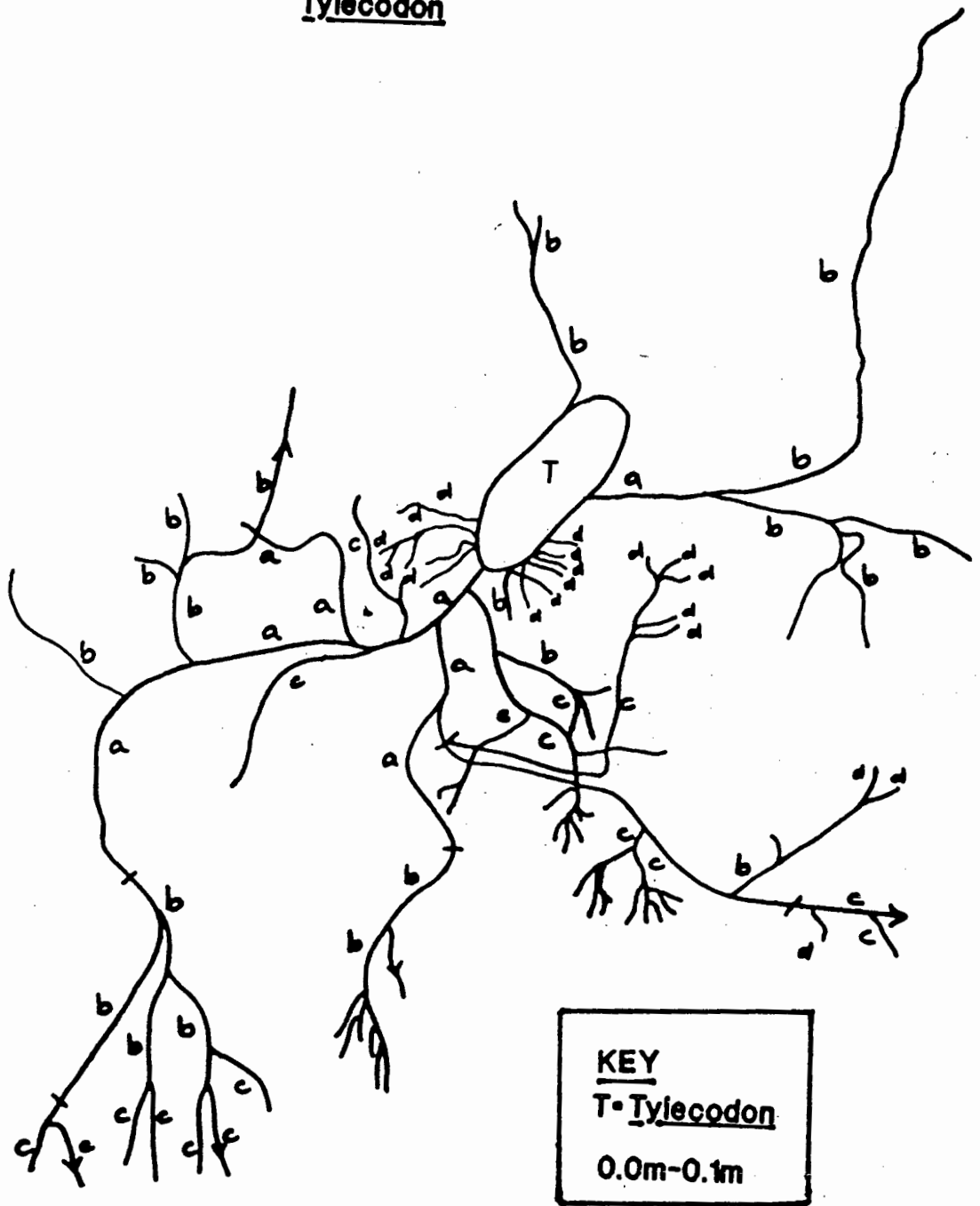


FIGURE 1.16: Root distribution (%root volume) at each soil depth of the patient Tylecodon in relation to three nurse plants.

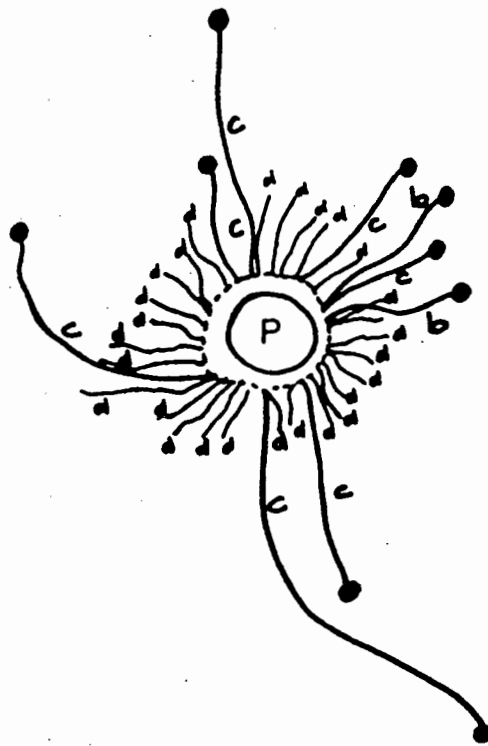
Tylecodon



20mm = 100mm

FIGURE 1.17: Plan of Tylecodon wallichii rooting pattern at 0.0m-0.1m depth, no roots below this depth (a,b,c,d refer to root diameter size classes, a=1-2cm; b=0.5-1cm; c=0.2-0.5cm and d= 0.2cm)

Pteronia



KEY
P = Pteronia
0.0m-0.1m
● to deeper levels

20mm = 100mm

FIGURE 1.18a: Plan of Pteronia pallens rooting pattern at 0.0m-0.1m soil depth (only 10% of the roots at this depth) (a,b,c,d refer to root diameter size classes, a=1-2cm; b=0.5-1cm; c=0.2-0.5cm; d= 0.2cm)

Pteronia

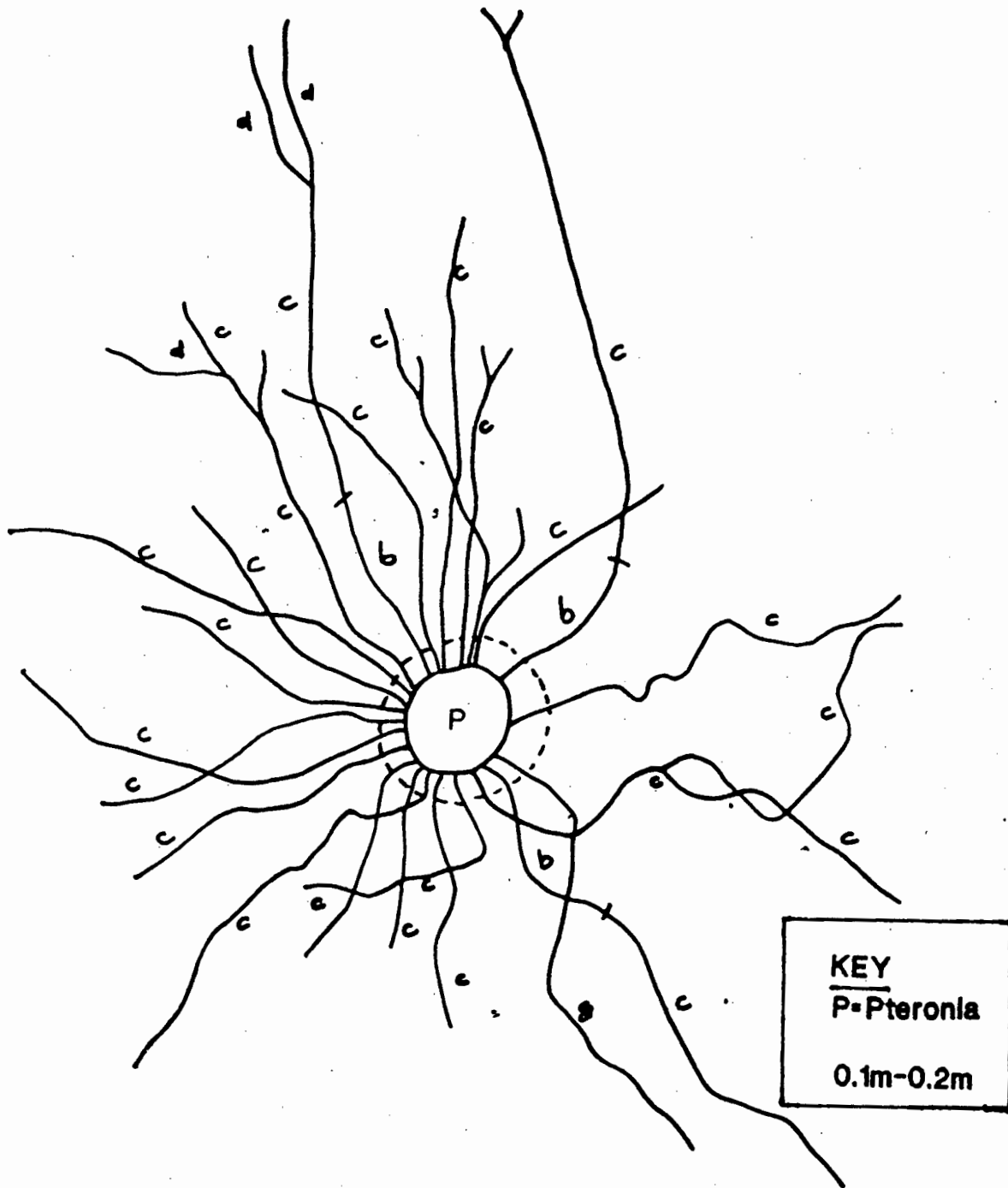


FIGURE 1.18b: Plan of nurse Pteronia pallens rooting at 0.1-0.2m soil depth (90% of the roots at this level and deeper) (a, b, c, d refer to root diameter size classes, a=1-2cm; b=0.5-1cm c=0.2-0.5cm; d= 0.2cm)

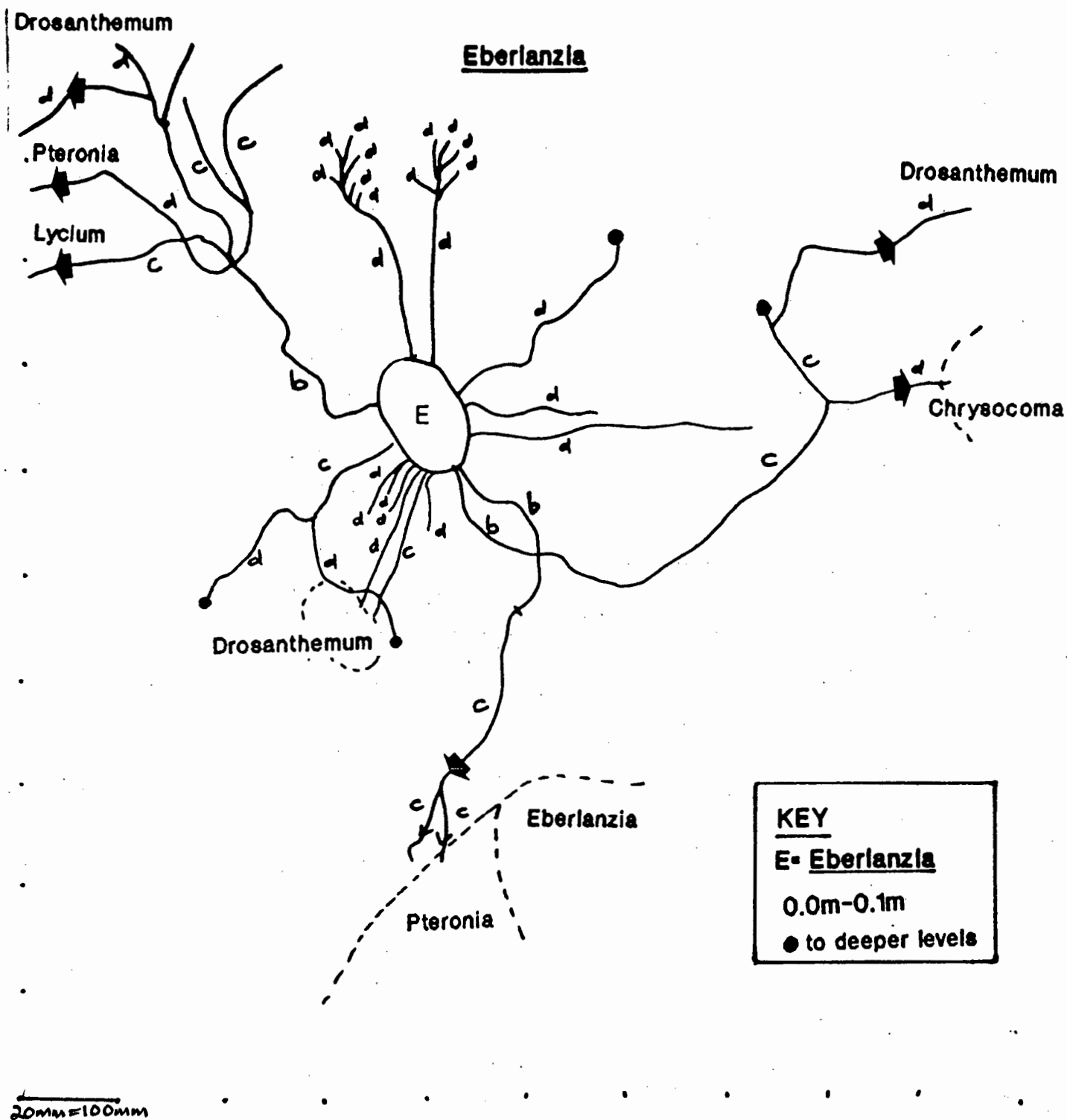


FIGURE 1.19a: Plan of nurse Eberlanzia rooting pattern at 0.0-0.1m soil depth (more than 40% of the roots at this depth) (a, b, c, d refer to root diameter size classes, a=1-2cm; b=0.5-1cm; c=0.2-0.5cm; d= 0.2cm)

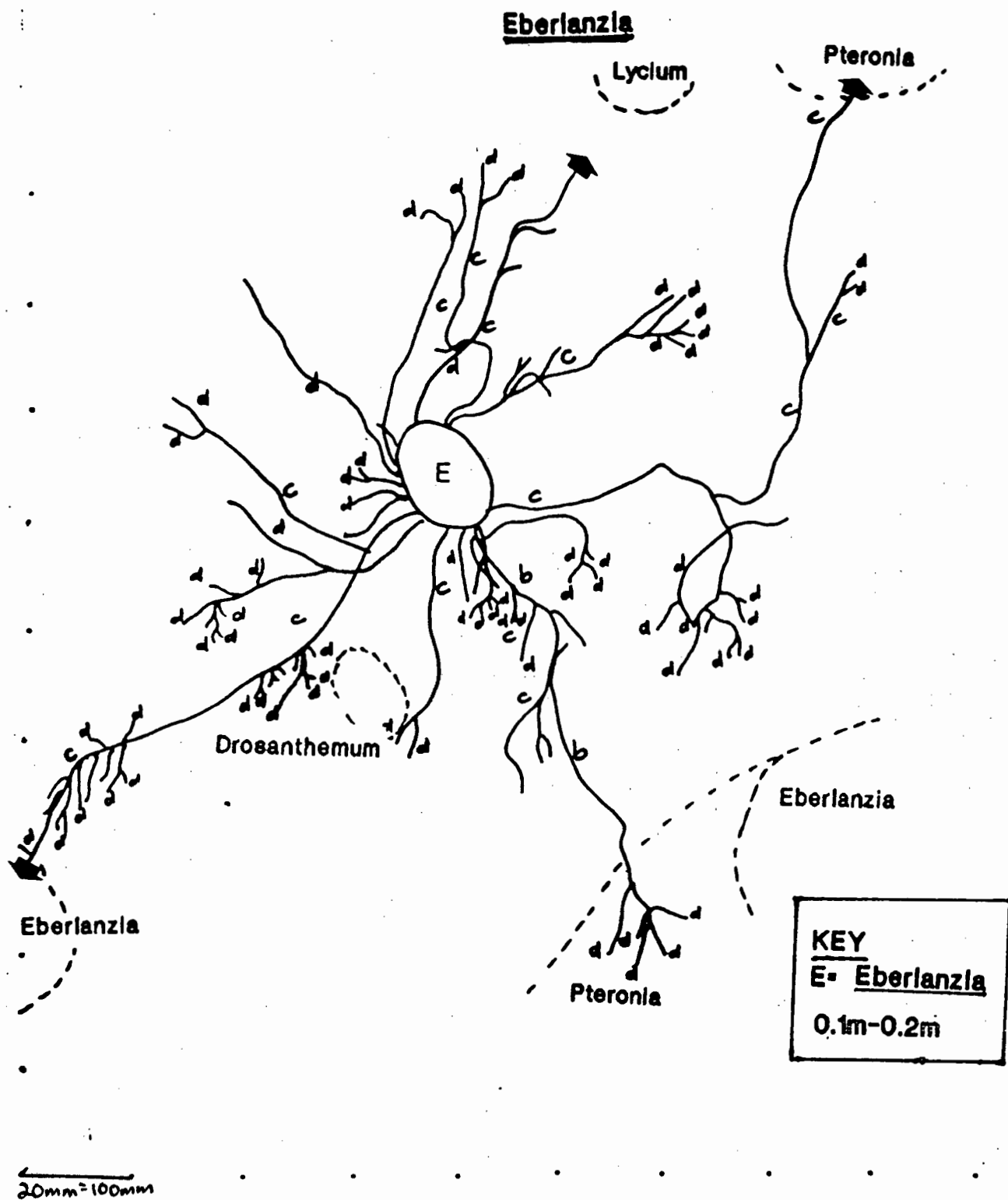
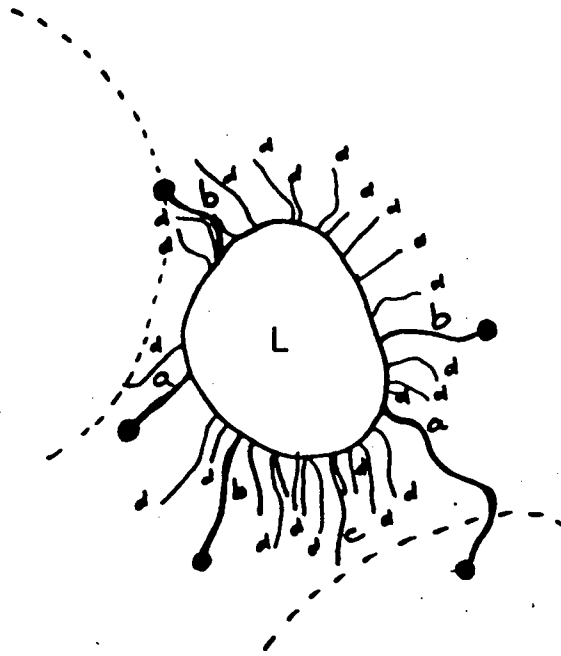


FIGURE 1.19B: Plan of nurse Eberlanzia rooting pattern at the 0.1-0.2m soil depth (60% of the roots at this depth) (a, b, c, d refer to root diameter size classes, a=1-2cm; b=0.5-1cm; c=0.2-0.5cm; d= 0.2cm)

Lycium

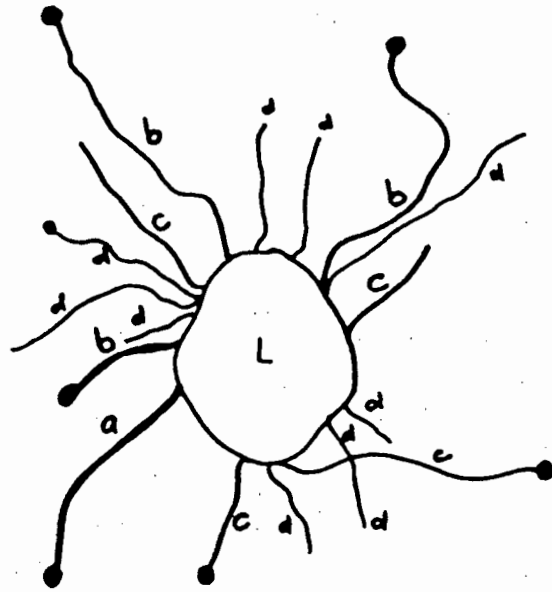


KEY
L = Lycium
0.0m-0.1m
● to deeper levels

20mm = 100mm

FIGURE 1.20a: Plan of Lycium rooting pattern at 0.0-0.1m soil depth (less than 10% of the roots at this depth) (a,b,c,d refer to root diameter size classes, a=1-2cm; b=0.5-1cm; c=0.2-0.5cm d= 0.2cm)

Lycium



KEY
L = Lycium
0.1m-0.2m
● to deeper levels

20mm = 100mm

FIGURE 1.20b: Plan of Lycium rooting at 0.1-0.2m soil depth (90% of the roots at this level and deeper) (a,b,c,d refer to root diameter size classes, a=1-2cm; b=0.5-1cm; c= 0.2-0.5cm; d= 0.2cm)

DISCUSSION

EXPOSED VERSUS NURSED

Tylecodon wallichii does not occur in the open exposed sites but only under the canopies of perennial shrubs. The quadrat method of investigation is descriptive and reveals only that no establishment of this plant is presently occurring in the open. This could merely be a result of wind blown seeds getting caught in the canopies of the shrubs. The transplant investigation however clearly shows that "patient" plants like Tylecodon wallichii are dependent on the nurse plants. Tylecodon wallichii individuals transplanted into the open died whilst those transplanted beneath the nurse plants showed evidence of new growth.

Seedling mortality in open sites and seedling survival beneath nurse plants in arid areas has been recorded in many studies (Steenbergh and Lowe 1969, Nobel 1980, Turner et al 1966). Protection afforded by the nurse plants include the amelioration of temperature extremes (Jordan and Nobel 1979, Nobel 1980, Steenbergh and Lowe 1969). Jordan and Nobel (1979) emphasized the importance of nurse plants in lowering soil temperature which in turn allowed more soil moisture to be retained and this extended the growing season for the patient Agave deserti. Nurse plants also offer concealment from herbivores (Niering, Whittaker and Lowe 1963, M^CAuliffe

1984). In this study there was no evidence of herbivory so survival and mortality are more likely to be related to the abiotic factors of temperature, moisture, photosynthetically active radiation (PAR) and soil nutrients.

Seedlings of desert plants are exposed to a severe microenvironment. For example in the first years of life of the Sahuaro cactus, its roots are in the top 1-2cm of the soil, its stem near the soil surface (Steenbergh and Lowe 1969). Any factor then which tends to modify those microenvironmental extremes of temperature and drought will have a profound effect upon the survival of the young plant (Geiger 1965 cited by Steenbergh and Lowe 1969).

A comparison of the microenvironmental conditions beneath the nurse Pteronia pallens and those in the open is made in an attempt to understand this mortality in the open.

A note must be made here that the logging period in December (Summer) was during unusually cool, cloudy weather. Since this is not representative of the Karoo in Summer only March Summer readings are discussed and compared with Winter temperatures.

The cooler daytime Summer soil temperatures and warmer night time temperatures in Winter beneath the nurse plant might explain the survival of the patient transplants in this microsite. I believe that the soil temperature maximum of 44°C in Summer and a minimum of nearly -1°C in Winter was lethal to the patient plant Tylecodon wallichii. This patient has succulent leaves and is therefore susceptible to

freezing damage, thus with soil temperatures reaching below zero in the open sites in Winter and not beneath the nurses, death of the exposed transplants might be explained.

Both extremes of temperature have been suggested as possible reasons for the mortality of plants in exposed sites in a number of studies. Steenbergh and Lowe (1976) found freezing survival of young Carnegieia gigantea individuals to be higher when under the nurse Cercidium microphyllum. Nobel (1980) demonstrated that nurse plants reduced IR loss to the sky, thus protected the meristems of C.gigantea juveniles from freezing damage. Plants beneath nurses in the current study however responded to the rain in May showing evidence of new growth, those in the exposed sites did not. This indicates that perhaps the latter were already dead. May being very early Winter it is unlikely that minimum temperatures at this stage were lethal and the Summer conditions of high soil temperatures and presumably minimal soil moisture were probably responsible for the death of the patients in the open.

Shading by the nurse plant decreases PAR available to the associated seedling and may reduce growth when compared with an exposed seedling (Franco and Nobel 1989). Though PAR levels beneath the canopies of the nurse plants were much lower than in the exposed sites (March, September and December) it appears quite insignificant since growth did not even occur in the open sites. Higher PAR levels were not advantageous since the deleterious effects of extreme temperatures were probably the overriding factors. PAR levels though low were sufficient to allow for substantial growth beneath the nurse.

Soil nitrogen levels beneath nurse plants have been found to be significantly higher than in adjacent open sites (Turner et al 1966, Garcia-Moya and McKell 1970, Franco and Nobel 1989). Infact, higher soil nitrogen levels may be significant when considering growth of patient plants since this may partially offset the reduced seedling growth caused by reduced PAR and competition with the nurse for water (Franco and Nobel 1989).

In the transplant experiment however, soil from beneath a nurse was used for transplants in the open, so that soil nitrogen levels were similar. Despite this, plants still died, indicating that other abiotic factors were more important. Whether varying nitrogen levels in different microsites are important to the success of patient species is discussed below.

To summarise, clearly Tylecodon wallichii requires a nurse plant for successful establishment. It cannot tolerate the physical conditions in the exposed sites, these being high Summer soil temperatures and perhaps low water availability as well as exposure to freezing in Winter.

NURSE SPECIFICITY

From the analysis of the distribution of patient species beneath the nine nurse species, clearly not all nurses are equally effective. Elytropappus rhinocerotis, Pteronia pallens and especially the Lycium species are more common as nurse plants whilst the dwarf, leaf succulent shrubs like Drosanthemum ligue and Eberlanzia ferox are 'poor' nurses. The observed number of patient species occurring beneath the other nurses (Pteronia paniculata, Helichrysum excisum, Galenia africana and Ruschia pungens) were intermediate between the more effective nurses and the 'poorer' nurses.

Initially, it was thought that the size of the nurse plants may be important in determining whether they were good or poor nurses ie. larger canopies provide a greater "sheltered" area and therefore would support a larger number of patient plants. The analysis of variance on the sizes of all nine nurse species and the regression analyses (nurse

diameter versus patient number) revealed however that canopy size was not important (see results).

Steenbergh and Lowe (1969) suggested that the association of nurse plants with others was not linked to particular species but rather to certain characteristics. If we consider other structural characteristics apart from canopy size for example height and branching, this also does not appear to be important since the preferred nurses (Elytropappus and Lycium) are structurally very different. This Lycium species seldom taller than 0.5 metres (pers obs) is a rather dense thorny shrub with branching close to the ground. Elytropappus on the other hand is often taller than 1 metre with less dense branching starting higher than ground level. So, comparing the more effective nurses, structure of the canopies in isolation does not appear to be very important. The poor nurses however do have similar structural characteristics. Both Eberlanzia and Drosantheum are dwarf, small leaf succulent shrubs with heights of approximately 0.5 metres. The fact that the latter two nurse species are quite erect in form might lend some support to the importance of shrub structure for seed trapping. It is interesting to note that the same Eberlanzia species in a study by Yeaton and Esler (1990) appeared to provide an ideal refuge for certain woody shrubs. The structural form of the species at their study site (near Prince Albert in the Karoo) differ to the Anyberg Eberlanzia plants in that they are less erect,

branching is at ground level and perhaps this canopy structure enhances seed and organic material trapping. Seed trapping alone does not explain the lack of patients under other species, see Chapter 2 where further studies revealed that initial establishment beneath this nurse could occur.

A closer examination of the microclimates beneath these different nurses may reveal whether the above ground structures are important or not. Here, only March (Summer) and June (Winter) soil temperatures are discussed. Air temperatures beneath all three nurses showed similar daily trends and were considered unimportant.

In the investigation, most of the patient plants were dwarf succulents except for Tylecodon wallichii. Lycium and Elytropappus are the favoured nurses for the dwarf succulents in general. Pteronia pallens in this study is neither a very good nor poor nurse when considering the dwarf succulent patients, however it will be referred to often since it is the favoured nurse for the patient Tylecodon wallichii (the main study species).

High soil temperatures beneath Eberlanzia nurses cannot be suggested as reasons to explain why dwarf succulents avoid this nurse since they can tolerate the high soil temperatures beneath Lycium. In Summer, the high soil temperatures beneath Lycium (similar to those in the open, see Fig 1.3) indicates that the avoidance of high temperature is not an important factor for the dwarf

succulents. The microclimate beneath Pteronia in Summer is much cooler and though probably not important to the dwarf succulents, it may well play a role in the success of Tylecodon beneath this nurse.

The night time Winter soil temperatures for Lycium and Eberlanzia are similar and therefore do not explain why Lycium is a more effective nurse. It could be suggested that for Tylecodon wallichii, the warmer night time temperatures beneath Pteronia in Winter may be significant when trying to determine why this species is the more effective nurse for this patient. In general, however, soil temperatures in Winter and Summer do not explain why some nurses are more effective than others.

PAR levels beneath the different nurse canopies show many fluctuations (a problem with instantaneous light readings). The trends are somewhat vague between the different nurse species and the only obvious difference is between the open sites and under nurses.

So far none of the above ground factors ie. canopy structures and their effect on the microclimate strongly indicate why some nurse plants are better than others. Physiological experiments on the temperature tolerances and light responses of the patient plants might help in determining how different nurses affect the establishment and success of patient plants.

Soil nitrogen levels are highest beneath Lycium when compared with other nurse species but significant differences were only detected between soil from the open and Lycium, not among the different nurses. Here again higher soil nitrogen levels may be significant for the success of the dwarf succulents but not necessarily for Tylecodon wallichii.

The occurrence of higher nitrogen levels in the soil beneath shrubs in comparison to soil in the open is common and has been found in a number of investigations (Turner et al 1966, Garcia-Moya and M^CKell 1970, Nobel 1989). The effect of different nutrient levels under different nurses on nurse specificity has not been examined elsewhere but Shreve (1942) commented on there being no young plants beneath the large succulents and semi-succulents of the North American deserts and suggested that this was because they cast little shade and drop no litter. In a study concerning shrub dependent desert annuals Muller and Muller (1956) suggested that these annuals would grow beneath those desert shrubs which accumulate mounds of wind blown organic debris, and that this may be correlated with the water holding capacity of organic colloids. Muller (1953) showed that the differential effects of Franseria dumosa and Encelia farinosa in harbouring shrub dependent herbs could be ascribed to the failure of the latter shrub to accumulate a mound of wind blown soil and organic debris favourable to the needs of such herbs. Gray and Bonner (1948) however

explained this difference between Encelia and Franseria in harbouring herbs in terms of a growth inhibiting toxin present in Encelia. When considering the dwarf succulents then, there is a clear "preference" for Lycium nurses. This nurse has a low dense canopy structure ideal for trapping wind blown material, it is deciduous and therefore contributes to the nutrient level in the soil beneath it and consequently soil nitrogen levels here are highest. These factors could explain why Lycium is an effective nurse for the dwarf succulent patient plant guild in the succulent Karoo.

It would be unrealistic to single out one microenvironmental factor determining why a nurse is effective or not, since a combination of factors are probably responsible, as discussed above. However, for the dwarf succulents found here I would emphasize less the effects of temperature and PAR beneath the different nurse species and more on the litter accumulation and its effects on addition of nutrients and soil moisture.

Different patient species or different guilds of patient species might require different environmental conditions. To understand why some nurses are more effective than others the physiological needs and tolerances of different patients would have to be examined in conjunction with the conditions beneath the different nurse species.

After critical establishment, subsequent survival of patients may depend on the compatibility of nurse and patient rooting systems.

Pteronia pallens is an effective nurse for Tylecodon wallichii and their rooting systems are separated in both vertical and horizontal space (see results). Eberlanzia ferox is a poor nurse for Tylecodon wallichii and in general for other patient plants. This nurse has a shallow rooting pattern, resulting in extensive overlap with most patient plants. This might result in some form of negative interference between the two, thus bringing about a negative pattern association. An effective nurse such as Lycium has the majority of its roots at soil levels much deeper than the common patient plants and therefore provides a more favourable below-ground environment for the various patient plants..

What has been shown in this chapter is that there is a dependence on nurse plants and that some plants make better nurse plants than others. The advantages of being nursed probably depend on a combination of environmental factors, above and below ground and that this would vary depending on each patient species requirements and characteristics.

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CHAPTER TWO

Nurse preference by one patient plant - *Tylecodon wallichi*

INTRODUCTION

In the first chapter it was established that not all nurse plants were equally effective. This aspect is pursued here by focussing on only one patient plant-*Tylecodon wallichi*.

This chapter examines the possible influences of 'nurse specificity' on the plant community. For certain plants in the Karoo nurses are important for regeneration and it has already been established that not all nurses provide equally favourable microsites for regeneration. This chapter investigates the causes of the patterns found in Chapter 1 by means of manipulative experiments to emphasise the phenomenon of nurse specificity.

Chapter two constitutes three sections. The first section is descriptive and concentrates on the success of the patient (in terms of size and fecundity) beneath four different nurse plants. *Pteronia pallens* appears to be one of the more effective nurses for *Tylecodon wallichi*, unlike *Eberlanzia ferox* which tends to be avoided. The association between *Pteronia* and *Tylecodon* is therefore established first.

Following this , a series of manipulative experiments were undertaken in the field to determine whether survival and reproductive success of the patient plant differed under two nurse plants-Pteronia and Eberlanzia.

Possible factors determining the success of the patient beneath Pteronia pallens are examined in the third section. Here a second Pteronia species, (Pteronia paniculata) which occurred on an adjacent but different soil from Pteronia pallens and Eberlanzia ferox was used. Though Tylecodon wallichii is occasionally nursed by this second Pteronia species, no large, reproductive individuals have been found beneath this nurse. This suggests that the Tylecodon patient is not as successful in terms of size and fecundity beneath this second Pteronia nurse. In the third section of the chapter, I investigate whether Tylecodon wallichii is specific to Pteronia pallens rather than Pteronia paniculata because of the nurse plants or because of the soils on which they occur.

So, two aspects are examined here, firstly, within one community type is there proof of certain shrubs being selected for as nurses more than others and secondly, across different plant communities how does soil or change in nurse plants explain changes in success of patients.

To my knowledge there has been no previous work done on the varying success of patient plants beneath different nurses. Emphasis in the past has always been on the successful establishment of seedlings under nurse plants generally compared to establishment in the open, and not on comparisons between nurses.

METHODS

1 (i) PATTERNS OF TYLECODON WALLICHI NURSE PLANT PREFERENCE

Beneath thirty randomly selected (Catana 1963) individuals of each of four different nurse species (Pteronia pallens, Eberlanzia ferox, Galenia africana and Ruschia pungens), the number of Tylecodon individuals were counted and measured for height and diameter. The number of patient Tylecodon plants that had flowered was also noted.

A similar investigation was undertaken but this time beneath dead Pteronia, dead Eberlanzia and dead Tylecodon plants. This was done so as to determine whether establishment was possible beneath dead plants as well.

The fecundity and size distribution data were examined by means of bar graphs.

(ii) EFFECTS OF DIFFERENT NURSES ON FLOWERING (REGRESSION TECHNIQUES)

One hundred standard sized Tylecodon plants (>15cm in diameter) were identified beneath fifty Pteronia pallens nurses and fifty Eberlanzia ferox nurses. In two 50m by 50m plots suitably sized Tylecodon plants were censused under every Pteronia and Eberlanzia encountered using the Wandering Quarter method (Catana 1963). The diameter and

height of each Tylecodon was measured and the number of flowering stalks per plant were counted.

In the data analysis the sizes and the number of flowering stalks of the Tylecodon patients beneath the two nurses was compared (t-test and Mann-Whitney U test respectively).

Tylecodon size was regressed against its number of flowering stalks for both nurse plants. The regression slopes were compared (Zar 1984).

2(i) ESTABLISHING THE PTERONIA-TYLECODON ASSOCIATION

In eight, 5m x 5m quadrats all Pteronia pallens, Eberlanzia ferox and other shrub species were measured for canopy diameters. All canopy areas were calculated in each quadrat and these values were used to determine the proportion of each nurse species in each quadrat. 'Other' species (all plants except Pteronia and Eberlanzia) canopy areas were pooled.

The occurrence of Tylecodon under every nurse species was noted. In the first investigation only the presence or absence of Tylecodon was noted. In the second investigation (see Tables 2.3 and 2.4) the number of times that Tylecodon occurred under any one nurse was also taken into account. Expected frequencies of Tylecodon were generated per quadrat depending on the relative area occupied by Pteronia pallens and Eberlanzia ferox (see Table 2.2).

This technique was based on a method used by Cody (1986).

The number of occurrences of Tylecodon wallichii under all Pteronia pallens nurses in one quadrat was multiplied by the proportion of Pteronia in that quadrat to generate the expected frequency of occurrence of the patient beneath Pteronia. The expected frequency beneath Eberlanzia was generated in a similar way. The observed and expected frequencies of Tylecodon were compared.

(ii) MANIPULATIVE EXPERIMENTAL METHODS TO INVESTIGATE
PATIENT PLANT SUCCESS

A number of transplants were done to experimentally test for differences in performance of the patient Tylecodon wallichii beneath two different nurses - Pteronia and Eberlanzia. Both young and mature Tylecodon individuals were used.

Twenty young Tylecodon plants were collected, measured and transplanted beneath Eberlanzia ferox. Another twenty Tylecodon plants were collected, measured and transplanted beneath twenty Pteronia pallens nurses.

Patient Tylecodon plants were monitored every third month (for a year) by measuring stem diameter, maximum leaf length and counting the number of leaves.

Since the Tylecodon plants were dormant and had no leaves, at the time of transplants, the diameters of all the plants were compared (by t-test) in the Eberlanzia and Pteronia treatment to check that there was no bias in size at the start of the experiment. Differences in growth between the patients under the two nurses were compared using a t-test. The maximum growth period was April, so leaf areas for this period only were compared statistically.

To experimentally test the effects of nurse plants on flowering, twenty adult Tylecodon plants were collected and measured for diameter and height. The number of flowering stalks were counted. Ten individuals were planted beneath Eberlanzia nurses and ten beneath Pteronia pallens.

The number of flowering stalks were counted again after the flowering season for Tylecodon wallichii in December (at Anysberg). The number of stalks before and after transplanting were compared using a non-parametric Mann-Whitney U test.

3. MANIPULATIVE EXPERIMENTS TO DETERMINE THE EFFECTS OF SOIL VERSUS NURSE CANOPY

The experimental design is outlined in Table 2.1.

Unlike in the previous section which involved manipulative experiments within one community using two different nurse species, this section examines the effects of soil versus nurse canopy in a different plant community (see Plate 6). Pteronia paniculata is the dominant nurse shrub in this

community and often has a second Tylecodon species beneath it (Tylecodon reticulatus (L.f.) Tolken,. This community has established on a different soil. The soil here is more sandy, rocky and red-brown in colour whilst the Pteronia pallens - Eberlanzia ferox community occurred on a sandy-clay-loam soil which had very few surface rocks and was dark brown in colour.

One hundred young Tylecodon wallichi plants were collected in February 1990. Each was transplanted in polystyrene cups so that the soil environment could be controlled. The bottom of these cups were removed so that the transplants were not completely isolated from the surrounding soil environment. Plants were potted in soil from either their common nurse (Pteronia pallens) or in soil from Pteronia paniculata, this constituted the soil control and soil treatment respectively. Fifty were transplanted in this way and all were placed beneath the common nurse Pteronia pallens. Twenty-five of the remaining fifty plants were transplanted beneath the second Pteronia species in soil from Pteronia pallens, this was the nurse treatment. The rest of the plants were transplanted beneath the second Pteronia species and in soil from this nurse as well. This constituted the combined soil and nurse treatment. Each plant was numbered and tagged.

All plants were measured for height and stem diameter at the start of the experiment. No leaves were present on collection of the plants as they were dormant. The transplants were monitored every second month, when stem diameter, maximum leaf length and the number of leaves were recorded. Tylecodon wallichii growth could in this way be compared for plants growing beneath their common nurse but on a foreign soil, in their common soil but beneath a foreign nurse and in a foreign soil beneath a foreign nurse.

To check that there was no plant size bias in the beginning of the experiment for the various treatments, all diameters were compared using a one-way analysis of variance.

To determine the effects of soil and nurse canopy and the combined effect, a two-way analysis of variance of the leaf areas of all the plants was done. Leaf areas during the maximum growth period were used (June 1990).

Leaf area estimates for Tylecodon were based on leaf length measurements. Twenty Tylecodon wallichii leaves were collected, measured for leaf length and leaf area was calculated using the formula for the area of a cylinder ($2rl$) since Tylecodon wallichii leaves are cylindrical. Leaf length was regressed against leaf area and the equation of the regression, $y = 0.059x + 10.17$ was used to determine all leaf areas from the maximum leaf lengths measured in the field. To arrive at values for whole plant leaf areas, leaf area (calculated from the maximum leaf length measurement) was multiplied by the number of leaves counted (in the field).

Table 2.1 :Transplant Experimental design to examine the effects of Soil versus Nurse Canopy (25 of each)

<u>Nurse Pteronia pallens</u>		<u>Nurse Pteronia paniculata</u>	
P.pallens Soil	P.paniculata Soil	P.pallens Soil	P.paniculata Soil
Control	Soil Treatment	Nurse Treatment	Soil and Nurse Treatment
1	2	3	4

KEY

- 1 = Pteronia pallens nurse canopy and P.pallens soil
- 2 = Pteronia pallens nurse canopy and P.paniculata soil
- 3 = P.paniculata nurse canopy and P.pallens soil
- 4 = P.paniculata nurse canopy and P.paniculata soil



PLATE 6: A different plant community adjacent to the main study site. It occurs on a different soil and the dominant shrub is Pteronia paniculata.

RESULTS

(i)

PATTERNS OF TYLECODON NURSE PLANT PREFERENCE :

SIZE AND FECUNDITY OF TYLECODON WALLICHI BENEATH DIFFERENT NURSES

From the bar graphs (figure 2.1) it is clear that many Tylecodon individuals establish beneath all four nurse plants (Pteronia pallens, Galenia africana, Ruschia pungens and Eberlanzia ferox). For the larger diameter classes however there is a decline in the number of plants occurring beneath all four nurses examined. Large Tylecodon plants (21-25cm diameter category and above) are found beneath Pteronia, Galenia and Ruschia but not Eberlanzia. Most of the large patient Tylecodon plants are found beneath Pteronia pallens.

Examining the size distribution of the patient plants beneath dead nurses (see figure 2.2) we can see that many young individuals are found beneath dead Pteronia, dead Eberlanzia and dead Tylecodon, indicating that initial establishment does occur beneath dead plants. Large Tylecodon plants were only found with dead Pteronia pallens and this is expanded on in the next chapter.

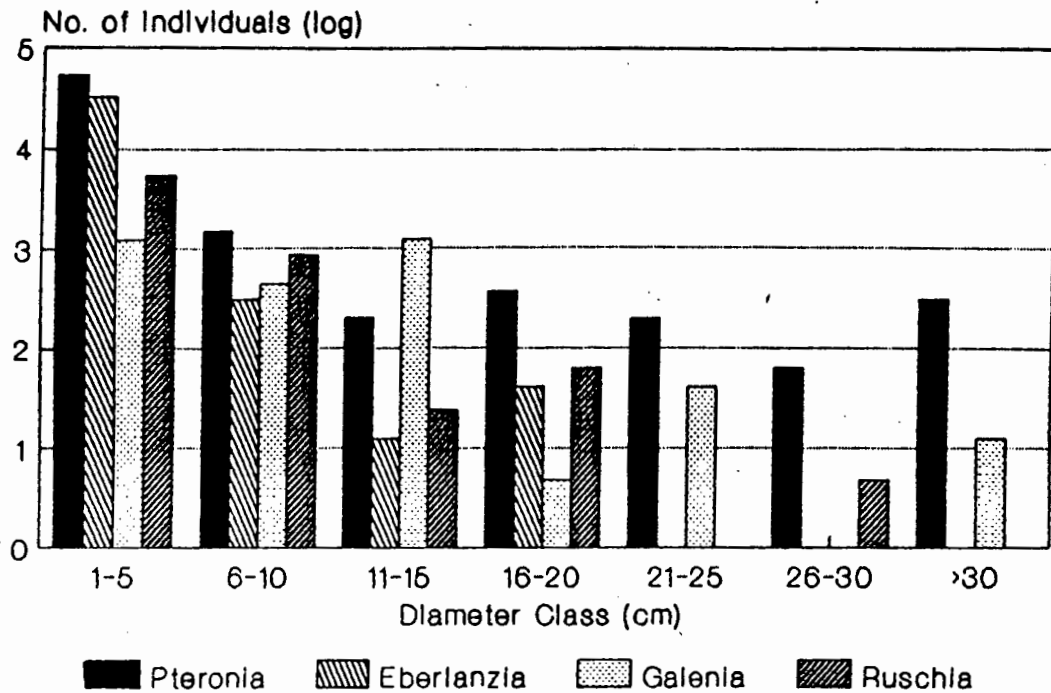


FIGURE 2.1: Tylecodon size distribution (using plant diameter) beneath four living nurses.

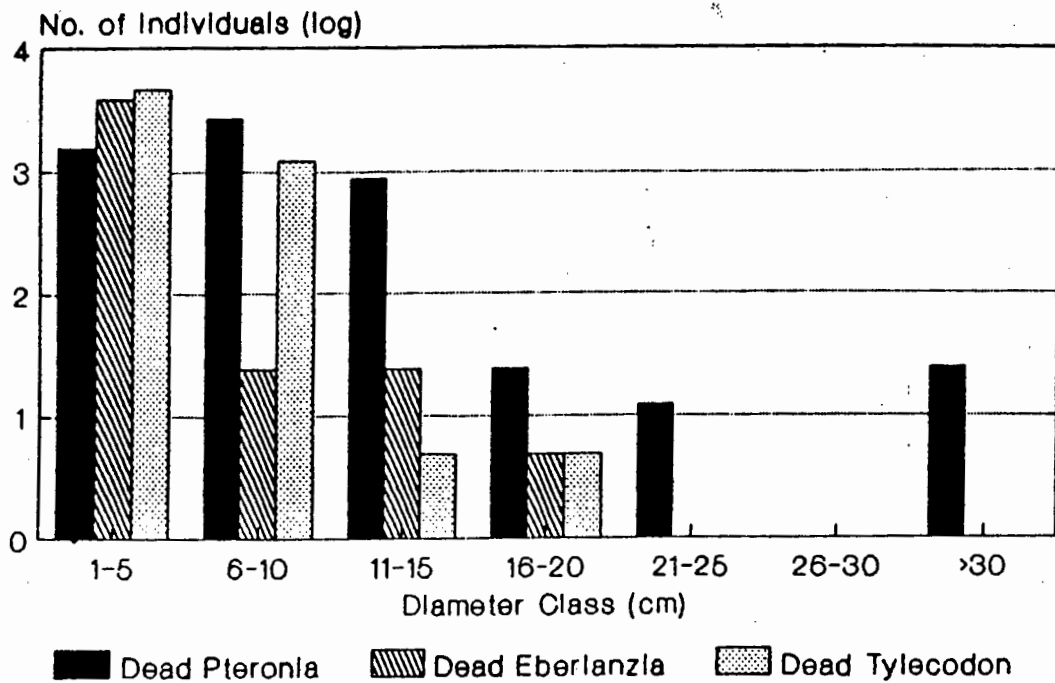


FIGURE 2.2: Tylecodon size distribution (using plant diameter) beneath four dead nurses.

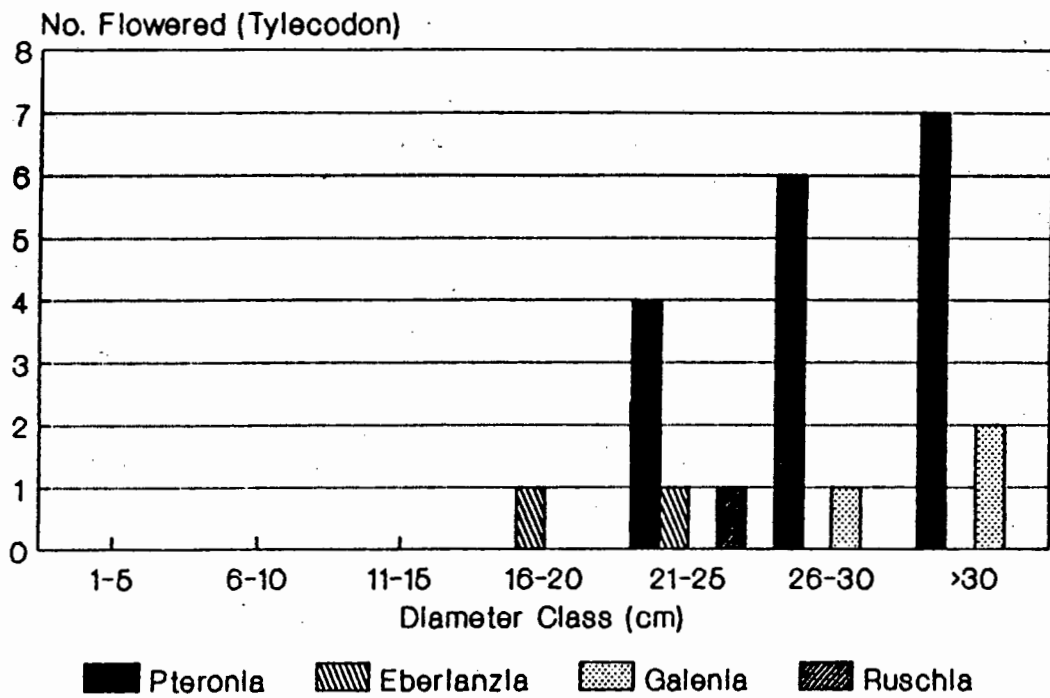


FIGURE 2.3: Distribution of reproductive Tylecodon plants beneath for living nurse plants

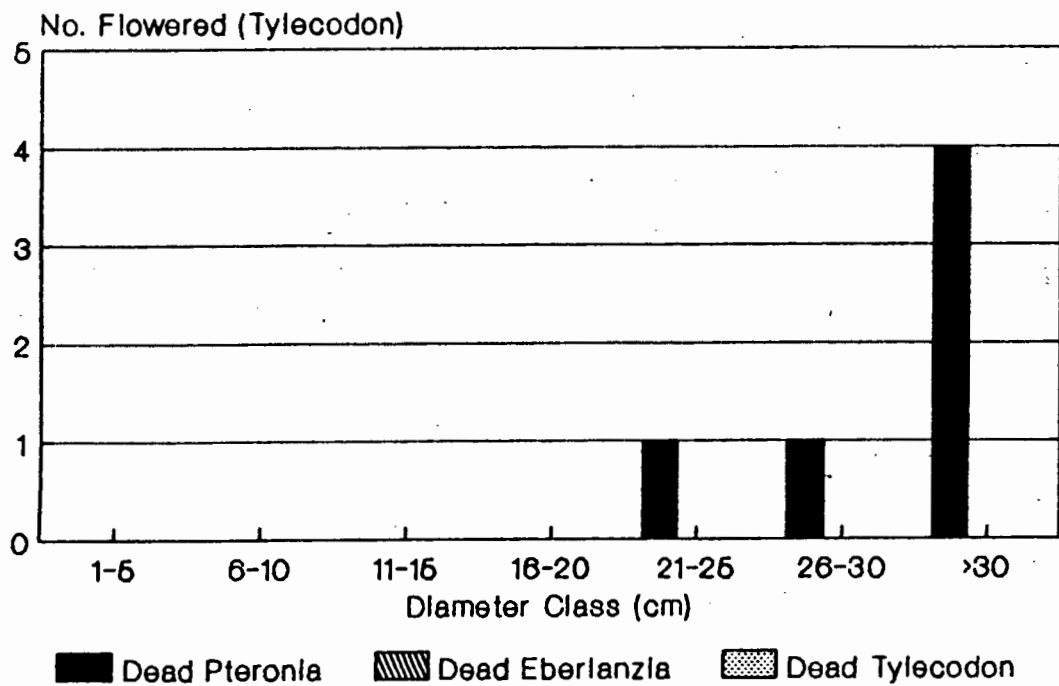


FIGURE 2.4: Distribution of reproductive Tylecodon plants beneath four dead nurse plants

In so far as the distribution of reproductive individuals of Tylecodon wallichi goes, most occur beneath Pteronia pallens (see figure 2.3). A total of twenty three reproductive individuals were found. Of these twenty three, seventeen were found beneath Pteronia pallens, two beneath Eberlanzia, three beneath Galenia and one beneath Ruschia. These occurrences were significantly different to that expected by chance (chi-square=29.69, $p < 0.001$). The chi-square contribution by Pteronia pallens was the largest (chi-square=22.01)

As regards Tylecodon under dead nurses reproductive individuals occurred only under dead Pteronia (figure 2.4).

2(i) ESTABLISHING THE PTERONIA-TYLECODON ASSOCIATION

(see Table 2.3)

From Table 2.3 it is clear that the occurrence of Tylecodon wallichi beneath Eberlanzia ferox is significantly less than expected by chance ($p < 0.001$)

The occurrence of Tylecodon wallichi beneath Pteronia pallens is not significantly different from what is expected by chance alone.

In terms of numbers of Tylecodon wallichi, Pteronia have significantly more Tylecodon patients under them than is expected and Eberlanzia have fewer Tylecodon patients beneath them than is expected by chance (in both cases $p < 0.001$).

Table 2.2 : Pteronia and Eberlanzia (EBER) plant cover and proportion in each quadrat.

QUADRAT	PTERONIA AREA	EBER AREA	TOTAL AREA	PTERONIA PROPORTION	EBER PROPORTION
1	5.71	3.29	9.01	0.634	0.364
2	8.49	3.90	12.39	0.685	0.315
3	7.27	5.02	12.29	0.591	0.409
4	9.74	4.72	14.46	0.674	0.326
5	9.63	3.22	13.15	0.732	0.245
6	6.58	3.93	10.76	0.612	0.365
7	5.71	3.11	8.95	0.638	0.348
8	7.75	4.21	12.16	0.637	0.346

(areas in m²)

Table 2.3 : Observed versus Expected occurrence of Tylecodon beneath Pteronia (Pt) and Eberlanzia (Eb)
(number of patient individuals not considered)

Quadrat	Pt obs*	Pt exp*	Eb obs	Eb exp
1	14	8.88	0	5.1
2	13	10.27	2	4.73
3	20	15.37	6	10.63
4	26	20.22	4	9.78
5	20	17.57	4	5.88
6	17	12.24	3	7.3
7	14	8.93	0	4.87
8	14	11.47	4	6.23

* obs = observed frequency
exp = expected frequency

Chi-square = 12.34 df = 7 p = 0.089 (ns) for Pteronia
Chi-square = 19.72 df = 5 p < 0.001 for Eberlanzia

Table 2.4 : Observed versus Expected occurrence of Tylecodon beneath Pteronia (Pt) and Eberlanzia (Eb) (number of patient individuals considered)

Quadrat	Pt obs	Pt exp	Eb obs	Eb exp
1	32	20.29	0	11.65
2	69	49.32	3	22.68
3	42	29.55	8	20.45
4	60	43.17	4	20.86
5	72	57.83	7	19.36
6	48	31.21	3	18.62
7	32	20.42	0	11.14
8	32	22.93	4	12.46

Chi-square = 49.07 df = 7 p <0.001 for Pteronia
 Chi-square = 87.81 df = 7 p <0.001 for Eberlanzia

2(ii) MANIPULATIVE EXPERIMENTAL RESULTS (PTERONIA VERSUS EBERLANZIA)

The above results clearly suggest nurse patient relations are species specific. The following experiment tested the validity of the pattern.

At the start of the experiment there was no bias in the sizes of the patients beneath Pteronia and Eberlanzia nurses on Tylecodon diameter (t-test, $p > 0.05$, $t = 0.087$ and $n=40$).

To determine success of the patients in terms of growth beneath the two nurses, leaf areas (in April, the maximum growth period) were compared. This was two months after transplanting. Leaf areas of the Tylecodon patients beneath the Pteronia nurse were greater than for those beneath Eberlanzia. Tylecodon leaf area averaged 158.35mm^2 beneath Pteronia pallens, whilst beneath Eberlanzia patient leaf area was 55.02mm^2 , (non-parametric Mann-Whitney U test, $p < 0.01$). $z = 0.0061$). Clearly Tylecodon wallichii patient plants are more successful in terms of growth beneath Pteronia than Eberlanzia.

1(ii) EFFECT OF DIFFERENT NURSES ON FLOWERING

The sizes of Tylecodon patients that occurred under Eberlanzia ferox and Pteronia pallens did not differ significantly. This was true whether, area ($t = 0.669$, $p = 0.5$) or diameter ($t = 0.986$, $p = 0.326$) was used.

However when the number of flowering stalks of Tylecodon patients (see Plate 7) were compared, there was a

significant difference, (Table 2.5 Mann-Whitney U Test, z statistic=-2.184 p<0.05)

In Table 2.5 the sizes and number of flowering stalks of the Tylecodon patients beneath Eberlanzia and Pteronia are presented. Since 15 of the 50 Eberlanzia nurses were mixed with other species acting as nurses, it was necessary to do two analyses comparing the number of flowering stalks and size. In the first analysis all fifty plants of each nurse were included. In the second, only those Tylecodon occurring exclusively under Eberlanzia and Pteronia were used.

In the regression analysis the number of flowering stalks was regressed against the diameter of the Tylecodon plants and against the canopy area of these patients. For both Pteronia and Eberlanzia there was a significant relationship (see Table 2.6).

Table 2.5 : Average sizes (canopy area) and number of flowering stalks of Tylecodon beneath Pteronia and Eberlanzia nurses.

NURSE SPECIES	ALL SAMPLES	STALKS (+SE)	EXCLUSIVE NURSE	STALKS (+SE)
	SIZE (CM ²) (+SE) n=50		SIZE (CM ²) (+SE) n=35	
Pteronia	686.04 (145.84)	7.82 (1.77)	731.74 (198.93)	9.8 (2.36)
Eberlanzia	502.68 (54.43)	5.8 (1.30)	357.77 (32.42)	4.8 (1.49)
	#	**	##	*

t-test on Tylecodon sizes beneath Eberlanzia and Pteronia
t=1.178, n=50, p=0.242 i.e. p>0.05.

t-test on Tylecodon sizes beneath Eberlanzia and Pteronia
t=1.854, n=35, p=0.071 i.e. p>0.05

** Mann-Whitney U test z=-2.184 p<0.05 (z=0.025)

* Mann-Whitney U test z=-3.4404 p<0.001 (z=0.0005)

Table 2.6 : Summarised regression results

NURSE	VARIABLES	r^2	r	SLOPE	INTER -CEPT
Pteronia	stalks vs diam	0.607	0.779	2.75	-3.09
Eberlanzia	stalks vs diam	0.510	0.714	2.41	-2.72
Pteronia	stalks vs area	0.615	0.784	1.38	-2.98
Eberlanzia	stalks vs area	0.510	0.714	1.20	-2.59

(stalks = log of the number of flowering stalks,
diam = log of the diameter of the patient)



PLATE 7: Flowering stalks of the patient plant
Tylecodon wallichii

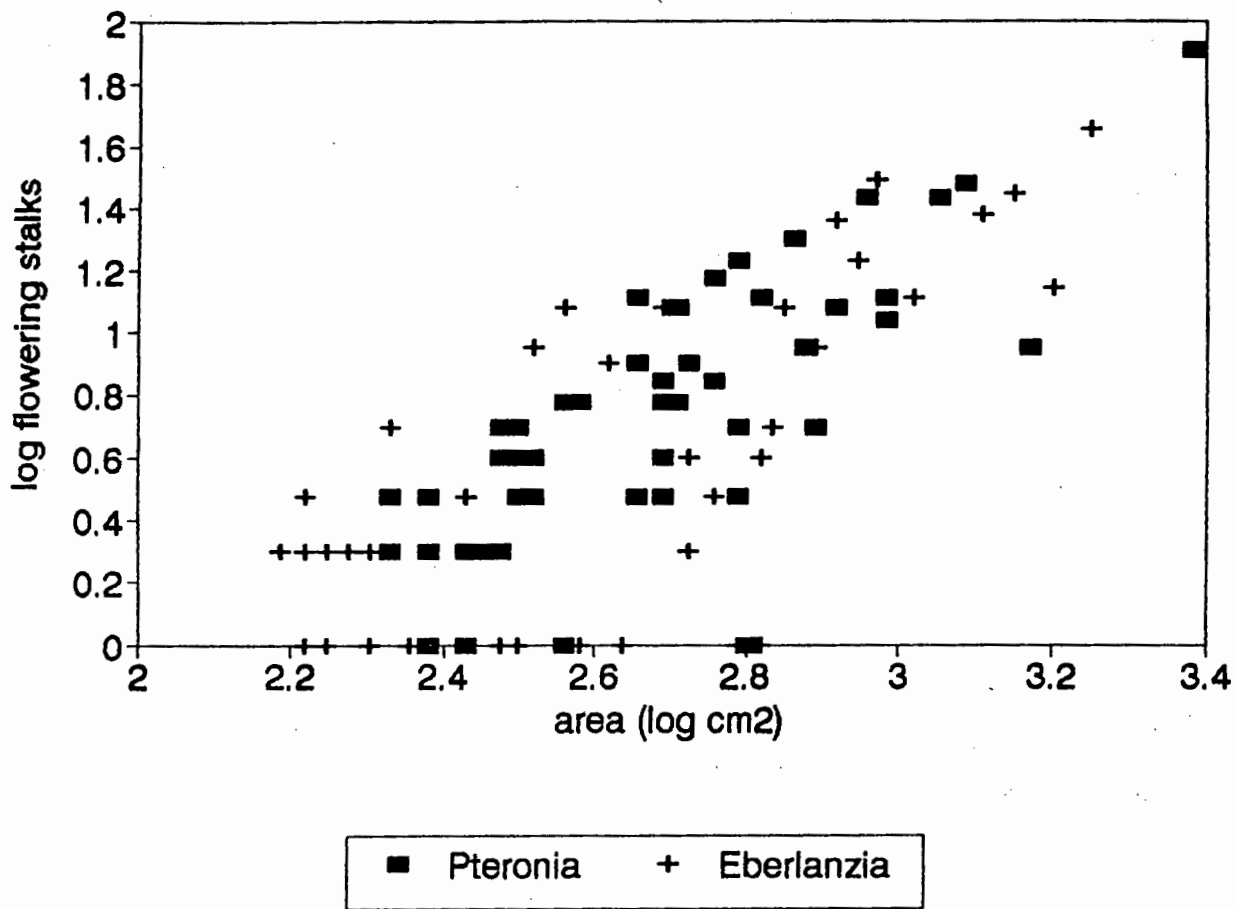


FIGURE 2.5: The relationship between Tylecodon canopy area and the number of flowering stalks beneath Pteronia and Eberlanzia.

Equations of the lines:-

PTERONIA: $y = 1.385x - 2.98$

EBERLANZIA: $y = 1.203x - 2.59$

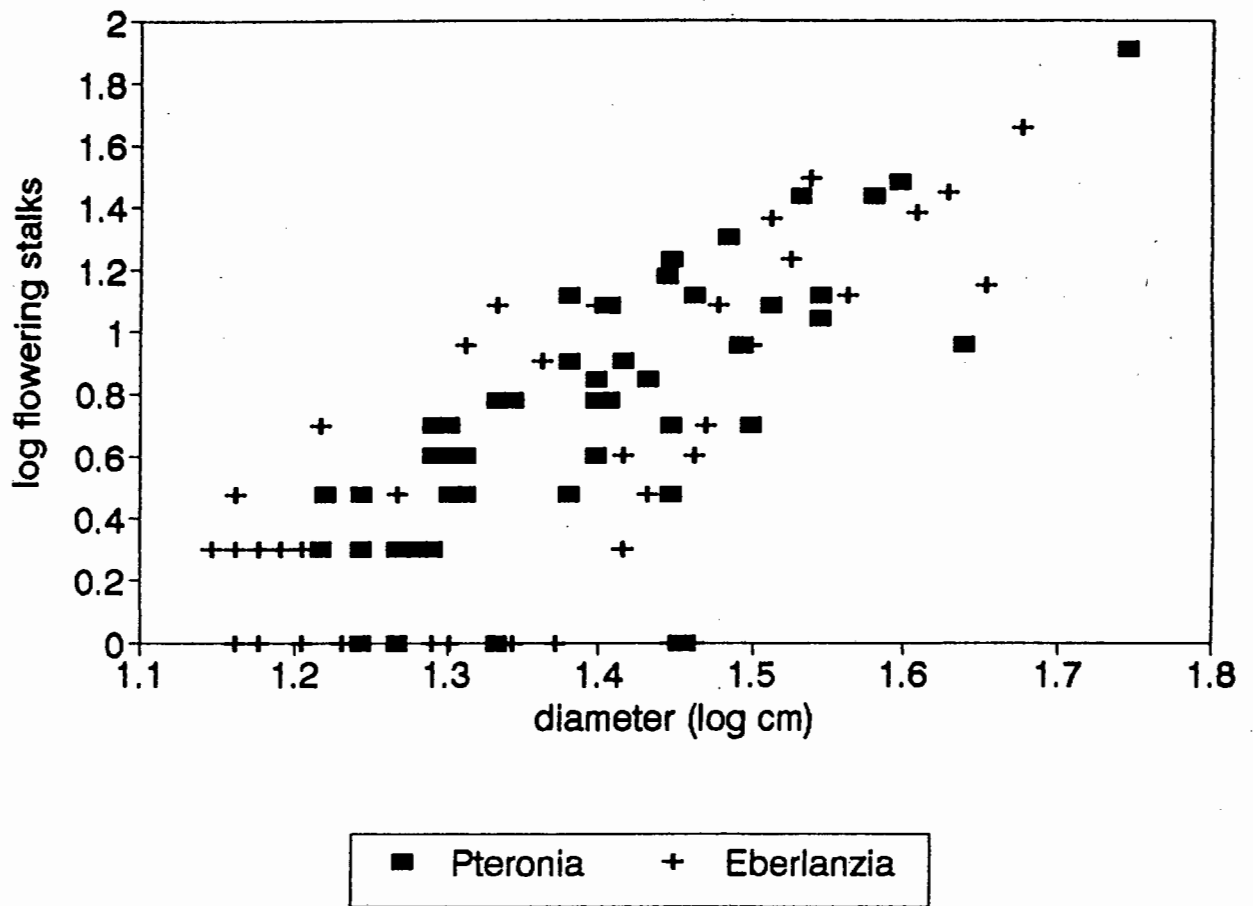


FIGURE 2.6: The relationship between Tylecodon plant diameter and the number of flowering stalks beneath Pteronia and Eberlanzia.

Equations of the lines:-

PTERONIA: $y = 2.74x - 3.09$

EBERLANZIA: $y = 2.41x - 2.72$

The regression slopes for the nurse species were statistically compared and were found not to differ significantly ($F=0.4917$ and $p>0.05$)(see Figure 2.6). These results show that for similar sized Tylecodon patients beneath a Pteronia and an Eberlanzia nurse, the number of flowering stalks do not differ.

In the Tylecodon adult transplant experiment, those transplanted beneath Pteronia had 10 more flowering stalks when compared to the number at the start of the experiment while patients beneath Eberlanzia had 13 more flowering stalks. A non-parametric test was run on the change in number of flowering stalks that the Tylecodon adults had at the start and at the end of the experiment, beneath the two nurses. No significant difference in the change in numbers of flowering stalks under Pteronia and Eberlanzia was apparent (Mann-Whitney U test, $p > 0.05$, $z=0.7212$, $n=20$).

3. TRANSPLANT EXPERIMENTS TO DETERMINE THE EFFECTS OF SOIL VERSUS NURSE CANOPY

The analysis of variance on the sizes at the start of the experiment showed that there was a size bias, (ANOVA F ratio=10.29 $p<0.001$ $df=99$). The plants in the combined soil and nurse treatment (see Table 2.1 to recall treatments) category as well as the control group were significantly larger than the separate soil treatment and nurse treatment

groups. The latter two were similar in size. This bias will be discussed below.

In the two-way analysis of variance, the soil treatment had a highly significant ($p < 0.01$) effect on Tylecodon leaf area. There was no significant effect of different nurse canopies ($p > 0.05$). The experimental treatments produced effects in the opposite direction from the original bias in plant sizes. Thus the results probably underestimate the magnitude of the effect of the different soils.

In summary, there is a definite effect exhibited by the patient plants when the soil in which they grow is changed. Transplants under different nurse canopies did not affect patient plant success.

DISCUSSION

SUCCESS OF TYLECODON WALLICHI IN TERMS OF SIZE AND GROWTH

The patient plant Tylecodon wallichi is clearly more successful under the nurse Pteronia pallens than other common nurse shrubs like Galenia africana, Ruschia pungens and Eberlanzia ferox. This appears to reflect growing conditions since transplant experiments showed that survival and growth (leaf area) of Tylecodon wallichi was significantly higher beneath this nurse than beneath Eberlanzia ferox.

In this section not only has a negative pattern association been revealed between Tylecodon wallichi and Eberlanzia ferox but experimental evidence of reduced growth from the transplants suggests that pattern is causal. In the first chapter, reasons as to why some nurses are better than others were examined. A nurse such as Eberlanzia does not provide as favourable an above ground microenvironment as does Pteronia in terms of temperature and light (PAR). The below ground rooting patterns of Eberlanzia are similar to the adult Tylecodon plants so that patterns of soil resource use may also overlap and limit close association. This would explain why no large adult Tylecodon plants were found under Eberlanzia in the Tylecodon size distribution section.

The transplanted Tylecodon plants were juveniles and perhaps rooting patterns are of less importance here in determining these initial stages of survival and growth . Possible causes of different growth and different nurses are discussed in Chapter 1.

SUCCESS IN TERMS OF FECUNDITY OF TYLECODON

From the investigation on the distribution of reproductive Tylecodon individuals, it was evident that Tylecodon reproductive success varies under different nurses. Only Pteronia pallens individuals had substantial numbers of flowering Tylecodon patients beneath them. This could either be due to a weaker flowering response under some nurses, or because patients beneath other nurses do not survive to reach reproductive age. The results (figure 2.3) suggest that few Tylecodon plants survive to reach maturity under Eberlanzia relative to Pteronia in a mixed stand. The survey of similar sized patients under the two nurse species showed that the number of flowering stalks that the Tylecodon individuals possessed were different (see Table 2.5). However, in the more appropriate analysis of the relationship between Tylecodon size and number of flowering stalks no significant differences were evidenced. So, there is no support for the hypothesis that there are differences in fecundity under the two nurse species.

That Tylecodon transplants had similar numbers of flowering stalks when transplanted beneath the two nurse species confirms this result. However, in this case I believe that the experimental period was too short to elicit treatment effects.

Thus, Tylecodon does not exhibit a weaker flowering response beneath Eberlanzia but has reduced survival in this microsite so fewer plants reach maturity.

In summary, both the transplant experiments and the pattern analyses of Tylecodon size distribution and the distribution of flowering patients, clearly support the phenomenon of nurse specificity for successful establishment, growth and (indirectly) reproduction of Tylecodon wallichii.

EFFECTS OF SOIL VERSUS NURSE CANOPY

While different nurses within one community do not provide equally favourable microenvironments for successful patient establishment and success this does not necessarily explain distribution patterns across different plant communities. Thus where different nurse plants occur on the same soil (for example Pteronia pallens and Eberlanzia ferox), nurse specificity may be determined by factors such as temperature and light. For the same patient plant however, another nurse occurring in a different community may provide a suitable above ground canopy, but the soil on which this nurse occurs may be unfavourable.

This was the case for Pteronia paniculata. In the transplant experiment using this Pteronia species it was evident that the soil type on which it occurred was less favourable to Tylecodon wallichii, though its nurse canopy was suitable. It is interesting to note that there is another Tylecodon species (T. reticulatus) that occurs predominantly on this soil, beneath the Pteronia paniculata nurse. So, even for one patient species, 'nurse selectivity' depends on a number of factors.

Yeaton and Esler (1990), showed that some Karoo shrubs provide ideal refuges for some plants but not others (e.g. Braunanthus providing a suitable establishment site for Pteronia pallens but not other members of the woody shrub guild in the area). They suggested that this specificity related to canopy structure for effective trapping of seeds and organic material and whether protection from herbivores is afforded to the 'patient' by nurse spinescence. The latter has also been discussed by McAuliffe (1984). In the current study however, not only are the main study species (Tylecodon wallichii and Pteronia pallens) unpalatable, but the role of canopy structure and 'trapping' does not appear to be one of the determining factors for nurse specificity. The 'poor' nurse Eberlanzia ferox, though apparently poorly structured for seed trapping does provide adequate conditions for initial establishment of Tylecodon wallichii. However subsequent growth and survival is definitely 'nurse specific'.

From these investigations, it is fair to claim that the patient plant Tylecodon wallichii will vary in success in terms of growth and reproduction beneath different nurse plants. This conclusion is based both on pattern analyses and transplant experiments.

So, in the Karoo, not only is it important to understand that nurse plants in general are required for the initial establishment and survival of some plants, but that specific requirements by the patient are needed for successful growth and reproduction. Only some nurse species provide these requirements and for the case of Tylecodon wallichii, Pteronia pallens is the nurse selected.

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CHAPTER THREE

Competitive Interactions between Tylecodon wallichii and its Nurse Pteronia pallens

Introduction

Earlier chapters indicate that facilitation is important in the establishment of some karoo plant species. However subsequent competitive interactions between the nurse and the patient may later become evident.

Competitive interactions between nurse plants and their patient plants have been illustrated in a number of studies (Yeaton 1978, Vandermeer 1980, M^CAuliffe 1984 and Franco and Nobel 1988). According to Yeaton (1978), the canopy of Larrea tridentata serves as a suitable site for Opuntia leptocaulis individuals but Opuntia later replaces Larrea.

M^CAuliffe (1984) expanded on the paloverde-sahuaros work undertaken by Vandermeer (1980) and showed that the close proximity of Sahuaros led to a relative increase in stem die-back of the nurse paloverde. This interaction appeared to accelerate the local loss of individual nurse trees and resulted in a predictable pattern of species replacement.

In this chapter, the apparent competitive interaction between Tylecodon wallichii and its common nurse Pteronia pallens is examined. It was shown in chapter one that Tylecodon wallichii tends to occur predominantly beneath the canopy of the perennial shrub Pteronia pallens. Though Pteronia appears to facilitate Tylecodon establishment in the arid Karoo environment, as the Tylecodon grows larger, stem die-back of the nurse in the vicinity of the Tylecodon has been observed. This indicates that there might be some competitive effect of the patient Tylecodon on the Pteronia nurse.

The initial part of this competitive study follows an approach used by M^CAuliffe (1984), whereby indices of nurse vigour and potential patient competitive effect are calculated from plant measurements and the distances between the nurse and the patient. This approach is therefore largely descriptive.

There are problems with a purely descriptive study. The pattern analysis does not take into consideration the ages of the respective plants. Nurse vigour might appear to decline due to an increased competitive effect by the patient but the loss of vigour may be due purely to natural senescence of the nurse and not be related at all to the patient.

In an attempt to actually prove that there is a competitive effect exerted by the patient on its nurse , a manipulative field experiment was necessary. Since the study area is arid, it was assumed that competition between the plants was for water, thus a physiological response in this regard was investigated. This constitutes the second section of this chapter.

There are several possible competitive mechanisms, one of which is the way in which a patient and a nurse exploit the soil. To complete this section on competitive interactions, an examination of the rooting patterns of both nurse and patient was undertaken. Here the Pteronia nurse - Tylecodon patient root interaction was determined.

METHODS

(i) DESCRIPTIVE METHOD

The procedure follows that of M^CAuliffe (1984) on the sahuaro (Carnegiea gigantea) and the nurse paloverde (Cercidium microphyllum) in the Sonoran desert.

One hundred nurse-patient pairs were chosen randomly (using the Wandering Quarter method (Catana 1963) for sampling. Twenty-five pairs for each of the following categories were sampled :- Pteronia with young Tylecodon plants (< 10cm tall), Pteronia with medium sized Tylecodon plants (10-20cm tall), Pteronia with large Tylecodon plants (20-60cm tall) and lastly dead Pteronia with Tylecodon plants.

The diameter of all dead branches were measured to compute the cross sectional area of each dead branch. These were summed and related to the base cross sectional area of the shrub. To attain an index of vigour for the nurse the total dead branch area was divided by the base area of the shrub and subtracted from one.

$$\begin{aligned} \text{Thus:- } V &= 1 - \sum_{i=1}^n \frac{(\pi (d_i / 2))^2}{(\pi (b/2))^2} \\ &= 1 - \sum_{i=1}^n \frac{(d_i)^2}{(b)^2} \end{aligned}$$

V = index of relative vigour

d = diameter at the base of dead branch

b = basal diameter

(M^CAuliffe 1984)

A Tylecodon patient was considered associated with a Pteronia if it was located within the boundaries of the nurse canopy. The height and two diameters of each associated Tylecodon was measured. The distance from the centre of the nurse to the central stem of the patient was also measured.

A value for the potential competitive effect of the patient Tylecodon was computed in two ways. In the first case the height was divided by the distance between the nurse and the patient and in the second the mean diameter was divided by this same distance. The latter potential competitive effect values were preferred in the analysis, as Tylecodon wallichii increases in horizontal growth more than vertical (unlike the sahuaro cactus that M^CAuliffe studied).

The canopy area of the nurse (which is circular) was used as a size index, so canopy diameters were measured. An estimate of the percentage canopy that was dead was also recorded.

Data were analysed using regression techniques.

Data collected for nurse plants that were completely dead gave unsuitable indices of vigour and so were not used in the analysis.

(ii) MANIPULATIVE EXPERIMENTAL PROCEDURE

To determine whether a competitive interaction was apparent between the patient (Tylecodon) and the nurse (Pteronia) a removal experiment was set up. The essence of this experiment was that should the patient be competing with the nurse, once the patient plant was removed, nurse plant performance should improve. It was assumed that competition was for water, thus an improvement in the water status of the nurse was expected once the patient competitor had been removed.

Twenty nurse-patient pairs were located in the field. All patients were adults. On the first day of setting up the experiment the stem xylem potential of all twenty nurse plants were measured using a pressure chamber (Scholander et al 1965).

At least two readings per plant were taken at midday when the plants were likely to be the most water stressed.

The Tylecodon patients of ten of the twenty pairs were removed after the xylem potential had been measured. Thus ten nurse plants had patient plants beneath them and with the other ten the patients were removed.

On the second day, the midday xylem potential of all twenty nurse plants were measured again. The midday xylem potential was measured again two weeks, one month and two months after the initial patient removals. Thereafter, the midday xylem potential was recorded every season at Anysberg.

This experiment therefore examined a time since removal response of the nurse plants and a seasonal response.

(iii) ROOT STUDY

The rationale behind this study was that should the nurse and patient be competing, and should competition be at root level then one would expect some degree of root zone overlap (in vertical and horizontal space). Root competition was therefore examined by direct observation of the rooting patterns.

Two adult Pteronia - Tylecodon pairs were excavated so that their root interaction could be examined.

The excavation procedure followed that of Higgins, Lamb and van Wilgen (1988). The mean crown diameter and height of each individual (in a pair) were measured and then cut off 10cm above the ground. The stump was tied and secured to the ground. A water pressure technique was used so a water tank was set up. Water was delivered under pressure through a 20mm hose fitted with an adjustable nozzle. Four 1,00m reference stakes (10cm calibrated) were driven into the ground radiating out along the four axes of each plant until the end of each plants root system was reached.

Approximately 10cm of soil was washed away at every stage of the excavation until the 100cm depth was reached. At each soil level, a 100cm x 100cm grid was placed over the stump of each plant. The plan view of the roots at each depth was then drawn to scale on graph paper. Separate drawings were made for every depth and for each plant. Roots were divided into four diameter classes - 1-2cm; 0.5-1cm; 0.2-0.5cm and <0.2cm.

Vertical root distribution analysis

Root data were quantified using root length and root volume in each diameter size class and at each soil depth.

Root length was calculated based on the initial scaled drawings on graph paper. Root volumes were calculated using the formula for the volume of a cylinder ($\pi \cdot r^2 \cdot l$). A midpoint was chosen for each diameter size class, for example, the diameter class 1.0cm - 2.0cm, 1.5cm was chosen so the radius was 0.75cm. The lengths of each root diameter size class, at each depth was multiplied by pi and the radius squared.

Horizontal root distribution analysis

Plan drawings of the roots of the two species were traced separately and laid one on top of the other. Both tracings were then placed on graph paper. In this way it was possible to determine what percentage root overlap there was between Pteronia and the patient Tylecodon. This was done at two scales (see Table 3.11).

Firstly all the squares that were occupied in horizontal space by all the roots were counted. From the total number of squares occupied by all roots, the squares which had both Pteronia and Tylecodon roots in them were counted. The percentage root overlap of Pteronia and Tylecodon was calculated in this way.

RESULTS

(i) DESCRIPTIVE RESULTS

Regression Analyses

The potential competitive effect of the patient Tylecodon (i.e. the ratio of its size to the distance from the nurse centre) was regressed against the vigour of the nurse Pteronia. This yielded a significant negative correlation ($r = -0.464$, $p < 0.001$, $n = 63$). As the size of the patient increased and its distance away from the nurse decreased, the competitive effect of the patient increased. The response of the nurse was a decline in vigour (see figure 3.1).

A significant positive correlation was found between patient competitive effect and the percentage dead of the nurse canopy ($r = 0.697$, $p < 0.001$, $n = 63$). As the competitive effect of the patient increased the percentage dead of the nurse canopy increased (see figure 3.2) (see Plates 8,9,10,and 11).

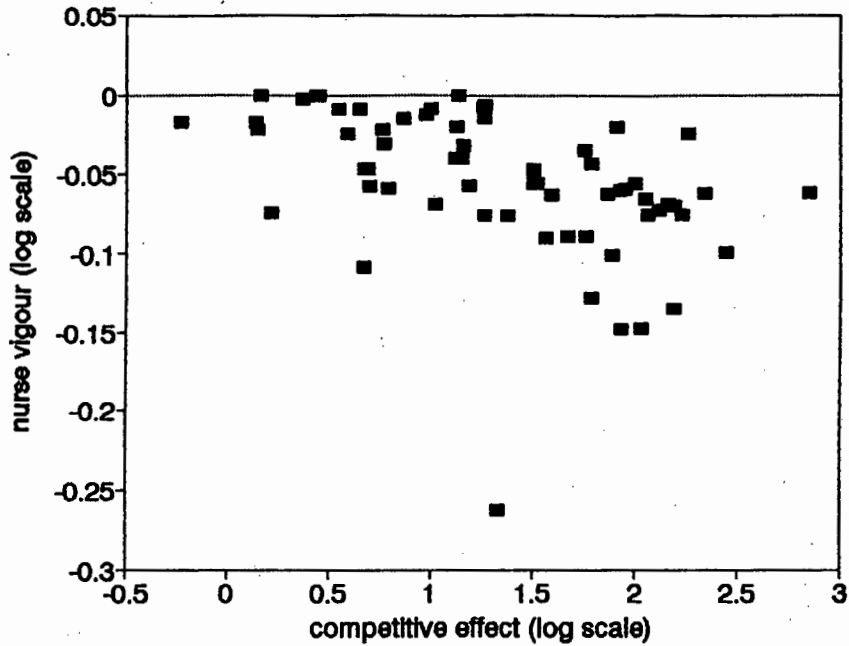


FIGURE 3.1: Showing the relationship between the competitive effect of the patient and the vigour of the nurse.
 ($r=0.464$, $p<0.001$, $df=63$)

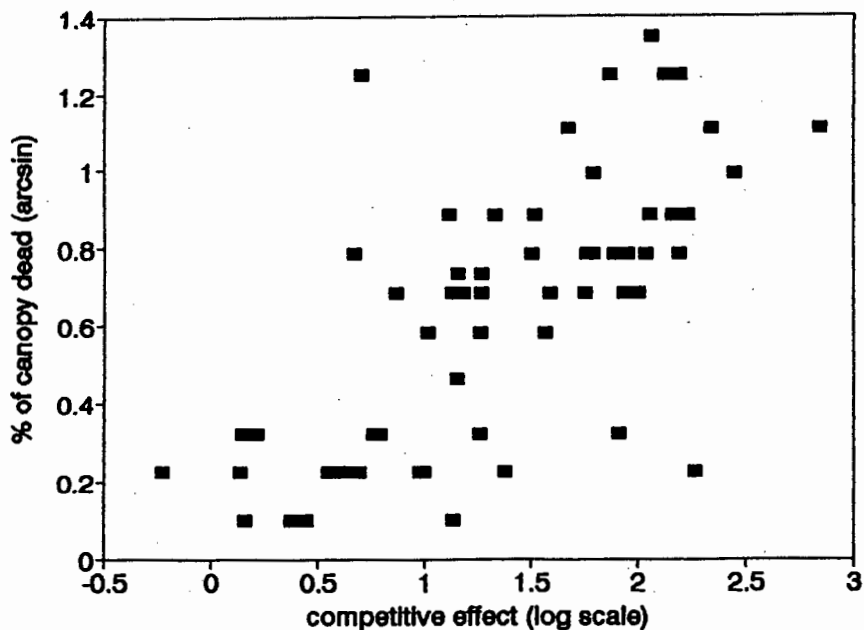


FIGURE 3.2: Showing the relationship between the competitive effect of the patient and the percentage of the nurse canopy that was dead. N.B. arcsin transformation on percentage data.
 ($r=0.696$, $p<0.001$, $df=63$)



PLATE 8: A vigorous nurse with a small patient beneath.



PLATE 9: A less vigorous nurse with a larger patient.
(note the proximity of the two species stems)



PLATE 10: The Pteronia nurse is being overtopped by the Tylecodon patient.



PLATE 11: The remains of the Pteronia nurse (left) next to a large, robust Tylecodon patient.

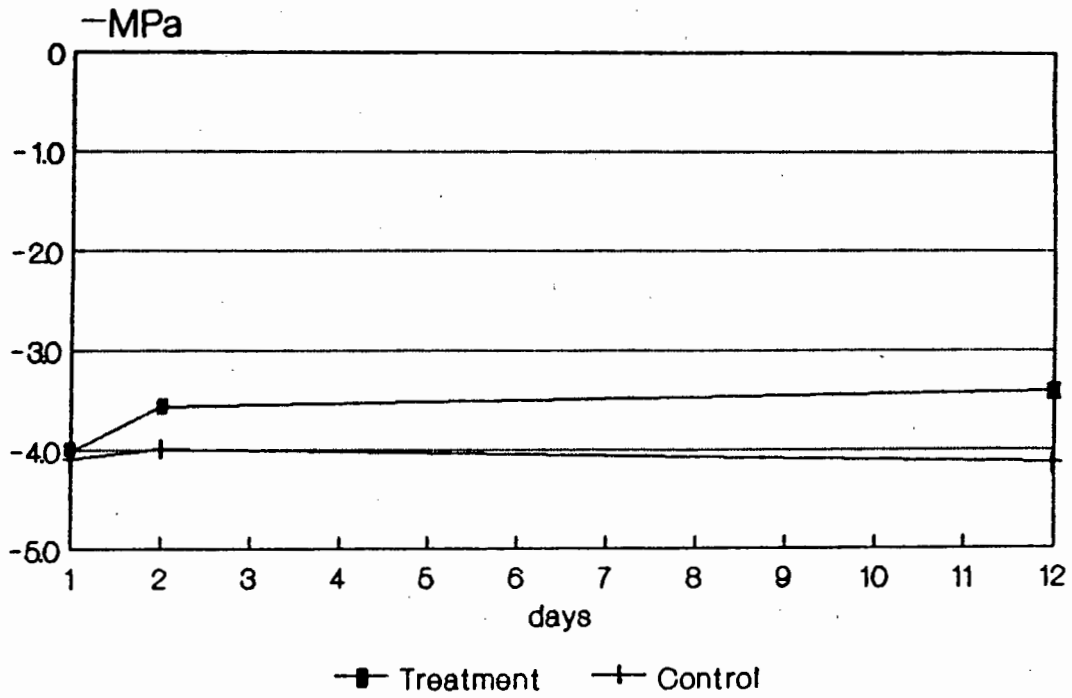


FIGURE 3.3: Xylem Potential of Pteronia treatment and control plants, (Treatments are without patients) at the start of the experiment and 2 and 12 days after removals

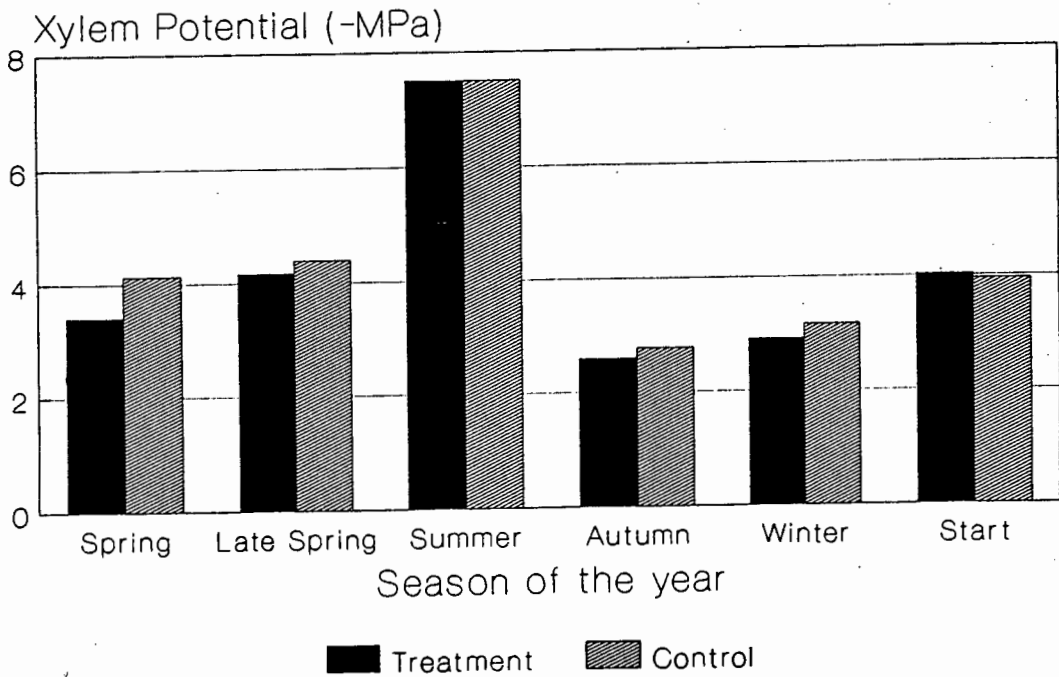


FIGURE 3.4: Seasonal xylem potential of Pteronia treatment and control plants (pre-treatment results also shown)

Table 3.1 : Water Potential (-MPa) response over time (days after removal of patient plants)(+SE)

Day	Month	t (+SE)	c	Difference	z	Significance
1	July	4.02 (.11)	3.94 (.14)	0.08	.677	ns
2	July	3.57 (1.65)	3.99 (1.77)	.42	.084	ns
12	August	3.41 (.20)	4.13 (.18)	.72	.042	p<0.05
72	October	4.17 (.16)	4.39 (.14)	.22	.479	ns
132	February	? ?	<7 ?	<7	? ?	? ?

t = treatment (without patients)
c = control (with patients)
z = statistic for Mann-Whitney U Test

(ii) MANIPULATIVE EXPERIMENTAL RESULTS

Before the patient plant removals from ten of the twenty nurse plants, all nurses had similar xylem potentials (see Table 3.1). On the second day, once the removal procedure had been carried out, there was a slight difference in xylem potential between those plants with patients and those without (control and treatment plants respectively). At this stage however the difference was not significant (see Table 3.1).

There was a significant difference in the water status of the plants only 12 days after the removals. A lower (more negative) xylem potential was evident for the nurse plants which still had patient plants beneath their canopies (see Table 3.1 and figure 3.3).

After two months, five months and ten months, no further differences were evident between treatment and control plants. Differences could not be determined in the late Summer (five month reading) as the xylem potential was often below -7MPa and this was the limit of the pressure chamber. Except for an initial response two weeks after removals, the xylem potential of the nurse plants with and without patient plants did not differ significantly. Though not significant, treatment plants always had higher xylem potentials than the controls (recall the latter still had patients beneath them).

Table 3.2 : Seasonal Water Potentials (-MPa) of Nurse plants with and without Patient plants (+SE)

Month	Season	t (+SE)	c (+SE)	Difference	z	Significance
August	Spring	3.41 (.2)	4.13 (.18)	.72	.042	p<0.05
October	Spring	4.17 (.16)	4.39 (.14)	.22	.479	ns
February	Summer	<7 (?)	<7 (?)	?	?	?
May	Autumn	2.6 (.09)	2.77 (.07)	.17	.183	ns
June	Winter	2.92 (.58)	3.17 (.09)	.25	.058	ns

t = treatment (without patients)

c = control (with patients)

z = statistic for Mann-Whitney U Test

Examining the water status of the plants in the different seasons revealed no differences between those nurses with patients and those without, except for late Winter (see Table 3.2 and Figure 3.4). Summer differences could not be determined.

(iii) ROOT STUDY

Vertical Distribution - Root length and Root area comparison of Pteronia and Tylecodon.

a) Root Length

For the first Pteronia - Tylecodon pair analysed, in all size classes, Tylecodon had 100% of its roots in the upper 10cm of soil whilst Pteronia had 21%, 11.7%, 21.1% and 0% respectively for each size class, at this 10cm depth (see Table 3.4).

For the second pair, again Tylecodon had 100% of tis roots for each diameter size class in the top 10cm of soil. Apart from the smallest size class (0.2cm) the percentages of root lengths for Pteronia were greatest for the 0.1m -0.2m soil depth which is below the level where all Tylecodon roots were situated (see Table 3.7 and Table 3.8). Only the small fibrous roots of Pteronia utilise this top 10cm as does Tylecodon.

Excluding the size classes and looking at total root length at the different soil depths, it is evident that Tylecodon has all its roots in the top 10cm while Pteronia has only 15% and 26% respectively of its roots at this depth (see Table 3.3 and Table 3.7).

b) Root Volume

For each root diameter size class, except the 0.5cm - 1.0cm class, Pteronia had its greatest root volume in the 0.2m - 0.3m soil depth (pair one). For all diameter size classes of the second Pteronia excavated the greatest root volume was found in the 0.1m -0.2m soil level. In both pairs Tylecodon root volume was limited to the upper 10cm (see Table 3.6 and Table 3.10 and Figure 3.6 and Figure 3.8).

In terms of total root volume, Tylecodon is very shallow rooted with 100% of its roots in the upper 10cm. Pteronia on the other hand is deeper rooted with 90% of its roots at depths below 10cm and only 10% in the top decimetre of soil, (see Figures 3.5, 3.6, 3.7 and 3.8)..

The roots of the two species also differ greatly in horizontal distribution, (see Figures 3.9 and 3.10).

For both scales and for both pairs of Pteronia and Tylecodon, the percentage root overlap between the nurse and the patient was less than 10% (see Table 3.11).

From the root study it is clear that not only are Pteronia and Tylecodon roots separated vertically in space but also horizontally.

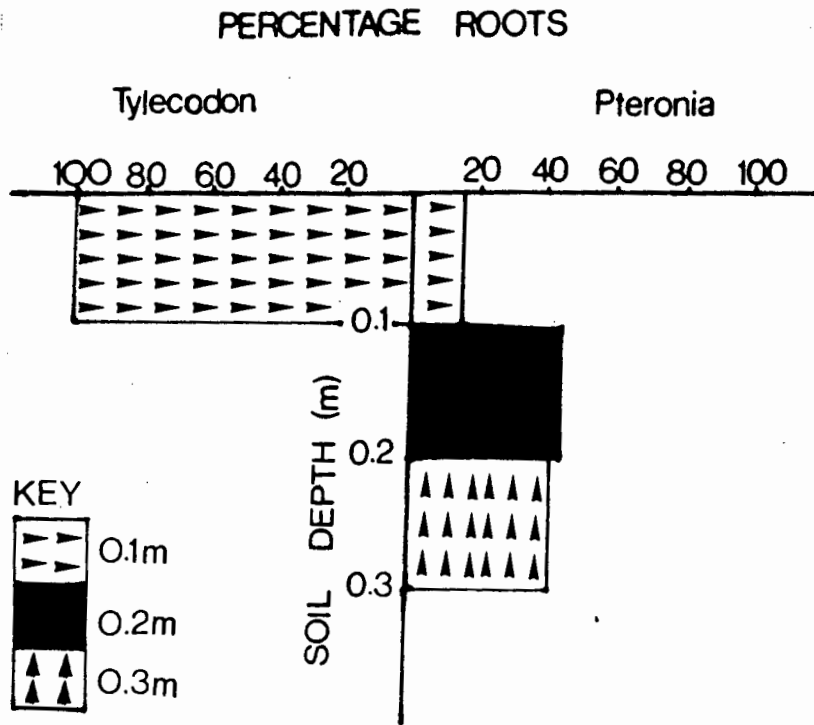


FIGURE 3.5: Vertical root distribution of Tylecodon and Pteronia (using root length data) at three depths.
PAIR ONE

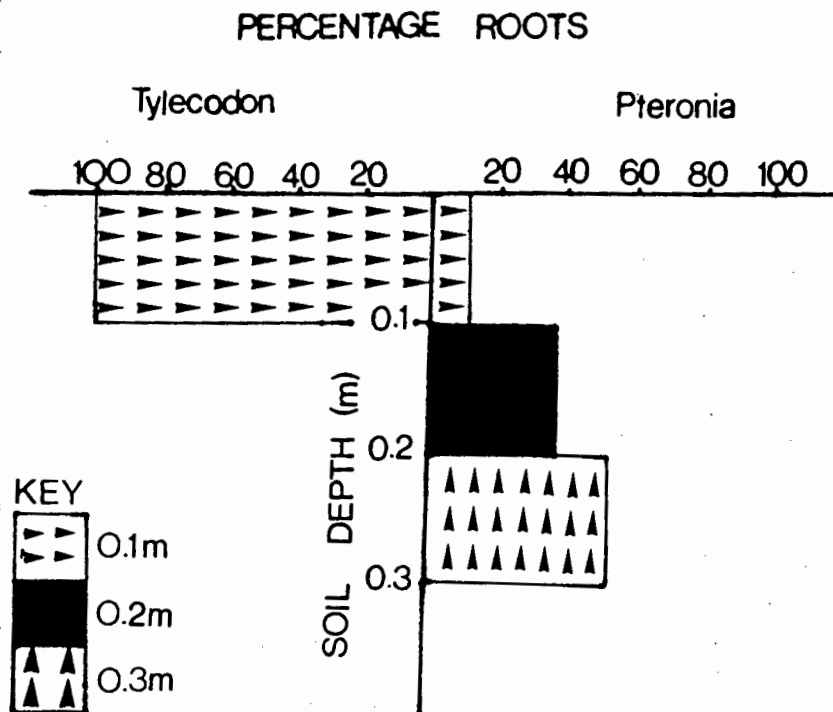


FIGURE 3.6: Vertical root distribution of Tylecodon and Pteronia (using root volume data) at three depths.
PAIR ONE

PAIR ONE

Table 3.3: Root lengths in each size class and percentage of total root length at that soil depth

Soil Depth		Root Diameter Size Class (cm)								TOTAL LENGTH	
		<0.2		.2-.5		.5-1.0		1.0-2.0		Pt	Tw
		Pt	Tw	Pt	Tw	Pt	Tw	Pt	Tw		
0-0.1	l	122	79	109	325	21	128	0	55	252	587
	%	48	13	43	55	8	23	0	9	15	100
0.1-.2	l	45	0	648	0	54	0	0	0	747	0
	%	6	0	87	0	7	0	0	0	44	0
0.2-.3	l	392	0	176	0	98	0	20	0	687	0
	%	57	0	26	0	14	0	3	0	41	0

Pt = Pteronia
 Tw = Tylecodon
 l = length
 % = percentage

Table 3.4: Percentage root length of total root length (at all soil depths) in each size class

Soil Depth (m)	Root Diameter Size Class (cm)							
	<0.2		.2-.5		.5-1.0		1-2.0	
	Pt	Tw	Pt	Tw	Pt	Tw	Pt	Tw
0-0.1	22	100	12	100	12	100	0	100
0.1-.2	8	0	69	0	31	0	0	0
0.2-.3	70	0	19	0	57	0	100	0
TOTAL LENGTH	559	79	933	325	173	128	20	55

Table 3.5: Root volumes (cm³) in each size class and percentage of total root volume at that soil depth

Soil Depth (m)		Root Diameter Size Class (cm)								TOTAL VOLUME	
		<0.2		.2-.5		.5-1.0		1.0-2.0		Pt	Tw
		Pt	Tw	Pt	Tw	Pt	Tw	Pt	Tw	Pt	Tw
0.0-.1	A	2.2	1.4	7.7	23	9.3	56	0	97	19	177
	%	11	0.8	40	13	48	32	0	55	10	100
0.1-.2	A	0.8	0	46	0	24	0	0	0	71	0
	%	1.1	0	65	0	34	0	0	0	38	0
0.2-.3	A	6.9	0	12	0	44	0	35	0	98	0
	%	7.1	0	13	0	44	0	36	0	52	0

Table 3.6: Percentage root volume of total root volume (at all soil depths), in each size class

Soil Depth (m)		Root Diameter Size Class (cm)								TOTAL VOLUME	
		<0.2		.2-.5		.5-1.0		1.0-2.0		Pt	Tw
		Pt	Tw	Pt	Tw	Pt	Tw	Pt	Tw	Pt	Tw
0.0-.1		22	100	12	100	12	100	0	100	10	100
0.1-.2		8	0	69	0	31	0	0	0	38	0
0.2-.3		70	0	19	0	57	0	100	0	52	0
TOTAL VOLUME (cm ²)		9.8	1.4	66	23	76	56	35	97	187	178

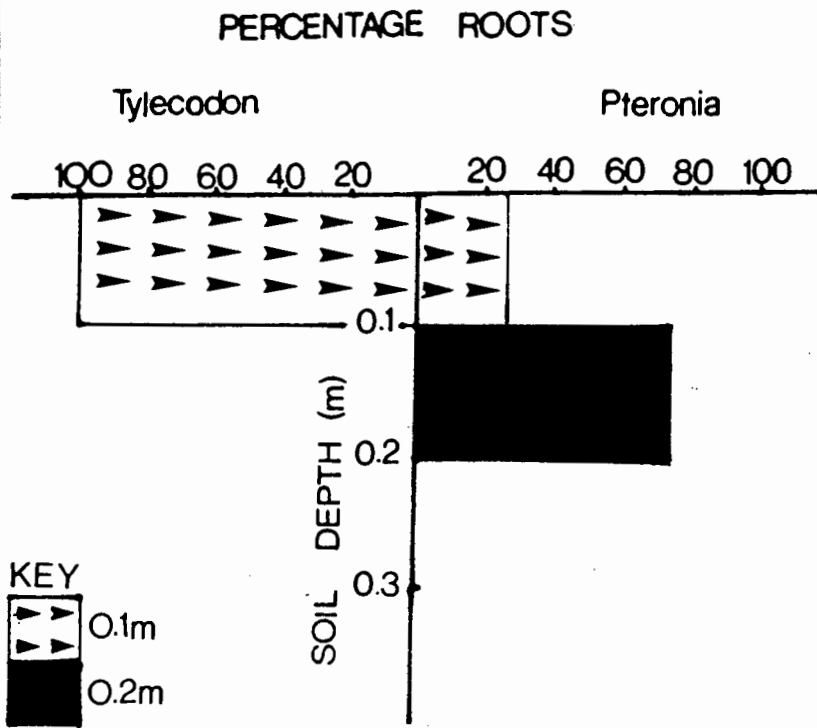


FIGURE 3.7: Vertical root distribution of Tylecodon and Pteronia (using root length data) at two depths.
PAIR TWO

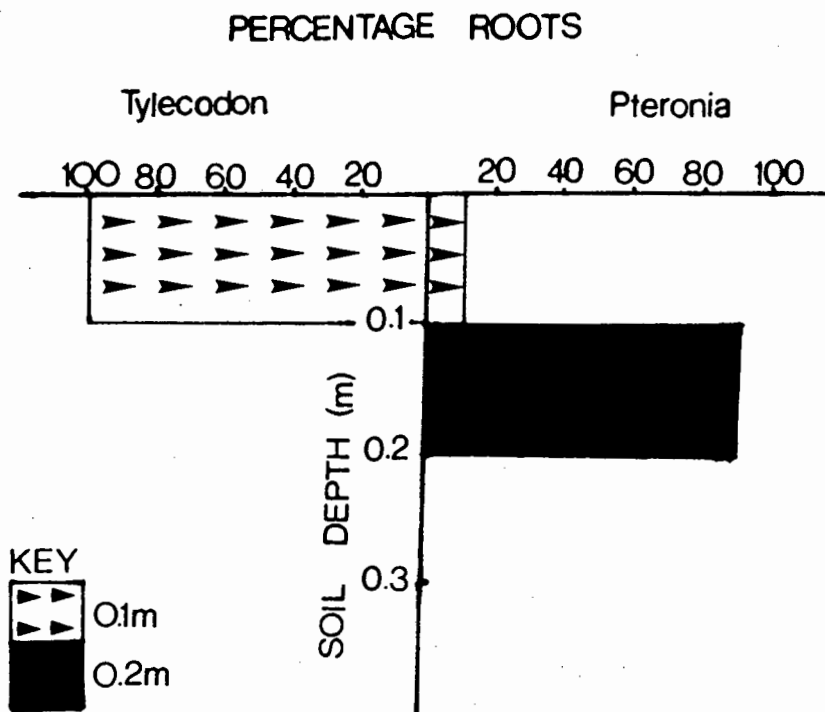


FIGURE 3.8: Vertical root distribution of Tylecodon and Pteronia (using root volume data) at two depths.
PAIR TWO

PAIR TWO

Table 3.7: Root lengths in each size class and percentage of total root length at each soil depth

Soil Depth (m)	Root Diameter Size Class (cm)										
	<0.2		.2-.5		.5-1.0		1.0-2.0		TOTAL		
	Pt	Tw	Pt	Tw	Pt	Tw	Pt	Tw	LENGTH		
0.0-.1	l	221	106	0	123	23	224	7	95	251	548
	%	88	19	0	22	9	41	3	17	26	100
0.1-.2	l	166	0	251	0	254	0	45	0	716	0
	%	23	0	35	0	35	0	6	0	74	0

Table 3.8: Percentage root lengths of total root length (at all soil depths) in each size class

Soil Depth (m)	Root Diameter Size Class (cm)									
	<0.2		.2-.5		.5-1.0		1.0-2.			
	Pt	Tw	Pt	Tw	Pt	Tw	Pt	Tw		
0.0-.1	57	100	0	100	8	100	13	100		
0.1-.2	43	0	100	0	92	0	86	0		
TOTAL LENGTH	387	106	251	123	277	224	52	95		

Table 3.9: Root volume (cm³) in each size class and percentage of total root volume at each soil depth

Soil Depth (m)	Root Diameter Size Class								TOTAL VOLUME		
	<0.2		.2-.5		.5-1.0		1.0-2.0		Pt	Tw	
	Pt	Tw	Pt	Tw	Pt	Tw	Pt	Tw			
0.0-.1	A	0.9	1.9	0	8.7	10	99	12	168	23	277
	%	3.9	0.7	0	3.1	43	36	53	60	9.9	100
0.1-.2	A	2.9	0	18	0	112	0	79	0	212	0
	%	1.4	0	8.4	0	53	0	37	0	90	0

Table 3.10: Percentage root volume of total root volume (at all depths) in each size class

Soil Depth (m)	Root Diameter Size Class (cm)							
	<0.2		.2-.5		.5-1.0		1.0-2.0	
	Pt	Tw	Pt	Tw	Pt	Tw	Pt	Tw
0.0-.1	24	100	0	100	8.3	100	13	100
0.1-.2	76	0	100	0	92	0	86	0
TOTAL VOLUME (cm ³)	3.8	1.9	18	9	122	99	92	167

Table 3.11: Horizontal overlap of Pteronia and Tylecodon roots

Pair	Scale 1 graph paper	Scale 2 grid	Total # squares	Common # squares	% overlap of roots
1	2cm x 2cm	10cm x 10cm	41	4	9.7
2			48	4	8.3
1	1cm x 1cm	5cm x 5cm	94	9	9.5
2			122	6	5

Pteronia — Tylecodon
PAIR ONE

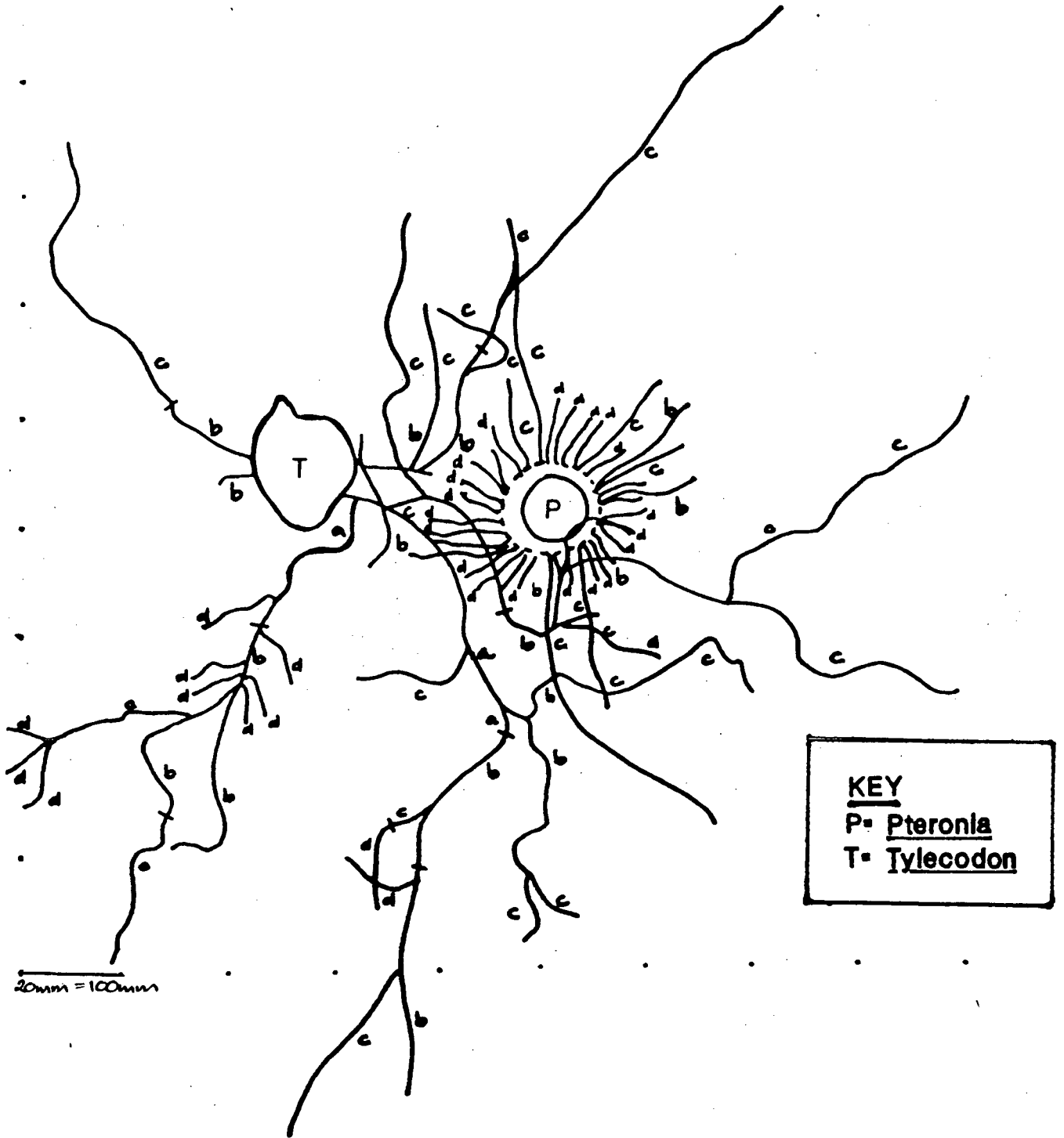


FIGURE 3.9: Horizontal root distribution of Tylecodon-Pteronia pair one showing virtually no overlap at the 0.0-0.1m soil depth (overlap less than 10%)

PAIR TWO
Pteronia — Tylecodon

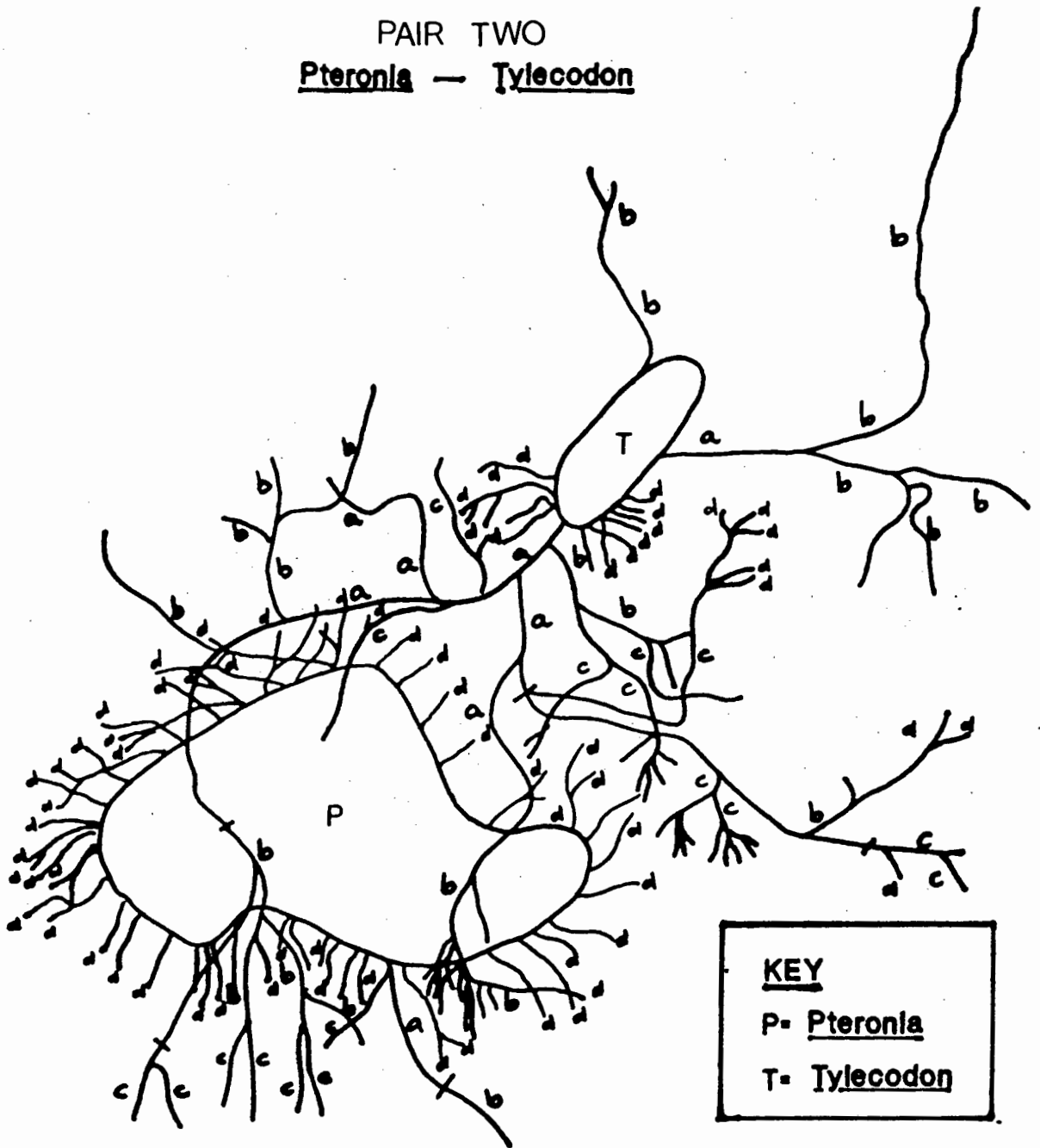


FIGURE 3.10: Horizontal root distribution of Tylecodon-Pteronia pair two showing very little overlap (less than 5%) at the 0.0-0.1m soil depth.

DISCUSSION

Competition in Arid Systems

Due to the increased potential competitive effect of the patient Tylecodon wallichii, nurse vigour declined and the percentage of the canopy that was dead increased. This supports the idea of a competitive interaction between the nurse and the adult patient. McAuliffe (1984) showed in the Sonoran desert that the nurse paloverde (Cercidium microphyllum) was adversely affected by the close proximity of the sahuaro cactus (Carnegiea gigantea). He claimed that the sahuaros lessened nurse vigour and also contributed substantially to paloverde tree mortality. Opuntia leptocaulis preferentially established beneath Larrea tridentata canopies (Yeaton 1978). Large Larrea individuals growing alone were more vigorous than individuals with Opuntia under their canopy while large Opuntia plants were associated with less vigorous Larrea individuals (Yeaton 1978). As with the majority of competition studies undertaken in arid and semi-arid regions, this section of the study is largely descriptive, based on observations of distribution and vigour of individuals. Few studies have concentrated on the mechanism of competition (Fowler 1986).

Most plant ecologists however, working in arid and semi-arid regions have assumed that the principal form of competition among plants is for water (Fowler 1986). Noy-Meir (1985) wrote, "Since drought mortality results from the exhaustion of the soil moisture resource, competition between plants for this resource should be an important factor". In McAuliffe's study (1984) on the sahuaro-paloverde association, root competition for water was suggested as the most likely cause of the loss of vigour and increased mortality of the nurse tree.

There are some experimental studies however which show conclusively that competition for water is of great importance. Some ecologists have examined the effects of competition on the water status of the affected plants on the water content of the soil, as well as upon measures of plant size, fecundity and/or survival (Friedman 1971, Friedman and Orshan 1975, Nobel and Franco 1986). Experimental removals of Larrea tridentata and/or Ambrosia dumosa around target plants of each species improved the water potential of individuals of other species (Fonteyn and Mahall 1981). Removal of Encelia farinosa individuals improved the water status and increased plant size and seed set of the remaining neighbouring conspecifics (Ehleringer 1984).

Another study, using modelling techniques, emphasized the physiological performance of the patient plant (Agave deserti) with and without the nurse (Hilaria rigida) (Franco and Nobel 1988).

Competitive mechanisms and Resource separation

In this study, to confirm the initial results of competition occurring between the Pteronia nurse and the Tylecodon patient, an experimental investigation was undertaken. Based on past work in arid regions, the assumption was that this competitive interaction was for water.

The xylem potential of the Pteronia nurses with patients (controls) and without patients (treatments) were not significantly different except for one Spring reading in August (1989). This was 12 days after the experiment was set up. In the following Winter (June 1990), xylem potentials of control and treatment plants still differed slightly but not quite significantly ($p=0.058$) and perhaps if a few more individuals were measured a significant difference would have been detected. For the remainder of the experiment, nurses with patients remained consistent in showing a slight, but not significant improvement in water status. I suspect that the one significant difference in Spring and the near significant difference in the following Winter was due to this being the active period of water uptake and prolific growth for both species but more especially Tylecodon wallichii. Most water is available at this time of the year but Tylecodon was probably intercepting some of the water before it infiltrated down to the Pteronia roots, and this is why lower xylem potentials were recorded for those nurses with patients.

A difference in xylem potential between control and treatment plants in Summer was not possible (see results)

but I believe a significant difference would have been unlikely. Tylecodon goes into a state of dormancy in Summer (pers.comm. Bruce Bayer) and survives on internal water resources, and is not actively utilizing soil moisture. The presence of this patient therefore would not have affected the water status of the control plants. In general, the lack of response by the nurse to patient removals can be explained in terms of the active period of water uptake for Tylecodon wallichii. Summer dormancy of the patient (already discussed) might well be advantageous to Pteronia nurse controls since the patients are tall and broad and therefore cast considerable shade on the soil below. This would reduce evaporation from the soil and retain soil moisture for longer (Shreve 1931). Treatment plants would not be sheltered in this way. In Spring and Autumn, Tylecodon is not actively taking up water since the primary period of water uptake for succulents is limited to the period immediately following rains (Fowler 1986). So even though less water is available at these times of the year, nurses with patients are not necessarily disadvantaged. This may explain why there was no improvement in the water status of the nurse plants without patients.

Some quantification of water uptake amounts and rates of the two species and evaporation rates from the soil is required to validate these comments.

A more likely explanation of why the xylem potentials of Pteronia treatment plants did not increase could be that Tylecodon was not competing with Pteronia for water due to

the separation of their rooting systems. Spatial separation of root systems has been suggested as a mechanism reducing or eliminating competition (Yeaton et al 1977). They demonstrated by near neighbour analyses that co-existence of two species in a simple community in the Sonoran desert could be explained by vertical partitioning of the soil profile by their root systems. Cody (1986) also suggested that growth form diversity of different root system morphologies might enable species co-existence. The separation or differentiation of niches among species is expected to reduce the intensity of competition among them and may thereby promote their co-existence. Niche separation among plants primarily takes the form of separation of resource use in space and/or time. The latter has already been discussed above.

The next step in this study was therefore to examine the rooting systems of the Pteronia nurse in relation to the Tylecodon patient to test the hypothesis that the nurse and the patient are not competing for water since their rooting zones are separate.

The root excavation study showed evidence that the roots of the nurse Pteronia and the patient Tylecodon are separated in vertical space (see results). Horizontal root overlap between Pteronia and Tylecodon was also minimal (see Table 3.11). It is apparent therefore that due to the separation of the nurse and patients rooting zones, they probably utilize separate water resources and are therefore not competing for water.

M^CAuliffe (1984) described the rooting patterns of the sahuaro (Carnegiea gigantea) and the paloverde (Cercidium microphyllum) and though they were separated in vertical space only, he still claimed that the competitive interaction exhibited between the two was for water. The plant's roots were apparently not separated in horizontal space. M^CAuliffe (1984) described the deeper root system of a paloverde tree and postulated that because it occurs beneath the shadow of the umbrella-like cover of sahuaro roots, the shallow network of sahuaro roots may intercept a large fraction of the available moisture before it could penetrate to the level of Cercidium roots. Die-back of the nurse was explained by root competition but no study was undertaken to prove this.

What must be emphasized in the current study is that competition for water between the nurse and the patient is weak despite the region being semi-arid. Based on the initial section of this chapter however, (where nurse vigour was shown to decline with increasing patient competitive effect) a competitive interaction does seem to occur, judging from the regression results. If they are not competing for water, how might the decline in nurse vigour be explained ?

One explanation could be the physical disturbance of the Pteronia canopy by Tylecodon adult patients. Tylecodon (see Plate 10) is a very robust leaf and stem succulent. Its growth rates are presumably rapid in comparison to the nurse. Pure physical pressure on the nurse canopy might cause this apparent deterioration of this canopy in the vicinity of the patient plant. As the patient plant grows larger, a greater disturbance of the nurse canopy results, and this gives the appearance of canopy "die-back" (see Plate 10 of Pteronia -Tylecodon at a late stage).

Another explanation might be one of light levels. Both the adult patient and the nurse are of similar heights and in some cases the Tylecodon patient has overtopped the nurse. These plants may simply shade the nurse and the section of the nurse canopy that would be most likely to suffer from inadequate PAR levels would be that closest to the patient. A light response investigation of Pteronia pallens would confirm this prediction. Franco and Nobel (1988) showed that reduced light levels beneath the nurse canopy of

Hilaria rigida caused reduced growth for the patient Agave deserti. Perhaps an overtopping patient plant may have a similar effect on its nurse.

Competition between the nurse and the patient might also be for nutrients, especially nitrogen and phosphorus. Nutrient requirements and uptake of Pteronia and Tylecodon would have to be studied to determine whether competition for nutrients is likely. However, these plants have different rooting zones, they exploit different nutrient resources so I would not emphasize nutrient competition as is the case with water.

Nurse-Patient Interactions and Vegetation change

Despite the fact that competition between Pteronia and Tylecodon does not appear to be for water, there is still this pattern of a decline in nurse vigour as patients get larger with the ultimate replacement of the nurse by the patient. This sort of species replacement has been evidenced in a number of studies (Vandermeer 1980, M^CAuliffe 1984, Yeaton 1978, Yeaton and Esler 1990). Yeaton (1978) claimed that there appeared to be a cyclical relationship occurring between Opuntia leptocaulis and Larrea tridentata. Vandermeer (1980) and M^CAuliffe (1984) described the sahuaro-paloverde relationship in the Sonoran desert, in a similar manner. M^CAuliffe (1984) stated that the competitive effects of the sahuaro on the nurse accelerated the rate at which individual trees (paloverdes) were lost from the system, thereby acting as an autogenic mechanism accelerating local plant replacement. Vandermeer (1980) drew a parallel between the sahuaro-nurse association in terms of population oscillations and the classic predator-prey system. M^CAuliffe (1984) discussed this further and stated that the loss of the 'prey' (paloverde) due to the 'predator' (sahuaro) was not instantaneous, and because of the time span over which this would occur (50-100 years) there would be multiple overlapping of generations of both plant populations.

Though the relative ages of Pteronia and Tylecodon are not known, Pteronia is a much longer-lived species and I believe that in the lifetime of one Pteronia a number of Tylecodon patients in series accelerate decline in nurse vigour, not just one. Casual observation in the study site shows much evidence for high mortality of large adult Tylecodon plants. This could be an indication of natural senescence and a relatively short life span.

Due to the above mentioned reason of overlapping generations and due to the fact that not all nurse plants or patient plants are the same ages, and also because their longevities are different, it may be explained why pure stands of Tylecodon are not found. I believe also that the time that Tylecodon adults stand alone is relatively short, since very few are found and many dead ones are present.

It is evident therefore that Tylecodon wallichii slowly replaces the long-lived, very common, dominant Karoo shrub Pteronia pallens and is one of the few Karoo plants that can do this. Using pattern analyses, Yeaton and Esler (1990) claimed that another Pteronia species, (P. empetrifolia) could replace P. pallens successionaly.

In conclusion, Pteronia pallens is the preferential nurse for Tylecodon wallichii (see Chapter 1 and Chapter 2), since it is most successful beneath this shrub. One of the reasons why Pteronia is such a good nurse for Tylecodon is due to the rooting patterns of the nurse and the patient being separate in vertical and horizontal space.

So, for a number of reasons (discussed in Chapter 1 and here) Pteronia facilitates Tylecodon establishment considerably. With time however, the larger the patient plant grows, the greater is the competitive effect it exerts on its nurse. Nurse vigour thus declines and eventually the Tylecodon replaces the Pteronia nurse. Whether this is a passive replacement, since the Pteronia is naturally less vigorous because it is older, or whether there is an active competitive force exerted on the nurse, is not certain. I would speculate that this "loss of vigour" is due to natural senescence but is accelerated by the physical pressures exerted by the patient on the nurse canopy (physical damage and reduced light levels). I base these statements however, on the findings of the water status investigation which yielded little evidence for active competition for water. Stronger evidence for active competition for another resource (eg light) is needed. There is definitely species replacement occurring but for reasons already mentioned, the community does not end up as a monospecific stand of Tylecodon wallichii.

This study highlights two points in particular about ecological studies in arid environments. Firstly, that

descriptive analyses are insufficient and need to be backed up by eco-physiological studies. Secondly, it should not be taken for granted that plants in arid areas are competing for water.

The important point in trying to understand arid plant community structure and dynamics, however, is not so much how species replacements occur but that they do occur. These successional sequences on the scale of an individual plant are predictable since the phenomenon of "nurse specificity" most definitely exists.

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CONCLUDING CHAPTER

Conclusion

The aim of this study was to determine the importance of plant-species interactions in the vegetation dynamics of the Succulent Karoo. The Karoo is a semi-arid rangeland and therefore might be viewed as an event-driven system (Mentis *et al* 1989) and since rainfall is highly stochastic, vegetation changes are seen to be unpredictable. Accepting that largely climatic events determine states and transitions of vegetation in arid lands, would it suffice to gain a predictive understanding of the effects of episodic rainfall events on vegetation change or are intricate biotic interactions equally important and therefore deserve further attention?

This study has shown conclusively that biotic interactions, specifically plant-plant interactions are complex and can considerably alter the vegetation in the Karoo. A significant rainfall event might provide suitable conditions for seed germination but depending on the availability of 'suitable space', establishment and survival of Karoo plant species might not occur. I have shown that at least some species in the Karoo require the 'space' beneath the canopies of larger plants, which are more favourable than adjacent exposed sites for initial establishment. Initial seedling establishment appears to be determined by abiotic

variables such as temperature, moisture, soil nutrients and PAR. Nobel and his colleagues (1988) have made conclusive studies of the physiology of nurse plant establishment in North America. The first three variables are more favourable beneath the canopies of the nurse plants and thus enhance seedling establishment. I must emphasise 'initial' establishment since not only do we need to gain an understanding of this initial facilitation but also of the species requirements until reproductive age is reached. While a Karoo shrub may offer suitable conditions for the initial establishment of a patient species, as the patient grows larger, the conditions beneath this nurse may no longer prove suitable. Patient plants may not be successful under some nurse species and therefore fail to reach maturity in such an association (e.g. as is the case with the nurse Eberlanzia and the patient Tylecodon). Another Karoo shrub (e.g. Pteronia pallens) may however provide suitable conditions for the patient throughout its life-history. Patient species requirements and tolerances as a juvenile and an adult need to be considered. In this study, the patient Tylecodon wallichii was nurse specific.

If we are to understand the role of plant-plant interactions in arid vegetation, we must accept firstly that some plants require nurses for initial establishment and secondly that depending on the patient species requirements and tolerances, some Karoo shrubs are more effective nurses than others.

Patient plants beneath their favoured nurses may be so successful in terms of growth that the initial commensal relationship, whereby the patient benefits and the nurse is unaffected (+0) (Abrams 1987) may change to a competitive interaction. At the start of such a changing relationship an almost 'predatory' interaction, rather than a competitive one could be described since the patient benefits and the nurse is disadvantaged (+ -) (Abrams 1987). However, I have referred to this interaction as a competitive one in Chapter 3 since in the long term, both nurse and patient are disadvantaged in the association (- -) The nurse dies and the patients offspring have fewer favourable sites available for establishment and survival to maturity. These competitive interactions lead to species replacements of the nurse by the patient.

It is interesting to note that Pteronia pallens is a widespread, long-lived unpalatable species which often dominates heavily overgrazed areas. Tylecodon wallichii may be one of the very few species that can oust Pteronia and in so doing provide establishment sites for more palatable species

In summary, this study has revealed the importance of intricate plant-plant relationships where initially facilitation of a patient plant by a nurse plant leads to competition and species replacement of the nurse by the patient. Since certain patient species are nurse specific, such species replacements are predictable.

Research Applications and directions for Future Research

The need for a predictive understanding of Karoo vegetation dynamics is crucial for sound farming and conservation practices (Cowling 1986, Hoffman and Cowling 1987, Mentis et al 1989). I believe that vegetation dynamics models such as the 'state and transition' model proposed by Westoby et al (1989) could form the basis of plant ecological research in the Karoo. If we were to concentrate more on predicting rainfall events in the Karoo, and describe in detail 'vegetation states' (using pattern analyses and experimental studies) we might achieve our goal. We have reason to be optimistic about the future of the Karoo if scientific research continues to grow in this important region of South Africa. Thus far, a model generating rainfall probabilities (Zucchini 1984) has been formulated, so, in relation to the state and transition model, work has begun on determining frequencies of climatic events. In so far as accurately describing vegetation states and transitions, a number of research projects are in progress in the Karoo. These studies focus on a number of variables thought to influence the vegetation dynamics and include work on seed banks, shrub responses to grazing and plant-plant interactions, to name but a few at the University of Cape Town alone.

It is encouraging that despite studies such as this one being extremely localised, there is supporting evidence for some of my findings in other areas of the Karoo (Tierberg)

as well as in other arid regions of the world (America). The processes studied here may thus be quite general to some growth form. We may well be addressing research questions more realistically.

The findings of this study may be indirectly applied to farming and conservation management. In trying to rehabilitate the much deteriorated Karoo veld for farming and conservation purposes, perhaps more specific studies on the regeneration sites of palatable versus unpalatable species and endangered dwarf succulents could be undertaken. Do the plants in question require nurse plants for successful establishment and survival? If so, which are the effective and which are the poor nurse plants? Do any of the palatable species replace non-palatables, or vice versa? Answers to these questions may explain the failure of many attempts to improve Karoo veld by sowing in seed and provide an indication of what changes can be expected from current veld composition.

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