Biology of Prosopis cineraria (Leguminosae) in the Sultanate of Oman

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BIOLOGY OF PROSOPIS CINERARIA (LEGUMINOSAE) IN THE SULTANATE OF OMAN

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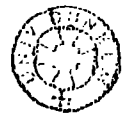

For Charlie, Mick, Karin and Kara

DECLARATION

The material contained in this thesis has been produced only by the author, and has not previously been submitted in any form for a degree in this or any other university.

ABSTRACT

This thesis presents the results of a four year study from 1986 to 1990 on the biology of the leguminous tree Prosopis cineraria (L.) Druce in the Sharqiya region of the Sultanate of Oman. Descriptive studies were performed on both the woodland habitat and the species. The suitability and methodology of utilising P.cineraria in future forestry programmes in Oman were also examined.

Field studies have shown that this drought-tolerant indigenous phreatophyte forms large mono-culture relic woodlands in the sandy deserts of the Sharqiya. It is well adapted to the harsh environment of shifting sand dunes, growing vegetatively through accumulated sand to form tree clumps.

Ecological studies have shown that the Prosopis woodland micro-environment supports wildlife not necessarily adapted to arid conditions. P.cineraria is an excellent multi-purpose tree for local people, particularly in providing fodder, fuelwood and shade protection. Over-exploitation and the general absence of natural reproductive regeneration has resulted in the decline in the condition of some Prosopis woodlands in Oman. To ensure their continued survival several methods of conservation were recommended.

Studies on the mature trees have shown that the morphological variability of this species in the Sharqiya was high, which contributed to its multi-purpose potential. This variability was both phenotypic and genotype in origin.

Glasshouse trials of P.cineraria in Durham have shown that seeds sampled from individual trees produced seedlings that were morphologically variable and were particularly tolerant to high salinities. Variation in morphology and salinity tolerance were related to both their geographical and parental origin.

Three P.cineraria field trials in Oman have shown that the climate and soil environment greatly affected seedling growth and morphology. Silvicultural recommendations derived from these trials have been proposed for the propagation of this species in Oman.

CONTENTS

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LIST OF ABBREVIATIONS

A1-A5	inter-provenance morphotypes determined by cluster analysis
AL-K	P.cineraria field trial in full sunlight at Al-Kamil
ANOVA	analysis of variance
B1-B6	intra-provenance morphotypes determined by cluster analysis
bA	basal area (cm^2)
CANOCO	canonical correspondence analysis
CEC	cation exchange capacity
cm	centimetre
CM1	treatment with 1:1 ratio of sand and manure
CM2	treatment with 2:1 ratio of sand and manure
CM3	treatment with 3:1 ratio of sand and manure
CPZ	Central Prosopis Zone
dbh	diameter of tree bole at breast height (cm)
DECORANA	detrended correspondence analysis
DF	degrees of freedom
DS	dune soil
DT	tree density ($treesha^{-1}$)
EC	electrical conductivity
Em	mean unit leaf rate (gcm^{-2})
EPZ	Eastern Prosopis Zone
F1-Fn	principal component functions
FAO	Food and Agricultural Organisation, Rome, Italy
FC	soil field capacity
Fm	mean leaf area ratio ($cm^2 g^{-1}$ plant dry weight)
h	hour
ha	hectare
IBPGR	International Board for Plant Genetic Resources, FAO, Rome, Italy
LAR	leaf area ratio ($cm^2 g^{-1}$ plant dry weight)
LWR	leaf weight ratio (gg^{-1} plant dry weight)
m	metre
mA	milli Ampere
MAF	Ministry of Agriculture and Fisheries, Muscat, Oman
MPa	mega Pascal
M1	natural seed moisture content
M2	partially imbibed seed moisture content
mm	millimetre
min	minute
MW	molecular weight
d	tree distance (m)

NAS	U.S. National Academy of Sciences
NPK	nitrogen, phosphorus, potassium fertiliser
NPK+T	NPK fertiliser with trace elements
NPK-T	NPK fertiliser without trace elements
NS	not significant ($p > 0.05$ unless stated)
n/d	not determined
OWSP	Royal Geographical Society's Oman Wahiba Sands Project
p	probability
PAGE	polyacrylamide electrophoresis
PAR	photosynthetically active radiation (400-700nm)
PCQM	point-centred quarter method
pers. comm.	personal communication
pers. ob.	personal observation
ppm	parts per million
P_v	mean seed viability period (days)
rev	revolutions
R_f	relative mobility
RGR	mean relative growth rate ($gg^{-1}week^{-1}$)
RWR	root weight ratio (gg^{-1} plant dry weight)
s	second
S1-S6	seed morphology classes
SLA	specific leaf area ($cm^2 g^{-1}$ leaf dry weight)
SWPZ	South-western Prosopis Zone
SQU	Sultan Qaboos University
SQU-1	P.cineraria field trial in full sunlight at SQU
SQU-2	P.cineraria field trial under shade at SQU
SD(σ)	standard deviation of the mean
SWR	stem weight ratio (gg^{-1} plant dry weight)
T1-T5	permanent transects across the EPZ
T1W-T5W	'wandering' transects across the EPZ
TEMED	N,N,N',N' tetramethyl-ethylenediamine
TRIS	Tris-(hydroxymethyl) aminomethane
TWINSPAN	two-way indicator species analysis
UTM	Universal Transverse Mercator
V1-V7	TWINSPAN vegetation classes
WAP	water-absorbing polymer
WS	Prosopis woodland soil
WSC	water storage capacity of wood (%)
wt	weight
WQM	'wandering quarter' method
yr	year
*	significance level $0.05 > p > 0.01$
**	significance level $0.01 > p > 0.001$
***	significance level $p < 0.001$

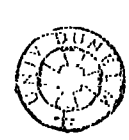
CHAPTER 1

GENERAL INTRODUCTION

Forests and woodlands cover nearly one third of the earth's land surface, supplying basic needs such as food, fuelwood, fodder and income to over 2000 million people (FAO, 1985). As a result of mismanagement, forest resources throughout the world are being continually degraded or destroyed.

Arid (less than 100mm rain annually) and semi-arid (less than 400mm annually) regions of the world exceed 64 million km^2, representing 43% of the continental land surface and 14% of the total earth surface. They are the major land resource in most developing countries, but as the demand for resources increase their availability decreases. There is therefore an urgent need for the responsible management of the world's arid and semi-arid land resources.

In arid environments, the generally low and sporadic nature of precipitation makes water availability the major limiting factor to the primary productivity and morpho-phenologic development of desert plants (DePuit, 1979). Desert plants are therefore opportunists, where their growth and development are critically dependent on favourable climatic conditions. The net primary productivity of a community is the rate of production of new biomass that is available for consumption by heterotrophic organisms (Begon et al., 1986). The net primary productivity in arid and semi-arid regions has been estimated at 25-400$gm^{-2}yr^{-1}$ and 250-1000$gm^{-2}yr^{-1}$ respectively, compared to up to 3000$gm^{-2}yr^{-1}$ in regions of abundant water (Fischer & Turner, 1978). Similarly, Whittaker (1975) has estimated the net primary productivity for the following ecosystems:



1. Extreme desert — 0-10gm^{-2}yr^{-1}
2. Desert & semi-desert shrub — 10-250gm^{-2}yr^{-1}
3. Woodland & shrubland — 250-1200gm^{-2}yr^{-1}

Access to predictable or permanent sources of water will promote the development of perennial vegetation communities which can eventually lead to the climax formation of desert woodland ecosystems. Desert woodlands are ecologically rich in plant and animal species diversity compared to the surrounding desert plains. They are an important resource to man and to indigenous wildlife, and often form ecological corridors in to dry regions by supporting species that are not specifically adapted to arid conditions.

Generally, desert woodlands lie in a fragile ecological equilibrium which is being disturbed by increasing pressures from man. One inevitable outcome of mismanagement of these areas is desertification, which has resulted in approximately five million hectares of new desert being formed each year (Walls, 1977). Causes of desertification include over-cultivation, over-grazing, poor irrigation practices and deforestation. In arid zones, the removal of the natural protective cover of the trees and shrubs, mainly for fuelwood and fodder, has rapidly enhanced the rate of desertification by exposing fragile and loose soils to wind erosion.

Perennial woody plants of arid and semi-arid regions have been used effectively in reafforestation practices in combating desertification and bringing about a restored and sustainable resource base to degraded lands. This practice is often referred to as social forestry. The tree species selected must be capable of surviving in the most extreme physical and climatic environments and must meet the demands of the local human population by providing at least the basic needs of food, fuelwood and fodder. These species must also be resistant to excessive grazing pressures and

over-exploitation. Trees that meet these requirements are called multi-purpose or multiple resource trees. The specific functions of multi-purpose trees in combating desertification, identified by Grainger (1983), include: rehabilitation of degraded lands; increase in vegetative cover; stabilisation of soils; reversal of water logging and salinisation; restoration of nutrient cycles; improvement of soil fertility and soil structure; and protection against wind erosion.

As a result of a major change in forestry policy in 1978 by the World Bank and FAO (World Bank, 1978; FAO, 1978) from commercial forestry (industrial wood plantations) to social forestry, the valuable role of multi-purpose trees in combating desertification has only recently been recognized. Studies have been primarily aimed at the selection of superior multi-purpose species, the analysis of their multiple resources, and the identification of methods for their controlled utilisation (Burley et al., 1984). To determine whether a tree species is suitably multi-purpose, it must be tested in trials under natural arid conditions. This subject is in its infancy compared to commercial trials screening for quality timber strains.

The genus Prosopis of the family Leguminosae (sub-family Mimosoideae) is recognised worldwide as a genus of economic and social importance in arid environments and has been reviewed extensively by a number of authors (see Simpson, 1977; Pedersen, 1980; Leakey & Last, 1980; and Pedersen & Grainger, 1981). In this genus, 44 species have been identified, of which 40 are from the new world (Burkart, 1976). The majority of Prosopis species in arid regions have long tap roots and shallow lateral roots so that water can be collected from deep underground and from the surface. As such, they are typical phreatophytes, defined by Simpson & Solbrig (1977) as woody perennial plants that survive in deserts by exploiting water rich

micro-habitats. Some American Prosopis species have been reported to have tap roots that penetrate down to 80m (Solbrig & Cantino, 1975). For phreatophytic growth, the soil environment must allow the roots to rapidly penetrate to considerable depths, so that these types of plants are usually restricted to dune areas, alluvial soils or habitats receiving water from run-off (Drew, 1979).

Phreatophytes also have physiological and morphological adaptations to survive in arid conditions. P.velutina and P.glandulosa can acquire water against forces of more than -1.5 MPa (Haas & Dodd, 1972), whilst the latter species has been shown to actively photosynthesise at xylem water potentials of less than -4.0 MPa, which is characteristic of xerophytes (Strain, 1970). In some Prosopis species during dry periods, midday stomatal closure occurs to reduce water losses (Mooney et al., 1977; Sen, 1973). These species also have pulvini at the base of each leaflet, leaf and petiole which are responsible for the closure of the leaflets at night, and the drooping of leaves during hot summer day temperatures. Morphological studies have shown that the size of Prosopis leaves decreases with increasing warmer and drier climatic conditions as a means of reducing whole plant transpiration (Solbrig et al., 1977).

Other sources of water in arid environments available to phreatophytes include unpredictable rainfall and atmospheric moisture in the form of fog, mists and dew. In the P.tamarugo woodlands of the Chilean Tamarugal Pampa, fog and mists were thought to sustain the water requirements of the trees through a mechanism of foliar absorption called reverse transpiration (Sudzuki, 1969). This mechanism has been reported in a number of species from a variety of habitats (see Stone, 1957; Levitt, 1972; and Pedersen 1979). Reverse transpiration is the uptake of atmospheric moisture water by the aerial parts of the plant and its movement through the plant and exudation through the roots into the soil (Pedersen, 1979). Dissolved

nutrients in the soil solution can then be taken up by the plant when the moisture is re-absorbed during normal transpiration. However, more recent research has indicated that P.tamarugo of the Tamarugal Pampa is a typical phreatophyte, exploiting the relatively shallow water table or capillary fringe through tap roots (Mooney et al., 1980; Acevedo et al., 1985). To phreatophytes, the regularity of atmospheric moisture in arid environments may be important in maintaining leaf turgor in the mature tree for optimal photosynthetic rates (Pedersen, 1979), and a regular source of moisture during seedling establishment.

Many of the drought tolerant Prosopis species are recognised as being excellent examples of multi-purpose trees (Simpson & Solbrig, 1977; Felker, 1979; Stienen, 1985). As a result of their multi-purpose properties, a number of Prosopis species have been selected for reafforestation, including: P.tamarugo in the Chilean Atacama desert (Thomsen & Hills, 1983; Torres, 1985); P.chilensis in Sudan (Wunder, 1966); P.pallida in Hawaii (Esbenshade, 1980); P.alba in Argentina (Kram, 1967); and P.juliflora in Rajasthan (Kaul, 1957) and in Costa Rica (Valdivia & Cueto, 1979). Several new world Prosopis species have also been specifically identified as important producers of fuelwood and fodder under severe environmental conditions of low rainfall and poor soils (NAS, 1979). However, some Prosopis species are considered serious pests because they rapidly spread into valuable agricultural land due to their easy propagation and ability to withstand adverse environmental conditions and heavy grazing (Beck et al., 1975). These species, which include P.juliflora, P.glandulosa and P.ruscifolia, have to be controlled through regular herbicide treatments.

Prosopis cineraria (L.) Druce has been identified as a potentially important multi-purpose tree for arid and semi-arid areas (Leakey & Last, 1980). It is a drought-tolerant tree indigenous to the Arabian Gulf, Afghanistan, Pakistan

and arid and semi-arid regions of India. It is only one of four Prosopis species that is exclusively indigenous to the old world. The other species are P.farcta, P.koelziana and P.africana (Burkart, 1976). Like many of the Prosopis species, P.cineraria is a typical phreatophyte, with tap roots over 30m in length (Khan, 1955). P.cineraria favours coarse, sandy and alkaline soils and grows well in the swales of dune-fields in Rajasthan and in the United Arab Emirates (Sharma, 1966; Satchell, 1978).

The nomenclature of P.cineraria is associated with a number of synonyms, dating back to the mid-18th century. The correct reference for this species and the chronological order of its synonyms according to Wickens, G.E., Royal Botanic Gardens, Kew, U.K. (pers. comm., 1987) is:

Prosopis cineraria (L.) Druce in Bot. Exchange Club Soc. Brit. Is. 3:422 (1913)

Syn. Mimosa cinerea L., Sp. Pl. 1:517 (1753) non M.cinerea L., Sp.Pl. 1:520 (1753) syn. of Dichrostachys cinerea (L.) Wight & Arn.

Mimosa cineraria L., Sp. Pl. 2:1500 (1763) based on M.cinerea L.

Prosopis spicigera L., Mant.:68 (1767)

Prosopis spicata Burm., Fl.Ind.:102 (1768)

Prosopis cineraria (L.) Mcbride in Contrib. Gray Herb. n.s. 59:16 (1919), comb.superfl.

The literature on P.cineraria (L.) Druce cited in this thesis also includes papers where the authors have used the synonyms P.cineraria (L.) Mcbride, and P.spicigera L.. For reasons of clarity, the species will be quoted as P.cineraria when referring to the tree, and as Prosopis when referring to the woodland habitats in which they form.

P.cineraria is the only indigenous representative of its genus in the Sultanate of Oman. Oman occupies an area

of approximately 300000 km² in the south-eastern Arabian Peninsula, between 16°40'-26°20'N and 51°50'-59°50'E (Lawton, 1985) and can be topographically divided into 245000 km² of sandy and gravelly deserts, 45000 km² of mountains and 9000 km² of coastal plain. Oman is typically arid, receiving between 50-250mm rainfall per annum and is generally characterised by its prevailing climate of long, dry, hot summers and short, mild, wet winters (Boulos, 1985). Rainfall is very unpredictable, and continuous drought periods of over three years can occur (pers. obs.). The most regular source of moisture in Oman is dew, which occurs in the winter and especially at night in cycles of three to five days (Anderson, 1988).

P.cineraria is vernacularly known as ghaf in Oman, and is predominantly found in the sandy deserts and the coastal plains in the north of the country. This species is morphologically distinct from P.juliflora which has been introduced into Oman as a fast growing ornamental tree in landscape and highway planting projects throughout the country. P.cineraria typically forms isolated woodland habitats, separated by large distances and natural geographical barriers. These habitats are very low in tree species diversity, to the extent that many occur as natural mono-cultures of P.cineraria.

Literature on P.cineraria is extensive, and has been comprehensively reviewed by Leakey & Last (1980). Prior to 1986, literature on the distribution and biology of P.cineraria in Oman was limited. Following the recommendations of Lawton (1980), a Forestry Section in the Ministry of Agriculture and Fisheries (Oman) was established to commence the task of monitoring and managing the indigenous woodlands of the country. This document identified the general distribution of P.cineraria in Oman, and the need for the future management of this species. Lawton (1985) also recognised the multi-purpose potential of P.cineraria which formed dominant woodlands in sandy

topography in Oman. In 1986, the Royal Geographical Society launched the Oman Wahiba Sands Project (Dutton, 1986, 1988). This four month project (January to April) involved the multi-disciplinary study of an isolated sand desert (Wahiba Sands) in the Sharqiya region of North-Eastern Oman (see figure 3.1). One of the objectives of this project was to carry out a systematic biological study of this desert ecosystem. The results of this project have shown that the dominant habitats of this region were Prosopis woodlands, which were identified as being a major biological resource to both wildlife and to man (Brown, 1988).

This thesis presents the results of research on the biology of the Prosopis woodlands in the Sultanate of Oman. The study of trees and the habitats in which they form has to be the study of 'short-cuts', since the long life and large size of trees makes many of the conventional methods of plant biology impossible or unrealistic (Harper, 1977). This necessitated the use of a number of disciplines to maximise the output of information on this species over a four year research period.

Field research was concentrated in the Sharqiya region of Oman, although the majority of the Prosopis woodlands throughout the country were visited during the study period. The logistical problems of working safely under desert conditions limited the degree of flexibility of the experimental designs. In the first four months' field work, excellent support was provided by the Oman Wahiba Sands Project. Under these conditions, research was carried out in three major Prosopis woodland provenances in the Sharqiya. Further field work was continued in only one of these provenances after the Oman Wahiba Sands Project ended in April, 1986.

The objectives of this thesis are the following: to determine the distribution and ecology of the Prosopis woodlands in Oman; to assess the multi-purpose properties

of both the tree and the habitat; to examine the morphological adaptations of the species to the arid environment; and to assess the suitability of this species for use in future social forestry plantation projects in Oman, and the propagation methods for their implementation.

This thesis has been divided into seven chapters, consisting of this general introduction (Chapter 1); a chapter on the general materials and methods (Chapter 2); four subject chapters of related disciplines (Chapters 3-6); and finally a summary chapter with conclusions and recommendations (Chapter 7). Each subject chapter has an introduction covering the relevant literature; a materials and methods section describing relevant experiments; a results and discussion section describing the analysis and interpretation of the data collected; and a summary section describing the conclusions and recommendations of the chapter. Chapter 3 presents the distribution, structure and ecology of the natural Prosopis woodlands in the Sharqiya. This is followed by the morphological description and variation of mature P.cineraria forming these woodlands (Chapter 4). In Chapter 5, the results of seedling studies under natural and artificial conditions are presented, with the objectives of determining the strategies of growth used in the natural establishment of P.cineraria and the morphological variability of seedling growth for ecotypic selection. Chapter 6 presents the results of P.cineraria seedling field trials in Oman, with the principal objective of obtaining silvicultural information on the species.

Attached to this thesis are five appendices. Appendix A presents the P.cineraria Slide Reference Collection of 45 colour photographs taken in the field by the author. These slides illustrate most subjects covered in this thesis, and have been arranged in subject order for easy access. Where relevant, slide numbers have been cited within the text of this thesis. Photographs of voucher specimens of

P.cineraria leaves, flowers and fruit collected in Oman are also included in this reference collection (slides 37-39). Appendix B lists the complete botanical names of all Prosopis species cited in this thesis. A Prosopis Seed Bank was designed to store the 103 seed accessions that were collected whilst performing the field work for this thesis. The format of the computer database in which the data was stored, together with a summary of the seed accessions collected are presented in Appendix C. Statistical summaries of data not included in Chapters 3, 4, 5 and 6 are presented in Appendix D. The chemical composition of well water data from bore holes in the Central Prosopis Zone determined by the Public Authority for Water Resources, Oman, are summarised in Appendix E.

CHAPTER 2

GENERAL MATERIALS AND METHODS

2.1 Navigation in the field

The majority of woodland cover in the Sharqiya was visited over a period of four years. Inaccessible areas were made available with the support of the Sultan's Armed Forces during the Royal Geographic Society's Oman Wahiba Sands Project (OWSP). The isolated locations of the primary study areas in the Sharqiya influenced the fieldwork methodology. In preparing and implementing experimental designs for the field, provisions were always made for working under safe conditions. A four wheel drive vehicle which was well equipped with a field first aid kit, vehicle spares, petrol, water and food provisions was essential.

Navigational aides for working in the Sharqiya consisted of 1:100000 K6611 series ordinance survey maps (National Survey Authority, Muscat, Oman), aerial photography (Petroleum Development Oman, Muscat, Oman), and, in some localised study areas, large scale satellite images (supplied by the OWSP). Navigation during the first excursions into the Sharqiya woodlands in 1986 was carried out using a MX6102 Magnavox satellite navigator (Magnavox Ltd., London, U.K.), which was installed in the vehicle. The MX6102 was used to dead-reckon the position of the vehicle by continually tracking satellites. The equipment was also used on the move, with the vehicle position being updated using speed and heading sensors. As access to this equipment was limited, it was primarily used to assess the distribution of woodlands in relation to the field maps so that they could be updated. For the majority of field work however, 1:100000 maps only were available. Precision map reading was often extremely difficult due to the absence of prominent physical features in the region.

2.2 Seed sampling strategies

Collections of P.cineraria seeds were made when they became available. Where possible, pods were collected whilst still attached to the trees to minimise seed damage through invertebrate infestation. From the Sharqiya, three provenance seed accessions and 100 seed accessions from individual trees of known morphology were collected (Appendix C). The precise location of individual trees within the woodlands was determined using the Magnavox MX6102. The seeds were immediately extracted from the pods, and seeds with intact testa stored temporarily in paper envelopes in the shade. A subsample of ten pods from each seedlot was made and the pod length and the number of healthy and damaged seeds per pod were determined. Damaged seeds were taken as those that would be unlikely to germinate. The extent of infestation in each seedlot was calculated as the number of damaged seeds, as a percentage of the total number of seeds from the pod sample.

2.3 In situ plots of seedling regeneration

Periods of heavy rainfall which occurred in late January and early February 1986 promoted herbaceous and ephemeral growth, and the germination of P.cineraria seeds within the woodlands. In situ plot studies were established in a Prosopis woodland near the town of Al-Kamil (see figure 3.1) to investigate the temporal and spatial vegetation responses to heavy rainfall. Four plots of $36m^2$ were marked out with wooden stakes, with the boundaries running north-south, and east-west. Each plot enclosed a central P.cineraria tree that was heavily in fruit. Recently matured pods were observed on the soil surface of all four plots. Plots 1 and 2 were protected by fencing whilst plots 3 and 4 were unfenced and subject to the normal grazing pressures of the area. For each plot, a grid system of 30cm x 30cm was used to map the positions of

individual plants. The plots were mapped two weeks and six weeks after the last rainfall (figure 5.4). Changes in the distribution and density of the P.cineraria seedlings were compared between the fenced and unfenced plots over the two sampling periods.

2.4 Assessment of genetic variation

1. Seed protein extraction and separation

P.cineraria seeds were imbibed for 18 hours to remove the testa. 0.5g of cotyledon material from 20 to 30 seeds were homogenised with a small amount of acid-washed silver sand and $3cm^3$ of 0.4M NaCl extraction buffer (pH 6.0), using a chilled (4°C) porcelain mortar and pestle. The homogenate was then briefly centrifuged to remove cell debris and silver sand. The supernatant was decanted into visking tubing and dialysed overnight against tap water at 4°C.

Polyacrylamide gel electrophoresis (PAGE) with a discontinuous buffer system was used to separate the extracted seed proteins, according to the method of Gates (1978). Each vertical slab gel (9.5cm x 7.2cm x 0.125cm) was made up of a 3% w/v acrylamide stacking gel and a 7% w/v acrylamide resolving gel. The composition and preparation of the acrylamide solutions have been summarised in table 2.1. Except for TRIS (Boehringer, Mannheim, West Germany), chemicals were supplied by Sigma Chemical Co., St. Louis, U.S.A.). The gels were prepared inverted using the Pharmacia GE-4 system (Pharmacia, Uppsala, Sweden) with a well former for ten samples (well volume of $0.025cm^3$), of which the outer wells were not used. After degassing under vacuum, the stacking gel was poured gently into the mould to a depth of 1.0cm from the wells. The gel front was made even by syringing $1cm^3$ of distilled water onto the surface of the gel, and left to

Table 2.1

Composition and preparation of polyacrylamide gels.

Solution 1	acrylamide	6.0g
	BIS-acrylamide	0.16g
	TEMED	0.15cm^3
	TRIS	3.03g
	Total volume	100cm^3 (made up with distilled water)
Solution 2	ammonium persulphate 150mg	
	Made up to 100cm^3 with distilled water	
Solution 3	TEMED	0.03cm^3
	1M HCl	6.0cm^3
	TRIS	4.57g
	Total volume	12.5cm^3 (made up with distilled water)
	Adjusted to pH 8.9	
Solution 4	acrylamide	7.0g
	BIS-acrylamide	0.183g
	Total volume	25cm^3 (made up with distilled water)

For one gel of 9.5cm x 7.2cm x 0.125cm dimensions:

1. 10cm^3 3% w/v stacking gel : 5cm^3 each of solutions 1 and 2

2. 16cm^3 7% w/v resolving gel: 2cm^3 solution 3, 4cm^3 solution 4 and 8cm^3 solution 1 with 2cm^3 distilled water

polymerise for 30 minutes, after which time the water was removed. Degassed resolving gel solution was then poured over the stacking gel, leaving room at the end of the mould to overlay the front with $1cm^3$ of distilled water. The gel was left to polymerise for 30 minutes before the well former was carefully removed from the stacking gel.

The gel was sealed into an electrophoretic tank (Pharmacia, Uppsala, Sweden) containing freshly prepared reservoir buffer (TRIS 0.606g, glycine 2.88g, made up to $1dm^3$ with distilled water). One drop of 0.1% bromophenol blue marker dye was added to each extract. One extract was loaded per well, using a clean syringe each time. Gels were ran using a constant current source of 10 mA/gel for 15 minutes, followed by 30 mA/gel, until the front marker dye had approached the bottom of the gel.

2. Staining for non-specific esterases

Esterase isoenzymes separated in the gels were stained according to the method of Markert & Hunter (1959). Tetrazotised o-dianisidine (Fast blue B) was dissolved in $1cm^3$ of pH 5.0 sodium acetate buffer ($14.8cm^3$ 0.2M glacial acetic acid and $35.2cm^3$ 0.2M anhydrous sodium acetate, made up to $100cm^3$ with distilled water). This was stirred into a solution of $30cm^3$ acetate buffer and $0.5cm^3$ of 1% w/v α-napthyl acetate in 70% v/v ethanol. The gel was immersed into the stain and incubated for about one hour and then washed in 50% v/v methanol. The distance moved by the marker dye and the leading and trailing edges of each band were measured with a millimeter ruler. The relative mobility (R_f) of the leading edge of each band was calculated, where R_f is the distance moved as a fraction of the distance moved by the marker dye.

2.5 Soil analysis

A total of 63 soil samples was collected from 20 woodland sites. At most sampling sites, a pit was dug to the maximum practical depth, which was usually to a depth of 1m. At some sites, soils were sampled directly from quarry faces or steep wadi banks. A description of the soil profile was made, including the depth of obvious soil horizons, moisture depth and the presence of roots. From each soil profile, samples were taken from 10cm wide bands around the pit wall at intervals of 20cm, starting from the soil surface. In one soil profile that was over 8m in depth, the sampling interval was increased to 1m.

The soil samples were sun-dried, placed in plastic bags, and returned to the laboratory for analysis of physical and chemical properties. Soil physical properties were based on the methods of Hodgson (1974) and Alexander (1988). Soil colour was determined using a Munsell Soil Colour Chart (Munsell Colour Co., Maryland, U.S.A.). Texture was qualitatively assessed on stone and root free moist soil by estimating the proportions of sand (2mm to 0.05mm), loam (0.05mm to 0.02mm) and clay (0.02mm to 0.002mm) using the procedure in table 2.2a. The size and abundance of stones in each sample was classified according to the descriptors listed in table 2.2b.

For the analysis of soil chemical properties, the samples were first passed through a sieve (2mm mesh) to remove stones and bulky organic material. The soil fractions were analysed with a soil test kit and colorimeter (Complete Soil Testing Outfit EL513-022; Paqualab Photometer EL430-550, ELE Ltd., Hemel Hempstead, U.K.). This equipment was used to determine the concentrations of exchangeable nitrate nitrogen $N(NO_3)$, ammonium nitrogen $N(NH_4)$, phosphate phosphorus $P(P_2O_5)$, potassium, calcium, magnesium, iron, chloride and sulphate sulphur $S(SO_4)$ to an accuracy of ± 5% at $1mgdm^{-3}$ (figure

Table 2.2

Methods of soil description based on Alexander (1988).

A. Soil texture

1. Roll out sample to a diameter of about 1cm
   1.1 will not work..... 2
   1.2 works..... 4

2. Check for bonding by rubbing between fingers
   2.1 no bonding..... 3
   2.2 bonding.....TEXTURE = LOAMY SAND

3. Grind down on palm of hand
   3.1 clayey material absent..... TEXTURE = SAND
   3.2 clayey material present..... TEXTURE = LOAMY SAND

4. Roll out sample to a diameter less than 0.5cm
   4.1 will not work..... TEXTURE = STRONG SANDY LOAM
   4.2 works..... 5

5. Rub between fingers close to ear
   5.1 loud crunch..... TEXTURE = SANDY LOAM
   5.2 soft or no crunch..... 6

6. Examine sliding surface
   6.1 dull..... TEXTURE = LOAM
   6.2 gleaming..... TEXTURE = LOAMY CLAY OR CLAY

B. Soil stoniness

STONE SIZE

Class	Descriptor	Size
1	very small stones	2-6mm
2	small stones	6mm-2cm
3	medium stones	2-6cm
4	large stones	6-20cm
5	very large stones	20-60cm

STONE ABUNDANCE

Class	Descriptor	Abundance
0	stoneless	< 1%
1	few stones	1-5%
2	common stones	6-15%
3	many stones	16-35%
4	abundant stones	36-70%
5	extremely abundant stones	>70%

supplied by ELE Ltd.). The soil test kit was used to the manufacturer's instructions with two modifications. The soils were extracted with water which was first distilled before being de-ionised, and an orbital shaker (Gallenkamp, Loughborough, U.K.) set at 200 rev.min^{-1} was used to standardise the extraction technique.

Soil pH using a PW9420 pH meter (Phillips, Pye Unicam Ltd., Cambridge, U.K.), and electrical conductivity using a Schott Geräte CG 857 portable meter (Camlab Ltd., Cambridge, U.K.) were determined on soil extracts prepared from 10cm^3 of soil in 50cm^3 of distilled and de-ionised water.

2.6 Seed extraction from pods

Seed extraction of small collections of pods was carried out by hand. The following procedure was developed to extract large numbers of seeds. Approximately 2-3 kg of sun-dried pods were placed into a strong plastic woven sack and beaten with a heavy wooden stick. Pod debris and loose seeds were passed through a 5mm mesh sieve to remove the larger fragments. The fine fraction was spread over the surface of a large bowl of water and gently stirred to allow seeds with intact testa to sink to the bottom. Damaged or hollow seeds and pod debris left at the surface were removed using a 1mm mesh sieve and discarded. The procedure was repeated until all the crushed material had been separated. The submerged seeds were collected from the bowl, excess water removed and then left on open trays to dry. As the seeds were submerged for less than five minutes, they rarely imbibed water. Those that did were considered damaged and discarded from the collection.

2.7 Seed germination

Seeds selected for sowing were scarified using coarse grained sandpaper, until scratches were clearly visible on the testa. The seeds were surface-sterilised in 5% sodium hypochlorite solution for five minutes, rinsed and then imbibed in distilled water for approximately 18 hours at 20°C. Imbibed seeds were placed between wet filter paper in petri dishes and stored at 20°C in the dark for 48 hours. Successfully germinated seeds were identified as those with at least 5mm of emerged radicles. Germinability was calculated as the number of germinated seeds, as a percentage of the total seed sample. Seed dormancy was measured on unscarified samples as those seeds failing to imbibe after at least 18 hours immersion in distilled water, but which germinated after scarification and repeated imbibition. This was expressed as a percentage of the total seed sample.

2.8 Sowing seeds

Only germinated seeds with 5mm of emerged radicle were selected for sowing. These seeds were consistently sown to a depth of 5mm, with the radicle orientated down into the soil.

2.9 Seed moisture content determination

Seed moisture content was determined from samples of approximately 200 seeds. The seeds were ground in a ball-bearing mill for short periods to minimise heat build-up and water loss through evaporation. Approximately 3g of ground seed were spread evenly over each of three pre-weighed dishes (10cm diameter). Fresh weights were determined before drying in a pre-heated oven at 130°C for one hour, according to the method of Evans (1972). The

samples were removed and cooled in a dessicater for 10 minutes and then weighed. The moisture content for each sample was determined as the weight of water as a percentage of the total weight of the seeds. The procedure of drying, cooling and weighing was repeated until the % moisture content of the three samples was consistent. The mean of these three samples was used as the % moisture content of the seeds.

2.10 Seedling harvests

Leaves were removed from the seedling and their area immediately determined by the method given in section 2.11. The stem was cut at the root collar and its length measured. The roots were carefully extracted from the soil with water and cleaned of adhering particles. The stem and roots were cut into small sections to facilitate drying. All plant material was dried in a ventilated oven at 80°C (Evans, 1972) for 24 hours, and the dry weights determined. The samples were re-dried for a further 24 hours and re-weighed to confirm the results.

2.11 Leaf area determination

Where possible, leaf areas were determined for each harvested seedling using a leaf area meter (Delta-T Devices LTD., Cambridge, U.K.). As leaf size was small, the shortest focal length of the equipment was used to maximise the resolution and accuracy. The meter was calibrated using a perspex sheet painted with black rectangles (10mm x 2mm) to represent the typical leaf size of the seedlings. To allow for the natural variation in the morphology of P.cineraria leaves, a second calibration was carried out. A small selection of leaves of varying size, shape, age and colour were permanently sealed between thick clear perspex sheets. The leaf area of this sample was then determined

using the calibrated area meter. Whenever the equipment was used thereafter, calibration was performed using both reference areas. Fully opened leaves were carefully arranged between solid strips of clear perspex in order to fill, but not exceed, the reference frame area. Multiple frames were necessary for most seedlings, and results were added cumulatively to give the total leaf area.

Leaf areas were also determined using leaf area calibration curves. This method was necessary when an area meter was not available, or when the seedlings that were harvested were too large to determine the total leaf area accurately. As the high correlation between leaf area and leaf dry weight can be susceptible to both ontogenetic drift and natural genetic variation (Evans, 1972), a calibration curve was prepared for each experiment to cover the ranges of seedling ages and treatments used. The leaf area for each of these seedlings was determined accurately using the leaf area meter before the leaf dry weights were determined. If the equipment was not immediately available, the leaves arranged between the perspex sheets were permanently recorded using a standard photocopier, for later determination. Leaf area was plotted against dry weight, from which regression equations were used to calculate the leaf areas for the remaining seedlings in the experiment.

2.12 Quantitative analysis of plant growth

The distribution of dry weight material between the different organs of young plants was examined. For each sampling period, mean dry weights for the plant organs and mean leaf area were determined. When the whole plant was harvested, leaf weight ratio (LWR), stem weight ratio (SWR), root weight ratio (RWR), specific leaf area (SLA), and leaf area ratio (LAR) were calculated according to Evans (1972). The distribution of dry weight and leaf area

of the plant over two sampling periods was assessed using relative growth rate (RGR) following the procedure of Evans (1972).

2.13 Statistical and computational methods

The mean values quoted in the text are given with their standard deviations. Three levels of significance were used in most statistical methods. The probability (p) and label of each significance level are summarised below:

Probability	Label
0.05> p >0.01	*
0.01> p >0.001	**
p<0.001	***

In this thesis, the following statistical methods, described by Parker (1973), were used:

1. Column by row frequency tables of categorical variables with chi-square
2. Pearson's product moment correlation coefficient on the continuous variables
3. One-way analysis of variance (ANOVA)

In one-way ANOVA's where all post hoc comparisons were required, a higher significant difference multiple range test (Tukey, 1977) was carried out. In one-way ANOVA's where only a selection of post hoc comparisons were required, the Bonferroni procedure (Wilkinson, 1988) was used in order to assign a more accurate protection level for determining the significance of each comparison. Two-way ANOVA, discriminant function analysis, principal components analysis and cluster analysis were used according to Manly (1986).

Statistical methods were performed using SPSS^{X} (McGraw Hill, 1986), which was run on the Northumbrian Universities Multiple Access Computer using the Michigan Terminal System in the University of Durham. Additional analyses using SYSTAT (Wilkinson, 1988), and data entry using the spreadsheet facility of SYMPHONY (LOTUS, 1985) were performed on an IBM AT computer (IBM U.K., International Products Ltd., Portsmouth, U.K.).

CHAPTER 3

HABITAT DESCRIPTION OF THE *PROSOPIS* WOODLANDS

3.1 Introduction

The spatial patterns of individual plants in natural vegetation communities are rarely random because their distribution is dependent upon plant form, age, seed dispersal mechanisms and environmental factors such as precipitation, temperature, humidity, soil nutrient and moisture availability, and soil structure (Greig-Smith, 1983). In the Namib desert, fog moisture was the most reliable source of water in the region and dominated the distribution and diversity of the vegetation (Pietruszka & Seely, 1985). In the Indian arid zone, the annual rainfall directly influenced the density of *P.cineraria*, such that 400-500mm of rainfall supported about 120 treesha^{-1}, whilst 200-300mm of rainfall supported less than 40 treesha^{-1} (Sharma & Joshi, 1982). Departure from a random distribution is further enhanced if there is interaction between plants, such as competition for available nutrients, or allelopathic interference. For example, the inhibition of growth of neighbouring plants around *P.juliflora* was suggested to be the result of phytotoxic extracts from the leaves or pods of the tree which have accumulated in the canopy soil (Sankhla *et al.*, 1965). An assessment of the distribution of the plants and the factors responsible for their departure from randomness provide information on the structure of the vegetation community in which the plants have formed.

In comparison to the surrounding desert plains, *Prosopis* woodland habitats are rich in plant and animal species diversity. Comparisons of vegetation in plots beneath and away from the canopy of *P.velutina* in Arizona and *P.chilensis* in Argentina have shown that annual grasses generally preferred open exposed areas, but many herbaceous perennials grew abundantly beneath these trees

(Mares, 1977). This distribution was attributed to the distinct micro-habitat beneath the canopy where there was protection from the sun, drought and grazing animals. The cooler temperatures beneath the trees provided increased atmospheric moisture which reduced evapo-transpiration from the plants and soil. Increased soil moisture also increased nutrient availability to the plants that grew beneath the trees.

Studies on the soil beneath the canopy (canopy soil) of P.juliflora have shown that the removal of the trees resulted in a significant decline in soil nutrients, including a large decline in available nitrogen, with smaller losses of available phosphate, potassium and sulphate (Tiedemann & Klemmedson, 1986). Similarly, the total nitrogen status of canopy soils of P.glandulosa in southern New Mexico was found to be more concentrated than the surrounding plains (Wright & Honea, 1986). Studies in Western Rajasthan on P.cineraria have demonstrated that the soils beneath the trees were higher in organic carbon, total nitrogen, available phosphate and soluble calcium, and had lower pH values (Singh & Lal, 1969). The effect of P.cineraria in Western Rajasthan on the productivity of range grasses growing in its vicinity was studied by Shankar et al. (1976). These authors found that the canopy increased the herbage yield, growth and species diversity of the surrounding natural pastures. This may be the combined effect of increased nutrient availability, supplemented by an increased soil moisture status (Gupta, 1975). Higher soil nitrogen in the canopy soil may be attributed to the presence of nitrogen-fixing root nodules which are found in many members of the Leguminosae (Peacock & McMillan, 1965). The extent of nodulation was greatest in Prosopis seedlings grown in moist, sandy soils (Bailey, 1976).

Ecological studies of Prosopis woodlands have shown that the high fauna species diversity was attributed to the

abundance of food, and/or protection and the reduction of the environmental extremes found in the surrounding deserts (Mares, 1977). As in most woodland habitats, the trees provide arboreal fauna with three major sources of food: leaves, flowers and fruit.

Invertebrates exploiting the Prosopis leaves are either generalist or specialist feeders (Cates & Rhoades, 1977). The generalists consume the less nutritious but also less toxic mature leaves, as well as other plant species in the woodlands. The specialists consume the young leaves, aided by their resistance to natural toxins that may be present. The leaves of P.cineraria are a rich source of crude protein of 14%-18% of dry weight (Bhimaya et al., 1964). They also have a high moisture content and are rich in ash, calcium and potassium, but poor in magnesium, sodium and phosphorus (Sharma, 1966).

Flowering varies between Prosopis species, but P.velutina, P.chilensis and P.flexuosa produce flowers at a predictable time because, as phreatophytes, they are generally independent of yearly fluctuations in rainfall (Simpson et al., 1977). Prosopis flowers are simple and unspecialised, forming long inflorescences (Burkart, 1976). The majority of the flowers do not develop to form mature fruit, which indicates that many of the estimated 10 million flowers produced per tree are sterile and only serve to attract pollinating insects to the fertile flowers (Solbrig & Cantino, 1975; Polhill et al., 1978).

The Prosopis fruit (pods) are a rich source of food to insects because they contain approximately 13% protein and 30% sucrose (Felker, 1979), and up to 7.6% fat (Beri et al., 1982). Insect infestation often results in fruit abortion and seed destruction (Kingsolver et al., 1977). A number of insects are highly specialised in utilising this food source, particularly bruchid beetles (Bruchidae) which reach pest proportions in many Prosopis species. For

example, in Texas (U.S.A.) the insect Chlorochroa ligata (Say) reduced P.glandulosa seed production by at least 70% by sucking juices from the immature seeds, whilst the seed beetle Algarobius prosopis (Le Conte) reduced viable seeds by 22% during its larval stage by consuming the seed cotyledons (Smith & Ueckert, 1974). Prosopis pods and seeds are among the oldest known foods and were used by prehistoric man in the Western Hemisphere, providing a source of protein and carbohydrate for many North and South American desert dwellers (FAO, 1981). The flour prepared from P.glandulosa pods was found to have water and oil absorption capacities superior to wheat flour, and contained comparable amounts of fibre to wheat bran (Zolfaghari et al., 1986). The Prosopis pods are also an important source of fodder to domestic livestock. For example, P.juliflora pods which contain 16.5% protein, 4.2% fat, 57.0% nitrogen-free extract and 16.9% fibre (as a percentage of dry weight), have been used in the feed concentrates of cattle and sheep without any negative effects on animal growth (Rao & Reddy, 1983).

The Prosopis woodlands are a major resource to man when the woodlands are distributed in arid or semi-arid environments and when they are composed of multi-purpose tree species. In the Indian Thar Desert, P.juliflora provides over 90% of the fuel needs of villagers, and also provides pods for fodder and wood for construction (Sharmar, 1981). The P.tamarugo woodlands of the Chilean Tamarugal Pampa reduce growing human pressure, provide multi-purpose tree products, sustain primary productivity for supporting domestic animals and provide recreational and research opportunities (Torres, 1985). The multi-purpose properties of these Prosopis woodlands have resulted in the implementation of plans for their long-term conservation and management.

The Prosopis woodlands of the Sultanate of Oman are also a major resource to wildlife and to man, particularly

where they are distributed in biologically unproductive aridland ecosystems receiving less than 50mm rain annually. Historically, the Prosopis woodlands played a critical role in the lifestyle of local nomads (bedu) by providing a permanent source of fodder for their livestock (principally camels, goats, sheep and donkeys), and food and fuelwood for themselves in times of drought when the traditional pastures were exhausted through over-grazing (Munton, 1988[a,b,c]; Webster, 1988). Traditional usage of the woodlands ensured that over-exploitation did not occur, so that the woodland resources would be available for the next drought period.

The study area for this thesis was the Sharqiya, which is the eastern region of the Sultanate of Oman (see figure 3.1). The area is also known as the Wahiba Sands, but will be referred to as the Sharqiya as it is more commonly known in Oman. The Sharqiya occupies an area of approximately 35000km² between 20°5' to 23°0'N, and 58°0' to 60°0'E. The area is dominated by a sand sea, consisting of unconsolidated sand dunes and aeolianite (Gardner, 1988).

The Prosopis woodlands of the Sharqiya are predominantly found in three geographically isolated provenances, and are generally aligned in a north-south direction. The Eastern Prosopis Zone (EPZ) and Central Prosopis Zone (CPZ) occur along the eastern and western margins of the sand sea respectively. The South-Western Prosopis Zone (SWPZ) consists of a series of woodlands along wadis (dry river courses which will flow during periods of heavy rainfall) in the alluvium and gravel plains to the southwest of the sand sea.

This chapter describes the distribution and characteristics of the Prosopis woodland habitat in the Sharqiya. The distribution of the trees within an accessible Prosopis woodland in the Sharqiya was examined,

to determine the spatial variation of tree density and tree size in this habitat. Analyses of the physical and chemical properties of the woodland soils were made, and the spatial influence of this species on the quality of the soil was assessed. Description and ordination of the understorey vegetation were performed on data collected after a period of heavy rainfall in February and March 1986, to identify specific community types and the factors involved in their distribution. The flora and fauna diversity of the Prosopis woodlands were also examined. This was followed by the assessment of the multi-purpose properties of P.cineraria and the resource potential of the Prosopis woodland habitat to man. The methods, extent and effects of exploitation of the Prosopis woodlands in the Sharqiya were also assessed.

3.2 Materials and methods

3.2.1 Field methods

Throughout the time spent in the field, records of observations were made on the wildlife, the available resources, the methods and extent of exploitation, and the general condition of the Prosopis woodlands. A photographic record of observations was taken whenever possible, and a selection of photographs are presented in Appendix A. Verbal information was collected from the bedu residing in the woodlands, including the local use of the woodland resources and their traditional management. Prosopis woodlands outside of the Sharqiya were visited, particularly the woodlands along the Batinah coast and in the proximity of Muscat (capital city), for observation and comparative purposes (see figure 3.1).

Samples of the flora from the Prosopis woodlands of the Sharqiya were collected and identified. Unknown plants were dried in presses and sent to the Herbarium of the

Royal Botanic Gardens (Kew, U.K.) for identification by T. Cope (pers. comm., 1987). Throughout the Oman Wahiba Sands Project (OWSP), plant material was also collected from the Sharqiya woodlands (Cope, 1988).

The OWSP fauna collection presented in Dutton (1988), was the principal data source for determining the species diversity of the fauna of the Prosopis woodlands. This collection covered the whole of the Sharqiya and included habitats as diverse as the coast and the sand sea. To determine the arboreal component of the collection, those species specifically sampled within, or in the vicinity of, the Prosopis woodlands were identified. For each animal phyla or class, species diversity was determined for the woodland habitat and for each of the three provenances and compared to the total diversity in the Sharqiya collection.

Ecological methods requiring long periods of intensive fieldwork were confined to the Eastern Prosopis Zone (EPZ) for logistical and safety reasons. Five parallel transects traversing the woodland were selected. The location of each transect was defined by the topography of the area, its ability to be located with some accuracy on field maps, and in sections of the woodland with minimal human disturbance (see figure 3.1). The starting point of each transect on the eastern margin of the EPZ was permanently marked with a wooden stake, and their position fixed by taking back-bearings from three prominent physical features to the east of the woodland. Along each transect, sampling points were selected by randomly generating integers between one and the length of each transect in metres, using a simple computer program. Each transect was carried out on foot as the woodlands were too dense to be crossed by vehicle. Along each transect, the sample points were paced out and marked with wooden stakes. The sampling points were then used to determine tree densities (section 3.2.2), and for the location of quadrats for studying the understorey vegetation (section 3.2.3).

3.2.2 Tree density and basal area determination

Tree density, defined as the number of trees per hectare was determined using two different plotless methods in the EPZ provenance of the Sharqiya. The point-centred quarter method (PCQM), according to Cottam & Curtis (1956), was performed on the five parallel transects (T1-T5) across the EPZ described in section 3.2.1. The wandering quarter method (WQM), according to Catana (1963), was performed on five 'wandering' transects (T1W-T5W) across the EPZ, using the same transect start points as the PCQM. Longitudinal transects down the woodland were not used for both methods because of navigational difficulties. The data from the WQM were also used to determine the changes in the distances between the trees across the study area, expressed as tree density according to the equation:

$$DT = 10000/d^2 \qquad \text{Equation 3.1}$$

Where: DT = tree density ($treesha^{-1}$)
d = mean distance between trees (m)

In both methods, the basal area of each tree sampled was calculated as:

$$bA = g^2/4\pi \qquad \text{Equation 3.2}$$

Where: bA = basal area (cm^2)
g = mean tree girth (cm)

3.2.3 Understorey vegetation description and ordination

A minimal sample area of $4m^2$ for examining the understorey vegetation in the Prosopis woodlands was determined using the method described by Shimwell (1971). At each sampling point a $4m^2$ quadrat was marked out with a tape measure, where the sampling point was consistently the bottom left corner of the quadrat in the direction of the

transect. In the area enclosed by the quadrat, the number of plants of each species present was recorded. The cover-abundance of each species was also determined using the Domin scale of plant cover (Bannister, 1966) presented in table 3.1. Total plant cover was determined for each quadrat. Unidentified ephemeral vegetation was divided into live and dead plants for cover determination.

A description of each quadrat site was made, which included the canopy shade (section 4.2.1); tree density and mean basal area (section 3.2.2); surface topography; and depth of loose soil.

The ordination of the understorey vegetation data was performed using three FORTRAN computer programs. Two-way indicator species analysis was performed using the program TWINSPAN (Hill, 1979b). TWINSPAN was used on the cover-abundance data to classify the species into community classes using a TWINSPAN two-way table. Detrended correspondence analysis was performed on species presence-and-absence data using the program DECORANA (Hill, 1979a). This method was used to order the species, the sample areas (quadrats) and the TWINSPAN vegetation classes. The product of the program was the formation of taxon and sample scores for four axes. In these analyses, axes 1 and 2 were only examined because they contained the majority of the variation in the dataset. Canonical correspondence analysis was performed using the program CANOCO (Ter Braak, 1987). CANOCO was used on a combined dataset made up of the presence-and-absence of species and the five variables measured at each quadrat site. This method was used to correlate the ordination of the species and the TWINSPAN vegetation classes with the measured environmental gradients.

Table 3.1

Domin scale of plant cover (Bannister, 1966)

Class	Cover
1	1-2 individuals
2	Less than 1 %
3	1 - 4
4	4 - 10
5	11 - 25
6	26 - 33
7	34 - 50
8	51 - 75
9	76 - 90
10	91 - 100

3.3 Results and Discussion

3.3.1 Description of woodland study areas (figure 3.1)

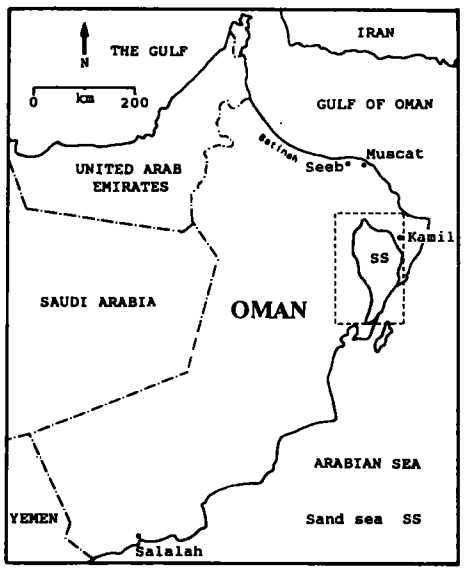
1. Eastern Prosopis Zone (EPZ)

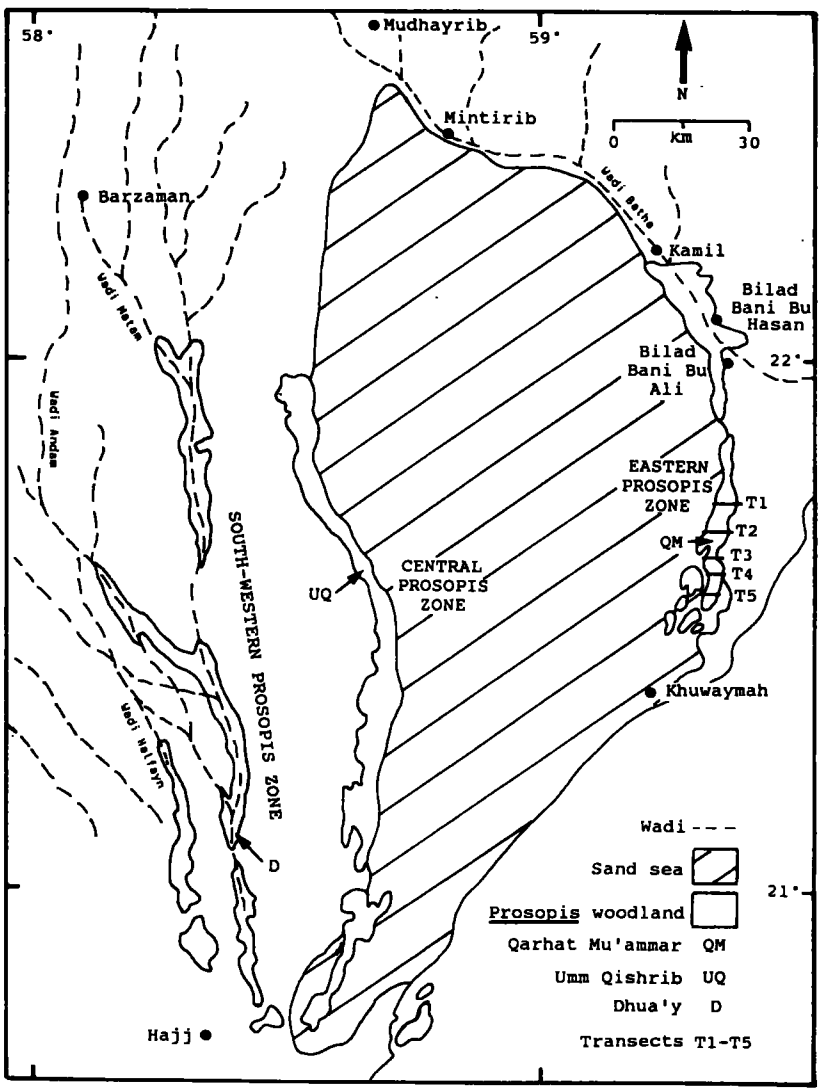
The EPZ is approximately 85km long and 20km at its widest point and is made up of a series of wooded areas along the east margin of the sand sea. Along the east and west margins of the woodland, sand has accumulated into ridges containing generally large trees of low density. These ridges are separated by stabilised undulating to flat sandy plains, with sporadic accumulations of small longitudinal dunes. The trees here form the woodland interiors and are generally smaller in size but greater in density than the margins. Trees also survive on the slip faces of the peripheral megadunes of the sand sea (slides 3-5). The unconsolidated sandy substrate of the woodlands and a proportion of the sand sea overlays a substantial aeolianite deposit (Gardner, 1988). Beneath the EPZ, at a depth of approximately 18m, is an aeolianite aquifer of good to moderate quality water with a specific conductance in the range 1510 to 3000 μmhos/cm (Jones et al., 1988). The northern limits of the EPZ is known as Wadi Libaydi'ah. To the south, the provenance runs parallel with and to the west of Wadi Qaymah, which is the southern exit of Wadi Batha.

Of the three woodland provenances in the study area, the EPZ is located nearest to the east coast, such that its climate is mostly influenced by a maritime effect (Chapter 6). During the winter months (November to March) moist, cool southeasterly winds blow inland off the sea, which results in precipitation in the woodlands in the form of dew. Dewfall is often very heavy, and in the EPZ occurs in cycles of approximately three to five days during the winter (Anderson, 1988). Exposure to moist winds is reduced in the north of the EPZ, by a barrier of moderately sized

Figure 3.1

Distribution of <u>Prosopis</u> woodlands in the Sharqiya, Sultanate of Oman.





rocky outcrops to the north-east of the woodlands. Aligning the east of the EPZ and extending to the outcrops in the north and to the coast in the south are a series of gravel and sabkhah plains. The latter are salt flats that are usually devoid of vegetation.

Approximately 200 bedu families of the Janabah and Al Bu 'Isa tribes have formed settlements in the EPZ, usually in the vicinity of wells (Webster, 1988). There are both temporary and permanent buildings here, of which the former are mainly constructed out of Prosopis wood (slide 25). There are a number of permanent brick houses, usually found adjacent to newly excavated fresh water wells. In the winter of 1986, the EPZ had the highest densities of goats and sheep in the Sharqiya, totalling 3-6 head/km² (Munton, 1988b), which represents a ratio of 6:1 livestock to people (Webster, 1988). In the south of the EPZ, the bedu and their livestock moved out of the woodlands after the rains in February, to browse on the open pastures to the east. In this way, the woodland forage was preserved for use after the open pastures were exhausted. This method of traditional use of the available resources was not observed in the north of the EPZ. This has been attributed to the proximity of the north-eastern villages such as Bani Bu Ali and Bani Bu Hassan where alternative livestock fodder can be purchased throughout the year (Munton, 1988b).

2. Central Prosopis Zone (CPZ)

The CPZ is the largest of the provenances, approximately 140km long and 30km wide, bordering the west margin of the sand sea. To the west of the CPZ, alluvial and gravel plains dominate the topography. The trees in the CPZ are widely scattered and the canopy is rarely continuous. The topography within the woodlands is predominantly small to medium mobile sand dunes, making access through the area extremely difficult. Trees are commonly found on the dune crests rather than in the

swales. An aquifer of siltstone and aeolianite origin is located beneath the CPZ, but at a depth of over 60m. The water was found to be of moderate to poor quality, with a specific conductance greater than 5000 µmhos/cm, and frequently exceeding 10000 µmhos/cm (Jones et al., 1988). The density of wells is low, and many appear to be abandoned or poorly maintained. The CPZ is known locally as Wadi Murayr and also as Wadi Al Wahiba. About 90 bedu families of the Al Wahiba tribe were estimated to reside in the CPZ during the winter of 1986, owning an average of 68 goats per family, which represents a livestock to people ratio of 11:1 (Webster, 1988). In comparison to the EPZ, there was a greater decrease in the livestock density and a more defined movement of bedu out of the CPZ in January to March 1986, as a result of the winter rains (Munton, 1988b).

3. South-Western Prosopis Zone (SWPZ)

In contrast to the EPZ and CPZ, the SWPZ is located in the complex alluvial fan system originating in the north-eastern mountains. The woodlands are predominantly found along three wadi systems, Wadi Matam, Wadi Andam and Wadi Halfayn. During periods of heavy rainfall in February 1986, these wadis flowed in a north-south direction, with the formation of small lakes that remained standing for over four weeks. After the rains, the water table was only several metres below the surface of the woodland and contained water which was potable. Consistent with the Prosopis woodlands of this study area, the substrate is predominantly small sandy dune fields. The woodlands of the provenance generally have a high tree density, with some of the largest trees in the Sharqiya. In some places the trees form a continuous canopy, where densely populated bedu settlements are usually located. The bedu are the Al Wahiba in the north and the Al 'Amr and Hikman tribes to the very south (Webster, 1988).

3.3.2 Woodland structure and tree distribution

1. Study area

An undisturbed but accessible part of the EPZ (slides 6 & 7) was chosen to carry out detailed studies on the spatial distribution of the trees, using the point-centred quarter method (PCQM) and the wandering quarter method (WQM) (section 3.2.2). The five PCQM transects (T1-T5) covered an area 9.1km in length and a minimum and maximum width of 760m and 1798m respectively (table 3.2). The five WQM transects (T1W-T5W) occurred in close proximity to the equivalent PCQM transects.

2. Transect variation

The PCQM data used to determine tree density (DT) as $treesha^{-1}$ for each transect are summarised in table 3.3a. Data from the WQM are summarised in table 3.3b and the separation of within (Y) and between (X) distances were used to determine tree density as $treesha^{-1}$ (DTw) for each 'wandering' transect (table 3.3c). As transect T3W did not have sufficient between-distances, DTw could not be calculated for this transect. This table shows that the number of clumps was highest in transects T2W and T5W. It also shows that there was a general decrease in the size of the clumps (Y) and an increase in the density of the clumps (decrease in X) down the study area. From each PCQM and WQM transect, the mean basal areas (bA & bAw) were calculated and used as indices of tree size.

The changes in transect tree density and basal area down the study area for each method are shown in figure 3.2. In the PCQM, tree density and basal area generally decreased southwards, with a localised increase in both variables in transect T3. In transects T1 and T3, both density and basal area were high, whereas in transects T2 and T4, the trees were of moderate basal area but low in

Table 3.2

Description of the PCQM sampling strategies used in each permanent transect (T1-T5) in the EPZ.

Transect	Woodland width(m)	Distance south from T1(km)	No. of total points	Sampling point distances (m)
T1	1798	0.0	20	5 145 153 173 351 384 386 499 581 672 729 812 924 953 960 1363 1591 1665 1690 1788
T2	1300	4.2	12	97 174 250 349 357 581 680 742 757 777 868 996
T3	1290	4.8	10	128 310 367 550 633 747 949 1103 1168 1259
T4	834	5.5	8	14 26 82 149 307 331 511 687
T5	760	9.1	6	75 140 257 555 613 723

Table 3.3

Tree density (DT) and basal area (bA) results determined by the point-centred quarter method (PCQM) and the wandering quarter method (WQM). Where: n = frequency of measurements; d = tree distance; DT = tree density (PCQM method); DTw = tree density (WQM method); bA = basal area (from PCQM data); bAw = basal area (from WQM data); Y = within clump distance; X = between clump distance; n/d = not determined.

A. Summary of PCQM data

PCQM transect	n	mean d (m)	DT (treesha^{-1})	bA (cm^2)
T1	76	11.16	80.29	645.08
T2	48	22.57	19.63	412.11
T3	40	13.34	56.24	558.22
T4	32	21.24	22.17	458.22
T5	24	15.77	40.21	355.09

B. Summary of WQM data

WQM transect	n	mean d (m)	SE	mode (m)	Limit of Y (m)	bAw (cm^2)
T1W	184	10.03	0.59	8.0	24.0	589.73
T2W	72	17.56	2.66	5.0	15.0	503.70
T3W	92	8.62	0.58	8.0	24.0	387.69
T4W	104	10.90	1.96	8.0	24.0	342.37
T5W	80	6.83	0.74	3.0	9.0	232.80

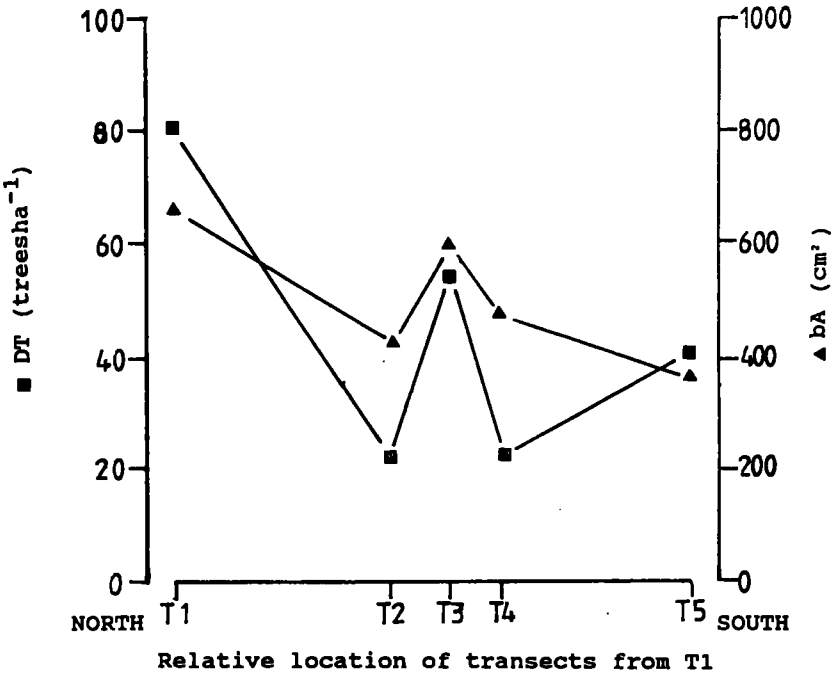
C. Separation of within (Y) and between (X) distances for tree density (DTw) determination by the WQM

WQM transect	No. clumps	No. Y	mean Y (m)	No. X	mean X (m)	SE of X mean	DTw (treesha^{-1})
T1W	6	175	8.76	9	34.67	2.77	79.53
T2W	15	44	7.86	25	34.92	6.29	27.65
T3W	0	95	8.54	0	n/d	n/d	n/d
T4W	5	96	6.20	8	67.38	13.96	85.10
T5W	13	59	3.59	20	16.28	1.42	181.35

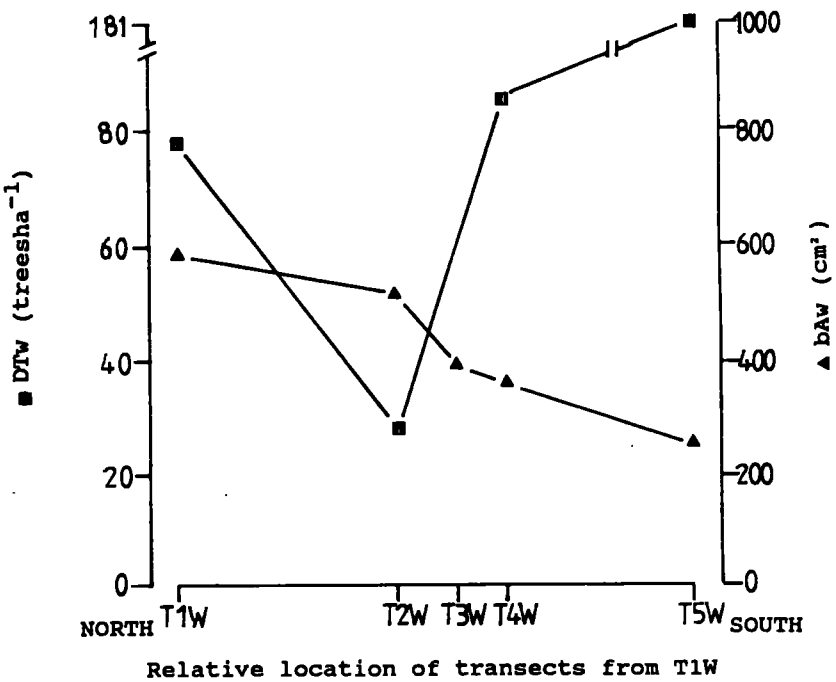
Figure 3.2

Longitudinal changes in Prosopis tree density (DT & DTw) and basal area (bA & bAw) down the EPZ, determined by the PCQM and WQM plotless methods.

A. Point-centred Quarter Method (PCQM)



B. Wandering Quarter Method (WQM)



density. Trees in transect T5 had the smallest basal areas in the study area and were moderate in density. The basal area of the trees determined from the WQM data also decreased southwards but to a greater extent. The density results for the PCQM and WQM were of the same magnitude in the two northern transects, but there was a greater increase in density using the WQM with increasing distance south. It can be seen that the major difference between the two methods were the smaller trees and higher density determined by the WQM for the southern transects.

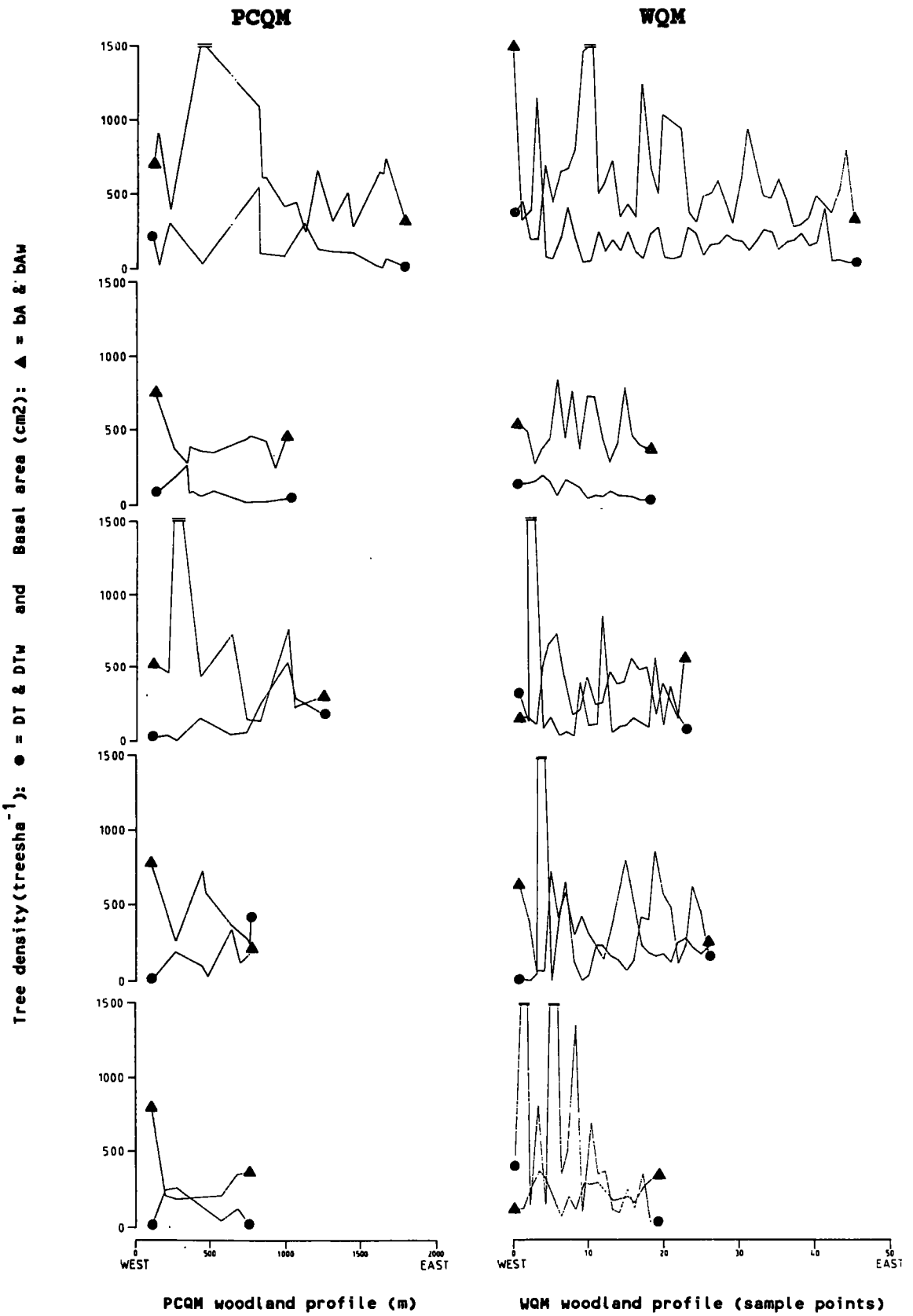
3. Tree spatial distribution

To identify the spatial distribution of the trees within the study area and the factors responsible for the departure between the two plotless methods, the sequential changes in tree density and basal area across the transects were examined. From the PCQM dataset, density and basal area were calculated for each sample point along each transect. The data from each WQM transect were divided into sets of four consecutive points, from which density and basal areas were determined. For each transect, density and basal area were plotted against distance west for the PCQM results and against schematic distance west for the WQM results (figure 3.3).

The profiles of tree density and basal area across the northern transects were very similar between the methods. Here, the trees in the eastern margin were generally moderate in size and occurred in low densities. Both tree density and basal area distinctly increased in a westerly direction and reached a maximum in the western margin. In the woodland interior, tree density and basal area were variable and were predominantly inversely related, so that they were arranged in a series of moderately dense clumps of small trees, separated by areas of large trees of low density. The ratio of basal area to density within the clumps slightly decreased westwards, but this ratio between

Figure 3.3

Transverse changes in <u>Prosopis</u> tree density (DT & DTw) and basal area (bA & bAw) across the EPZ, determined from the PCQM and WQM data.



the clumps increased greatly in the same direction. Thus, in an east to west direction in the north of the study area, there was an increase in density and a decrease in the size of the trees in clumps, in contrast to a decrease in density but a large increase in size of trees between the clumps (figure 3.4).

The differences between the two plotless methods were clearly shown by the profiles in the south of the study area (transects 3, 4 & 5) in figure 3.3. The inverted relationship between tree density and basal area of the clumps was very pronounced in the southern profiles. These clumps consisted of much higher tree densities and much smaller trees than those in the north. This trend increased both in a southerly and westerly direction. The trees between the clumps marginally increased in tree density and decreased in tree size with increasing distance southwards (figure 3.4).

The structure of the woodland study area has shown that the solitary trees in the between-clump gaps decreased in density but increased in size towards the western margin and generally decreased in both tree density and size southwards. The tree clumps also increased in number and decreased in size towards the west and south of the woodland. In the same directions, the density of the trees within the clumps increased and their size decreased. From these results it is suggested that there are two distinct tree habits responsible for sustained tree life under conditions of continued exposure to sand encroachment. The first habit includes those trees that are sufficiently large enough to survive sand encroachment, by being resistant to both physical damage and complete sand inundation. In areas of bulk movement of sand into the woodlands, trees less than a certain size will eventually die out, leaving large solitary trees such as those found in the between-clump gaps of the western margin in the north of the study area. The second habit for sustained

Figure 3.4

Spatial distribution of <u>Prosopis</u> trees in the EPZ in relation to tree size. Where symbol size represents the tree size.

Northern transects(T1-T2) **Southern transects (T3-T5)**

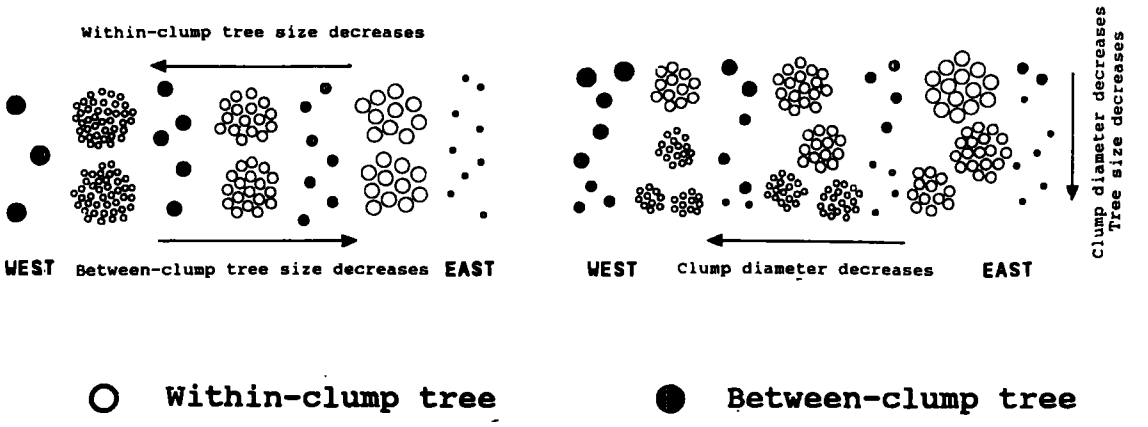
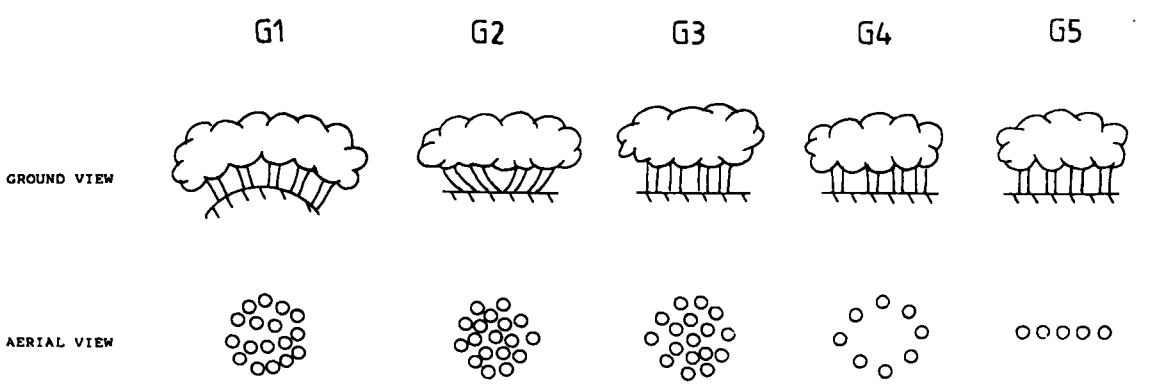


Figure 3.5

<u>Prosopis</u> tree distribution patterns (G1-G5) within clumps.



tree life is the formation of tree clumps which are high in tree density, but are generally low in tree size. These clumps increase the resistance of small-sized trees to damage by sand encroachment. The longitudinal megadunes of the sand sea are encroaching the woodlands at an incident angle from the south-west (Warren, 1988a). This suggests that sand encroachment through the penetration of the megadunes into the woodland is highest towards the south of the study area and along the western margin, and is responsible for the clumping habit of the trees here.

4. Vegetative regeneration and clump formation

Evidence of vegetative regeneration was found in all the woodlands of the study area in the form of suckers, which were usually offshoots from the lateral roots (slide 15). Physically damaged tissue of the lateral roots and the branches off the tree bole were found to be the sites of greatest vegetative regeneration.

In the mensuration of 321 trees from the EPZ and CPZ (Chapter 4), 23 trees had definite vegetative growth, where the suckers were observed growing from their exposed lateral roots. In addition, at least 30 trees had sucker-like growth, but because the lateral roots were not exposed these observations could not be confirmed. In the same dataset, 40.5% of the trees were found in tree clumps and 11.8% were found arranged between a clumped and solitary habit. The distribution pattern of trees within these clumps were classified into five groups (figure 3.5). Group G1 clumps (slide 13) were found on sandy mounds, where the tree boles converged to a central point. The diameter of these clumps varied from as small as 3m, to greater than 15m. Group G2 clumps (slide 12) were also formed by tree boles converging to a central point and were comparable in size to group G1 clumps, but were differentiated by being found on flat ground. The remaining three groups were classified on the basis of the spatial

pattern of erect-stemmed trees on flat ground, where group G3 clumps (slide 14) were made up of trees in dense circles, group G4 clumps in rings and group G5 clumps in crossed rows.

Two tree clumps of group G1 and G2 morphology were selected and the sand around the tree boles was mechanically excavated. In each clump, the trees forming the clump were found to be from the same plant, which were connected at a depth of between 1.0m-2.5m below the surface. Since it was not practical to continue this method, an assessment of the genetic relationship between trees within clumps was carried out by comparing the distribution of non-specific esterase isoenzymes in their seeds (sections 2.4). Of the clumps examined in both the EPZ and CPZ, the isoenzyme band patterns for individual trees within clumps were either identical, or demonstrated marginal variation (figure 3.6). Even in clumps of close proximity, the isoenzyme band variation was less in trees from within the clumps than between the clumps.

The relationship between trees within clumps suggests that the clumps have been formed vegetatively from suckers off the lateral roots (lateral vegetative growth). Clump formations may also occur from single trees if they are submerged in sand above their primary or secondary branches to form two or more clear boles. If the branch boles continue to grow (vertical vegetative growth) faster than the rate of sand accumulation, they may eventually form clumps of mature-sized trees (figure 3.7a and slide sequence 10-12). If the rate of vertical vegetative growth is less than the rate of sand accumulation, then the clumps will eventually be completely submerged in sand (figure 3.7b). The penetration of the megadunes into the western margin of woodlands suggests that the clumps have been formed primarily by vertical vegetative growth of submerged single trees. The convergence of the tree boles to a central focal point in the groups G1 and G2 suggests that

Figure 3.6

Two examples of seed non-specific esterase isoenzyme band patterns sampled from Prosopis trees within clumps. Each gel produced from seeds sampled off individual trees.

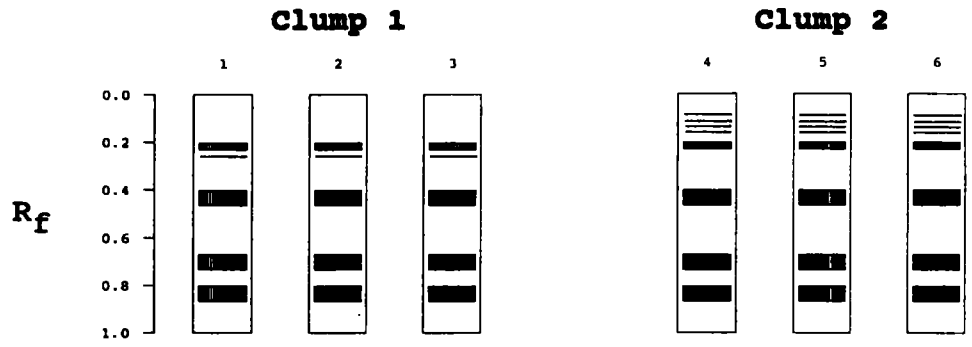
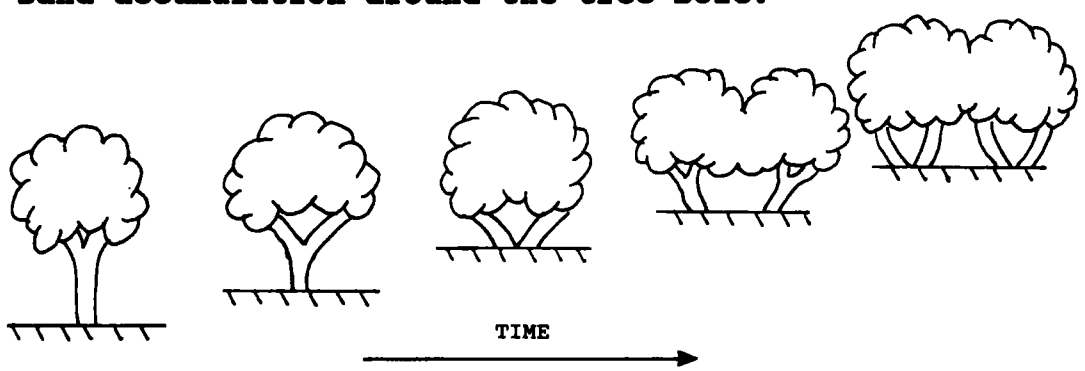


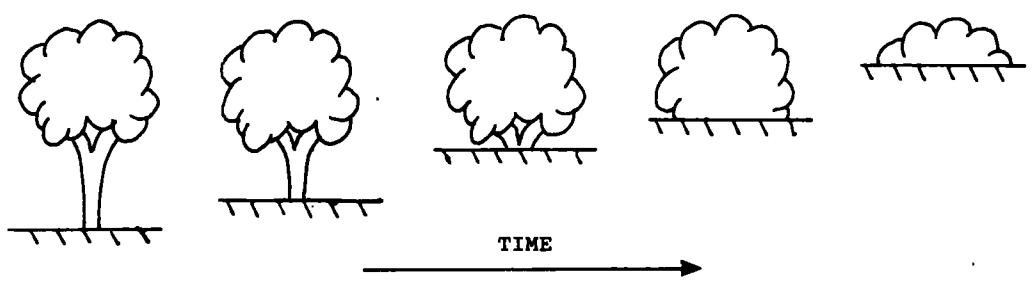
Figure 3.7

Influence of sand accumulation and vertical vegetative growth on Prosopis clump formation.

A. Vertical vegetative growth is greater than the rate of sand accumulation around the tree bole.



B. Vertical vegetative growth is less than the rate of sand accumulation around the tree bole.



these clumps have also been formed through vertical vegetative growth. The distribution of trees in the remaining three groups suggests they are the result of lateral vegetative growth. This latter growth may be responsible for the spread of the trees into the between-clump gaps found in the south of the study area.

5. Prosopis woodland ontogeny

The adaptive response of vertical and lateral vegetative growth of P.cineraria to sand encroachment may have been a major factor in both the survival of the Prosopis woodlands and the formation of the monocultures in the Sharqiya. As the sand accumulates, the trees will continue to survive the effective drop in the aquifer depth by having their original roots in the aquifer or its capillary fringe. This would explain the phreatophytic survival of trees in the extensive sand dune system of the CPZ where the aquifer is more than 60m deep. Other tree species unable to respond to sand encroachment in the same way as P.cineraria will have eventually died out. In the absence of factors favouring reproductive regeneration identified, in Chapter 5, species diversity will have decreased and new reproductive growth of P.cineraria will have been inhibited. This will have resulted in the formation of monoculture woodlands of closely related trees.

From the distribution and structure of the present Prosopis woodland provenances in the Sharqiya, an hypothesis for the ontogeny of the woodlands is suggested. Prior to the evolution of the sand sea, the distribution of woody perennial vegetation was probably based on earlier patterns of drainage from the mountains in the north and on earlier pluvial periods such as the most recent that occurred between 12500 and 6500 years before present (Clark & Fontes, 1990). The development of the sand sea through the accumulation of material from the northern mountains

and the movement of marine deposits from the coast (Allison, 1988) may have promoted the formation of the Prosopis monoculture woodlands. The present Prosopis woodlands along the margins of the sand sea (EPZ and CPZ) may therefore be the surviving remnants of ancient vegetation communities. If vegetative growth was and still is the principal survival strategy to sand inundation, then the present trees may also be genetically related to the trees surviving over 12000 years ago during the last pluvial period.

3.3.3 Prosopis woodland soils

1. General variation in soil chemical properties

Samples of 63 woodland soils were taken from 20 pits excavated to a depth of 1m in the EPZ (section 2.5). The mean ion concentrations, mean electrical conductivity (EC) and mean pH of these soils are summarised in table 3.4, and a statistical summary of the data is presented in Appendix D. The mean values were compared to plant-free sand dune soil sampled to the east of the woodlands. The data show that in the woodland soils, calcium was the major ion, with high levels of chloride and sulphate and approximately equal concentrations of potassium and magnesium. In contrast, the dune soil had higher chloride levels than calcium, low levels of sulphate and four times more magnesium than potassium. Most of the ion concentrations were higher in the woodland soils than in the dune soil, which included almost eight times more sulphate, at least three times more potassium and iron, almost double the concentration of nitrate and calcium and marginal increases in phosphate. Dune soil had almost twice as much magnesium as the woodland soils, with small increases in both chloride and ammonia. The nitrogen, phosphorus, potassium (NPK) ratio in the woodland soils was approximately 2:1:28, in contrast to the dune soil which was 1.4:1:12. All soils

Table 3.4

Comparison of woodland soil (WS) and dune soil (DS) chemical properties ($mgdm^{-3}$). Electrical conductivity (EC) in μS.

Ion	Woodland soil (WS) (maximum n=63)	Dune soil (DS) (n=1)	Ratio (WS/DS)
N	31.56	16.50	1.91
P	15.49	12.00	1.29
NH_4	5.47	6.20	0.88
Fe	0.22	0.07	3.14
K	434.48	145.00	3.00
Ca	2484.13	1500.00	1.66
Mg	323.91	600.00	0.54
Cl	1730.16	1875.00	0.92
SO_4	864.97	113.00	7.65
EC	1265.56	703.10	1.80
pH	8.28	8.3	1.00

sampled were alkaline and within a small pH range.

The higher sulphate levels in the woodland soils may be linked to the high concentrations of sulphate ions found in the aeolianite aquifer beneath the woodlands (Jones et al., 1988). The higher levels of nitrate in the woodland soil may be the combined result of the nitrogen-fixing properties of the trees (Basak & Goyal, 1975), and the presence of organic matter from the woodland detritus. The high concentrations of calcium in both types of soil can be attributed to the calcium carbonate rich sand-sea in the proximity of the soil sampling sites (Allison, 1988).

The variation in the chemical properties of all the woodland soils sampled was examined using principal components analysis (section 2.13). The first two components of this analysis accounted for 50.3% of the variation in the data and were only examined (figure 3.8a). The first principal component (F1) was dominated by sulphate, potassium, calcium and chloride, which were the major ions by weight in the soils. These major ions were in contrast to phosphate, ammonia and iron which had large negative score coefficients. The second principal component (F2) was dominated by magnesium and nitrate in contrast to chloride and, to a lesser extent, sulphate.

A scatter plot of these components (figure 3.8b) shows that chemical properties of the woodland soils were very variable. As the soils were ordinated evenly along F1, the relative proportions of the major ions with respect to phosphate, ammonia and iron were highly variable in the soils sampled. The ordination of soils along F2 shows that the highest concentrations of magnesium and nitrate occurred in soils containing intermediate concentrations of the major ions, phosphate, ammonia and iron.

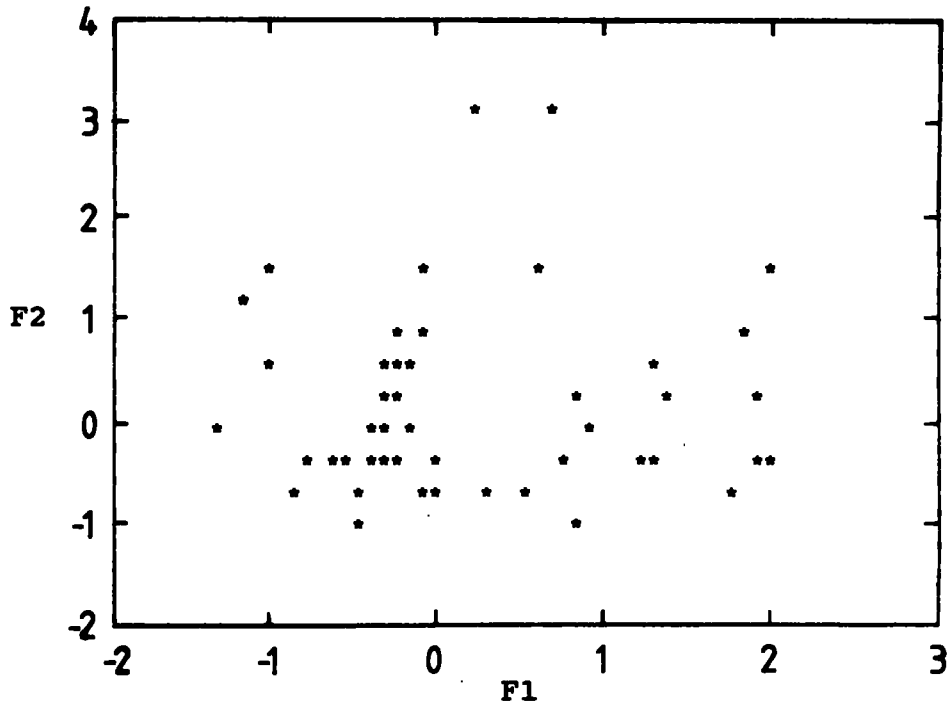
Figure 3.8

Results of a principal components analysis performed on the chemical properties of *Prosopis* woodland soils (n=63) from the EPZ.

A. Score coefficients of the first two principal components.

	Principal components	
	F1	F2
% of variation of data	32.3	18.0
SO_4	0.297	-0.063
K	0.256	0.191
Ca	0.217	0.131
Cl	0.201	-0.109
P	-0.195	0.135
NH_4	-0.191	0.087
Mg	0.032	0.510
N	-0.004	0.509
Fe	-0.164	0.046

B. Scatter plot of the first 2 principal component scores for each soil sample.



2. Variation in soil properties with depth

Two typical woodland soil profiles to a depth of 1m are presented in figure 3.9. Of the soils sampled, a total of 9 Munsell colours were distinguished. These were predominantly shades of yellow, yellow/brown and brown, though in some samples light grey was identified. There was no particular change in the colour with increasing depth. There were very few stones in the soil and those that were present were small to very small and were confined mostly in the surface layers. Soil texture was predominantly loamy sand, with a tendency to increasing amounts of loam with depth. Sandy loose dry soil was almost always found at the surface, where the highest levels of visible detritus occurred. Below 30cm from the surface, the soils were tightly packed to extremely compact, but rarely cemented. Partially cemented soils were occasionally found at the lower depths.

At each of four soil sampling depths (0-10cm; 30-40cm; 60-70cm; 90-100cm) mean ion concentrations were calculated (figure 3.10). One-way ANOVAs of each ion concentration between depths have shown that only phosphate and iron were significantly different, as a result of their higher concentrations at the surface. Nitrate concentrations did show a trend of increasing with depth. Lower nitrate concentrations at the surface may be a result of its uptake by shallow rooted understorey vegetation. However, Singh & Lal (1969) have found that total nitrogen in the soil beneath the canopy (canopy soil) decreased with increasing depth, which was related to the decline in organic matter down the soil profiles. The same authors found that all nutrients decreased with depth, which was also found for phosphate, ammonia and iron in the woodland soils. Phosphate was consistently higher in concentration at the surface which was attributed to the highest levels of organic matter here. This ion was relatively constant with increasing depth. Highest levels of chloride were found at

Figure 3.9

Two examples of typical soil profiles in the Prosopis woodlands. Figures in parentheses are the detritus content (% of total weight) for each depth.

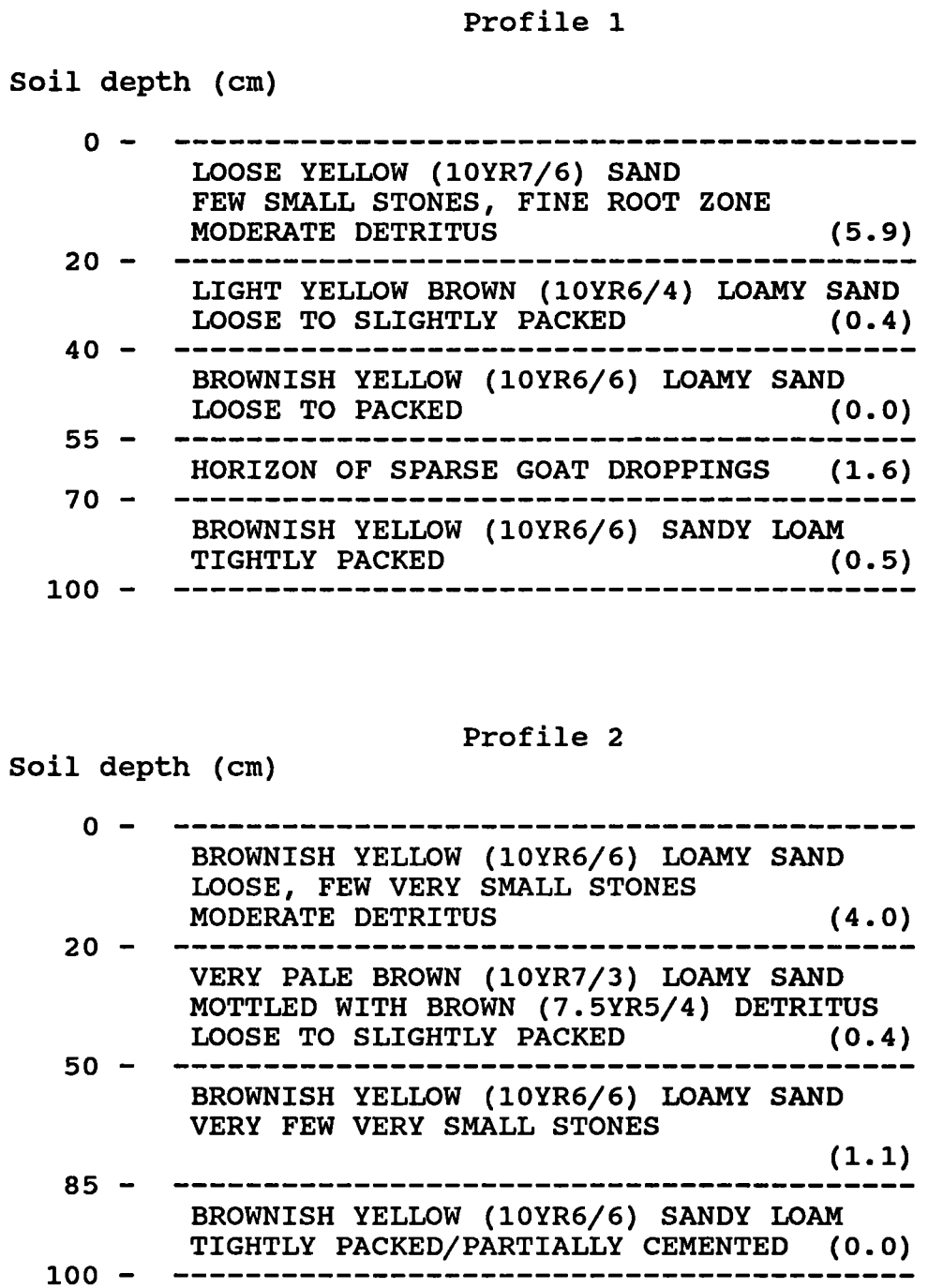


Figure 3.10

Variation in woodland soil chemical properties with depth of soil pit (surface n=20; 20-40cm n=20; 60-70cm n=15; 90-100cm n=8).

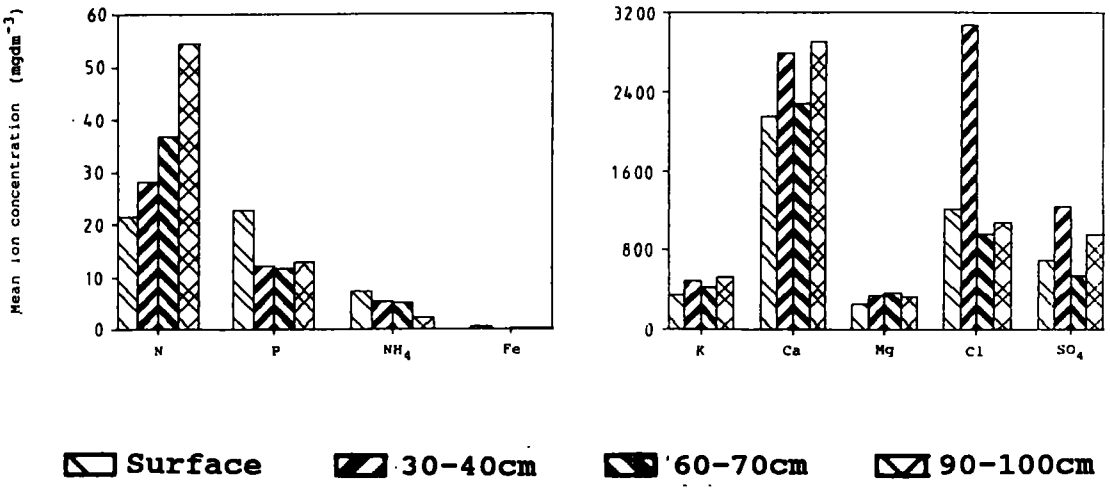
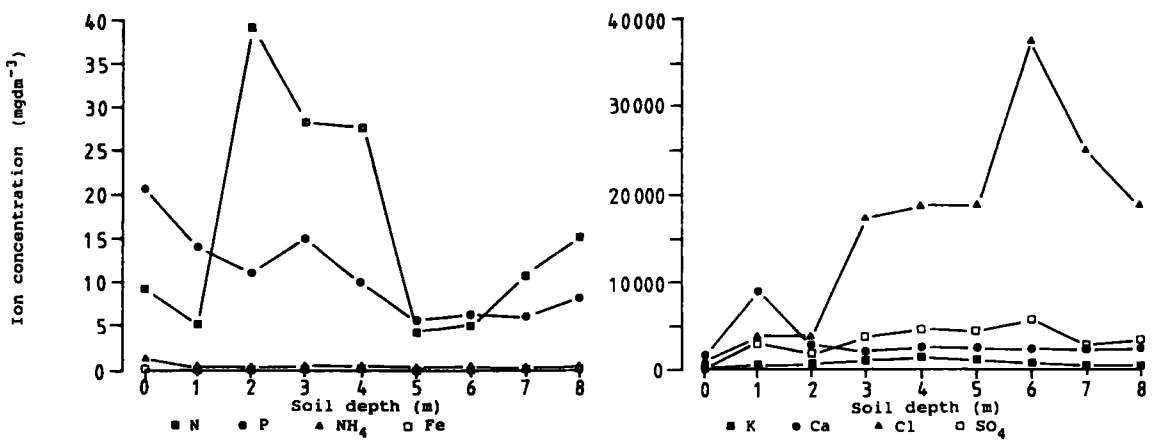


Figure 3.11

Vertical variation in woodland soil chemical properties sampled from a pre-excavated pit (1 soil sample at each depth).



a depth of 30-40cm, which may be attributed to the downward leaching of the ions from surface water. The removal of the chloride deposits by digging pits deeper than 40cm would improve the local soil conditions for the transplantation of seedlings.

In the EPZ, a deep pre-formed excavation allowed the sampling of soil at 1m intervals to a depth of 8m. The soil was yellow (10YR7/6) at the surface to 1m, changing to very pale brown (10YR7/3) between 1-5m and to light grey (10YR7/2) after 5m. The loam component of the soil increased with depth, with sand at the surface, strong sandy loam between 1-3m and sandy loam deeper than 3m. Common stones of very small to small size were found at the surface only, where there were also low amounts of detritus present. The soil was loose and dry at the surface and damp and compact below 1m deep.

A vertical profile of the chemical properties of the sampled soils is presented in figure 3.11. Maximum concentrations of nitrate were found between 1m and 5m, which may be related to the depth at which nitrogen-fixing rhizobia are most active. These results suggest that nitrogen fixation occurs deep in the soil and supports the results of Felker & Clark (1982), where P.glandulosa var. torreyana grown in greenhouse trials was shown to fix nitrogen at depths greater than 2.7m from the surface. The highest concentrations of phosphate were found at the surface, which decreased with increasing depth. Ammonium and iron were also highest at the surface, but they were hardly detected below 1m. A substantial increase in chloride was observed down the profile, reaching a maximum at a depth of 6m, where concentrations over 38000mgdm^{-3} were detected. This accumulation of chloride may be of a localised nature caused by greater lateral movement of water and dissolved ions to the pit wall. The highest calcium concentrations of 8000mgdm^{-3} occurred at a depth of 1m, but decreased to a constant level of 2000-3000 mgdm^{-3}

below 2m. Sulphate and potassium levels were relatively constant down the profile, but both were lowest at the surface. Soil pH was high at the surface (pH 8.6) which rapidly dropped to pH 7.0 at 2m and then generally increased with depth to over pH 8.0.

3. Geographical variation in soil properties

The geographical variation in the physical and chemical properties of the EPZ soils was examined along a longitudinal transect down the northern half of the provenance (see figure 3.1). The soil profiles were typical of the *Prosopis* woodlands presented in figure 3.9, where only colour and texture showed some geographical variation. From north to south, the soils changed gradually from very pale brown (10YR7/4, 10YR7/3) to brownish yellow (10YR6/6), concomitant with an increase in sandy texture.

From each of five sites along the transect, two pits were excavated to a depth of 1m. A maximum of four soil samples were collected from the soil profile of each pit. The mean ion concentrations for each site were determined and then plotted against distance from the northernmost site (figure 3.12). The concentration of nitrate varied along the length of the transect, but generally increased southwards. Marginal increases in phosphate and ammonia were also detected southwards. In contrast, calcium, chloride and sulphate decreased in concentration southwards, whilst potassium and magnesium remained constant. These results show that the soils can be partitioned along this transect into those of high salinity with low nutrients in the north and those of low salinity and high nutrients in the south. These results may be linked to the closer proximity of the northern *Prosopis* woodlands to several large towns, where agricultural practices and heavy utilisation of the woodland resources may have contributed to the decline in the condition of the soils here. Other factors such as geological variation,

Figure 3.12

Variation in woodland soil chemical properties along a longitudinal transect in the EPZ (n=38 soil samples).

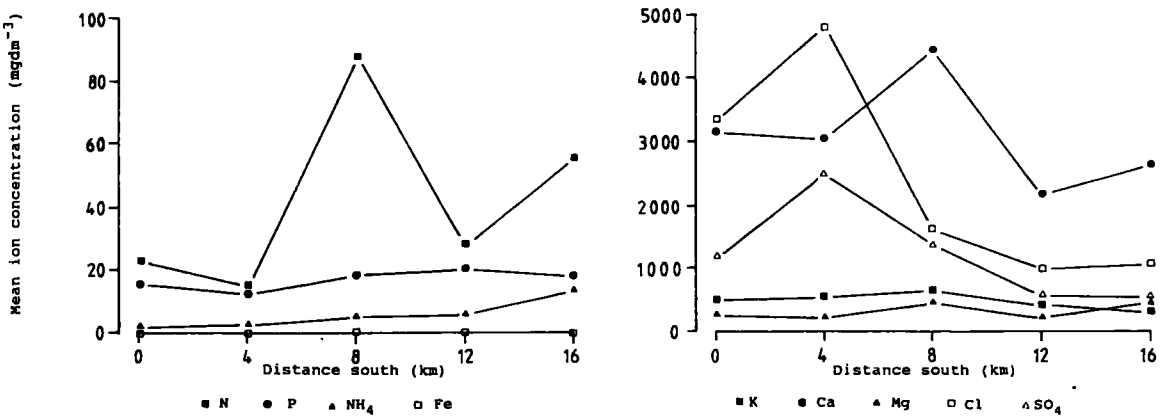
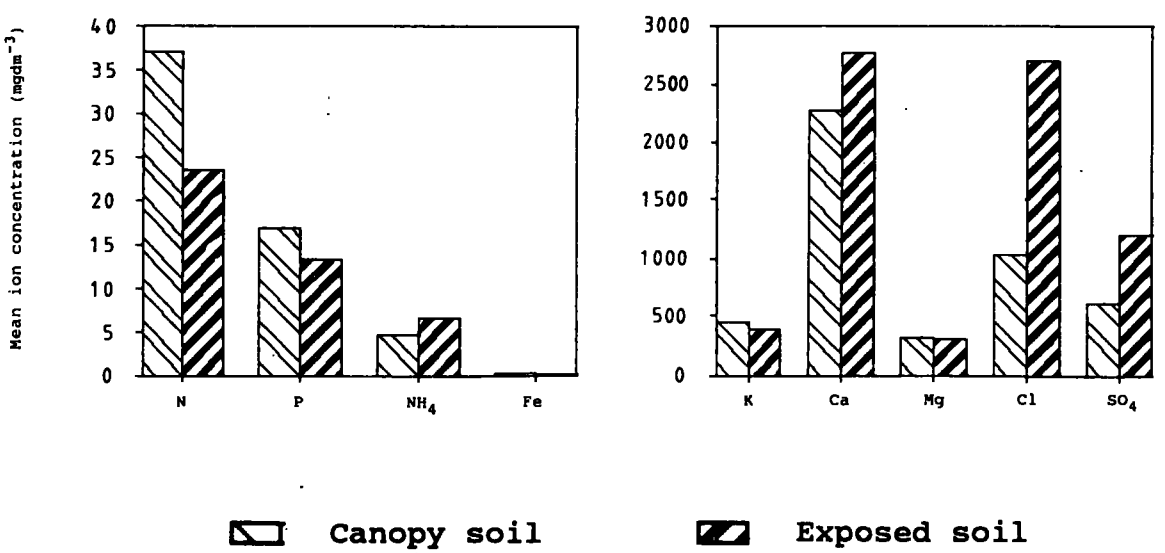


Figure 3.13

<u>Prosopis</u> canopy influence on soil chemical properties (canopy soil n=37; exposed soil n=26).



aquifer depth and soil water may have also contributed to this variation.

4. Canopy influence on soil chemical properties

As the canopy of the Prosopis woodlands in the study area was not usually continuous (pers. obs.), the influence of the canopy on the soil chemical properties was assessed. At each of 9 randomly selected woodland sites in the EPZ, two pits were excavated. The first pit was located immediately beneath the tree canopy at 1m from the bole. The second pit was located at least 25m from the first pit, in an area of the woodland where the canopy was not continuous. The mean ion concentrations of soil samples to a depth of 1m taken from beneath the canopy (canopy soil) and away from the canopy (exposed soil) are summarised in figure 3.13. Except for iron and chloride, there were no significant differences in the chemical properties between the canopy and exposed soils. However, this figure illustrates the general influence of the canopy on the chemical properties of the soil. Soil iron ($p<0.01$), nitrate and phosphate were higher beneath the canopy, whilst chloride ($p<0.01$), calcium, sulphate and to a lesser extent ammonia were found higher away from the canopy.

A solitary tree within a fixed sand dune system in the EPZ was selected to examine the spatial influence of the tree on the chemical properties of the surrounding soil. The subject tree was located in an area of very low tree density, where disturbance by people and livestock was low. The nearest neighbour to the subject tree was more than 200m away, so that the interaction between trees with respect to the soil composition was assumed to be minimal. The subject tree was large, over 10m in height with an erect stem and a girth of 212cm. It had a spherical canopy of healthy foliage, with a canopy diameter of approximately 12m. A transect starting at 1m from the tree bole was randomly selected and soil pits were dug at 1m, 6m, 11m,

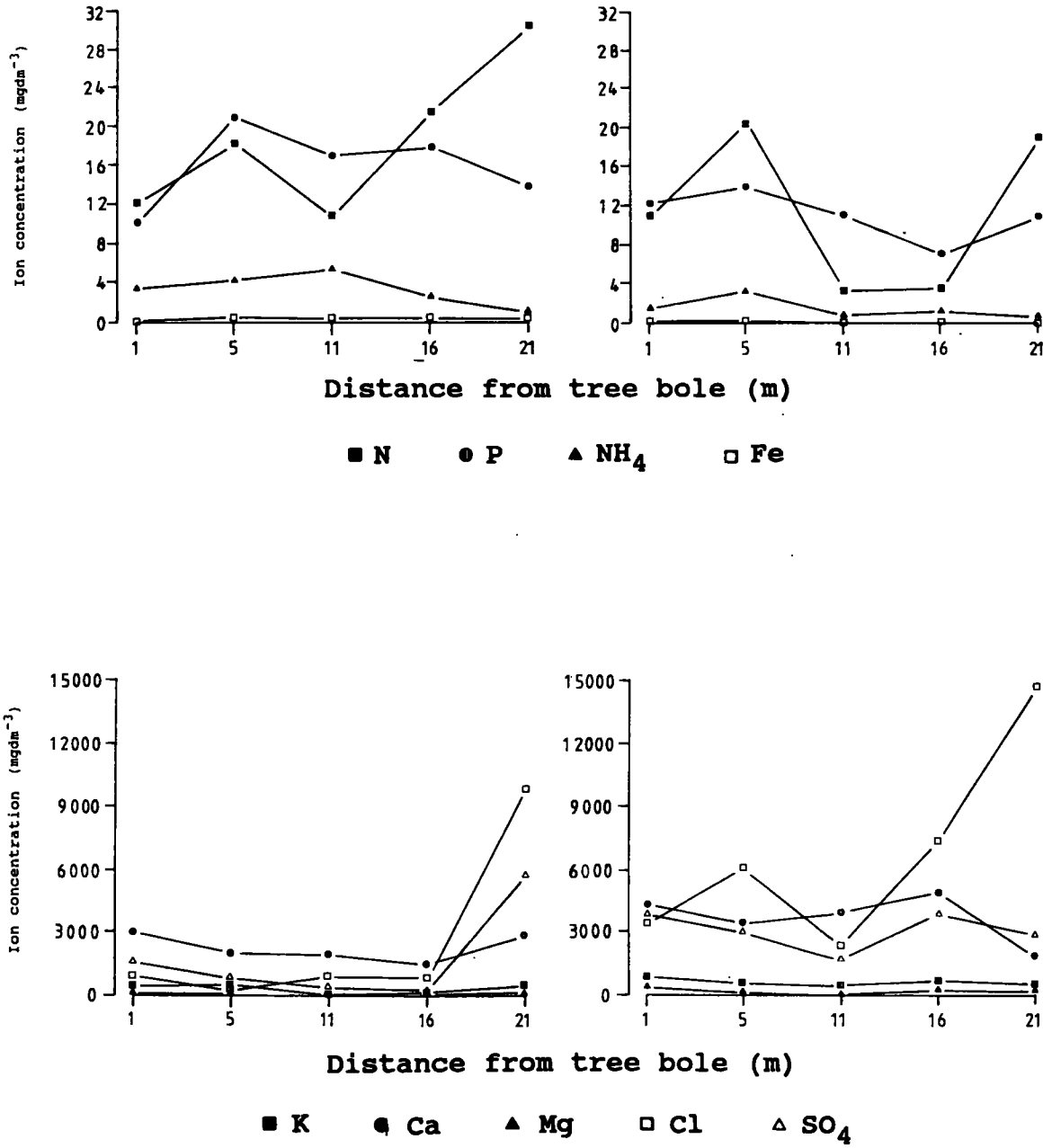
16m and 21m away from the tree. Only pits 1m and 6m were located beneath the tree canopy. Due to the underlying compact to partially cemented substrate, soils were sampled only at the surface (0-10cm) and at 30-40cm deep.

The ion concentrations at the surface and 30-40cm deep were plotted against distance from the tree bole (figure 3.14). At the surface, a very large increase in soil chloride and sulphate and, to a lesser extent, calcium was detected between 16m and 21m from the tree. At 30-40cm deep, the levels of these ions were higher, but chloride levels greatly increased between 11m and 16m from the tree, while sulphate and calcium did not show any obvious increment in concentration. The lower salt concentrations beneath the canopy may be the result of the leaching of the salts deep into the soil from dewfall dripping from the canopy, or the actual uptake of salts by the tree. Nitrate was variable along the transect at both depths and this increased with distance away from the tree at the surface, but generally declined at 30cm. At both depths, nitrate was found to be higher towards the fringe of the tree than near the bole. This was also found for phosphate, which at both depths decreased in concentration beyond the tree fringe. At the surface, iron increased away from the bole, but no changes were detected at 30-40cm. The soils generally increased in pH away from the tree, with a pH range of 7.4 to 9.1. This has been suggested by Shankar et al (1976) to be the result of the higher organic content beneath the canopy which lowers the soil pH.

These results show that the chemical composition of the soils beneath the tree canopy may be an important factor in the distribution of understorey vegetation (see section 3.3.4), by providing micro-habitats of available nutrients and low levels of salinity.

Figure 3.14

Spatial influence of a single <u>Prosopis</u> tree on soil chemical properties (soils sampled at 0cm-10cm and 30-40cm from 5 pits n=10).



3.3.4 Woodland flora

1. Vegetation description of the **Prosopis** woodlands

A total of 36 species of plants from at least 18 families were recorded in the Prosopis woodlands (table 3.5). In the sandy woodlands of the Sharqiya, the trees were almost exclusively P.cineraria, to the extent that the majority of these woodlands were natural monocultures (slides 6-9). However, in Prosopis woodlands on wadi edges, gravel plains and rocky outcrops, five other tree species were also recorded, but in very low abundance. Of these species, Acacia tortilis was the most common, particularly in the Prosopis woodlands established on sandy gravel soils. Mature A.tortilis trees in the Sharqiya ranged from stunted bushes to moderate sized trees. Acacia ehrenbergiana in the Sharqiya was usually smaller and more bushy than A.tortilis and was found mainly along wadi edges of the gravel plains to the west of the sand sea. Salvadora persica was found in a number of Sharqiya habitats, including wadi banks, gravel and sandy plains. Specifically in the sandy areas to the west of the sand sea, S.persica was rarely found in a solitary habit, but took the form of a creeper using P.cineraria as a host for support. Maerua crassifolia was found only on gravel plains and rocky outcrops in the north of the Sharqiya and to the west of the sand sea. This tree was always heavily grazed by livestock. Ziziphus spina-christi was found more in gravely and rocky substrates in the edges of wadis in the SWPZ.

The understorey vegetation included at least 15 dicotyledons and 11 monocotyledons. Before the rains of February 1986 and March 1987, the perennial xerophytes in the woodlands were generally open in their distribution and formed scattered vegetated tufts and clumps. After the rains, ephemeral growth greatly increased the vegetation cover of the woodlands. This was most pronounced immediately beneath the canopy of the trees where the

Table 3.5

Systematic list of Prosopis woodland flora in the Sharqiya. Species identification by T. COPE (pers. comm., 1987), and COPE (1988).

Family	Species	Vernacular name
Trees		
Leguminosae	Prosopis cineraria (L.) Druce	ghaf
	Acacia tortilis (Forssk.) Hayne	samur, semr
	A.ehrenbergiana Hayne	salam
Salvadoraceae	Salvadora persica L.	rak, arak
Capparaceae	Maerua crassifolia Forssk.	sarh
Rhamnaceae	Ziziphus spina-christi (L.) Willd.	sidr
Ascomycetes	Ramalina lacera (With.) Laundon	
	Diploicia canescens (Dickson) Massel	
	Xanthoria parietina (L.) Th. Fr.	
Gasteromycetes	Montagnea arenaria (DC.) Zeller	
Understorey vegetation		
DICOTYLEDONS		
Amaranthaceae	Aerva javanica (Burm.f.) Spreng.	ra'
Boraginaceae	Heliotropium kotschyi Guerke	rimram
	Arnebia hispidissima (Lehm.) DC.	
Carylophyllaceae	Polycarpaea repens (Forssk.) Asch.	
Cruciferae	Dipterygium glaucum Decne.	'alqa
Euphorbiaceae	Euphorbia granulata Forssk.	
	Chrozophora sabulosa Karelin & Kir.	
Leguminosae	Cassia italica (Mill.) Lam.ex.Steud.	'ishriq, kharkhash
	Indigofera sp.	
Menispermaceae	Cocculus pendulus (J.R.et G.Forst.) Diels.	
Neuradaceae	Neurada procumbens L.	
Polygonaceae	Calligonum comosum L'Her	'arta, 'abal;dhakar
Tamaricaceae	Tamarix arabica Bunge	
Zygophylloceae	Zygophyllum qatarense Hadidi	tharmad
	Tribulus pentandrus Forssk.	hahit bidar, shurayshira
MONOCOTYLEDONS		
Cyperaceae	Cyperus aucheri Jaub. & Spach	thidda
Gramineae	Cenchrus pennisetiformis Hochst. & Steudel	
	Coelachyrum piercei (Benth.) Bor	
	Dactyloctenium aristatum Link	
	Eragrostis barrelieri Daveau	
	Lasiurus scindicus Henr.	dha'i
	Panicum turgidum Forssk.	tharmam
	Setaria viridis (L.) P. Beauv.	
	Stipagrostis plumosa (L.) Munro	nussi
	S.sokotrana (Vierh.) de Winter	
	Tragus berteronianus Schultes	

vegetation was often continuous (slides 16-18). Including the ephemeral species identified after the rains, species diversity in the woodlands was found to be almost double that of the surrounding desert plains. Zygophyllum qatarense as a perennial succulent was the dominant understorey species in the Prosopis woodlands. It was also found in abundance on open dune fields and desert plains. Its dominance in both habitats was primarily because of its unsuitability as fodder. Even after three years of continued drought when most of the vegetation was extensively browsed or had died back, this species was rarely eaten by livestock. Z.qatarense was most abundant in areas of disturbance, such as near bedu habitation or in woodlands that have been extensively exploited for timber and forage.

Calligonum comosum was also a common perennial of sandy habitats, that grew as a sparsely leafed shrub, up to 1m or more in height. It was more abundant on the open plains than in the woodlands. The perennial herb Cyperus aucheri was commonly found on the tops of sand dunes or where the substrate was particularly mobile or unstable. As a perennial grass, Panicum turgidum was the most abundant of the gramineae identified and grew in bushes to about 1m in height. Chrozophora sabulosa also was commonly found in the understorey vegetation as a small shrub less than 40cm in height.

Three species of lichen growing on P.cineraria have been identified by D.L. Hawksworth, CAB International Mycology Institute (pers. comm., 1987). The distribution of the species was not determined, but Ramalina lacera, a foliose lichen was the most abundant, found on both live and dead branches of P.cineraria. This lichen may be an important food source to some woodland fauna. The crustose lichen Diploicia canescens was more frequent on dead branches and may speed up wood decay for the release of nutrients back into the soil.

2. Understorey vegetation survey

A quadrat survey along transects T1 to T5 in the EPZ (section 3.2.1) was carried out in May 1987, to assess the understorey vegetation response to a period of heavy rainfall that fell in the area in March 1987. In 57, 4m² quadrats, 15 species and two ephemeral groups were identified in the understorey vegetation (table 3.6). Those ephemerals that could not be positively identified due to the absence of taxonomic features such as the flowers and fruit, were divided into those that were alive (EPH.L) and those that had died back (EPH.D). Included in the live ephemeral group, Coelachyrum pierci, Setaria viridis and Cenchrus penniseteformis were later identified. Species frequency and mean Domin cover (section 3.2.1) for each transect have also been summarised in table 3.6. Only three species (Z.qatarense, C.sabulosa and A.hispidissima) and both ephemeral groups were found present in all transects. The ephemeral vegetation was generally high in frequency and cover both down and across the woodland. Species diversity decreased slightly southwards, but vegetation cover was approximately constant.

Species correlation using 2x2 contingency tables and chi-square was carried out on the presence or absence data of pairs of species in the 57 quadrats, to determine those species that were significantly associated at $p<0.05$. Five species (Z.qatarense, A.hispidissima, P.repens, E.granulata and T.pentandrus) and the dead ephemeral group were found to be positively correlated to each other, to the extent that only one combination of species pairs was not significant (Z.qatarense and T.pentandrus). Except for the significant correlations between C.aucheri and N.procumbens, and between C.sabulosa and E.barrelieri all other combinations of species were not significantly associated in their distribution.

Table 3.6

Summary of species and data used in the ordination of *Prosopis* woodland understorey vegetation. Where F = transect frequency; C_m = transect mean domin cover.

		Transect									
		1		2		3		4		5	
Code	Species name	F	C_m	F	C_m	F	C_m	F	C_m	F	C_m
Pc	*Prosopis cineraria*	0	0	15	2.7	12.5	3	0	0	0	0
Zq	*Zygophyllum qatarense*	50	4	5	3	50	6.3	50	5	83.3	6.2
Ah	*Arnebia hispidissima*	41.7	3.2	5	3	0	0	0	0	0	0
Cs	*Chrozophora sabulosa*	50	3	25	3	12.5	3	40	3	16.7	3
Da	*Dactyloctenium aristatum*	66.7	2.6	30	2.8	75	2.5	70	3.3	50	1
EPH.L	Live ephemerals	91.7	2.9	85	2.4	87.5	3	40	2.5	66.7	4
EPH.D	Dead ephemerals	23.1	8.7	85	5.6	75	3.8	80	4	50	4.7
Tp	*Tribulus pentandrus*	25	3	5	2	0	0	0	0	0	0
Eg	*Euphorbia granulata*	25	2.7	5	2	0	0	0	0	0	0
Eb	*Eragrostis barrelieri*	33.3	2.5	10	3	0	0	30	2	0	0
Pr	*Polycarpaea repens*	25	2.3	5	2	0	0	0	0	0	0
Np	*Neurada procumbens*	8.3	3	0	0	12.5	2	0	0	0	0
Ca	*Cyperus aucheri*	0	0	0	0	12.5	3	0	0	0	0
Tb	*Tragus berteronianus*	0	0	0	0	12.5	6	20	4	0	0
Aj	*Aerva javanica*	0	0	0	0	12.5	3	0	0	0	0
Ci	*Cassia italica*	0	0	0	0	0	0	10	1	0	0
Hk	*Heliotropium kotschyi*	0	0	0	0	12.5	3	0	0	16.7	3

3. Understorey vegetation ordination

A divisive classification of the understorey vegetation was performed by two-way indicator species analysis using the computer program TWINSPAN (section 3.2.3). A two-way table produced by TWINSPAN is replicated in table 3.7a. By separating the dichotomous divisions, seven vegetation classes (V1-V7) were determined, and number coded for easy reference (table 3.7b). The vegetation classes were then identified on a map of the study area (figure 3.15) to observe the general trends in their distribution both down and across the woodland.

Vegetation class V1 was dominated by Z.qatarense and the live ephemeral group. Present also were the four herbaceous species that were significantly correlated to each other. This community was found only in the north-eastern part of the study area. Vegetation classes V2 and V3 were similar in that Z.qatarense was co-dominant with either the live ephemeral group (class V2) or dead ephemeral group (class V3). Both classes had the shrub C.sabulosa, but class V3 also contained three identified annuals (E.barrelieri, T.berteronianus and D.aristatum) which suggests that these species formed a major component of the dead ephemeral group. These two classes were rather scattered through the study area and did not show any trends in their distribution. Vegetation class V4 was dominated by C.sabulosa, but both ephemeral groups were present. This community was found only in two quadrats towards the interior of the woodland. Vegetation classes V5 and V6 consisted of both ephemeral groups and D.aristatum, but with or without Z.qatarense respectively. Vegetation class V6 was found in the north of the study area where Z.qatarense was infrequent, whilst vegetation class V5 was found in the south where Z.qatarense was dominant. C.aucheri (class V7) as a sand coloniser was found only on the western margin in areas of shifting sand dunes.

Table 3.7

Results of a divisive classification of the understorey vegetation by TWINSPAN. See table 3.6 for species labels.

A. TWINSPAN two-way table

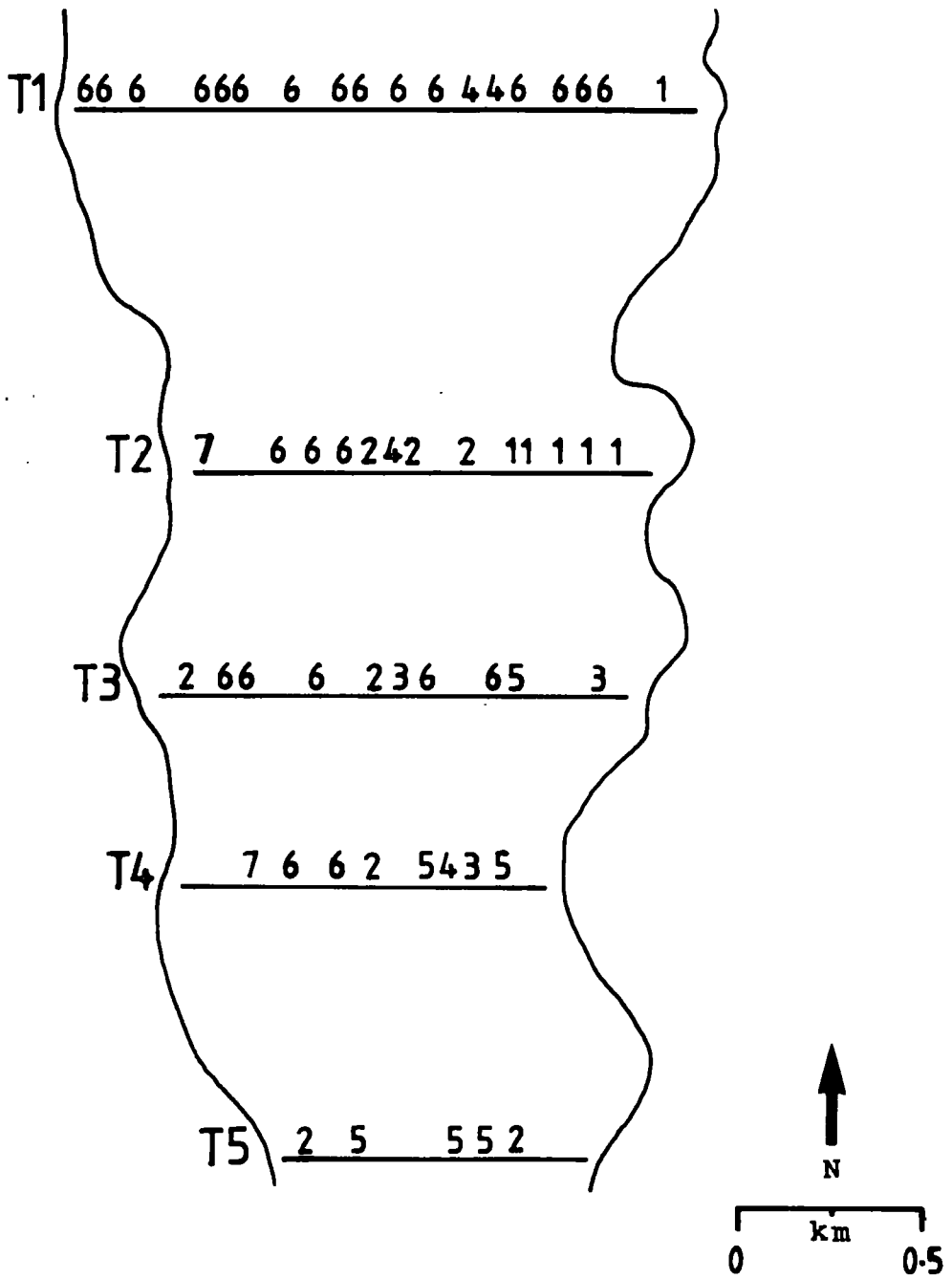
```
                                    QUADRAT

          112111 53411145 344 2213 4 55335 224423442222223 2241112222 31
          ...... ........ ... .... . ..... ............... .......... ..
          341125 15167966 215 6783 2 24413 123846795813117 9141111112 81
                   0                      00        5 27   3 012149   3
VEGETATION
  CLASS     1       2      3   4     5        6a        6b             7

SPECIES

  Tp      1-111- -------- --- ---- - ----- -------------- ---------- --  111111
  Ah      111211 -------- --- ---- - ----- -------------- ---------- --  111110
  Pr      111--1 -------- --- ---- - ----- -------------- ---------- --  111101
  Eg      -111-1 -------- --- ---- - ----- -------------- ---------- --  111100
  Ci      ------ ------1- --- ---- - ----- -------------- ---------- --  1110
  Aj      ------ -------- --- ---1 - ----- -------------- ---------- --  110111
  Np      1----- -------- --- ---1 - ----- -------------- ---------- --  110110
  Cs      -121-- ---12121 -11 1111 - ----- ----1--1------- ---------1 --  11010
  Eb      -1--11 -------- -11 --1- 1 ----- ----1---------- ---------1 --  11001
  Tb      ------ -------- -11 11-- - ----- 1------------- ---------- --  11000
  Hk      ------ -------1 --- ---- - ----- -------------- ---------- 1-  101
  Zq      1112-2 3222-222 422 ---- 3 33233 -------------- ---------- --  100
  EPH.L   211111 211111-- 1-- 1-11 - 11111 11-1111-1111111 11111-1111 --  0111
  Da      ---111 -1-111-- 11- ---1 1 11111 1-11-11211----- 1-111---11 --  0110
  EPH.D   ------ -------- 111 11-1 3 22233 111122222332222 3335545444 --  0101
  Pc      ------ -------- --- ---- - ----- --------111---1 ---------- --  0100
  Ca      ------ --1----- --- ---- - ----- ---2---------- ---------- 31  00

          000000 00000000 000 0000 0 00000 000000000000000 0000000000 11
          000000 00000000 000 0000 1 11111 111111111111111 1111111111 01
          000000 00000000 111 1111 0 00000 111111111111111 1111111111
          000000 11111111 000 1111 0 11111 000000000000000 1111111111
          011111 00011111 011 0001   00011 000000001111111 0000000001
           00111 01100011  01 001    001   000011110001111 000111111
```

B. Species composition of TWINSPAN vegetation classes

Class	Species composition
V1	Zq/EPH.L + Tp, Ah, Pr, Eg
V2	Zq/EPH.L (+ Cs)
V3	Zq/EPH.D (+ Cs, Eb, Tb, Da)
V4	Cs + EPH.L, EPH.D
V5	Zq/EPH.D/EPH.L/Da
V6.1	EPH.D (low abundance)/EPH.L (+Da)
V6.2	EPH.D (high abundance)/EPH.L (+Da)
V7	Ca

Figure 3.15

Geographical location of TWINSPAN vegetation classes.



Detrended correspondence analysis using the program DECORANA was performed on the cover-abundance data (section 3.2.3). As the first two axes of the analysis accounted for 74.9% of the variation in the data, only these were examined. The quadrat scores for both axes are presented as a scatter plot in figure 3.16. Each quadrat point on this plot was marked with its TWINSPAN vegetation class. In this ordination, the vegetation classes were clearly separated, with only a marginal overlap between some of the classes. Quadrats with high positive scores for axis 1 were located on the western margin of the woodland. In contrast, quadrats with the lowest scores on axis 1 were predominantly from the eastern margin. This suggests that axis 1 may be a function of increasing distance west, or a function of topographical or environmental differences between the two marginal areas. The quadrats within the woodland interior were scattered positively along axis 2, which indicates that the function of this axis may be related to micro-environmental conditions of the woodland interior.

Ordination of the understorey vegetation was also carried out by canonical correspondence analysis using the program CANOCO (section 3.2.3). This analysis was performed on the cover-abundance data with five variables (tree density, mean basal area as an index of tree size, slope, immediate shade, loose soil depth), which were determined at each quadrat site (section 3.2.1). As the first two axes accounted for 81.1% of the variation in the data, only these axes were examined. A scatter plot of the quadrat scores marked with the appropriate TWINSPAN vegetation classes for the first two axes is shown in figure 3.17a and a scatter plot of the species scores for the same axes is shown in figure 3.17b. A 135° clockwise rotation of the CANOCO plot of the TWINSPAN classes (figure 3.17a) shows a similar ordination pattern to the DECORANA plot in figure 3.16. In the CANOCO analysis, tree density and shade in contrast to loose soil depth were the

Figure 3.16

DECORANA plot of quadrat scores for axes 1 & 2, superimposed with TWINSPAN vegetation classes. Where figures in parentheses are the percentages of variance associated with each axis.

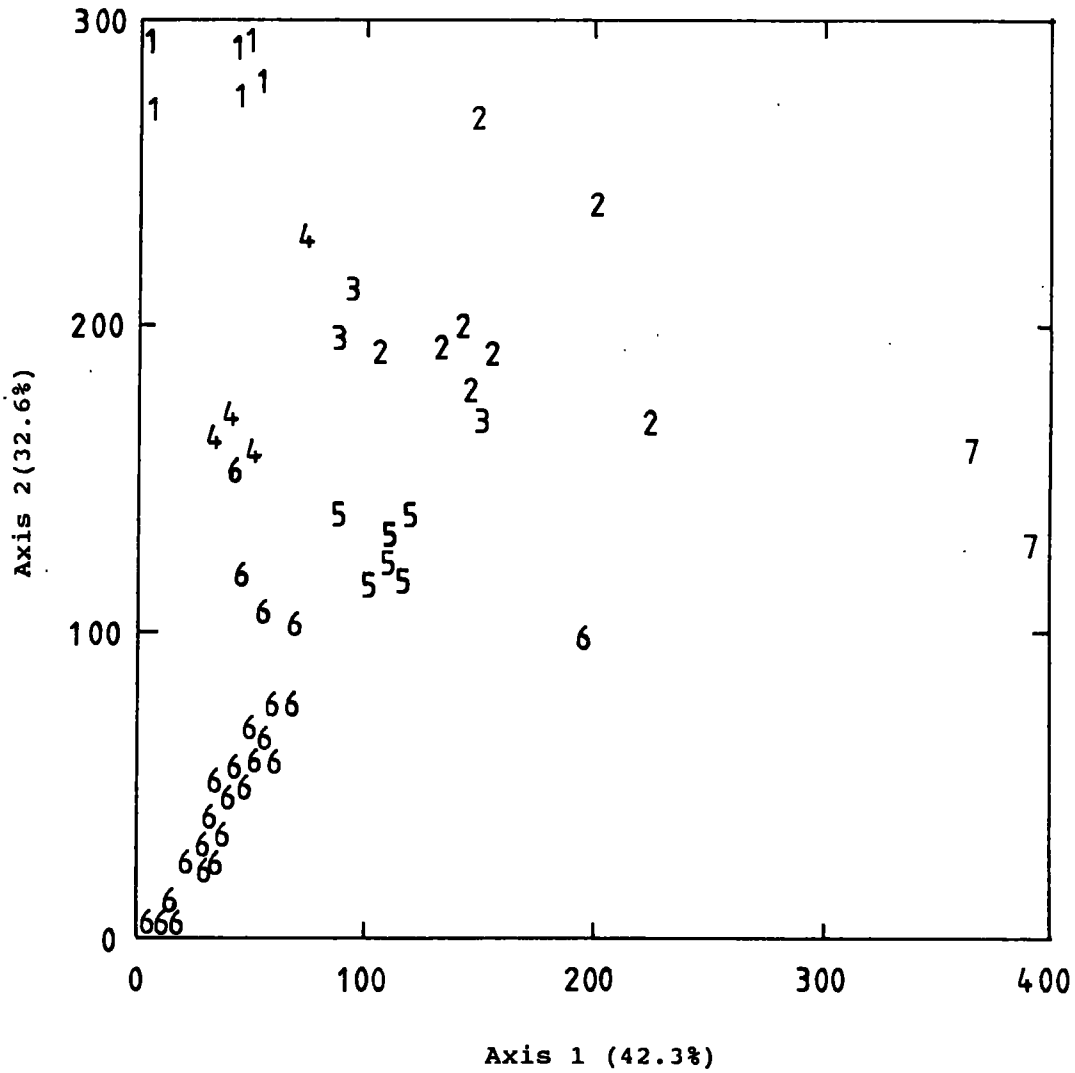
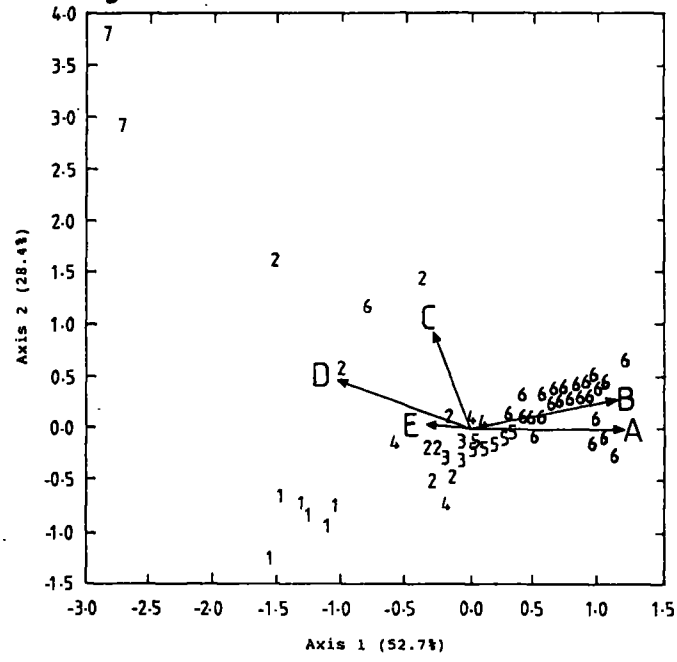


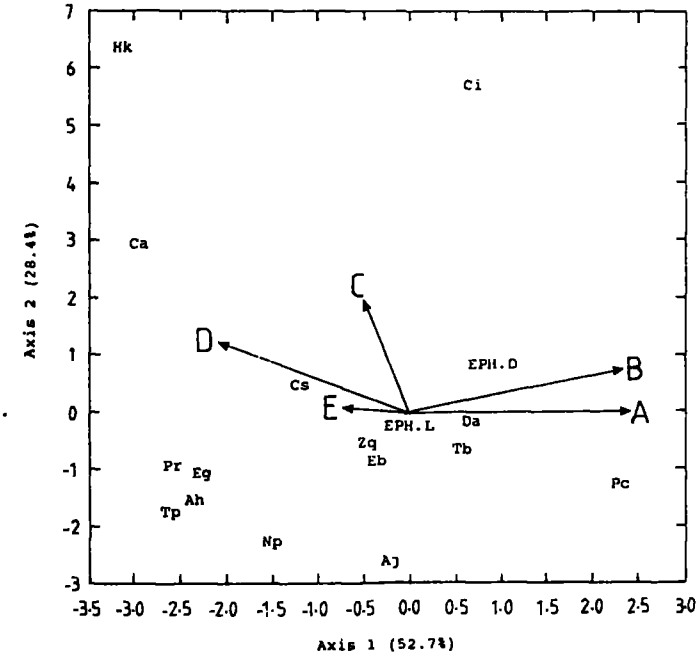
Figure 3.17

Ordination of the Prosopis woodland ephemeral vegetation by canonical correspondence analysis, using the program CANOCO. Where figures in parentheses are the percentages of variance associated with each axis.

A. CANOCO biplot of quadrat scores for axes 1 & 2 (superimposed with TWINSPAN vegetation classes) and 5 environmental gradients.



B. CANOCO biplot of species scores for axes 1 & 2 and 5 environmental gradients.



A Tree density B Shade cover C Tree size D Soil depth E Slope

influencing functions of axis 1, whilst tree size and to a lesser extent loose soil depth and shade were the predominant functions of axis 2. Slope had only a minimal influence on the ordination of the vegetation.

Specific environmental factors influencing the ordination of both the TWINSPAN vegetation classes and the individual species were identified from the CANOCO plots. Vegetation class V1 was clearly separated from other communities by being found in parts of the woodland of low tree density and shade, in deep soil and where the trees were moderate in size. The exclusively ephemeral vegetation class V6 was found where tree density and shade were high and where the soils were firm. The vegetation classes V6, V5, V3 and V2 were spread in order along a decreasing gradient of tree density and shade, which can be explained by the ordination of the component species. There was a high abundance of dead ephemerals in parts of the woodland where tree density and shade was highest. As the density and shade decreased, there was an increase in the abundance of the live ephemerals and an increase in D.aristatum. Further decreases in density and shade led to an increase in the abundance of Z.qatarense and an increase in C.sabulosa. Vegetation class V4, composed of C.sabulosa with both ephemeral groups, was rather scattered around the axes intercept. This community was only found in the woodland interior and towards the east margin. C.aucheri (class V7) and H.kotschyi were similar in their ordination in that they were found in deep soils, in areas of low density and shade along the western margin, but the latter species was more associated with large trees.

Species diversity and distribution in the understorey of the Prosopis woodlands were therefore heavily influenced by the canopy shade. Shade cover will protect sensitive understorey plants from the high air and soil temperatures that can reach over 50°C and 80°C respectively in the summer in the open plains (pers. obs.). Concomitant with

reduced temperatures beneath the tree canopy, slower windspeeds will favour higher humidities and reduced evapotranspiration of the vegetation and the soils. The vegetation immediately beneath the trees will also benefit from the higher concentrations of soil nutrients and the lower soil salinity (section 3.3.2). In this way, the micro-environment beneath the trees has favored the growth of vegetation that one would not normally expect to find in the arid conditions of the Sharqiya.

The species in the dead ephemeral group were more abundant in areas of high tree density and shade than those in the live ephemeral group. This suggests that the species in the former group were the least adapted to arid conditions but were the first ephemerals to respond to the rains by colonising and then dominating the prime areas beneath the canopy. These species were the first to die back when moisture became limited. The distribution of the live ephemeral group in the canopy fringes and in the between-clump gaps suggests that its constituent species were more tolerant to arid conditions than those in the dead ephemeral group. The zonation of live and dead ephemeral groups in the woodland along gradients of varying degrees of shade cover may have promoted a higher diversity of ephemeral plants to exist than would normally have been expected.

3.3.5 Woodland fauna [1]

1. Invertebrates

The invertebrate fauna from the Prosopis woodlands included 26 families (table 3.8), which account for 68.4% of the invertebrate families identified in the Sharqiya collection (section 3.2.1). At least 82 species were collected from the woodlands, which represent more than half the total species found in the Sharqiya. Of these

[1] In this section, the OWSP fauna collection (Dutton, 1988) was used to analyse the distribution and diversity of the Prosopis woodland fauna in the Sharqiya.

Table 3.8

Systematic list of invertebrate families identified in the *Prosopis* woodlands of the Sharqiya. Data source from Buttiker & Buttiker (1988); Popov (1988); Wiltshire (1988); Collingwood (1988); Chhotani (1988); Crosskey & Buttiker (1988); Lane & Buttiker (1988); Ferrara & Taiti (1988).

CLASS: ARACHNIDA

Arachnidae (Gall mites): *Eriophyes prosopidis* Saksena

CLASS: INSECTA

Orthoptera (grasshoppers):

- Pyrgomorphidae
- Cyrtacanthacridinae
- Tropidopolinae
- Truxalinae
- Stenopelmatidae

Isoptera (termites):

- Hodotermidae
- Rhinotermidae
- Termitidae

Homoptera: Aphididae (Greenflies)

Coleoptera (beetles):

- Bruchidae (bruchids)
- Tenebrionidae: *Ammogiton* sp., *Erodius* sp.

Lepidoptera Macro-heterocera :

- Cossiade
- Psychidae
- Geometridae
- Sphingidae
- Lymantriidae
- Noctuidae
- Tortricidae: *Cryptophlebia* sp.
- Melelonthidae

Diptera:

- Phlebotominae (sandflies)
- Simuliidae (blackflies)
- Cecidomyidae (Gall midges): *Lobopteromyia prosopidis* Mani

Hymenoptera:

- Formicidae (ants)
- Apoidea (Carpet and Honey bees)

CLASS: CRUSTACEA

- Eubelidae; *Periscyphis vittatus* Omer-Cooper

invertebrates, 49 species were found exclusively in this habitat. The majority of these species were insects (97.6%), of which the moths (Macro-Heterocera) from mainly the EPZ and SWPZ were the highest in species diversity (table 3.9). Out of the 28 species of ant (Hymenoptera) in the Sharqiya collection, 19 were identified in the Prosopis woodlands (table 3.10a). Ant species diversity in both the CPZ and SWPZ was more than double that in the EPZ. Four termite species (Isoptera) were mainly found in the EPZ and SWPZ (table 3.10b). Nine species of grasshopper (Orthoptera) were recorded in the Prosopis woodland, representing 63.3% of the total species in the Sharqiya (table 3.10c). All were generalists in terms of habitat preference and were mostly identified in the EPZ.

High species diversity of insects in the Prosopis woodlands can be attributed to the abundance of food (leaves, flowers, nectar, pollen, pods) and suitable micro-habitats (within the canopy, beneath fissured bark) in the trees. This diversity is enhanced by the understorey vegetation and by the abundance of surface micro-habitats of woodland detritus and fallen dead wood.

A number of insect species identified in the Prosopis woodlands were present as pests, to the extent that they may be having a detrimental effect on the ecology of this habitat. P.cineraria seed infestation by moth larvae (slide 39) was particularly heavy in the Sharqiya woodlands (see Chapter 4). At least two species of moth were responsible, but these have only been identified to the genus in one species (Cryptophlebia sp.) and to the family in the second species (Melelonthidae) by W. Buttiker (pers. comm., 1988). Tephrina pervaria and T.disputaria were also potential pests, particularly the latter which is known to be a serious defoliator of Acacia mollissima plantations in Morocco (Rungs, 1954 cited by Wiltshire, 1988). Other moth pests in the woodlands have been identified as Spodoptera exigua, S.litura and Helicoverpa armigera which are

Table 3.9

Provenance distribution of larger moths (Macro-Heterocera) in the Prosopis woodlands of the Sharqiya. Data source from Wiltshire (1988). Collecting sites within the provenances are Qarhat Mu'ammar (EPZ); Umm Qishrib (CPZ); Dhu'ay (SWPZ); Wadi Andam (SWPZ). Where + = presence in provenance; * = species identified only in the Prosopis woodland habitat.

SPECIES (n=34)	WOODLAND PROVENANCE			
	EPZ	CPZ	SWPZ	
Paropta l-nigram * (Bethune-Baker)			+	
Amicata murina (Klug)		+		
Idaea mimetes * Brandt	+		+	
Tephrina disputaria (Guenee)			+	
T.pervaria (Lederer)	+	+	+	
Atomorpha hedemanni Christoph balouchistana Werhrli	+			
Agrius convolvuli * (Linnaeus)	+			
Hyles livornica (Esper)	+			
Casama vilis Walker	+			
Spodoptera exigua (Hubner)	+			
S.litura * (Fabricius)		+		
Platysenta viscosa (Freyer) persicola * (Strand)	+			
Helicoverpa armigera * (Hubner)	+			
Eublemma bistella (Wiltshire)			+	
E.rushi (Wiltshire)	+		+	
Acontia biskrensis Oberthur orientalis * Brandt			+	
Entelia blaniatrix * Guenee	+			
Ctenoplusia limbirena * (Guenee)	+			
Achae catella * (Guenee)	+			
Pericyma signata Brandt	+		+	
Heteropalpia acrosticta *(Pungeler)	+		+	
Gnamptonyx innexa (Walker)	+			
Clytie devia * Swinhoe			+	
Drasteria kabylaria (Bang-Haas)	+	+	+	
Anumeta asiatica Wiltshire	+			
A.eberti Wiltshire zaza Wiltshire	+			
A.hilgerti Rothschild popovi Wiltshire	+	+		
A.astrosignata Walker	+	+	+	
A.spilota Ershoff harterti Rothschild	+	+	+	
Acrobyla kneuckeri Rebel	+	+	+	
Armada maritima Brandt			+	
A.gallagheri Wiltshire	+			
Acantholopes circumdata Walker	+		+	
Hypena abyssinialis Guenee	+			
	==========			WOODLAND
Species total	26	8	16	34
% species in woodland	76.5	23.5	45.7	100
% species in Sharqiya (n=57)	45.6	14.0	28.1	59.6

Table 3.10

Provenance distribution of ants (Hymenoptera), termites (Isoptera) and grasshoppers (Orthoptera) in the *Prosopis* woodlands of the Sharqiya. Ant species from Collingwood (1988); termites from Chhotani (1988); grasshoppers from Popov (1988). Collecting sites within the provenances are Qarhat Mu'ammar (EPZ); Umm Qishrib (CPZ); Dhu'ay (SWPZ); Wadi Andam (SWPZ): Wadi Matam (SWPZ). Where + = presence in provenance; * = species identified only in the *Prosopis* woodland habitat.

SPECIES	WOODLAND PROVENANCE			
	EPZ	CPZ	SWPZ	
A. ANTS (n=19)				
Pachycondyla senaarensis (Mayr)		+		
Crematogaster antaris Forel			+	
Messor planiceps * Stitz			+	
Tetramorium sericeiventre Mayr		+		
Monomorium abeillei Andre		+		
M.barbatulum * Mayr		+	+	
M.mayri Forel			+	
M.phoenicium Santschi		+		
M.venustum (Smith)			+	
Tapinoma melanocephalum (Fabricus)		+		
Acantholepis gracilicornis Forel		+		
Camponotus aegyptiacus Mayr		+		
C.fellah * Tohme	+		+	
C.sericeus * (Fabricus)		+	+	
C.thoracicus * (Fabricus)			+	
Cataglyphis desertorum (Forel)	+	+		
C.livida * Andre	+			
C.laevior * Stitz			+	
C.niger * Andre		+	+	
	==========	==========	==========	WOODLAND
Species total	3	11	10	19
% species in woodland	15.8	57.9	52.6	100
% species in Sharqiya (n=28)	10.7	39.3	35.7	67.9
B. TERMITES (n=4)				
Anacanthotermes saudiensis Chhotani & Bose		+	+	
Psammotermes hybostoma Desneux	+		+	
Heterotermes omanae sp.nov.	+		+	
Microcerotermes spp.	+			
	==========	==========	==========	WOODLAND
Species total	3	1	3	4
% species in woodland	75	25	75	100
% species in Sharqiya (n=14)	21.4	7.1	21.4	28.6
C. GRASSHOPPERS (n=9)				
Pyrogomorhpa conica tereticornis (Brulle)	+			
Tenuitarsus angustus (Blanchard)		+	+	
Schistocerca gregaria (Forsskal)	+			
Sphingonotus rubescens (Walker)	+			
Ochrilidia geniculata (I.Bolivar)	+			
O.persica (Salfi)	+			
Truxalis procera Klug	+			
Leva sp.	+			
Lezina armata Popov			+	
	==========	==========	==========	WOODLAND
Species total	7	1	2	9
% species in woodland	77.8	11.1	22.2	100
% species in Sharqiya (n=14)	50	7.1	14.3	64.3

widespread migrants that feed on cultivated crops, flowers or low lying herbs (Wiltshire, 1988). The same author has identified Paropta 1-nigram from the SWPZ, which is a tree borer that is very widespread in the Arabian peninsula. This species may have been responsible for the abundance of bore holes in P.cineraria from all three provenances of the Sharqiya (pers. obs.).

Coleopteran bruchids (Bruchidae) were abundant in the Prosopis woodlands, both on the trees and on the ground (pers. obs.). These insects have also caused severe seed infestation because the larvae grow inside the developing seeds and ovi-positing adults have mouth parts capable of penetrating the hard testa of mature seeds (Johnson, 1983). There were several gall-forming pests on P.cineraria leaves, rachis and flower spikes (pers. obs.). These have been identified by W. Buttiker (pers. comm., 1988) as Lobopteromyia prosopidis (gall midge) and Eriophyes prosopidis (gall mite). Infection of the immature flower spikes by gall mites (slide 37) was particularly common and appears to cause a physiological shedding of the developing flower buds. The galls were extremely abundant throughout the canopy of most trees in the Sharqiya provenances and may have a considerable effect on the total seed production.

2. Reptiles

Thirteen species of reptile were found in the Prosopis woodlands, representing 46.4% of the species identified in the Sharqiya collection (table 3.11). Species diversity was highest in the EPZ and SWPZ, from which seven of these species were found exclusively in the woodlands. These animals were divided into two groups: those that were associated with P.cineraria trees, and those that were found in woodland margins or its vicinity and migrate into the woodlands to exploit the food resources (Gallagher & Arnold, 1988). These authors included in the former group,

Table 3.11

Provenance distribution of reptiles (Reptilla) in the Prosopis woodlands of the Sharqiya. Data source from Gallagher & Arnold (1988). Where + = presence in provenance; * = species identified only in the Prosopis woodland habitat.

SPECIES (n=13)	WOODLAND PROVENANCE			
	EPZ	CPZ	SWPZ	
Acanthodactylus schmidti Haas	+			
Bunopus tuberculatus Blanford *	+	+	+	
Hemidactylus turcicus (Linnaeus) *	+	+	+	
Pristurus minimus Arnold	+		+	
P.rupestris Blanford *	+	+	+	
Stenodactylus arabicus (Haas)	+		+	
S. doriae (Blanford)		+	+	
Mesalina adramitana Boulenger *			+	
Scincus mitranus muscatensis Murray	+		+	
Varanus griseus (Daudin)	+		+	
Diplometopon zarudnyi Nikolski *	+	+	+	
Psammophis schokari (Forsskal)		+		
Echis carinatus sochurecki (Stemmler) *	+			
	==========			WOODLAND
Species total	10	6	10	13
% species in woodland	76.9	46.1	76.9	100
% species in Sharqiya (n=28)	35.7	21.4	35.7	46.4

Hemidactylus turcicus, Pristurus rupestris, Bunopus tuberculatus, Echis carinatus sochurecki and to a lesser extent the tree snake Psammophis schokari. The extended range of Echis carinatus sochurecki into the Sharqiya was attributed to the favourable conditions and suitable micro-habitat provided by the woodlands. The remaining reptile species identified were placed in the second group, which were opportunist feeders in the woodlands but living in the surrounding desert plains.

3. Birds

Birds were the most diverse of vertebrate species in the Prosopis woodlands with 29 species, of which 22 of these were recorded exclusively in this habitat (table 3.12a). The Prosopis woodland biotope in the Sharqiya was the third largest in bird species diversity (25.2% of total in the collection), superseded only by the biotopes 'sea & shore' and 'cultivation & wet wadis' (Gallagher, 1988). Resident breeders and passage migrants were the dominant bird type, with smaller numbers of winter visitors and migrant breeders and no summer visitors (table 3.12b). Bird species diversity was highest in the EPZ, which may be attributed to its close proximity to the species-rich coastal zone and its distribution along set migratory routes. The CPZ had the lowest numbers of bird species, which may be an artifact of the variable sampling strategies between the provenances. The birds exploit the Prosopis woodlands for food (invertebrates, leaves and flowers), roosts, perches, nest material (sticks, twigs, leaves, lichen), nest sites and protection from the sun and from wind and sand blast. In return, the birds may play an important role in the pollination of the Prosopis flowers and the dispersal of the seeds away from the parent trees. The multiple resources provided by the woodlands have been recognized by Gallagher (1988) to be responsible for attracting birds into a region in which they were not necessarily adapted. In this way the woodlands have acted

Table 3.12

Birds (Avifauna) identified in the Prosopis woodlands of the Sharqiya. Data source from Gallagher (1988). Where RB = resident breeder; MB = migrant breeder; PM = passage migrant; WV = winter visiter (not breeding); + = presence in provenance; * = species identified only in the Prosopis woodland habitat.

A. Provenance distribution of birds in the Sharqiya

SPECIES (n=29)		WOODLAND PROVENANCE			
		EPZ	CPZ	SWPZ	
Great Cormorant	Phalacrocorax carbo			+	
Long-legged buzzard	Buteo rufinus		+		
Kestrel	Falco tinnunculus	+		+	
Peregrine	F.peregrinus	+	+		
Grey francolin	Francolinus pondicerianus	+	+	+	
Spotted thick-knee	Burhinus capensis	+			
Collared dove*	Streptopelia decaocto	+	+	+	
Turtle dove*	S.turtur	+		+	
Palm dove	S.senegalensis	+		+	
Bruce's scops owl	Otus brucei	+			
Little owl	Athene noctua	+		+	
Pallid swift	Apus pallidus	+			
Little green bee-eater	Merops orientalis	+		+	
Blue-cheeked bee-eater*	M.superciliosus	+			
Indian roller	Coracias benghalensis	+			
Yellow wagtail	Motacilla flava	+			
White wagtail	M.alba	+	+		
Yellow-vented bulbul	Pycnonotus xanthopygos	+	+	+	
Rufus bush robin	Cercotrichas galactotes	+			
Black redstart	Phoenicurus ochruros	+	+	+	
Desert lesser whitethroat*	Sylvia minula	+	+	+	
Arabian babbler	Turdoides squamiceps	+	+		
Purple sunbird	Nectarinia asiatica	+		+	
Isabelline shrike*	Lanius isabellinus			+	
Great grey shrike	L.excubitor	+	+	+	
Brown-necked raven	Corvus ruficollis	+	+	+	
House sparrow	Passer domesticus	+			
Yellow-throated sparrow*	Petronia xanthocollis	+	+	+	
Scarlet rosefinch*	Carpodacus erythrinus		+		
		==========			WOODLAND
	Species total	25	13	16	29
	% species in woodland	86.2	44.8	55.2	100
	% species in Sharqiya (n=115)	21.7	11.3	13.9	25.2

B. Summary of bird status within provenances

	Resident breeder	Migrant breeder	Passage migrant	Winter visitor
EPZ	17	6	14	8
CPZ	8	1	8	7
SWPZ	10	2	8	6
	==========			
TOTAL	18	6	17	10

as corridors for the extended range of a number of species into the sand sea.

4. Mammals

The mammals of the Prosopis woodlands have been listed in table 3.13. Pipistrellus kuhli ikhwanius (Cheesman and Kuhli's pipestrelle) was identified in the EPZ (Gallagher & Harrison, 1988). This insectivorous bat can be used as an indicator of the abundance of invertebrates which it needs to feed on. Bat activity was highest on the fringes of the woodlands, where predatory flight was uninhibited by the trees (pers. obs.). There were permanently breeding populations of Ichneumia albicauda (white-tailed mongoose) in the EPZ, Vulpes vulpes (red fox) populations in both the EPZ and CPZ and Felis sylvestris (wild cat) in the CPZ (Linn, 1988). Ichneumia albicauda has no obvious adaptations to surviving in desert conditions and must rely on the woodland resources for food and protection. Vulpes vulpes was more common in the Prosopis woodlands, but less adapted to arid conditions than V.ruppelli (Ruppell's sand fox). As a result of the availability of prey, it has been estimated by I. Linn (pers. comm., 1987) that the woodland foxes have hunting ranges which are considerably smaller than foxes inhabiting the open plains. Gazella gazella arabica (Arabian gazelle) was occasionally observed in the margins of the CPZ (pers. obs.). Low numbers of gazelle can be attributed to the presence of human habitation (bedu) in the woodlands and the competition with domestic livestock for food. Other indigenous mammals such as Canis lupus (wolf), Felis caracal (caracal) and Felis margarita (sand cat), have been thought to have used, or continue to use, the woodlands for hunting and as a habitat (I. Linn, pers. comm., 1987). Feral cats (Felis cattus) and feral dogs (Canis familiaris) have been observed in numbers in the vicinity of bedu inhabitation (pers. obs.).

Table 3.13

Indigenous and feral mammals in the *Prosopis* woodlands of the Sharqiya. Small mammals from Gallagher & Harrison (1988); large mammals from Linn (1988).

A. SMALL MAMMALS (n=2)

Chiroptera sp. Several species observed but only one identified
Pipistrellus kuhli ikhwanius Cheesman & Hinton (Kuhli's pipestrelle)

Gerbillus cheesmani arduus Cheesman & Hinton (Cheesman's gerbil)

B. LARGE MAMMALS (n=7)

Vulpes ruppelli (Ruppell's sand fox)
V. vulpes (Red fox)
Canis familiaris (Feral dog)
Felis sylvestris (Wild cat)
F.cattus (Feral cat)
Ichneumia albicauda (White-tailed mongoose)
Gazella gazella arabica (Arabian gazelle)

3.3.6 Woodland resources and their exploitation

The multi-purpose resources of the Prosopis woodlands to the bedu of the Sharqiya and the exploitation of these resources were assessed in the field. This was achieved by repeatedly visiting bedu camps in the woodlands. Where possible the observations made were supported by photographic records. A summary of the multi-purpose properties of P.cineraria observed in the Sharqiya is presented in table 3.14. This table shows that this species is a very important multi-purpose tree in the Sharqiya, which is enhanced by its resistance to prolonged periods of drought (slide 23), which allows it to flourish in conditions where the majority of other vegetation has died back. From observations made in the field, the most important properties of this species were found to be the perennial abundance of leaves and pods used as fodder for domestic animals (slide 19); fuelwood (slide 20); and shade protection (slides 21 & 22). The multi-purpose properties of P.cineraria is comparable to those described for P.glandulosa growing in North America (Felker, 1979).

Seven different methods were observed to be in use in the exploitation of the trees for fodder and fuelwood in the Prosopis woodlands:

1. hand-selection of healthy leaves and pods in the tree canopy
2. collection of fallen pods from the ground
3. collection of dead wood for local use (slide 20)
4. small scale controlled lopping of branches (slide 26)
5. indiscriminate large scale lopping of branches causing severe deformities and often death of tree (slides 27 & 28)

Table 3.14

Multi-purpose properties of *P.cineraria* identified in the Sharqiya.

1. Foliage	An extremely important resource, especially during continuous periods of drought, when the canopy foliage remains abundant whilst the majority of the surface vegetation has died back or been exhausted through over-grazing. The leaves are rich in moisture and nutrients, with a crude protein content between 14% to 18% dry weight (Bhimaya *et al.*, 1964; Sharma 1966).
2. Wood	An extremely valuable and readily used resource, used as a source of fuel for cooking and heating. The wood burns with an intense flame for long periods of time. The wood is known to have a high calorific content of 1720 joules/kg (Kaul & Jain, 1967).
3. Shade	Very important to bedu and livestock during the high summer temperatures, which can exceed 50°C in the open plains. Bedu camps and livestock pens are often constructed beneath the tree canopy. Camels are often tethered here.
4. Drought tolerance	As a phreatophyte, the tree will retain a full canopy of dense leaves and will flower and produce copious quantities of fruits in periods of continuous severe drought.
5. Salinity tolerance	Existing woodlands in highly saline soils will support both man and wildlife when less tolerant herbaceous plants will not survive. Seedlings can be propagated under saline media, which allows the utilisation of this species in degraded or poor quality soils.
6. Coppicing	The vegetative growth is fast, and responds well to both pruning and controlled lopping. Damaged surface lateral roots often results in the development of rapid sucker growth and the propagation of tree clumps.
7. Shelter-belts	The tree canopy provides protection to habitation in the woodlands from wind and sand blast, and reduces evaporation of water from the soil surface. Sand encroachment into towns and cultivated land is reduced when in proximity to the woodlands.
8. Sand fixation	In mature trees, a complex web of surface lateral roots are responsible for stabilising the sand in the immediate vicinity of the trees. This allows the understorey vegetation to colonise the fixed sandy soil and flourish.
9. Soils	Woodland soil is high in organic matter derived from the trees, understorey vegetation and arboreal wildlife. Soil nutrient availability is higher and saline conditions lower in the vicinity of the canopy (section 3.3.1). This favours ephemeral growth after periods of rain, which makes excellent pastures for both arboreal wildlife and domestic livestock.
10. Building materials	As a timber, the species is comparatively poor due to its twisting irregular growth. It is used however as a major building material by bedu, in fence construction around their homes, and in the making of animal pens and grain stores.
11. Flowers	When available these are used as supplementary fodder for livestock.
12. Fruit	Very nutritious livestock dietary supplement. These are collected from the tree by thrashing the canopy with sticks.
13. Scientific/ touristic value	As a habitat for a diverse range of desert wildlife, the woodlands of Oman are ideal for long term scientific research, with potential for controlled tourism in reasonably accessible areas.
14. Others	Includes the utilisation of seasoned wood for the handles of tools (pers. obs.); potential medicinal properties of both *P.cineraria* and the understorey vegetation (pers. obs.); exploitation of gum residues (Anderson & Farquhar, 1982).

6. large scale collections of fallen dead wood through excursions into the woodlands by people outside of the Sharqiya

7. tree felling (axed or pulled over using a tow rope attached to a vehicle) for fodder, fuelwood and timber

The influence of man on the condition of the Prosopis woodlands of the Sharqiya was also recorded. The greatest influence was found on the woodland margins in close proximity to towns or villages, where tree felling and over-lopping was common (slides 29 & 30). This has caused the encroachment of small sand dunes into the woodland interiors. Over-lopping was most common in the CPZ, although evidence of this practice was found throughout the Sharqiya woodlands, particularly in the vicinity of abandoned bedu settlements. Herds of up to 20 head of domestic goat and sheep were regularly observed in the three provenances, but large herds exceeding 50 animals were found to severely affect the understorey vegetation through grazing and trampling (slide 22). These herds required large quantities of fodder that had to be lopped from the trees. The number of roads and tracks in the EPZ and SWPZ were very high, which has led to the destruction of the understorey vegetation and the fragile soil structure. In the vicinity of the bedu settlements, large deposits of rubbish have encouraged feral animals into the woodlands which may compete with the arboreal wildlife for food and range, affect the gene pool of these species through hybridisation, and introduce new diseases into the habitat (Linn, 1988). Non-degradable rubbish was found to be very common in some of the larger more permanent bedu settlements in the woodlands.

The over-exploitation of the woodland resources has led to a decline in the condition and stability of this habitat (slides 29 & 30). In areas of heavy exploitation, woodland recovery can only be achieved through immediate

rigorous management practices. An increase in the number of bedu permanently settling in the woodlands; the increase in the populations of domestic animals; the divergence from traditional methods of utilising the woodland products; and the increase in the entrepreneurial utilisation of the resources by both resident and non-resident people in the woodlands has promoted the rate of deforestation in this region.

3.4 Conclusions and recommendations

The results presented in this chapter describe the structural and ecological uniqueness of the Prosopis woodlands in the Sharqiya, their importance in supporting wildlife and livestock in areas of low productivity and in providing resources to people resident in the region. As a consequence of the multi-purpose properties of P.cineraria, the woodlands are subjected to increasing over-exploitation that is destroying them at a rate where their recovery will eventually become impossible.

The Prosopis woodlands within the Sharqiya have been used to study the spatial distribution pattern of desert trees. The study of the predominantly monoculture woodlands in the Eastern Prosopis Zone (EPZ) has minimized the effect of inter-species interactions. The differences in tree density and basal area found between the point-centred quarter method (PCQM) and the wandering quarter method (WQM) may be partially explained by the differences in their sampling strategies. These included a greater number of sample points for each transect dataset, which were continuous across the woodland when using the WQM. In the north of the study area, the two methods produced similar results for tree density. However, towards the south of the study area where the clumping habit was found to increase, there was a departure in the results between the methods,

with the WQM estimating higher tree densities. As the WQM was designed for estimating tree density in non-random tree distributions (Catana, 1963), the results have shown that the WQM was sensitive to both a low clumping habit in the north of the study area and a high clumping habit in the south.

The formation of the Prosopis monocultures in the Sharqiya was attributed to the encroachment of sand in to the woodlands, in which this species was able to adapt to the changing environment by growing vegetatively above the accumulated sand to form tree clumps. Tree clumps in the Sharqiya were formed by either lateral vegetative growth, or through vertical vegetative growth of individual trees. Based on the data collected, it is proposed that the relic Prosopis woodlands of the Sharqiya that exist today are the surviving remnants of larger woodlands established over 12000 years ago during the last pluvial period. The vigorous vegetative growth of this species should be exploited in the regeneration of existing woodlands where water supplies and resources are minimal.

Studies have been carried out on the effects of P.cineraria on the quality and structure of its soil. A large variation in the chemical properties of the woodland soils was found. In a number of ways the results presented here are comparable to existing studies on this species carried out in Rajasthan, India (see Sharma, 1966; Singh & Lal, 1969; Shankar et al, 1976). The arboreal soils were found to be of high pH, with only a small number approaching neutrality. Trends of higher nutrient availability and lower salinity were found beneath the tree canopy compared to the adjacent surrounding plains. The nutrient-rich soils beneath the tree canopy should be selected for the propagation of P.cineraria, as the species-specific nutrient levels will enhance seedling growth (see Chapter 6).

For most of the woodland soils examined, soils to a depth of 1m were predominantly loose to compact sand to loamy sand, with very few stones and very low levels of organic matter. Soil horizons were rare and the physical properties of the surface soil were the most variable between the sites.

Plant species diversity in the Prosopis woodlands was found to be almost double that of the open plain, with 36 species forming the understorey habitat. This high species diversity was, in part, a result of ephemeral growth after heavy rainfall in February 1986 and March 1987. A total of seven vegetation communities were detected in the understorey habitat. This high species diversity was attributed to the micro-environment beneath the tree canopy consisting of: available nutrients and water; low salinity; small decrease in soil pH; and shade protection. In this way, the micro-environment has favoured the growth of vegetation that one would not normally expect to find growing in the arid conditions of the Sharqiya.

The results presented here have shown that the Prosopis woodlands support an abundance of fauna, to the extent that many of the species in the Sharqiya fauna collection of the Oman Wahiba Sands Project were found in the woodlands. The systematic lists can not be considered complete but should be used as a basis for future field research. Despite the differences in the arboreal fauna, the ecology of the Prosopis woodlands in the Sharqiya was essentially similar to studies of Prosopis woodlands growing in Arizona and Argentina (Mares, 1977). Several insect species have been identified as pests, to the extent that they may have a detrimental affect on the overall ecology of the woodland habitat. Attention should be given to the collection of pest-free seeds, and the identification of strains that are naturally resistant to infection for genetic conservation purposes.

The Prosopis woodland habitat in the Sharqiya encourages wildlife to thrive in conditions in which they would not normally be found. The woodlands represent corridors for the colonisation of the desert interior and allow species to extend their natural range. High fauna species diversity has been maintained by the provision of food, habitats and protection. The differences between the three woodland provenances in the Sharqiya with respect to fauna diversity may be a product of the non-systematic sampling between the woodlands. Higher species diversity in the EPZ than in the CPZ may be attributed to the greater length of time spent in the EPZ, which was also far more accessible. However, the EPZ and SWPZ are dense woodlands, often with large areas of continuous canopy. These would provide optimal conditions for the establishment and maintenance of a diverse range of species.

P.cineraria in the Sharqiya has been identified as a very important multi-purpose tree for the region, which is enhanced by the habitat in which it forms in areas of generally low natural resources. The most important resources provided by P.cineraria in the Sharqiya are the provision of fodder, fuelwood and shade protection. Over-exploitation of these resources through tree-felling and uncontrolled lopping practices has resulted in the degeneration of the woodlands. In some areas, the rate of exploitation will soon result in irreversible damage if no steps are taken for their conservation and management.

CHAPTER 4

MORPHOLOGICAL DESCRIPTION OF MATURE P.CINERARIA

4.1 Introduction

In comparison to populations of higher animals, plant populations show greater phenotypic variability. This complexity and diversity in the plant population is the combined result of developmental variation, environmentally induced variation and genetic variation (Jones & Luchsinger, 1987). In a fluctuating environment, survival is dependent upon the phenotypic and genotypic plasticity of the plant to respond to change (Solbrig et al., 1977). Phenotypic plasticity is the ability to express a genotype as different phenotypes according to external environmental conditions. A major cause of phenotypic plasticity is the persistent meristematic tissue during the life of the plant. As a result, the individual plant is susceptible throughout most of its life span to variation induced by environmental factors such as water, light, temperature, nutrients and soil. Under arid conditions, variation can be caused by water and temperature stress, wind and sand blast, fragile soil structure, bulk soil movement and the destructive influence of browsing animals. Briggs & Walters (1984) suggest that the extent of phenotypic plasticity differs between taxa; that different characters of the phenotype show different degrees of plasticity; and that phenotypic plasticity is under genetic control. Genotypic plasticity within a population will maximise survival through evolution and adaptation, as well as maintain the ability of the population to respond to genetic vulnerability to disease and infection.

Taxonomically, the new world Prosopis species are very difficult to separate as a result of extensive morphological variation and natural hybridisation between species (Graham, 1960; Burkart, 1976; Ffolliott & Thames, 1983a). As a consequence, many of these species have now been re-classified into a number of sub-species. A number

of polymorphic isoenzyme systems have been used to determine the genetic relationship between different new world Prosopis species and their natural hybrids (Solbrig & Bawa, 1975; Naranjo et al., 1984; Saidman, 1986). However, there is an absence of literature on the relationship between phenotypic and genotypic variation within these species. This is also true for P.cineraria, except that tree height has been used to measure the phenotypic variability of different populations grown from seeds of known genetic origin (Solanki et al., 1984).

The quantification of morphological variation in a woodland population requires a representative sample of trees on which a number of suitable measurements are taken for statistical analyses (Solbrig et al., 1977). The identification of morphological variability in a species is commonly used in forestry for the selection of superior trees for their utilisation. This method can also be used to classify trees within a natural population into morphological groups. The distribution of these morphological groups and the genetic relationship within and between groups can be used in the identification of specific ecotypes (groups of plants of the same species which are genetically adapted to a particular habitat). Statistical approaches in the analysis of tree morphology have been performed on a number of new world Prosopis woodlands. Multivariate techniques were effectively used in the identification of morphologically unique groups, or morphotypes of P.chilensis using a broad range of tree variables sampled from several woodlands in Chile (Contreras, 1985). Similarly, P.tamarugo in the Chilean Tamarugal Pampa was characterised into biotypes based on easily measured variables for the identification of trees best suited for fodder production (Briner, 1985).

The relationship between a number of morphological characteristics will often be highly correlated because they are inherited as character complexes (Solbrig et al.,

1977). This has been exploited in forestry management, where practical information can be derived from efficient field sampling techniques. Whisenant & Burzlaff (1978) used this methodology to predict the fresh weight of highly variable individual trees from a simple regression equation with the easily measured variable stem area 60cm above the ground. In P.cineraria, regression equations have also been used to estimate fresh weight (Kaul & Jain, 1967), and biomass production in terms of pod and seed yield (Kaul et al., 1964; Muthana, 1985) using simple field measurements such as diameter of bole at breast height, and length of clear bole (from the ground to the primary branches).

Burkart (1976) described P.cineraria by the following characteristics:

Trees to 6.5m
Cortex cinereous
Prickles internodal, scattered, straight, somewhat acroscopic, conical with broad bases
Leaves 1-3 jugate, glabrous or puberulous
Petiole and rachis 0.5-4.0cm long, the pinnae 2-7cm long
Leaflets 7-14 jugate, ovate, straight to subfalcate, without nerves (or 2-4 nerved at base, the midrib excentric) mucronate, 4-15mm long x 2.0-4.5mm broad, greyish when dry
Stipules foliaceous, deciduous
Racemes spiciform, 5-13cm long, several together, subpaniculate
Peduncle with amplexicual bract (or two bracts united), this caducous and leaving an oblique scar 1.5-2.0mm long
Bractlets ovate, sessile, 0.5-0.8mm long, caducous
Pedicels 0.5-1.5mm long when mature
Flowers yellow, glabrous
Calyx truncate, 0.8-1.2mm long
Corolla 3.5mm long glabrous, the petals rolled back in age
Anthers 0.8-1.0mm long
Pistil glabrous
Fruit slender, elongate 8-19cm long (including the stipe 0.8-2.0cm), subcylindric-torulose, 4-7mm in diameter, glabrous
Pericarp thin, brittle
Endocarp segments thin, longitudinal, little developed
Seeds distant, longitudinal ovate, 6mm long, the tegument with open horse-shoe fissural line on faces

The gross morphology of P.cineraria in Northern Oman is diverse, ranging from large trees to stunted bushes (pers. obs.). This species is a typical phreatophyte, with tap roots exceeding 30m in length to reach the permanent water table (Khan, 1955). As a phreatophyte, P.cineraria is capable of surviving over three years of continuous drought in Oman, during which the trees retain a dense healthy canopy and are able to flower and produce fruit (pers. obs.). P.cineraria flowers within four years from germination and reaches maturity at about 20 years of age (Leakey & Last, 1980).

In this chapter, a morphological description of mature P.cineraria in the Sharqiya has been made, with the objective of providing information on the phenotypic plasticity of this species in Oman. The results were also used to contribute towards the identification of suitable trees for their utilisation for fuelwood, forage, timber, and environmental protection. A preliminary assessment of morphological variation was first carried out in the field by classifying the trees into distinct morphotypes. These morphotypes were described and the most abundant were assayed for genetic differences by examining the distribution of non-specific esterase isoenzymes extracted from their seeds. This was followed by the mensuration of trees throughout the EPZ and CPZ (inter-provenance population), and of trees from five transects (T1-T5) from the EPZ (intra-provenance population) described in Chapter 3. A statistical morphometric analysis was performed on all the trees to determine the relationships between the measured variables. A statistical classification of tree morphology using multivariate techniques was then performed separately on the inter- and intra-provenance populations. The objectives of this classification were to quantify the morphotypic variation in the Sharqiya trees, and to determine the distribution and exploitation potential of the morphotypes identified.

Relationships between tree morphology and both pod morphology and seed infestation were then examined, to determine if there were any morphological influences on seed regeneration. This study was aimed at identifying distinct morphological characteristics in seed-bearing trees for the future collection of high quality seeds. The geographical variation in seed infestation between the EPZ and CPZ provenances was also examined.

4.2 Materials and methods

4.2.1 Tree mensuration

A total of 15 characteristics were recorded from 321 trees in the Sharqiya, consisting of seven continuous variables and eight categorical variables (table 4.1). A 3m pole was placed vertically next to the tree. At a paced distance of 15m from the bole, the pole was used as a visual reference for estimating tree height to the nearest half metre. This method was first standardised using trees of known height which were calculated trigometrically using a clinometer and measuring tape. The maximum distance between the canopy fringes (canopy diameter) was determined using a measuring tape laid out on the ground passing alongside the tree bole. Tree girth at 1m from the ground was measured with a tape meter to the nearest centimetre. In trees with branches below 1m, the mean of the girths was calculated. Branching height was defined as the height from the ground to the primary branches, which was measured with a tape. Root habit height and spread were measured directly with a tape to the nearest metre. Canopy shade cover was used as an assessment of the foliage density, and determined as the maximum shade cover expected beneath the canopy as a percentage of the area of the tree shadow. The condition of the foliage was qualitatively assessed, taking into account the vigour and colour of the leaves.

Table 4.1

Tree mensuration variables. Variables allocated with upper-case labels were statistically analysed.

A. Continuous variables

1. Tree height (m); HEIGHT
2. Maximum crown diameter (m); CANDIAM
3. Girth at breast height (cm); GIRTH
4. Branching height (m); BRANCH.HT
5. Canopy shade cover (%); SHADE
6. Root habit height (m)
7. Root habit spread (m)

B. Categorical variables

1. Canopy shape
   CANSHAPE
   1. sphere
   2. dome
   3. spindle
   4. irregular

2. Stem habit
   STEMTYPE
   1. erect
   2. leaning
   3. twining

3. Branching form
   BRANTYPE
   1. divergent
   2. non-divergent

4. Foliage condition
   FOLIAGE
   1. poor
   2. moderate
   3. excellent

5. Tree habit
   HABIT
   1. stem solitary
   2. clumped
   3. unknown

6. Surface root habit
   0. none
   1. lateral
   2. enlarged base

7. Root suckers
   0. no
   1. yes

8. Presence of fruit
   0. no
   1. yes

4.3 Results and discussion

4.3.1 Field classification of tree morphology

1. General description and distribution of tree morphotypes

A total of 13 different morphotypes of P.cineraria were identified in the Sharqiya which are described in table 4.2. The relative abundance of these morphotypes is presented in table 4.3. Type 1, 3 and 8 trees were found in all three provenances and were the most abundant of the morphotypes. Type 1 trees (slides 31 & 32) formed woodlands where the canopy was open, whilst type 3 trees (slide 33) formed dense woodlands where the canopy was usually continuous. Type 8 trees (slide 34) were easily identified by the multiple primary branching at ground level to 1m and were mostly found in exposed areas and shifting dune fields. In some of these trees, up to 13 primary branches were observed (slide 35), but trees with 2-3 primary branches were the most common. Type 5 trees were differentiated by having at least three similar sized branches from the primary axis at 2m or more above the ground. Very tall trees were rare in the Sharqiya, but in the remoter parts of the EPZ and SWPZ, trees up to 12m (type 6) and over 20m (type 7) were found. With the remaining morphotypes, there was an increasing departure from the common morphological forms and a decrease in their size (slide 36). The smallest morphotype was a low lying heavily thorned shrub (type 13) found on the woodland margins, or scattered on sandy dune fields.

2. Statistical comparisons

Frequency tables with chi-square and one-way ANOVAs were performed on the variables collected from 297 trees between the dominant tree types 1, 3 and 8 (table 4.4). In the former method, the attribute frequencies greater than 20% in each category, and in the latter the mean values for

Table 4.2

Description and distribution of P.cineraria morphotypes in the Sharqiya. Where + = present in provenance; - = absent from provenance.

TREE TYPE	LOCATION EPZ	CPZ	SWPZ	DESCRIPTION
1	+	+	+	Straight trunk, divides into 2, main branches, thereafter highly branched. Canopy spherical or dome shaped. Usually the largest type of tree.
2	+	+	+	Straight trunk, does not divide into 2 main branches, but the trunk continues up into the canopy with small stems branching out. Canopy spherical, or dome shaped.
3	+	+	+	S-shaped trunk, often twisted, does not divide into 2 main branches. Canopy spherical or dome shaped. Dead stems usually found down the length of the trunk.
4	+	+	-	Straight trunk, with dead stems down trunk to ground level.
5	-	+	+	Straight trunk, dividing into many (3 or more), similar branches from the same axis.
6	+	-	-	Straight trunk, upto 12m, dividing into 2 main branches within canopy. Canopy distinctly cigar-shaped.
7	+	-	-	Very tall tree with straight trunk, some reaching heights over 20m. Branches into 2 main stems within the canopy. Canopy spherical.
8	+	+	+	Multi-stemmed (2 or more), stems dividing from ground level to a height of 1 metre, often exceeding 10 in number. Canopy either separate for each stem, or merges.
9	+	+	+	Bush like, single-stemmed, highly branched, with canopy down to ground level. Reaches 2-6m in height.
10	+	+	+	As in type 9, but multi-stemmed.
11	+	+	+	Small single tree in the centre of very thorny low lying shrubby suckers. Tree is protected from browsing animals.
12	+	+	+	Low bush (1-2m), single-stemmed, highly branched and heavily thorned. Canopy relatively sparse.
13	+	-	+	Ground hugging shrub, very heavily branched. A distinct thorny surface layer that protects the underlying healthy green leaves from browsing animals. Maximum heights of 0.5m.

Table 4.3

Relative abundance of P.cineraria morphotypes identified in the field. Tree types 2, 4, 6, 7, 10 and 13 were not sampled because of their low frequency in the Sharqiya.

	Field morphotype	Number	Frequency (%)
	TYPE 1	176	54.83
	TYPE 3	69	21.49
	TYPE 8	52	16.20
	TYPE 9	11	3.43
	TYPE 5	7	2.18
	TYPE 12	4	1.25
	TYPE 11	2	0.62
TOTAL	7	321	100.00

Table 4.4

Description of the commonest morphotypes (types 1, 3 & 8) by variables (n=297 trees).

A. Dominant attribute frequencies in descending order and their significance using chi-square. Where / = variables which are equal in frequency.

		Type 1	Type 3	Type 8
CANSHAPE	***	spherical, dome	spherical, dome	spherical/irreg.
STEMTYPE	***	erect, lean	twine	erect/lean, twine
BRANTYPE	***	diverge	diverge, non-diverge	diverge
FOLIAGE	**	moderate, good/poor	moderate, poor	moderate, poor
HABIT	NS	solitary, clump	solitary/clump	clumped, solitary

B. Significance results of one-way ANOVAs of continuous variables by categorical variables for each morphotype with group means

		Type 1	Type 3	Type 8
HEIGHT (m)	***	6.30	5.28	6.32
GIRTH (cm)	***	89.19	65.22	72.48
CANDIAM (m)	***	4.86	3.29	5.24
BRANCH.HT (m)	***	2.29	1.91	0.45
SHADE (%)	NS	54.90	48.99	49.65

the continuous variables were used to describe the dominant characteristics for each of these morphotypes. The significance between these mean values was determined using Tukey's multiple range test (section 2.13). These three morphotypes were highly significantly different in all variables except tree habit and canopy shade. Type 1 trees were primarily solitary in habit and had mostly spherical canopies, erect stems and generally the healthiest foliage condition of the three morphotypes. This tree type had significantly larger girths than types 3 and 8, but its height and canopy diameter were not significantly different to type 8. The major difference between types 1 and 8 was the significantly lower ramification in the latter. Type 8 trees had mainly either spherical or irregular shaped canopies and, in contrast to the other tree types, they were found more in clumps than as solitary trees. Type 3 trees were significantly smaller in height and canopy diameter than both types 1 and 8 and had predominately twining stems and the greatest abundance of non-divergent branching. These trees also had similar girths to type 8 trees, and their habit was either solitary or in clumps.

3. Genetic variation

The non-specific esterase isoenzymes of seeds sampled from the dominant tree morphotypes in the EPZ and CPZ were separated using polyacrylamide gel electrophoresis (section 2.4). The variation in the distribution of the isoenzyme bands between seed samples was used as a general indicator of genetic variation between the parent trees. The typical distribution of the isoenzyme bands for seeds collected from individual trees of type 1, 3 and 8 morphology are illustrated in figure 4.1. The isoenzymes were clearly divided into five main bands (bands 1-5), from which only band 1 was further resolved into five distinct sub-bands. Using all seed samples examined, band and sub-band frequencies were calculated for each provenance and for each tree type within each provenance (table 4.5). Band 2

Figure 4.1

Examples of seed non-specific esterase isoenzyme band patterns sampled from Prosopis tree of types 1, 3 and 8 morphology.

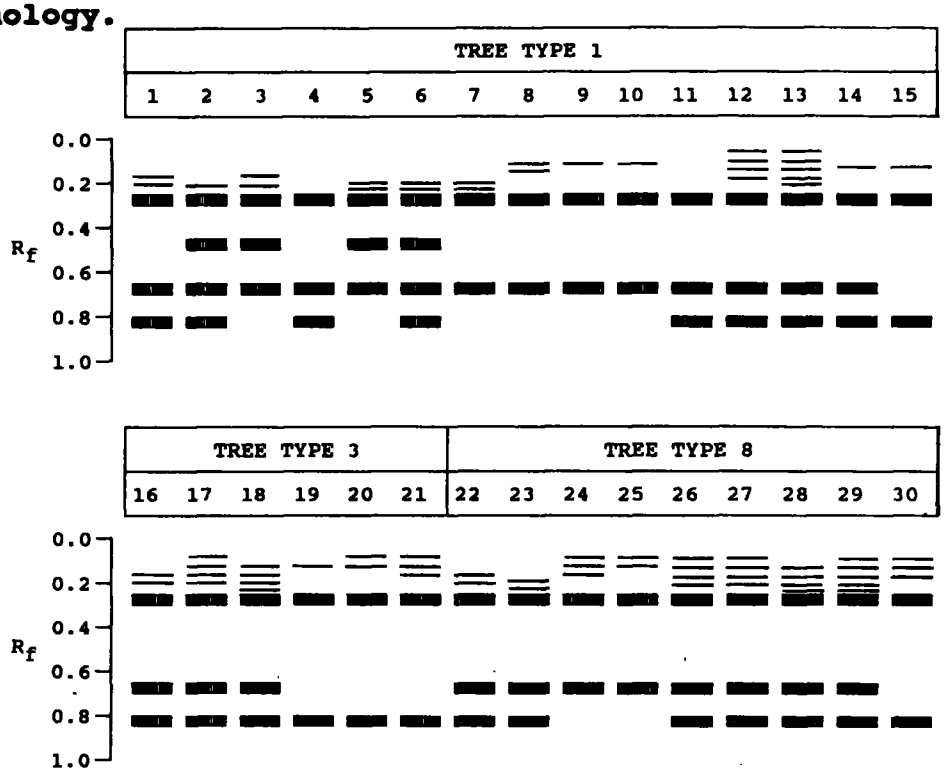
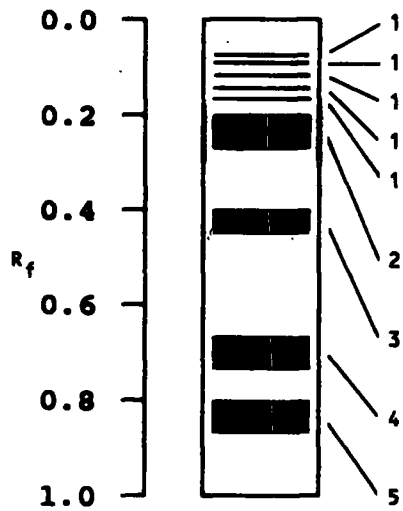


Table 4.5

Frequency of non-specific esterase isoenzyme bands of seeds between provenances and between parent tree types, determined from 36 seedlot accessions. Where 1.0 = isoenzyme band present in all samples; 0.0 = isoenzyme band absent in all samples.



BAND	EPZ PROVENANCE			CPZ PROVENANCE			
	TYPE 1 (n=14)	TYPE 8 (n=6)	TOTAL (n=20)	TYPE 1 (n=4)	TYPE 8 (n=6)	TYPE 3 (n=6)	TOTAL (n=16)
1.1	0.0	0.50	0.15	0.50	0.83	0.50	0.53
1.2	0.36	0.33	0.35	0.50	1.0	0.83	0.79
1.3	0.21	0.50	0.30	1.0	1.0	0.67	0.84
1.4	0.43	0.50	0.45	0.50	0.67	0.50	0.59
1.5	0.21	0.17	0.20	0.25	0.33	0.17	0.26
2	1.0	1.0	1.0	1.0	1.0	1.0	1.0
3	0.29	0.0	0.20	0.0	0.0	0.0	0.0
4	0.86	1.0	0.90	0.75	0.67	0.50	0.58
5	0.36	0.50	0.35	1.0	1.0	1.0	0.95

was found in all samples and was consistently the most heavily stained in the gels. Band 3 was unique, as it only occurred in some of the seed samples collected from type 1 trees in the EPZ. The major differences in the distribution of the esterases between the provenances were that band 4 frequency was high in the EPZ but low in the CPZ, and that sub-bands 1.1, 1.2 and 1.3 and band 5 frequencies were high in the CPZ but low in the EPZ. In tree types 1 and 8 in the EPZ, band 4 frequency was high, whereas bands 1 and 5 were low. As the precise locations of the seed samples within the provenance were known (section 2.1), it was also determined that band 5 demonstrated the most intra-provenance variation, by increasing in frequency in a southerly direction. In contrast, seeds sampled from both tree types in the CPZ had higher frequencies of bands 1 and 5, but lower frequencies of band 4. Band 4 was also more frequent in the south of this provenance. The distribution of esterase bands in type 3 trees in the CPZ was similar to both types 1 and 8, but the frequencies of band 4 and the sub-bands of band 1 were generally lower.

The greater genetic variation between the provenances than between the parent tree morphotypes may be attributed to their biologically isolated distribution. For genetic conservation of this species in the Sharqiya, supplementary provenance collections of seeds within each provenance should be made. The low genetic variation between types 1 and 8 within each provenance suggests that the departure in gross morphology between the morphotypes was the product of phenotypic plasticity rather than genotypic variation. Factors that influence phenotypic plasticity can be divided into those that are active and those that are passive. Active factors are those that cause the plant to respond to change, such as the damage of the apical tissue during early growth through wind and sand blast, or through browsing animals, which enhance multi-stemmed growth typical of type 8 trees. In contrast, passive factors are those that do not directly affect a response in the plant,

such as the transformation of type 1 morphology into type 8 morphology through the accumulation of sand to just below the primary branches. Active factors such as browsing animals exploiting the lowered canopy will then stimulate vertical vegetative growth, according to the hypothesis proposed in Chapter 3. If the rate of sand accumulation is greater than the vertical growth, the tree will gradually be buried in sand. Under these conditions, tree morphotypes 9 through to 13, which decrease in size from a bushy tree to a ground-hugging shrub, can be considered the interim stages before the tree is completely submerged in sand.

4.3.2 Morphometric analysis of P.cineraria

1. Analysis of results

This section presents the results of a statistical morphometric analysis of 10 of the 15 variables recorded from 321 mature trees in the Sharqiya (section 4.2.1). The variables involving the roots (height, spread, habit and suckers) and the presence of fruit were not included in this analysis because of both their low frequencies and their outlying influence on tree morphology. A statistical summary of the data is presented in Appendix D. The data for tree height, canopy diameter and canopy shade approached a normal distribution, whilst the data for girth and branch height were marginally skewed to the left. As the logarithmic transformation of girth and branch height to normalise their distribution did not affect the significance of the results, these variables were left untransformed in this study. The majority of the attribute frequencies exceeded 20% in most categorical variables, with the exception of spindle (7.1%) and irregular (18.0%) canopies and non-divergent branching (10.9%).

2. Continuous variables

A probability half-matrix determined by Pearson's correlation coefficient on the continuous variables is shown in table 4.6. There were high positive correlations between most of the continuous variables at $p \leq 0.01$. This was expected since tree height, canopy diameter and girth were measurements of the overall size of the tree. Only branching height was not significantly related to both canopy diameter or canopy shade.

3. Categorical variables

Frequency tables using chi-square have shown that there were significant associations between most of the categorical variables (table 4.7). The dominant attribute frequencies responsible for the significant associations show that the best foliage condition and level of shade were found in spherical and dome canopied trees. Pointed and irregular canopies contained foliage of poor to moderate condition, which offered less shade protection. In spherical and dome canopied trees, all stem types were found but were dominated by erect stems. In contrast, spindle and irregular canopy trees had mostly twining stems. The best foliage condition was found in erect stems and rarely in twining stems. Erect stems were mostly from solitary trees, in contrast to leaning and twisted trees that were associated in clumps. The foliage condition was generally higher in solitary trees than in those forming clumps.

4. Comparisons between continuous and categorical variables

The significance results of one-way ANOVAs of the continuous variables by the categorical variables are summarised in table 4.8. Significant variations from the means were examined using Tukey's multiple range test. The significant difference between tree height and canopy shape

Table 4.6

Significance half-matrix determined by Pearson's correlation coefficient using all trees in the population (n=321). All significant correlations are positively correlated.

	HEIGHT	CANDIAM	GIRTH	BRANCH.HT
HEIGHT				
CANDIAM	***			
GIRTH	***	***		
BRANCH.HT	**	NS	***	
SHADE	***	***	**	NS

Table 4.7

Significant associations between categorical variables using frequency tables with chi-square on all trees in the population (n=321).

	CANSHAPE	STEMTYPE	BRANTYPE	FOLIAGE
CANSHAPE				
STEMTYPE	**			
BRANTYPE	NS	*		
FOLIAGE	**	*	**	
HABIT	NS	*	NS	**

Table 4.8

Significance results of one-way ANOVAs of continuous variables by categorical variables using all trees in the population (n=321).

	HEIGHT	CANDIAM	GIRTH	BRANCH.HT	SHADE
CANSHAPE	**	***	***	***	***
STEMTYPE	**	***	***	NS	NS
BRANTYPE	NS	NS	*	***	NS
FOLIAGE	*	***	NS	*	***
HABIT	NS	NS	**	NS	NS

was a result of spindle canopied trees being significantly shorter than all other trees. Trees with erect stems were significantly taller than those with twining stems. The trees with moderate foliage condition were significantly taller than those with poor foliage condition. There was no significant relationship of tree height between both branching type and tree habit.

There was a highly significant relationship between the canopy diameter and its shape, where the diameter of dome canopies were significantly larger than all other canopy shapes. There was no significant difference between the diameters of spherical and irregular canopies. Canopy diameters of trees with erect stems were significantly larger than diameters of trees with twining stems. Trees with both moderate and good foliage condition had significantly larger diameters than trees with poor foliage condition. As with tree height, there were no significant differences in the canopy diameter between either branching form or tree habit.

Girth was highly significantly different between canopy shapes, where dome canopy trees had the largest girths. However, there was no significant difference between girths of spherical and irregular canopy trees. Erect stemmed trees had significantly larger girths than trees with leaning or twining stems, of which the girths of the latter stem types did not significantly differ. Girths were significantly larger in solitary trees and also when the branching was non-divergent.

Branching height was significantly different between canopy shapes, caused by the higher ramification in spherical canopied trees than irregular canopied trees. Branching was significantly higher in trees that had poor foliage condition than in trees with moderate foliage condition. The common divergent form of branching was significantly lower in height than non-divergent branching.

The significant difference of canopy shade between the canopy shapes was caused by the higher shade of spherical and dome canopied trees compared to spindle and irregular canopied trees. As expected, the degree of shade was significantly higher in canopies of good foliage condition. Canopy shade was not related to stem type, branch type or tree habit.

The integration of the continuous variables with the categorical variables have contributed towards the separation of the trees into two morphologically distinct groups. The first group consisted of solitary trees which were generally tall, with correspondingly large girths and canopy diameters. Their canopies were either spherical or dome shaped, and they had erect stems which divergently branched high up the stems. The foliage condition was generally very good, and the canopy shade was generally high. The trees in the second group were more heterogenous in their morphology, and were smaller in size, with irregular or spindle shaped canopies. The canopy shade was low and the foliage was poor in condition. Their stems were either twining or leaning, and primary branching was low to the ground. As these trees were more associated in clumps, their morphology may be a product of vertical vegetative growth of submerged solitary trees described in Chapter 3. The stems within the clumps have either been forced over by the bulk movement of the sand, or are the divergent branches of the partially submerged canopy.

4.3.3 Inter-provenance classification of tree morphology

1. Analysis of results

As different sampling strategies were used in the inter-provenance (EPZ, CPZ and SWPZ) and intra-provenance (transects T1-T5) populations, these datasets were treated separately in further analyses. In this section, results

are presented on the classification of the trees in the EPZ and CPZ populations (n=93 trees) into morphologically similar groups. The SWPZ population of five trees was excluded in this inter-provenance analysis because of the low number of trees sampled.

The variation in tree morphology between the EPZ and CPZ provenances was first examined using frequency tables with chi-square and t-tests. Discriminant function analysis was then used to determine whether it was possible to significantly discriminate between trees from the EPZ and CPZ using the continuous variables and four dichotomously re-classified categorical variables (table 4.9). Tree habit was not used in this analysis as it was not a direct measure of tree morphology.

The classification of individual trees into morphologically similar groups was performed using two multivariate methods. The highly significant correlation between the continuous variables measuring the overall size of the trees (see table 4.6) made it difficult to classify tree morphology effectively. This was resolved using the method of Arriaga et al. (1988), where principal components analysis was performed on the most highly correlated variables (tree height, canopy diameter and girth) to produce uncorrelated linear combinations of the variables that describe the dominant morphological characteristics of the trees. These morphological indices were used with the variables branching height and canopy shade in a cluster analysis. This clustering method divided the trees into a selected number of groups by maximising the variation between the groups, relative to the variation within the groups. As the variables were different in scale (principal component scores, distance in metres and % respectively), these were standardised, so that each variable had a mean of zero and a standard deviation of one (Manly, 1986). The geographical distribution of the cluster groups was then determined by mapping the individual trees.

Table 4.9

Dichotomous re-classification of categorical variables for use in discriminant function analysis.

	Dichotomous variables	
	1	2
CANSHAPE	spherical & dome	pointed & irregular
FOLIAGE	poor	moderate & good
STEMTYPE	erect & twining	leaning
BRANTYPE	non-divergent	divergent

Table 4.10

Variation in the morphology of 93 trees between the EPZ (n=58) and CPZ (n=35) populations.

A. Dominant attribute frequencies and their significance using chi-square.

	CANSHAPE	STEMTYPE	FOLIAGE
LOCATION	***	***	***
EPZ	spherical	erect/lean	moderate, poor
CPZ	irreg., dome/spherical	twine, erect/lean	moderate

	BRANTYPE	HABIT
EPZ	diverge	clumped
CPZ	non-diverge	clumped

B. Significance results of one-way ANOVAs of continuous variables by provenance, with provenance means.

	HEIGHT (m)	CANDIAM (m)	GIRTH (cm)	BRANCH.HT (m)	SHADE (%)
LOCATION	NS	NS	NS	**	NS
EPZ	7.15	6.33	87.02	2.14	50.43
CPZ	7.10	5.71	87.81	1.33	57.00

2. Variation in tree morphology between provenances

The variation in tree morphology between the EPZ and CPZ are presented in table 4.10. These results show that the EPZ-trees had mainly spherical canopies, erect and leaning stems, moderate to poor conditioned foliage and divergent primary-branching high above the ground. In contrast, CPZ-tree had predominantly irregular canopies, twining stems, moderate foliage and non-divergent primary-branching closer to the ground. The trees in both provenances were predominantly from a clumped habit, and there were no significant differences in the tree height, canopy diameter, girth and canopy shade between the provenances.

This variation in tree morphology accounted for the significant discrimination ($p<0.001$) between the EPZ and CPZ determined by discriminant function analysis, such that 76.3% of the trees were classified into the correct provenances. The analysis required only three variables, canopy shape, stem type and branch type, which accounted for most of the morphological variation between the provenances.

3. Morphological classification of provenance trees

Principal components analysis performed on the inter-provenance data produced three principal components (table 4.11a). The first principal component (F1) accounted for most of the variation in the data, and was dominated by all three variables. This component was used as an index of tree size, where trees that had positive F1 scores were large in size, whilst trees with negative F1 scores were small in size. The second and third principal components (F2 and F3) accounted for 22.1% of the variation in the data. F2 was dominated by the tree height and canopy diameter in contrast to its girth, and was used as an index of girth dominance. Trees that had positive scores for F2

Table 4.11

Morphological classification of inter-provenance (EPZ & CPZ) trees (n=93).

A. Score coefficients for the first 3 principal components determined by principal components analysis.

	PRINCIPAL COMPONENT		
	F1	F2	F3
% OF VARIANCE	77.9	15.3	6.8
HEIGHT	0.391	0.550	-1.579
CANDIAM	0.390	0.568	1.566
GIRTH	0.351	-1.244	0.017
INDEX	Tree size	Girth dominance	Canopy dominance

B. Summary statistics of cluster analysis (5 clusters).

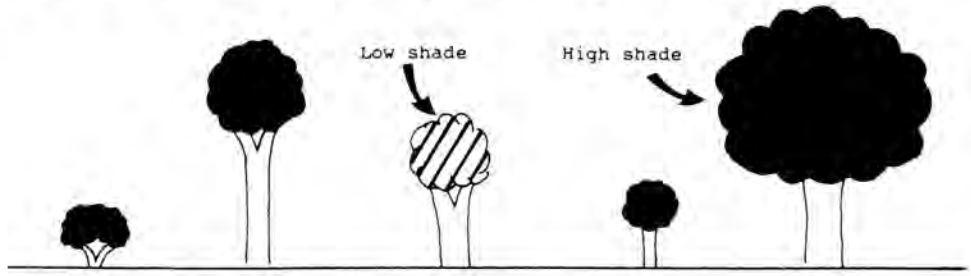
VARIABLE	BETWEEN GROUPS	DF	WITHIN GROUPS	DF	F-RATIO	SIGNIFICANCE
TREE SIZE (F1)	30.758	4	33.242	60	13.879	***
GIRTH DOMINANCE (F2)	24.222	4	39.778	60	9.134	***
CANOPY DOMINANCE (F3)	11.630	4	52.370	60	3.331	*
BRANCH.HT (m)	59.625	4	32.375	88	40.517	***
SHADE (%)	58.447	4	33.553	88	38.323	***

C. Morphological description of trees within each cluster group using the group means of the standardised variable.

	CLUSTER GROUP				
	A1	A2	A3	A4	A5
N	28	9	35	18	3
TREE SIZE (F1)	-0.27	1.42	0.19	-0.46	3.07
GIRTH DOMINANCE (F2)	0.64	-0.93	-0.55	-0.02	-1.46
CANOPY DOMINANCE (F3)	-0.33	-0.11	0.13	-0.32	1.17
BRANCH.HT (m)	0.36	2.34	2.21	2.95	3.10
SHADE (%)	58.39	63.33	34.57	72.78	65.00

Figure 4.2

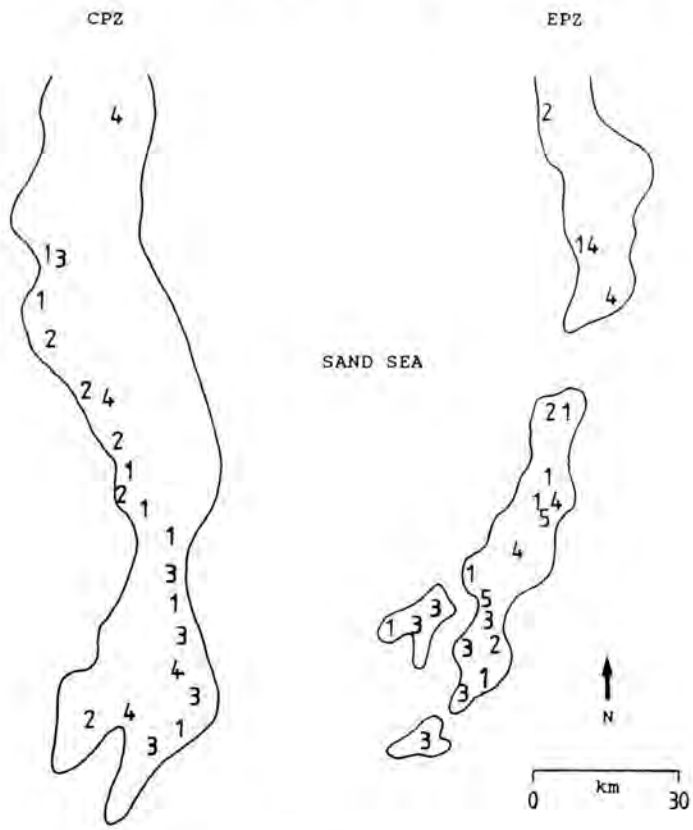
Summary description of <u>Prosopis</u> tree morphotypes determined by inter-provenance cluster analysis, with continuous variables illustrated schematically and categorical variables with attribute frequencies greater than 20%.



	A1	A2	A3	A4	A5
CANSHAPE	irregular	sphere	sphere/dome	sphere	sphere
STEMTYPE	twine	erect	erect/lean	erect/lean	erect/lean
BRANTYPE	diverge/ non-diverge	diverge	diverge	diverge	diverge
FOLIAGE	moderate	ALL	poor/moderate	moderate	moderate
DIST	clump	solitary	clump/solitary	clump	clump/solitary

Figure 4.3

Geographical distribution of inter-provenance cluster groups (A1-A5) in the Sharqiya. Map scale for latitude axis only.



had small girths in relation to the size of the tree, whilst trees with negative scores had dominant girths. F3 was dominated by the canopy diameter in direct contrast to tree height and was used as an index of canopy dominance for the tree. Trees that had positive scores for F3 had dominant canopies, whilst trees with negative scores had small canopies in relation to their height.

Five cluster groups (A1-A5) were produced from the inter-provenance population by cluster analysis (table 4.11b). All five variables significantly contributed to the separation of the trees into the cluster groups. A morphological description of the trees in these groups are presented in table 4.11c, which are schematically summarised in figure 4.2.

A1-trees were small in size, with both low girth and canopy dominance. They had mostly twining stems, but had the largest number of non-divergent stems of any other group. They were multi-stemmed, almost at ground level and had irregular and, to a lesser extent, spherical and dome canopies. The canopy shade was moderate to high and the leaves were generally moderate in condition. A4-trees were similar in size and canopy dominance to A1-trees, but were separated by having marginally more dominant girths, higher branches in both erect and leaning stems and only spherical canopies. However, they were both mainly associated in clumps and their foliage abundance and condition were comparable. A2-trees were large in size with dominant girths and a small canopy. They were solitary trees and their stems were erect with high branches. Their canopies provided high shade cover, but the leaves were variable in their condition. A3-trees were the most abundant in the inter-provenance population, which were intermediate in both size and canopy dominance and had dominating girths. The trees were associated more in clumps and their stems were either erect or leaning with high branches. The canopy was either spherical or dome shaped and was sparse in

foliage and generally poor to moderate in condition. Three trees of A5 morphology were selected out on the basis of their very large size, dominant girths and very dominant canopies. They had either erect or leaning stems with spherical canopies of dense foliage of moderate condition.

4. Geographical distribution of cluster groups in the provenances

Individual trees from each of the cluster groups in the inter-provenance population were identified and their approximate distribution within the EPZ and CPZ were mapped (figure 4.3). Each point on this map represents areas of trees with the same cluster morphology, which clearly shows that A3-trees were distributed towards the south of both provenances. Trees of A1, A2 and A4 morphology occurred throughout the study area and formed the basic morphological structure of the woodlands. The three A5-trees were specific to the EPZ.

4.3.4 Intra-provenance classification of tree morphology

1. Analysis of results

In this section, results are presented on the classification of the trees sampled from the transects in the EPZ (n=223 trees). Following the methods described above (section 4.3.3), statistical tests and discriminant function analysis were used to describe the morphological variation between the transects, and both principal components analysis and cluster analysis were used to classify individual trees into morphologically similar groups. The geographical distribution of the cluster groups in the transects was also determined.

2. Variation in tree morphology between transects

The morphological variation between the transects are presented in table 4.12. These results show that all transect trees had predominantly spherical or dome canopies, but in transects T1 and T5, which were the north and south limits of the study area, there were also high frequencies of trees with irregular canopies. Trees with erect stems were more common in the northern transects, whilst trees with leaning stems were more common in the southern transects. There was a general improvement of the foliage condition with increasing distance southwards, and an increase in the clumping habit in the same direction which supports the results presented in Chapter 3. Non-divergent branching was not common in this population of trees. There were no significant differences in the canopy diameter or branching height between the transects, but there were significant decreases in both the tree height and girth and significant increases in the canopy shade with increasing distance southwards.

All variables except branch height were required to significantly discriminate between most of the transects (table 4.13) using discriminant function analysis. There were significant discriminations between all combinations of transects except transects T3 and T4, resulting in 43.1% of the trees being correctly classified. The value of the F-statistic was lowest between transects T3 and T4, but increased with increasing distance between pairs of transects. The first two discriminant functions accounted for most of the variation in the data (75.6%), in which the variables tree height, canopy diameter, girth, canopy shade and foliage condition had the greatest effects. This analysis shows that the greater the distance between transects, the greater the difference in the magnitude of these particular variables. Hence, the significant differences between the transects were based on significant changes in the morphology of the trees down the study area.

Table 4.12

Variation in the morphology of 223 trees between transects (T1 n=79; T2 n=48; T3 n=40; T4 n=32; T5 n=24).

A. Dominant attribute frequencies and their significance using chi-square.

LOCATION	CANSHAPE ***	STEMTYPE ***	FOLIAGE ***
T1	spherical, dome/irreg.	erect, twine	poor, moderate, good
T2	spherical, dome	twine, erect	moderate, poor
T3	spherical, dome	erect, lean	good, moderate
T4	spherical, dome	erect, lean/twine	poor, moderate
T5	spherical, dome/irreg.	lean/twine/erect	good, moderate

LOCATION	BRANTYPE ***	HABIT ***
T1	diverge	solitary
T2	diverge	solitary
T3	diverge	solitary, clumped
T4	diverge	solitary/clumped
T5	diverge	clumped, solitary

B. Significance results of one-way ANOVAs of continuous variables by transects, with transect means.

	HEIGHT (m)	CANDIAM (m)	GIRTH (cm)	BRANCH.HT (m)	SHADE (%)
LOCATION	***	NS	***	NS	***
T1	5.79	3.81	85.89	1.94	47.59
T2	5.53	3.49	68.79	1.89	46.67
T3	5.34	4.06	75.23	1.83	60.73
T4	4.70	3.53	67.72	1.46	42.97
T5	4.51	3.50	61.33	1.73	63.54

Table 4.13

Intra-provenance discriminant function analysis results (n=223).

A. F statistics and significance levels between pairs of transects after using 8 discriminating variables.

	T1	T2	T3	T4
T2	3.471 ***			
T3	4.149 ***	2.983 **		
T4	4.568 ***	3.659 ***	1.927 NS	
T5	7.546 ***	5.546 ***	2.078 *	3.887 ***

B. Discriminant function coefficients. Where * = variables with greatest effect on the function.

	DISCRIMINANT FUNCTION			
	1	2	3	4
% VARIANCE	55.9	19.7	18.9	5.5
HEIGHT	-0.875*	1.074*	-0.262	0.475
CANDIAM	0.927*	-0.379	-0.791	0.095
GIRTH	-0.628*	-0.827*	1.097	-0.154
SHADE	0.392	-0.945*	0.877	0.150
FOLIAGE	0.123	1.366*	0.066	0.011
STEMTYPE	0.353	-0.189	0.086	0.338
CANSHAPE	0.155	0.156	0.584	-0.646
BRANTYPE	0.242	0.171	0.375	-0.228

3. Morphological classification of transect trees

The three principal components produced from the intra-provenance data shown in table 4.14a were comparable to those determined from the inter-provenance principal components analysis (table 4.11a), such that F1 was an index of tree size, F2 an index of girth dominance and F3 an index of canopy dominance. Using these principal components with the variables branch height and canopy shade, six morphologically similar groups of trees (B1-B6) were produced by cluster analysis (table 4.14b). A morphological description of the trees in these groups are presented in table 4.14c, which are schematically summarised in figure 4.4.

There were morphologically comparable cluster groups between the inter- and intra-provenance populations. B4-trees were similar to A1-trees, but rarely had non-divergent branching and irregular and dome canopies, and commonly had all stem types. B2-trees were similar in size and girth dominance to A4-trees, but had less dominant canopies. These trees were more solitary in habit, had mostly erect and twining stems and all canopy shapes, and their foliage was sparse and in poor condition. B3-trees were very abundant in the study area and were large trees with dominant girths and intermediate in canopy dominance. They were mainly solitary trees with erect and, to a lesser extent, leaning stems. Their spherical or dome canopies provided high shade cover with foliage that was good to moderate in condition. B1-trees were as abundant as B3-trees and were intermediate in size and canopy dominance and low in girth dominance. These trees had all stem types and occurred more frequently as solitary trees. They also had all canopy shapes, which provided moderate shade cover and consisted of foliage that was generally poor to moderate in condition. As a large group of trees, these were the most heterogenous in morphology, which suggests they could be further divided into smaller sub-groups. B5-

Table 4.14

Morphological classification of intra-provenance (T1-T5) trees (n=223).

A. Score coefficients for the first 3 principal components determined by principal components analysis.

	PRINCIPAL COMPONENT		
	F1	F2	F3
% OF VARIANCE	82.6	10.2	7.2
HEIGHT	0.373	0.378	-1.689
CANDIAM	0.367	1.024	1.266
GIRTH	0.360	-1.436	0.459
INDEX	Tree size	Girth dominance	Canopy dominance

B. Summary statistics of cluster analysis (6 clusters).

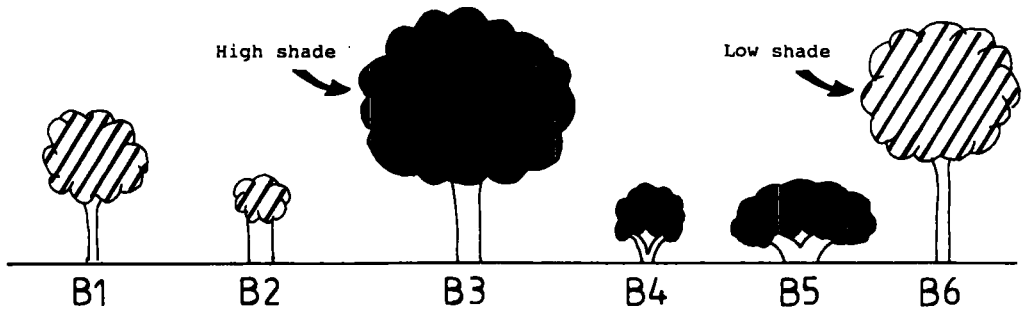
VARIABLE	BETWEEN GROUPS	DF	WITHIN GROUPS	DF	F-RATIO	SIGNIFICANCE
TREE SIZE(F1)	106.417	5	108.583	210	41.162	***
GIRTH DOMINANCE (F2)	93.712	5	121.288	210	32.451	***
CANOPY DOMINANCE (F3)	75.334	5	139.666	210	22.654	***
BRANCH.HT (m)	133.416	5	88.584	217	65.364	***
SHADE (%)	94.423	5	127.577	217	32.122	***

C. Morphological description of trees within each cluster group using the group means of the standardised variable.

	CLUSTER GROUP					
	B1	B2	B3	B4	B5	B6
N	64	47	64	44	3	1
TREE SIZE(F1)	0.03	-0.43	0.96	-0.73	-2.85	0.39
GIRTH DOMINANCE (F2)	0.82	-0.10	-0.68	0.26	-1.68	3.66
CANOPY DOMINANCE (F3)	-0.01	-1.05	0.38	0.18	2.58	2.43
BRANCH.HT	2.93	1.26	1.78	0.98	0.13	2.50
SHADE	45.00	24.77	67.27	63.18	60.00	20.00

Figure 4.4

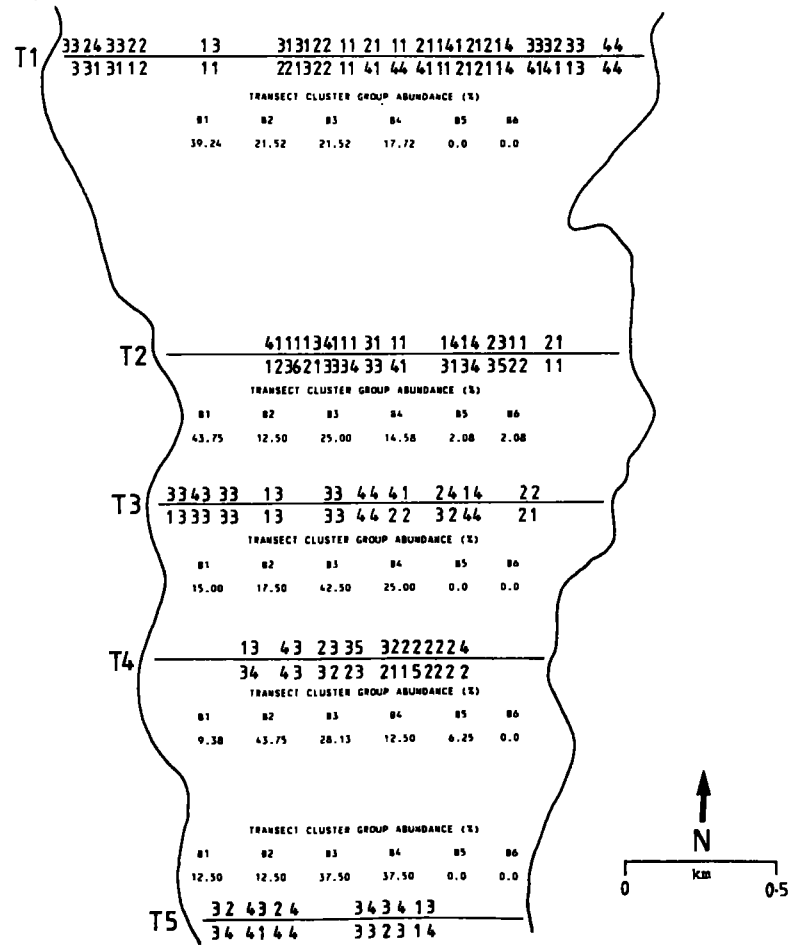
Summary description and abundance of <u>Prosopis</u> tree morphotypes determined by intra-provenance cluster analysis, with continuous variables illustrated schematically and categorical variables with attribute frequencies greater than 20%.



	B1	B2	B3	B4	B5	B6
CANSHAPE	sphere	ALL	sphere/dome	sphere	sphere	sphere
STEMTYPE	erect/lean	erect/lean	erect	ALL	erect	erect
BRANTYPE	diverge	diverge	diverge	diverge	diverge	diverge
FOLIAGE	poor/moderate	poor	good	moderate	moderate	poor
DIST	solitary/ clump	solitary/ clump	solitary	clump/ solitary	solitary/ clump	solitary

Figure 4.5

Geographical distribution of intra-provenance cluster groups (B1-B6) in the EPZ.



trees were very small and multi-stemmed, but were unique in having both dominant girths and dominant canopies. A single moderate sized B6-tree was separated out in the analysis because of its very low girth dominance and very high canopy dominance.

4. Geographical distribution of cluster groups in the transects

The relative abundance of trees in each cluster group in each transect and their geographical distribution are shown in figure 4.5. B1-trees were clearly distributed towards the north of the study area and were the dominant tree type in transects T1 and T2. They were scattered throughout the length of each of these transects, with no trends of being associated together in clumps. B2-trees were found in all transects, but were most dominant in the eastern end of transect T4. B3-trees were most frequent towards the western margin, particularly in transect T3. As the largest of the morphotypes, these trees would be the most suitable to resist physical damage through the encroachment of sand into the woodland margins. In transect T3, there was also a distinct zonation of B3-trees to the west and B4-trees to the east. B4-trees increased in abundance towards the south of the study area and, as in B2- and B3-trees, their nearest neighbours were similar in morphology. Trees of B5 and B6 morphology were found only in the interior of the woodland.

These results show that the distribution of B1- and B4-trees accounted for the majority of variation between the transects, where the frequency of B1-trees decreased and B4-trees increased in a southwards direction down the study area. In the woodland interior and the eastern margin, the smaller morphotypes were more frequent. This was most apparent in transects T3 and T4, where there were more B4- and B2-trees respectively towards the eastern margins of the transects. However in transect T5, B4-trees were also frequent to the west of the transect, which can be

attributed to the greater clumping habit in response to the mega-dunes which have clearly penetrated the woodland here (Chapter 3).

4.3.5 Multi-purpose properties of classified trees

This section assesses the multi-purpose properties of trees in the cluster groups determined from both the inter- and intra-provenance populations. The objective of this assessment was to define a selection procedure for isolating superior multi-purpose trees for future utilisation in Oman. Tree properties were divided into a number of categories: timber for commercial use; fuelwood through tree felling; fuelwood by lopping; fodder by lopping; fodder directly accessible to livestock; low lying shelter belts for crops; shelterbelts for tree plantations; shade protection; soil stabilisation; and miscellaneous properties. For each cluster group of trees, each of these categories was assessed using a grading system of poor (1), moderate (2), or good (3).

The results of this assessment are presented in table 4.15. This table shows that A1-, B4- and B5-trees were the most suitable for supplying fodder, which was enhanced by having canopies that were directly accessible to grazing animals. They were also suitable as shelterbelts for crops by reducing wind and sand blast at ground level. Trees of A2, A5 and B3 morphology were suitable for providing fuelwood and fodder through controlled lopping practices and suitable for providing substantial shade. A3-trees were suitable for providing low-grade timber for general use. B1-trees were more suitable for fuelwood production rather than for timber because of their twining stems, whilst trees of A4 and B2 morphology were more suitable for providing wood for tools and fence posts.

Table 4.15

Assessment of multiple-purpose properties of the morphotypes determined by cluster analysis. Where 1 = poor; 2 = moderate; 3 = good; NR = not recommended.

A. Inter-provenance cluster groups

PROPERTY		A1	A2	A3	A4	A5
FUELWOOD:	Felling	1	NR	2	1	NR
	Lopping	1	2-3	2-3	1	3
FODDER:	Lopping	1-2	2	1-2	1-2	3
	Unaided	3	1	1	2	1
SHELTER-:	Crops	3	1	1	2	1
BELT	Trees	1	1	2	2-3	1
SHADE		1	1-2	1	1	3
SOIL PROTECTION		3	1	1	1-2	1
TIMBER		1	NR	2-3	1-2	NR
OTHERS			social use		tools & fences	social use

B. Intra-provenance cluster groups

PROPERTY		B1	B2	B3	B4	B5	B6
FUELWOOD:	Felling	2	2	NR	1	1	NR
	Lopping	2	1	3	1	1-2	2-3
FODDER:	Lopping	2	1	3	1	1	1-2
	Unaided	1	2-3	1	3	3	1
SHELTER-:	Crops	1	1-2	1	3	3	1
BELT	Trees	2-3	2-3	1	1	1	1-2
SHADE		2	1	3	1	1	2-3
SOIL PROTECTION		1	1-2	1	3	3	1
TIMBER		2	1-2	NR	1	1	NR
OTHERS			tools & fences	social use			social use

4.3.6 Morpho-geographical influences on seed regeneration and infestation

From each of 86 seedlots collected from the EPZ (n=54) and CPZ (n=32), a subsample of 10 intact pods was made at the time of collection to determine mean values for the variables pod length (PODLENGTH), viable seeds per pod (VIABSEED) and seed infestation (INFESTATION) (section 2.2). A statistical summary of the data is presented in Appendix D. In this section a statistical analysis was performed to determine the influences of tree morphology and provenance origin on the regeneration and infestation of the seeds. The significance results between the variables are summarised in table 4.16.

The number of viable seeds was highly positively correlated to the length of the pod and negatively correlated to the degree of infestation, which was consistent for both provenances. There was no significant correlation between seed infestation and pod length, which suggests that the size of the mature pods does not play a part in the selection of trees by ovi-positing insects. This would be the case if the insects lay their eggs in the tissue of immature pods. This corresponds to the method of infection by adult Lepidoptera in the new world Prosopis species, whose larvae are often responsible for the total destruction of the seeds (Johnson, 1983). There was also no significant correlation between the legume variables and tree height, girth and branching height for each provenance population.

The significant relationships between the tree canopy variables (shade and foliage condition) and the legume variables for each provenance are summarised in figure 4.6. There were strong negative correlations between the canopy shade of the EPZ-trees and both pod length and viable seeds. Similarly, EPZ-trees had significantly longer pods with larger numbers of healthy seeds when their canopies were of poor condition. This suggests that there is a

Table 4.16

Significance results between legume variables and tree morphology for all data (TOTAL) and for each provenance (EPZ and CPZ), using correlations and one-way ANOVAs.

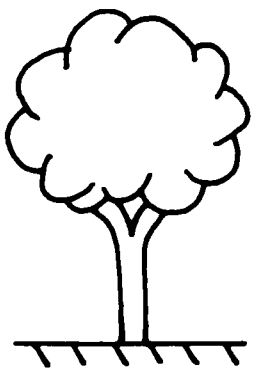
	PODLENGTH	VIABSEED	INFESTATION	CANDIAM	SHADE	STEMTYPE	BRANTYPE	FOLIAGE
PODLENGTH								
TOTAL	-	-	-	*	***	*	*	**
EPZ	-	-	-	NS	***	NS	*	**
CPZ	-	-	-	*	NS	*	NS	**
VIABSEED								
TOTAL	***	-	-	NS	**	NS	*	**
EPZ	***	-	-	NS	***	NS	NS	**
CPZ	***	-	-	NS	NS	*	NS	***
INFESTATION								
TOTAL	NS	***	-	NS	*	NS	NS	NS
EPZ	NS	***	-	NS	*	NS	NS	NS
CPZ	NS	**	-	NS	**	NS	NS	*
PROVENANCE								
TOTAL	NS	NS	***	-	-	-	-	-

There were no significant correlations between the legume variables and HEIGHT, GIRTH or BRANCH.HT. There were also no significant variations in the means of the legume variables between the attributes of CANSHAPE and HABIT.

Figure 4.6

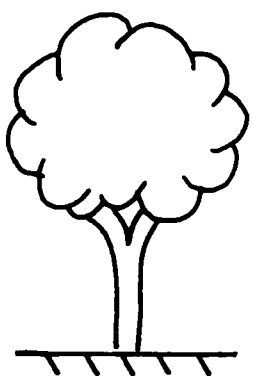
Summary of significant relationships between the legume variables and the canopy composition variables (SHADE and FOLIAGE) for each provenance. Where NS = not significant (p>0.05) between variables.

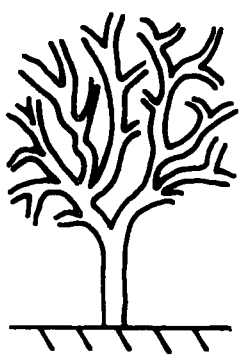
A. Eastern *Prosopis* Zone



CANOPY COMPOSITION	GOOD SHADE	GOOD FOLIAGE	POOR SHADE	POOR FOLIAGE
INFESTATION RATE	High	High	Low	Low
POD LENGTH	Small	Small	Large	large
VIABLE SEEDS	Few	Few	Many	Many

B. Central *Prosopis* Zone





CANOPY COMPOSITION	GOOD SHADE	GOOD FOLIAGE	POOR SHADE	POOR FOLIAGE
INFESTATION RATE	Low	Low	High	High
POD LENGTH	NS	Large	NS	Small
VIABLE SEEDS	NS	Many	NS	Few

relocation of dry matter from the leaves into the production of the seeds. Seed infestation in this provenance was positively correlated to the degree of shade, so that seeds were more infested in canopies with denser foliage. There was also a significant increase in infestation with increasing improvement of the foliage condition. The lush growth in the canopy may therefore be an important signal in attracting ovi-positing invertebrates to the trees.

In contrast to the EPZ-trees, the canopy shade of the CPZ-trees was negatively correlated to seed infestation and was not correlated to either pod length or number of viable seeds. However, these trees had significantly longer pods, higher numbers of healthy seeds and lowest infestation levels when their canopy was of good foliage condition. These results suggest that heavy seed infestation has influenced the defoliation of the trees in this provenance. Defoliation may have been promoted directly by large populations of adult insects feeding on the leaves, or indirectly through physiological injury by the insect larvae. In this provenance, trees with a healthy canopy that produce copious quantities of high quality seeds may be resistant to infestation by insects.

Pod length and number of viable seeds did not significantly differ between the provenances, but seed infestation was significantly higher in the CPZ (48.4%) than the EPZ (33.5%). Factors influencing the provenance variation in seed infestation in the Sharqiya include:

1. variation in the distribution, density and diversity of pest species

2. presence of specific predators, such as the higher bird species diversity in the EPZ due to its closer proximity to the coast (Chapter 3)

3. greater maritime influence on the EPZ (Chapter 3)

4. geographical changes in morphology and physiology of the trees affecting their natural resistance to infection

5. spatial and temporal staggering of flowering and fruiting within each provenance influencing the degree of infestation at the time of sampling

The coastal influence in lowering the degree of seed infestation is supported by the fact that high quality seeds were collected from natural stands of P.cineraria woodlands along the Batinah coast (pers. obs.).

4.4 Conclusions and recommendations

The results presented in this chapter have shown that the morphology of mature P.cineraria in the Prosopis woodlands of the Sharqiya was extensive, ranging from very large, tall trees to stunted ground-hugging bushes.

The identification of 13 morphotypes in the field was important in the in situ assessment of morphological variation in P.cineraria, and in the selection of morphologically distinct trees for genetic analysis. The most abundant morphotypes were shown to be highly significantly different in their morphology. The distribution of non-specific esterases extracted from seeds was used as an estimate of genetic variation between individual trees. Active and passive factors were responsible for the extensive morphological diversity of the trees, in response to the changing environment of shifting sand dunes.

The greatest genetic variation determined by the frequency of non-specific esterases extracted from seeds was found between the provenances, rather than between tree types. Provenance genetic variation was attributed to the

biologically isolated distribution of the woodlands. For genetic conservation of this species in the Sharqiya, supplementary provenance collections of seeds within each provenance should be made. Collected seeds should be divided into those for storage (Chapter 5), and those for genetic analysis using more than one isoenzyme system and a higher resolution PAGE technique.

A morphometric analysis of all the trees measured in the Sharqiya has resulted in the separation of the trees into two distinct groups. The first group consisted of large solitary trees which were generally homogenous in their morphology and in very good condition. In contrast, the second group consisted of smaller trees that were more associated in clumps; were morphologically more heterogenous; and were poorer in condition. The development of clumps through vertical vegetative growth of submerged solitary trees (Chapter 3) appears to be an important adaptation for the survival of the tree in a highly mobile environment, but results in the decline in the condition of the stems and branches within the clumps. This suggests that the metabolic and physiological requirements of the solitary trees have been sustained by their phreatophytic growth. Extended vertical vegetative growth in response to continuous sand submergence appears to have resulted in large changes in the morphology of the exposed stems and branches, and changes in the phreatophytic capacity of the tree caused by the greater distances between the soil surface and the water table.

Morphological variation in mature P.cineraria was found between the provenances. EPZ-trees had mainly spherical canopies, with foliage of moderate to poor condition. Their stems were usually erect, and primary branching was high. In contrast, CPZ-trees had irregular and, to a lesser extent, dome and spherical shaped canopies. They usually had twining stems which branched close to the ground, and had the highest frequency of non-divergent branches. These

morphological differences between the provenances appear to be both genotypic and phenotypic in origin, as a result of natural genetic variation between the provenances, and environmental differences either side of the sand sea. The greater exposure to wind and sand blast in the CPZ (Chapter 3) may be responsible for the abundance of trees in this provenance that have a morphology typical of trees partially submerged in sand. Undetermined factors such as differences in the ontogeny of the provenances, and the age of the individual trees may also influence the morphological variation between the provenances. The major differences in the height and salinity of the aquifer water between the two provenances (Chapter 3) suggests there may also be a physiological effect on tree growth.

Cluster analysis was used to separate the trees in to significantly different morphological groups. Genotypic studies will be necessary to determine whether these cluster groups are genetically adapted to the habitat in which they are found, for ecotypic identification in the Sharqiya. The further the trees were geographically apart, the greater was their morphological variation. In the EPZ, there was an increase in the canopy dominance and a decrease in the tree size towards the south of the study area, as a result of a decrease in both the height and girth in the same direction, with no change in the canopy diameter. In addition, the canopy shade cover, foliage condition and the degree of clumping increased southwards.

The survival responses of the morphotypic groups determined by cluster analysis can be summarised into those that form clumps, those that are naturally protected, and those that are resistant to change. Trees of A1, A4, B2, B4, and B5 morphology are the major components of clumps, and it is suggested that they are the products of both vertical and lateral vegetative growth described in Chapter 3. These trees can also exist in a solitary habit in protected parts of the woodlands. Solitary trees of A2, A5,

and B3 morphology are sufficiently large to survive exposed areas such as the margins fronting the sand sea, and between the within-clump gaps.

The multi-purpose properties of P.cineraria in the Sharqiya can be attributed to the extensive morphological variation found in the species. Morphotypes of particular relevance in Oman were those used for fuelwood, fodder and shade protection (Chapter 3). A variety of morphotypes identified in these studies satisfied these criteria. Their future exploitation depends upon the genotypic and environmental influences on gross morphology. The distribution of these morphotypes are now known for the Sharqiya, so that the next stage in their utilisation is to carry out germplasm collections of selected morphotypes. The material collected must be used to assess the performance of the morphotypes under both nursery and field conditions, using seed material or micro-propagated clones. The large solitary morphotypes should be severely restricted in their exploitation, as they offer the greatest stability to the woodlands. These trees are the most likely to tap the aquifer water throughout periods of severe drought, and will contribute new biomass to the ecosystem when most other vegetation has died back.

The insects lay their eggs in the tissue of immature P.cineraria pods, resulting in the destruction of more than 70% of the seeds in some accessions. This corresponds to the method of infection by adult Lepidoptera in the new world Prosopis species, whose larvae are often responsible for the total destruction of the seeds (Johnson, 1983).

Of the tree variables measured in the EPZ, only the canopy shade cover and foliage condition were related to the degree of seed infestation. The lush growth in the canopy may therefore be an important signal in attracting ovi-positing insects to the trees. In this provenance, larger pods were found when the canopy was sparse and in

poor condition. This suggests that there is a pronounced relocation of photosynthates from the leaves into the production of the pods. In contrast, high infestation levels were found in CPZ-trees of low shade cover and poor foliage condition. Since seed infestation was found to be significantly higher in the CPZ, these differences may be linked to higher densities of pests, and to the distribution of specific pest species. Higher infestation levels in the CPZ may be responsible for the poor foliage condition and defoliation of the trees.

The results have shown that the correlations between the degree of seed infestation and tree morphology were affected by the distribution of the trees within the Sharqiya. Further studies are required to define the morphological characteristics that indicate important traits such as high seed production and natural insect resistance. Such studies will allow the development of efficient seed collections and the selection of high yielding and resistant strains for future development and utilisation.

CHAPTER 5

PROPAGATION, GROWTH AND MORPHOLOGY OF P.CINERARIA SEEDLINGS

5.1 Introduction

The most vulnerable stages in the life-cycle of plants are the seeds and the early growth of the seedlings. Particularly under arid conditions, specific phenological and morphological adaptations are necessary for the permanent establishment of the plant. These include seed dormancy to survive long continuous dry periods, rapid responses to unpredictable ephemeral water, rapid growth characteristics for the exploitation of more permanent sources of water, and an early tolerance to water and salinity stress. As a result, morphological and often genetic variation in desert species are generally high, particularly in trees which are very susceptible to environmentally induced variation. This variation will increase the adaptability of the species within a population to a changing environment.

In the analysis of the variants in a wild population, the sampling strategy of germplasm material is extremely important. The germplasm available includes whole plants by digging them up and transplanting them, cuttings, tissue culture and the seeds. In the case of tree species, the collection and propagation of seeds is often the only method available. The sampling procedures for exploring plant genetic resources should be aimed at the fullest possible recovery of genetic variation, including within-population variation and geographical patterns of variation (Ford-Lloyd & Jackson, 1986). To maximise the genetic variation, the sample size and area should be as large as possible, and preferably random rather than selective. This will result in the capture of genetic diversity associated with the adaptations to differences in the environment. Such optimum sampling strategies with 95% certainty should result in the collection of all alleles occurring in the population at a frequency greater than 5% (Marshall &

Brown, 1975).

Information on the reproductive biology of a species is necessary for the implementation of optimum seed sampling strategies. P.cineraria reaches reproductive maturity after approximately four years (Leakey & Last, 1980), with the development of many bright yellow inflorescences (4 to 20cm in length). Each inflorescence is composed of many small unspecialised flowers attached to a single spike. The flowers at the base of the spike reach maturity before those at the tip. Of these flowers, only a small percentage will develop fruits, since each spike is only capable of carrying a certain load of fully matured pods. A large number of the flowers in each inflorescence will therefore not have a reproductive function, and may simply be involved in the production of nectar and pollen for the pollinators (Polhill et al., 1978).

Seeds collected for genetic or economic importance are stored under specific conditions to maximise their viability. Factors affecting seed viability are many, but are principally dominated by the storage temperature and the moisture content of the seeds. For example, seed viability is doubled for each 5°C fall in temperature or for each 2% drop in seed moisture content (Harrington, 1963). Methods of predicting seed viability under storage conditions have been extensively studied by Roberts (1972, 1973). Under known storage parameters, it is possible to estimate the deterioration in seed viability over any given storage period. In this way, one can predict the optimal storage treatment and the length of the storage period that will ensure high seed viability.

Pollination of P.cineraria in the Sharqiya is predominantly by invertebrates that use the flowers for food and for breeding sites (Chapter 3). Other pollinators include birds and bats. Following the fertilisation of the ovules, fruit maturation commences with the development of

a soft, vulnerable exocarp containing the developing seeds. These are spaced evenly along the fruit, varying in number from 3 to 25 per pod (Chapter 4). The mature pods are long (4 to 25cm), flattened, torulose structures with tough glabrous exocarps and fleshy mesocarps. The mature seeds have been described by Burkart (1976) as distant, longitudinal ovate, 6mm long, with an open horse-shoe fissural line on the tegument. Seeds of P.cineraria from the United Arab Emirates were divided into four morphological groups which germinated at different rates under a range of temperatures, and which produced seedlings with different growth rates (Sankary, 1982).

Shedding of the pods from the tree allows the seeds to become available for dispersal. In several new world Prosopis species, a degree of co-evolution has occurred between the trees and the native mammals (Mooney et al., 1977). In return for the nutrient-rich pods, the mammals both disperse the seeds, and increase their chances of survival following germination. The chewing of the pods may remove the hard exocarp as well as scarifying the seeds. By passing through the digestive tract, the seeds will be freed from larvae, bruchids and parasites, and the seeds deposited in the droppings have a better chance of establishing themselves. Seeds from these species have very hard and resistant teguments which provide effective protection from mechanical and chemical damage. The thick tegument also maintains seed dormancy, which allows the seeds to retain their viability for over 50 years (Glendening & Paulsen, 1955). In an environment with long periods of continual drought and unpredictable rainfall, seed dormancy ensures the survival of the species.

Conditions for successful seedling establishment in arid environments are rarely available which accounts for the limited age stratification of trees in desert woodlands. Trees that produce protein and energy rich seeds and fruit in areas of low productivity will inevitably

become host to a wide range of generalist and specialist parasitic fauna. This is a particular problem in P.cineraria, where both the pods and seeds are important sources of nutrient-rich food (Chapter 4). Seed destruction through invertebrate infestation is extremely advanced in the new world Prosopis species, and causes major problems during the collection, processing and distribution of their seeds (Johnson, 1983; Ffolliot & Thames, 1983b).

Mature seeds arriving on the soil surface through dispersal are often buried to form the seed bank. These seeds must be in a particular condition and require specific stimuli before they will germinate (Hartman & Kester, 1983). The seeds must be viable, non-dormant and with the embryo quiescent. The seeds must be subjected to the appropriate environmental conditions which include available water, suitable temperature and oxygen levels, and often light. The number of seedlings appearing from the seed bank has been described by Harper (1977) as a function of the number of 'safe sites' offered by the environment. For the successful development of the seedlings, these 'safe sites' must be free of hazards such as predators, competitors and toxic soil constituents. Within these 'safe-sites', the seeds will imbibe water which softens the tegument and hydrates the protoplasm. Hydration activates the synthesis of enzymes, resulting in cell elongation and the emergence of the radicle (Berlyn, 1972). Stored fats, proteins and carbohydrates in the endosperm of the seeds are digested to smaller compounds and translocated to the growing points of the embryo axis. Cell division in the growing points of the embryo axis results in the growth of the seedling. The development of a photosynthetic surface in the shoots will reduce the dependence of the seedlings on their seed reserves.

Following germination, the seedlings increase in size through the elongation in the stems and roots and increases in cross-sectional area (Harper, 1977). Woody plants are

not dependent on the growth made in a single season because their meristems can be held high on the perennial woody stems. Generally the early periods of life of the woody perennial are usually devoted to gaining height, whilst the reproductive period is delayed. Specifically in desert plants, elongation of roots downwards to more permanent sources of water is an adaptation that maximises the survival of the plants in arid environments. Reproduction can be delayed for 20 years or more, so that a long juvenile period is a characteristic feature of trees. The woody perennial accumulates dead structures and is dependent on a small proportion of living tissue. This strategy of growth departs from the annuals growing under arid conditions, which develop extensive cambium, phloem and wood parenchyma which are then a respiratory burden to the plant.

The growth, development and variability of plants in their natural environment are often very difficult to monitor. Hence, to assess the variability of plants sampled from wild populations, the plants must be grown under standardised environmental conditions, following the method pioneered by Turesson (1922). Plants taken from habitat extremes or phenotypically different parents must be analysed in this way to determine whether the phenotypic characteristics are the product of environmentally induced variation, or the genetic response through adaptation to that habitat (Langlet, 1971). The quantitative assessment of plant variation can be either destructive through harvests, or the non-destructive repeated scoring of plants over defined growing periods.

In this chapter, the variability of P.cineraria from the morphogenesis of the seeds to the growth and development of the seedlings has been described. The ability of the seeds to remain viable for long periods of time were examined by testing the germinability of seeds stored under five different storage treatments. Factors

affecting the natural establishment of P.cineraria seedlings in the Sharqiya were then examined. This included the study of the seed bank in the Prosopis woodlands, methods of seed dispersal, and the spatial and temporal survival of seedlings that germinated naturally after periods of heavy rainfall.

As a means of following the seedling growth under standardised environmental conditions, trials were set up under glasshouse conditions in the University of Durham Botanic Gardens. As it was impractical to mimic the conditions in the field, the principal objectives of these trials were to assess the variability in the growth and morphology of seedlot accessions sampled from individual trees throughout the EPZ and CPZ. Variation in the seedling size and morphology between the seedlots were then compared to their geographic origin and to their parent phenotype. The glasshouse trials were also used to screen a number of these seedlots for salinity tolerance, and to assess the growth and morphology of seedlings under three salinity treatments. Correlations between salinity tolerance and seedlots sampled from known areas of high salinity were also performed. Four harvests of randomly selected glasshouse grown seedlings were performed to determine the relative growth rate (RGR) of this species under standardised environmental conditions.

5.2 Materials and methods

5.2.1 Seed morphology

The variation in seed morphology was assessed by classifying the seeds from the provenance seedlot accession EPZ/1 (Appendix C) into distinct morphological classes. In each class the general morphology was described, and the colour of the testa determined using a

Munsell Soil Colour Chart (Munsell Color Co., Maryland, U.S.A.). The maximum length, width and thickness of 20 seeds from each morphological class were measured. A random sample of 1000 seeds was taken and sorted into each of these classes. The seed class frequency was calculated as the number of seeds in the class, as a percentage of the total number of seeds in the sample. The mean seed weight for each class was determined, and expressed as the number of seeds per kg.

5.2.2 Seed storage viability

Using the methods of Roberts (1972, 1973) the relationship between the storage temperature, seed moisture content and the period of seed viability was used to predict the optimum storage conditions for P.cineraria seeds. The method required a series of germination tests of seeds of at least two moisture contents stored under at least two temperatures. In this study five storage treatments were tested (see table 5.4). For each treatment, the % viability was determined as the number of germinated seeds as a percentage of the total number of seeds in the sample. A seed survival curve of % viability against storage time on probability paper was then used to determine the mean viability period (P_V), taken as the time in storage to get 50% viability. The standard deviation (σ) was also determined from the curve as the change in time over one standard deviation from the mean. These were used to calculate the first viability constant K_σ using the equation:

$$K_\sigma = \sigma / P_V \qquad \text{Equation 5.1}$$

The relationship between mean viability period, moisture content and storage temperature (Roberts, 1972) has been described by the equation:

$$\log P_v = K_v - C_1m - C_2t \qquad \text{Equation 5.2}$$

Where: m = % seed moisture content
t = storage temperature (°C)
K_v, C_1m & C_2t = viability constants

This equation was used to calculate the remaining three viability constants (K_v, C_1, C_2) from the different storage conditions, using substituted simultaneous equations. These constants were then used to construct a viability nomograph for P.cineraria according to the method of Roberts & Roberts (1972).

The five storage treatments were prepared in the following way. Mature P.cineraria seeds were collected from the trees in the first week of February 1986 to minimise the effect of insect infestation. These seeds with a natural moisture content (section 2.9) of 8.26% (M1) were immediately stored at 20°C in hermetically sealed plastic bags (treatment 1). A batch of approximately 150 seeds was sampled from treatment 1 after 300 days storage and again after 400 days storage. As the effect of drying M1 seeds in a ventilated oven at 45°C for 48 hours did not significantly decrease their moisture content, a second moisture content of 13.02% (M2) was prepared in the following way. Seeds were immersed in distilled water for six hours, and those that were fully imbibed were discarded from the sample. The remaining seeds were thoroughly dried and a random selection were used to determine their moisture content. Four batches of seeds from treatment 1 were sampled after 150 days storage, of which two of the batches were immediately converted to M2 moisture content. The two M1 seed batches were then stored separately at -20°C (treatment 2) and 4°C (treatment 3), and the two M2 seed batches at 20°C (treatment 4) and 4°C (treatment 5). From each of treatments 2-5, approximately 150 seeds were sampled after a period of 150 days in storage. Seeds from treatment 2 were also sampled after 250 days in storage. For each of the five storage treatments the seed viability was determined for each storage period.

5.2.3 Preparation of glasshouse trials in Durham, U.K.

Seedling trials of P.cineraria were established in a glasshouse (University of Durham Botanic Gardens) in June 1986. These trials were maintained for the duration of the summer period in which the micro-environmental conditions of warm temperatures and long daylengths inside the glasshouse were maximum at this latitude. As a result of a seasonal drop in both temperature and daylength at 15 weeks of age, morphological measurements (section 5.2.6) were only performed on seedlings up to 13 weeks of age. Throughout the monitoring period of the trials, no extra heating inside the glasshouse was used.

Plastic plant pots (15cm diameter, 20cm height) were filled with sand culture medium, prepared from washed soil-free sand (1-2mm particle diameter), with a complete nutrient solution based on Evans's modification of Shive's solution (Evans & Nason, 1953). A concentrated (x100) nutrient stock solution was prepared and diluted when required to the following concentration:

Salt	Molarity	ppm
$Ca(NO_3)_2.4H_2O$	0.005	
K_2SO_4	0.0025	
KH_2PO_4	0.0005	
$MgSO_4.7H_2O$	0.002	
KCL		9.0 Cl
$FeSO_4.7H_2O$ (in place of Fe-versenate)		0.5 Fe
$MnSO_4.H_2O$		0.25 Mn
H_3BO_3		0.25 B
$ZnSO_4.7H_2O$		0.25 Zn
$CuSO_4.5H_2O$		0.02 Cu
$Na_2MoO_4.2H_2O$		0.02 Mo

Each pot was sown with 4-6 germinated seeds that had been scarified using coarse-grained sand-paper (section 2.8). The pots were watered every 48 hours with $30cm^3$ tap water, and treated weekly with $30cm^3$ of freshly diluted nutrient solution.

5.2.4 Glasshouse accession trial

Seedlings were grown from 38 seedlot accessions sampled from individual trees of known geographic origin in the Eastern and Central Prosopis Zones (Chapter 3) and known parent morphology (Chapter 4). The selection criteria for these seedlots from the 103 seedlot accessions stored in the P.cineraria Seed Bank (Appendix C) was aimed at maximising the geographical distribution of the seedlots within the provenances and including the dominant parental morphotypes (table 5.1).

5.2.5 Glasshouse salinity trial

Seedlings from 11 of the 38 seedlot accessions examined in the accession trial were used in a salinity trial of P.cineraria. The accessions were selected to cover the largest geographical range of P.cineraria in the Sharqiya (table 5.2). For each of these accessions, a further three pots were planted with 4-6 seedlings. After four weeks irrigation with tap water, the pots were then treated every 48 hours with $30cm^3$ of 4%, 2% and 1% salt solutions, which represented both the ionic composition and concentration range of the aquifer water in the Sharqiya. Water analysis data (Appendix E) supplied by the Public Authority for Water Resources (Ruwi, Oman) from seven bore holes in the Sharqiya were used to determine the mean ionic weight ratio for chlorine, sulphate, calcium, sodium and magnesium, which together accounted for 97.7% of the mean ion weight in solution. For each of the ions, the mean weight ratio was used to calculate the mean ionic mole ratio:

	Cl	SO_4	Ca	Na	Mg
Mean ionic weight ratio	40.97	20.59	3.9	28.97	3.25
Mean ionic mole ratio	1.154	0.214	0.097	1.260	0.134
Approx. ionic mole ratio	12	2.5	1	13	1

Table 5.1

Seedlot selection criteria for the assessment of seedling morphological variability.

Seedlot accessions	Seedlot No.	Provenance origin	Parent type
1-8	8	EPZ	type 1
9-13	5	CPZ	type 1
16,23	2	EPZ	type 3
14,15	2	CPZ	type 3
17-22	6	CPZ	type 3
24-27	4	EPZ	type 8
28-32	5	CPZ	type 8
35-39	5	CPZ	type 5
41	1	EPZ	type 5
TOTAL	38	2	4

Table 5.2

Seedlot selection criteria for the assessment of seedling morphological variability between salinity treatments. Where + = seedlings grown in salinity treatment; n/d = not determined.

	Seedlot accessions	Provenance origin	Parent type	Salinity treatment 1%	2%	4%
	5	EPZ	1	+	+	+
	7	EPZ	1	+	+	+
	9	CPZ	1	+	+	+
	11	CPZ	1	+	+	+
	13	CPZ	1	+	+	+
	14	CPZ	1	+	+	+
	17	CPZ	3	+	+	+
	20	CPZ	3	+	+	+
	30	CPZ	8	+	+	+
	32	CPZ	8	n/d	+	+
	38	CPZ	5	n/d	+	+
TOTAL	11	2	4	9	11	11

Four salts (Sigma Chemical Co., St. Louis, U.S.A.) were used to satisfy this ionic mole ratio, from which the mole ratio and then the molecular weight ratio for these salts were determined. The weight of each salt was then calculated for the preparation of one litre 4% w/v stock solution:

Mole ratio	8NaCl	: $2.5Na_2SO_4$	: $CaCl_2$	: $MgCl_2$	TOTAL
Weight ratio	468	355	111	95.3	1029.3
Weight ratio at 4% w/v (g)	18.19	13.80	4.31	3.70	40

As $CaCl_2.2H_2O$ and $MgCl_2.6H_2O$ were hydrated, their weights were corrected to allow for the extra water component. The salt constituents in one litre of 4% w/v salt stock solution are summarised below:

1. NaCl			= 18.19g
2. Na_2SO4			= 13.80g
3. $CaCl_2.2H_2O$	(MW = 147)	(147/111)4.31	= 5.71g
4. $MgCl_2.6H_2O$	(MW = 203.3)	(203.3/95.3)3.70	= 7.89g

The 2% and 1% solutions were prepared by serial dilution of the 4% stock solution. To maintain the salinity regimes, the pots were flushed with nutrient solution every week to minimise salt accumulation in the soil.

5.2.6 Seedling morphology

For both the accession and salinity trials, seedling morphology was measured using the following parameters:

1. Shoot height (mm), from the cotyledonary node to the apical meristem; HEIGHT
2. Stem diameter (mm), 5mm below the cotyledonary node; STEMDIAM
3. Number of nodes, not including the cotyledonary node; NODES
4. Number of pinna; MAT.LVS

5. Number of immature pinna; IMMAT.LVS

6. Maximum number of leaflets per pinna; LEAFLETS

7. Length of longest thorn (mm); THORNS

Stem diameter was measured to the nearest half millimetre using a stem gauge constructed from thick card according to the specifications of Evans (1972). Mature pinna were selected as those with fully formed green leaflet that were open during daylight. All other pinna were counted as being immature. The variables allocated with upper-case labels were statistically analysed.

Mensuration was first performed on 7 week old seedlings. This allowed time for the plants to adapt to the conditions in which they had been placed, and minimised the disturbance to plant growth (Evans, 1972). Morphological data were collected from each seedling every two weeks for a period of six weeks. Seedlings were labeled in order to record the growth of individual plants. Due to the number of seedlings recorded at each date, the sampling was staggered over three days and was consistently maintained throughout the study.

5.3 Results and discussion

5.3.1 P.cineraria seeds and seedlot accessions from Oman

1. Seed collections

Whenever available, P.cineraria seeds were collected in the three Prosopis provenances (EPZ, CPZ & SWPZ) of the Sharqiya. A total of 103 seedlot accessions of P.cineraria were collected over a four year period and stored in the P.cineraria Seed Bank (Appendix C). Seeds were sampled throughout the year, but varied between areas and also between adjacent trees. Trees heavily in fruit were

frequently found next to morphologically similar trees that were neither in fruit nor in flower. Shedding of the pods was not automatic on reaching maturity, as matured pods were observed still attached to branches that had both new flower and fruit development. Mature pods taken off the trees produced the best quality seeds with respect to low insect infestation, and were easiest to extract from the pods. This variability in seed production is common in forest trees, which is attributed to a variety of adverse conditions that inhibit flower induction (Hartman & Kester, 1983). These include the competition from an excessively large seed crop from the preceding season; stress produced by inadequate nutrition, water and extremes of temperature; and defoliation caused by insects or disease. This makes germplasm conservation very difficult, as precise periods for extensive seed collections can not be easily predicted. Since genetically related trees may start seed morphogenesis at the same time, the final seed collections may not be as genetically diverse as anticipated.

2. Seed morphology

The morphological dimorphism of P.cineraria seeds collected from the Sharqiya was high. Provenance collections of seeds showed maximum dimorphism, whilst seeds sampled from individual trees showed minimum dimorphism. A sub-sample of seeds from the accession EPZ/1 had a mean seed weight of 23000 seedskg^{-1}. On the basis of seed shape, colour and size (section 5.2.1), six morphologically distinct seed classes (S1-S6) were identified in this accession (table 5.3). The most frequent seed class was S3, which contained seeds that were the second largest in both size and weight in the sample. Class S4 seeds were the second most frequent in the sample, and were generally the smallest in size. Class S2 seeds were separated from class S3 seeds by being particularly elongated, although the colour, thickness and weight were comparable. The largest seeds in the sample were those in

Table 5.3

Physical description and frequency of 6 seed morphological classes identified from a 1000 seed sample from a general seed accession collected from the Eastern *Prosopis* Zone (EPZ). Where 7 seeds from this sample were of miscellaneous morphology.

	SEED CLASS					
	S1	S2	S3	S4	S5	S6
MUNSELL COLOUR	dark brown 7.5YR3/4	dark brown 7.5YR3/4	dark brown 7.5YR3/4	dark brown 7.5YR3/4	brownish yellow 7.5YR5/4	brownish yellow 7.5YR5/4
SHAPE	oval/ square	elongate	oval/ square	oval/ elongate	oval/ elongate	oval/ elongate
SEED DIMENSIONS						
LENGTH						
Mean	7.7	7.3	6.3	5.3	6.6	5.4
S.D.	0.5	0.3	0.4	0.4	0.5	0.3
WIDTH						
Mean	5.1	4.0	4.5	3.3	4.5	3.6
S.D.	0.3	0.2	0.2	0.3	0.3	0.4
THICKNESS						
Mean	2.4	2.4	2.5	2.2	2.5	2.1
S.D.	0.3	0.3	0.3	0.3	0.2	0.3
WEIGHT OF 12 SEEDS (g)	0.738	0.5 75	0.592	0.306	0.567	0.320
AREA OF 12 SEEDS (cm^2)	3.6	2.6	2.6	1.6	2.7	1.7
% FREQUENCY IN 1000 SEED SAMPLE	3.7	11.5	51.7	19.1	10.1	3.2

class S1 which were low in frequency. This variability in seed morphology was higher than that found for P.cineraria collected from the United Arab Emirates (Sankary, 1982), although three of the four classes identified by Sankary corresponded closely to classes S4, S5 and S6 in this study. The relationship between form and function in the seed classes could not be clearly identified, with the exception of the lighter coloured seeds which rarely had to be scarified to induce germination. The majority of the dormant seeds left after 18h soaking in water were those from classes S3 and S4. Specific care should be taken in collecting the morphologically different seeds in the population, as a means of maximising genetic variability in the germplasm collection.

3. Breaking seed dormancy

Seed dormancy of P.cineraria from the Sharqiya was high, reaching 70% or more in the majority of the seedlots collected. The rate of germination of unscarified seeds after being imbibed in water for 18h was slow and very variable, ranging from two days to over six weeks when left under suitably moist conditions. To increase the bulk germination of seeds, several methods of breaking seed dormancy without affecting seed viability were examined. Studies were performed on a collection of seeds that did not imbibe after 18h immersion in water. Abrasion of the seed tegument using coarse-grained sandpaper was found to be the most suitable method for scarifying large numbers of seeds, and was used whenever possible (section 2.7). Methods of breaking seed dormancy including scalpel incisions, immersing seeds in boiling water for various lengths of time, and using various molarities of sulphuric acid, were all unsuccessful for P.cineraria seeds. A resistance to sulphuric acid was also characteristic of P.nigra seeds (Rolfo, 1963). However, Mahmond & El-Sheikh (1978) successfully broke the dormancy of P.chilensis seeds using concentrated sulphuric acid, and Winer (1983) has

shown that the pre-treatment of P.chilensis seeds using sulphuric acid improved the rehabilitation of this species in the arid conditions of northern Sudan.

4. Seed storage viability

The viability of P.cineraria seeds stored under five different treatments (section 5.2.2) are presented in table 5.4. Highest viabilities were found in seeds of M1 moisture content stored at 4°C, followed closely by M1 seeds stored at 20°C for both 300 and 400 days. Lowest viabilities occurred in seeds of M2 moisture content stored at 20°C. The partially hydrated protoplasm of M2 seeds stored at 20°C may have caused the premature activation of the quiescent embryo, resulting in seed fatalities due to the absence of suitable germinating conditions. Seed viability of M1 seeds stored at -20°C was 56.85% after 150 days, but in a second test 100 days later the whole batch of seeds failed to germinate as a result of a fungal infection with Aspergillus niger. This suggests that freezing had a detrimental effect on germination by increasing the susceptibility of the seeds to infection.

The effect of the storage treatment on the rate of seed germination after 18h soaking in water was examined (figure 5.1). Seeds of M1 moisture content stored at 20°C and 4°C were very high in seed dormancy of 84.3% and 86.0% respectively. Dormancy was maintained in these seeds for 70 days of continued exposure to moist conditions. Seeds of M2 moisture content stored at 20°C and 4°C had lower numbers of dormant seeds which may have been influenced by the method in which the M2 seeds were prepared (section 5.2.2). The cooler storage temperature of 4°C also enhanced the germination rate and reduced seed dormancy of M2 seeds. The germination rate of M1 seeds stored at -20°C was found to be opposite to M1 seeds stored at 20°C and 4°C., such that germination was high in the first 10 days after imbibition and seed dormancy was very low (6.0%). Low numbers of

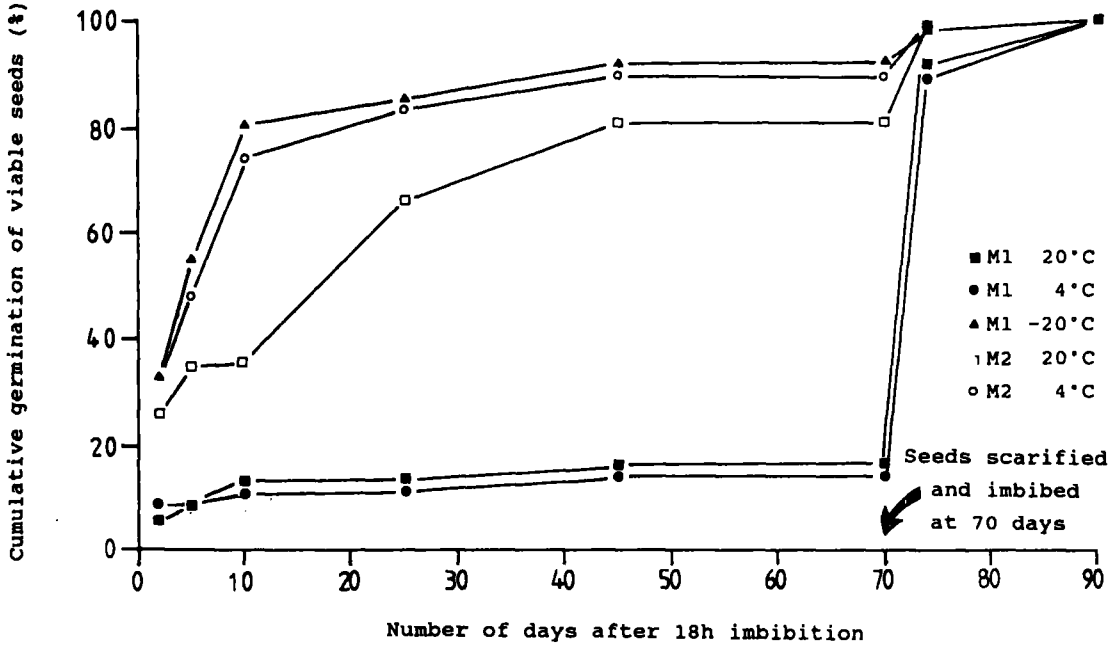
Table 5.4

Summary of germination tests of seeds stored under different storage treatments. Where M1 = 8.262% seed moisture; M2 = 13.019% seed moisture; a,b = repeated samples within storage conditions; n/d = not determined.

	Storage treatment	Storage (days)	Seed age (days)	Total seeds	Total viable	% viability	% dormant
1.	M1 20C a	300	300	181	153	84.53	84.31
1.	M1 20C b	400	400	164	134	81.71	n/d
2.	M1-20C a	150	300	146	83	56.85	6.02
2.	M1-20C b	250	400	FAILED	DUE	TO FUNGAL	INFECTION
3.	M1 4C	150	300	124	107	86.29	85.98
4.	M2 20C	150	300	154	20	12.99	20.00
5.	M2 4C	150	300	156	57	36.54	8.77

Figure 5.1

Germination rates of viable seeds retrieved from 5 different storage treatments.



dormant seeds when stored at -20°C suggests that the seed coat has been damaged by the low temperatures, perhaps as a result of freeze fracturing. Since the gaseous exchange in the seed tissue is thought to be important in maintaining seed viability (Harrington, 1972), this suggests that the damaged seed coat at -20°C caused a change in the gaseous exchange which reduced seed viability.

The seed survival curves for each storage condition are presented in figure 5.2, from which the mean viability periods (P_v) and standard deviations (σ) were used to determine the first viability constant K (table 5.5). For M1 seeds at 4°C, the mean viability period was 1925 days, which shows that seeds stored under these conditions would reach 50% viability after approximately five years. Seeds of M2 moisture content stored at 20°C would reach 50% viability in just over two months storage. Seeds of M1 moisture content stored at 20°C would reach 50% viability after 1265 days, or approximately 3.5 years. The survival curve of this storage condition intercepted the y-axis at 91% viability. As the seeds were placed under this storage condition immediately after they were sampled from the tree, this value represents the viability of the seeds at the time of seed maturation.

The remaining three viability constants (K_v, C_1, C_2) determined from four combinations of three sets of different storage conditions using equation 5.2, are presented in table 5.6. The four viability constants were then averaged, and used to construct the seed storage nomograph presented in figure 5.3. This nomograph can be used to estimate the time taken for the viability of P.cineraria seeds to fall to any given level at any given temperature or moisture content, or can be used to find the various combinations of temperature and moisture content necessary to maintain the viability above a given value for a given storage period.

Figure 5.2

Survival curves of seeds stored under 5 different storage treatments for determining their mean viability periods (at 50% viability). Where viability % is plotted on a probability scale.

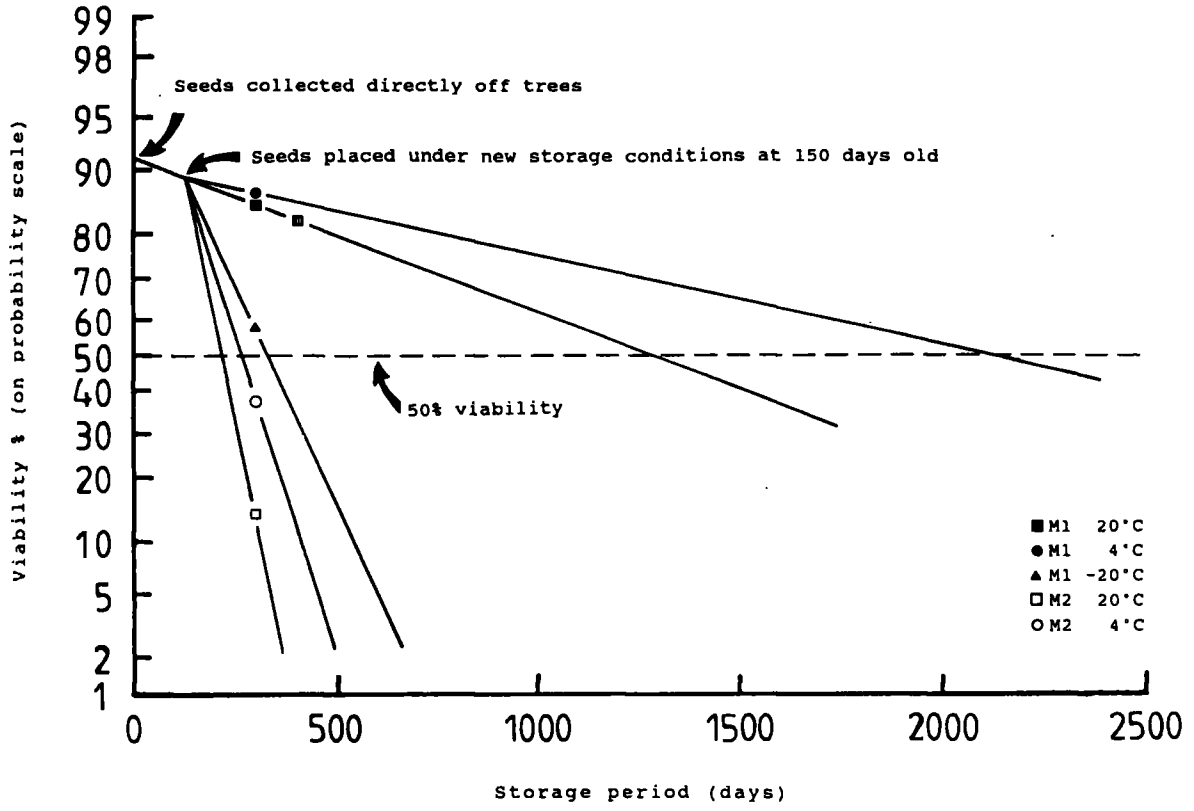


Table 5.5

Mean viability period (P_v) and its standard deviation (σ) determined from seed survival curves for 4 storage treatments.

Storage treatment	Mean viability period (P_v)	Standard deviation (σ)	K_σ constant (σ/P_v)
1. M1 20°C	1265	940	0.743
3. M1 4°C	1925	1625	0.844
4. M2 20°C	77	65	0.844
5. M2 4°C	115	100	0.870

Table 5.6

Summary of seed viability constants (K_v, C_1 & C_2) determined for 4 combinations of 3 sets of different storage treatments.

	Treatment combination	K_v	C_1	C_2
A.	1. M1 20°C 3. M1 4°C 5. M2 4°C	5.452	0.257	0.011
B.	1. M1 20°C 3. M1 4°C 4. M2 20°C	5.435	0.255	0.011
C.	3. M1 4°C 4. M2 20°C 5. M2 4°C	5.451	0.257	0.011
D.	1. M1 20°C 4. M2 20°C 5. M2 4°C	5.424	0.255	0.011
	Mean	5.441	0.256	0.011

Figure 5.3

Viability nomograph for P.cineraria.

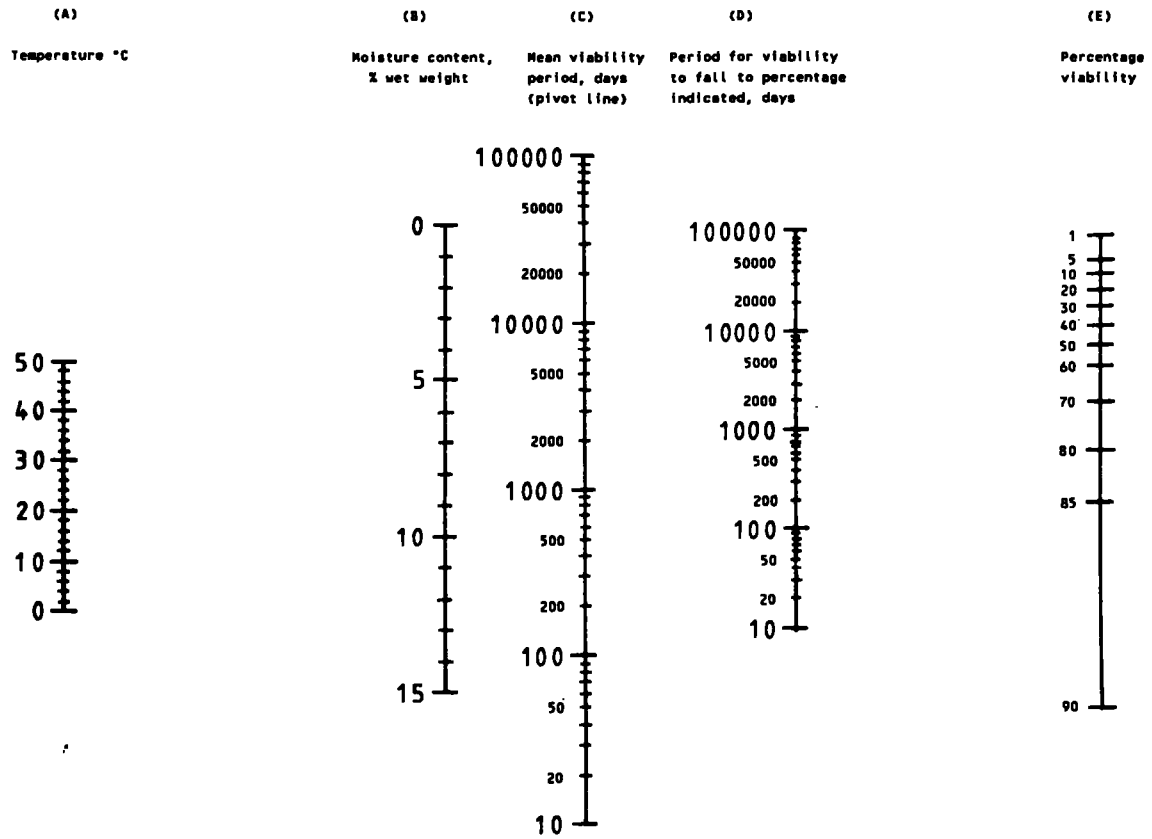
Methods for using this nomograph (after Roberts & Roberts, 1972).

1. To estimate the time taken for viability to fall to any given level at any given temperature and moisture content.

Put a ruler on the required temperature scale (scale A) and moisture content (scale B). Note the value indicated on scale C (this gives the mean viability period). Using this point on scale C as a pivot, move the ruler to indicate any required percentage viability on scale E. The value now indicated on scale D is the time taken for viability to drop to the percentage viability chosen.

2. To find the various combinations of temperature and moisture content necessary to maintain viability above a given value for a given period.

Select a minimum level of viability required on scale E. Select required storage period on scale D. Put a ruler through both points and note the value it indicates on scale C. Using this point on scale C as a pivot, move the ruler through scales A and B. Any position of the ruler indicates a combination of values for temperature (scale A) and moisture content (scale B) which, during the required storage period, viability would be expected to fall to the chosen value.



5.3.2 Factors affecting natural seedling establishment

1. Prosopis woodland seed bank

In the analysis of the physical and chemical properties of Prosopis woodland soils described in Chapter 3, a total of 63 samples were collected and sieved with a 2mm mesh (section 2.5). The large debris extracted from all these soils contained no intact seeds. To quantify the distribution and density of seeds in the Prosopis woodland seed bank, two pits were excavated beneath different trees that were heavy in fruit production. Approximately 4kg samples of soil were taken at four depths, 0cm-10cm, 30cm-40cm, 60cm-70cm and 90cm-100cm, and examined for seeds. There were no intact seeds in both pits below 30cm deep. A maximum of only 10 intact seeds were found loose on both soil surfaces with a small number of recently fallen damaged pods.

The absence of a seed bank in the woodland soil suggests that the seeds of P.cineraria, are not resistant to the environmental conditions of the Sharqiya. Scarification of seeds by the abrasive action of the sand will promote germination in suitably moist soils. Deeply buried seeds that have germinated will die because of the failure of the plumule to reach the surface. These results are comparable to the observation that the seed banks beneath woodland habitats contain small numbers of seeds from the climax trees, in contrast to the seed-rich seed banks from the climax species of arable land or annual grasslands (Livingstone & Allesio, 1968). Harper (1977) has suggested that this is due in part to the larger tree seeds that are heavily predated and vulnerable to decomposition, and in part to the delayed reproduction of the climax trees through effective seed dormancy strategies. Specifically for P.cineraria in the Sharqiya, the absence of a seed bank can also be attributed to environmental damage and to heavy seed infestation by insects (Chapters 3 & 4).

2. Seed dispersal vectors

The absence of large numbers of seed at the soil surface suggests that mature seeds are rapidly dispersed away from the parent tree once they have reached the woodland floor. The role of domestic livestock (goat, sheep, camels and donkeys) grazing in the woodlands as dispersal vectors of P.cineraria seeds was studied by examining fresh animal droppings from beneath the canopy of trees heavy in fruit production. In all the droppings sampled, no intact seeds were found, although evidence of testa fragments were observed. This suggests that the seeds are both damaged by the mechanical action of mastication and are egested whilst chewing the cud. These results show that there is insufficient evidence to support a co-evolutionary strategy between the vertebrates and the establishment of P.cineraria, which occurs in several new world Prosopis species (Mooney et al., 1977). The presence of other vectors of seed dispersal in the woodlands include birds and bats (Chapter 3). Wind and sand shift were the main abiotic vectors for seed dispersal. Strong winds caused mature pods to fall away from the parent trees. Seeds that were released from the pods were light enough to be carried along with the sand or buried beneath shifting dunes.

3. Natural seedling establishment

Under favourable conditions, the initial growth of P.cineraria follows the pattern determined by epigeous germination, where the hypocotyl elongates and raises the cotyledonary leaves above the ground. Natural seedling establishment in the vicinity of mature P.cineraria trees after a heavy period of rainfall in early February of 1986 was assessed in the presence and absence of livestock grazing pressures (section 2.3). The vegetation beneath two fenced and two un-fenced plots, each of 36m², was surveyed two and six weeks after the rains (figure 5.4) to

Figure 5.4

Temporal and spatial effects of natural seedling regeneration in fenced and unfenced *in situ* plots at Al-Kamil, taken 2 and 6 weeks after heavy rainfall in mid February, 1986.

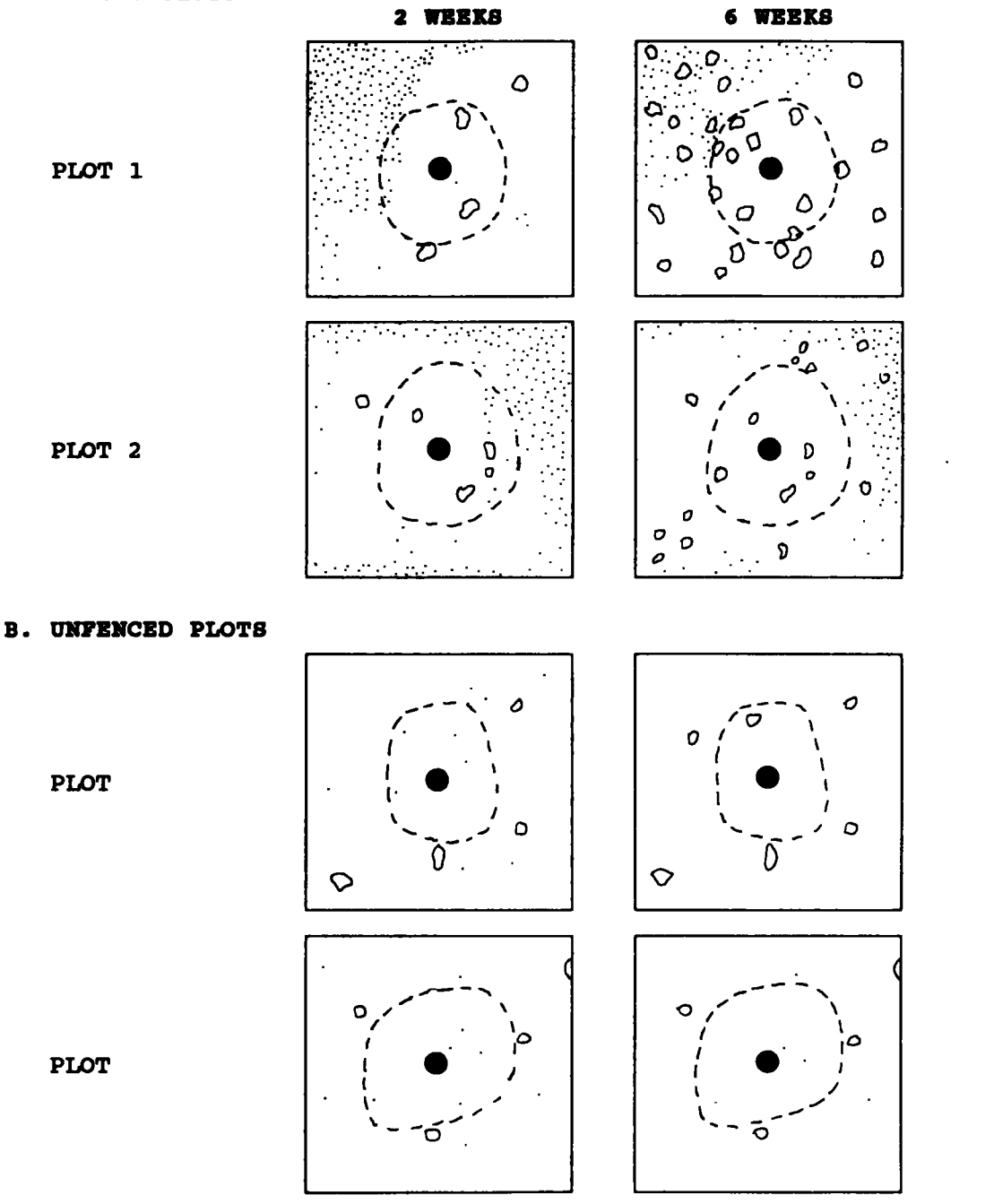


Table 5.7

Results of *in situ* plot studies of natural seedling regeneration taken 2 and 6 weeks after heavy rainfall in mid February 1986.

		TIME AFTER HEAVY RAINFALL				
		2 WEEKS		6 WEEKS		
	Plot	No. seedlings	Density 1 (m^2)	No. seedlings	Density 2 (m^2)	Density 2/ Density 1 ratio
A. Fenced	1	210	5.83	90	2.50	0.43
	2	180	5.00	102	2.83	0.57
	Mean	195	5.42	96	2.65	0.48
B. Un-fenced	3	10	0.28	0	0	0
	4	10	0.28	4	0.11	0.39
	Mean	10	0.28	2	0.06	0.20
Fenced/Un-fenced density ratio			19.36		44.17	

determine the spatial and temporal changes in P.cineraria establishment (table 5.7). Two weeks after the last rainfall seedling density was almost 20 times higher in the fenced plots than in the unfenced plots, which increased to more than 44 times after six weeks. These results clearly demonstrate the impact of heavy grazing pressure on seedling establishment, which can be attributed to the nutritionally rich P.cineraria seedlings that are selectively grazed by the livestock (pers. obs.). In the fenced plots, seedling density decreased by more than half between the two sampling dates, compared to a five fold decrease in the unfenced plots.

The density of seedlings within the fenced plots was highest away from the immediate canopy shade for both sampling dates, which suggests that shade had an inhibitory effect on early seedling growth. The failure of new world Prosopis seedlings to survive beneath the tree canopy has been observed by Haas et al. (1973), in which they also attribute this to the seedlings' intolerance to the canopy shade.

There was a high cover-abundance of Zygophyllum qatarense seedlings at six weeks, which were almost absent at two weeks. Particularly in plot 1 at six weeks, Zygophyllum qatarense seedlings had occupied the spaces previously taken up by P.cineraria seedlings. New growth of this succulent was greatest immediately beneath the tree canopy. These results suggest that plant competition has also affected seedling establishment, such that optimal growth of P.cineraria seedlings occurred under full sunlight where plant competition was lower. The absence of P.cineraria seedlings beneath the canopy may also be due to the allelopathic influences of the parent trees in the same way as P.juliflora, which inhibits the growth of neighbouring plants and inhibits seed germination (Sankhla et al., 1965).

5.3.3 Glasshouse accession trial of P.cineraria

1. Analysis of results

A P.cineraria accession trial was performed under glasshouse conditions in the University of Durham Botanic Gardens (sections 5.2.3 & 5.2.4). Between 7 and 13 weeks of age, morphological measurements (section 5.2.6) were performed on four to six labelled seedlings from each seedlot at four sampling dates, separated by two week intervals. A total of 636 seedlings were measured over the trial period. A general statistical summary of the data is presented in Appendix D. Each variable was standardised to have a mean of zero and a variance of one. Except for shoot height and leaflets/pinna, all other variables were normally distributed. As the transformation of shoot height and leaflets/pinna to normalise their distribution did not generally affect the significance levels in the statistical methods used, the results presented here were determined using un-transformed, standardised variables.

The developmental, geographical and parental variation in seedling morphology and the interactions between these factors were first statistically examined using all the seedlings measured. This was followed by a multivariate analysis to determine the variation in seedling morphology between the 38 seedlot accessions.

2. Developmental variation in seedling morphology

The establishment of even-aged seedlings was complicated by the variable germination period after the scarified seeds were fully imbibed. Variation in growth between seedlings was enhanced by the time required to shed the seed coat from the cotyledonary leaves, occurring between one and five weeks in the seedlings examined. Once the seed coat was shed, further variation was observed in the time required to turn the exposed cotyledonary leaves

green, ranging from two days to over four weeks. The development of the plumule was also not consistent between seeds from individual seedlots.

The tallest seedlings at 13 weeks of age were just under 40mm in height and seedlings with the thickest stems of just under 1.8mm in diameter were woody. At this age the seedlings had a maximum of 6-8 nodes bearing fully developed pinnate leaves. The leaves had a maximum of 8 pairs of pubescent straight leaflets per pinna (leaflets/pinna). Internodal woody thorns developed within 30 days of germination that were broad-based with either straight or slightly acroscopic spikes.

Pearson's correlation coefficient performed on the data has shown that the majority of the variables were positively correlated ($p<0.01$) to each other (table 5.8), as a result of the increase in the number or size of individual characteristics with increasing size of the seedlings. Only the number of mature and immature leaves were not correlated, due to the generally constant production of immature leaves compared to the increase in the mature leaves with increasing seedling age.

The results of one-way ANOVAs of seedling morphology by seedling age are presented in table 5.9, together with the mean values of the seedling variables for each age group. The significant differences between the mean values were examined using Tukey's multiple range test. At 13 weeks, the mean shoot height was 22.47mm which represented an increase of just under 9mm in six weeks. The mean stem diameter increased from 1.41mm to 1.59mm and the mean number of nodes from just under two to over four in the same period. The mean number of mature leaves increased from just under one with about eight leaflets/pinna to just under three with about 10 leaflets/pinna. The mean thorn length increased from 0.26mm to 1.20mm over the sampling period. Except for the number of immature leaves, the

Table 5.8

Pearson's correlation coefficient half-matrix of standardised variables determined from 636 seedlings. All correlations are positive and significant at $p<0.01$, with the exception of mature leaves by immature leaves ($p>0.05$).

	HEIGHT	STEMDIAM	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS	THORNS
HEIGHT	1.000						
STEMDIAM	0.436	1.000					
NODES	0.732	0.516	1.000				
MAT.LVS	0.717	0.534	0.915	1.000			
IMMAT.LVS	0.267	0.116	0.409	0.054NS	1.000		
LEAFLETS	0.399	0.294	0.546	0.517	0.173	1.000	
THORNS	0.724	0.422	0.635	0.666	0.129	0.378	1.000

Table 5.9

Developmental variation in seedling morphology. Summary of group means and significance results of one-way ANOVAs of seedling morphology by seedling age (n=159 seedlings sampled in each age period).

	HEIGHT (mm)	STEMDIAM (mm)	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS ($pinna^{-1}$)	THORNS (mm)
AGE(WEEKS)	***	***	***	***	NS	***	***
7	13.69	1.41	1.93	0.76	0.81	8.12	0.26
9	17.58	1.50	3.03	1.67	0.84	8.90	0.83
11	20.36	1.56	3.83	2.42	0.87	9.51	1.10
13	22.47	1.59	4.25	2.85	0.88	9.92	1.20

seedling variables were highly significantly different with age ($p<0.001$). This was a result of most variables increasing in magnitude with increasing age. However, there was no significance in the shoot height, stem diameter and thorn length of seedlings between 11 and 13 weeks of age. The number of leaflets/pinna generally increased with age, but there was no significant difference in this variable between 9, 11 and 13 weeks of age. The reduction in variability with increasing seedling age may have been influenced by the onset of cooler temperatures and shorter day lengths in the glasshouse towards the end of the trial (section 5.2.3).

3. Geographical variation in seedling morphology

One-way ANOVAs of seedling morphology by provenance origin show that shoot height was highly significantly different between provenances ($p<0.001$), as a result of the taller seedlings of EPZ origin (table 5.10a). This suggests a bio-geographical variation in the rate of shoot height growth. The remaining morphological variables were not significantly different between the provenances.

Using discriminant function analysis on the seedling data, the two provenances were significantly discriminated at $p<0.001$ level, such that 59.24% of the seedlings were classified into the correct provenances (table 5.10b). This analysis required only four discriminating variables, which were dominated by shoot height in contrast to the number of nodes, the length of the thorns and, to a lesser extent, the number of leaflets/pinna. These variables were expressed in the form of one discriminant function, from which the mean scores for this function for EPZ and CPZ were -0.258 and 0.159 respectively. This shows that EPZ seedlings were separated from CPZ seedlings by being characteristically taller with fewer nodes, shorter thorns and, to a lesser extent, marginally fewer leaflets/pinna.

Table 5.10

Geographical variation in seedling morphology (n=636).

A. Summary of group means and significance results of one-way ANOVAs of seedling morphology by provenance origin (EPZ n=244; CPZ n=392).

	HEIGHT (mm)	STEMDIAM (mm)	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS (pinna^{-1})	THORNS (mm)
PROVENANCE	***	NS	NS	NS	NS	NS	NS
EPZ	20.08	1.51	3.25	1.91	0.87	9.27	0.83
CPZ	17.56	1.52	3.26	1.93	0.83	9.01	0.85

B. Discriminant function analysis on seedling variables between provenances.

1. F-statistic and significance between provenances

	EPZ
CPZ	6.436 ***

2. Standardised discriminant function coefficients

Total variance explained (%)	100
HEIGHT	-1.690
NODES	0.928
LEAFLETS	0.349
THORNS	0.771

4. Parental variation in seedling morphology

One-way ANOVAs of seedling morphology by parental origin show that all variables except the number of immature leaves were significantly different between the parent types (table 5.11a). This was mainly as a result of the significantly higher values for most of the variables in type 5 seedlings. Type 3 seedlings had significantly smaller stem diameters than all other seedling types, whilst type 8 seedlings had significantly more leaflets/pinna than both type 1 and type 3 seedlings.

Discriminant function analysis was also performed on the morphological data to quantify the variation in the seedlings of different parent types (table 5.11b). This analysis required only four variables (thorn length, leaflets/pinna, stem diameter and shoot height) to correctly classify 36.7% of the seedlings and resulted in the significant discrimination between all combinations of parent types. Three discriminant functions were produced in this analysis. As the first two functions accounted for 81.6% of the variation in the data, only these were examined. The first function was dominated by the thorn length in contrast to shoot height and number of leaflets/pinna, whilst the second function was dominated by stem diameter in contrast to shoot height. A scatter plot of the mean scores of these two functions for each parent type is presented in figure 5.5. This plot clearly shows that type 1 and 8 seedlings were the most similar in morphology, whilst type 3 and 5 seedlings had the greatest departure in morphology. The combined effects of the first two functions show that type 5 seedlings had the longest thorns of all seedling types. Type 3 seedlings had the shortest thorns and the most leaflets/pinna of all seedling types. Although type 1 and 8 seedlings were the closest in morphology, they were significantly differentiated as a result of type 1 seedlings which tended to be taller, with smaller stems and shorter thorns than type 8 seedlings.

Table 5.11

Parental variation in seedling morphology (n=636).

A. Summary of group means and significance results of one-way ANOVAs of seedling morphology by parent tree type (type 1 n=220; type 3 n=168; type 8 n=156; type 5 n=92).

	HEIGHT (mm)	STEMDIAM (mm)	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS (pinna^{-1})	THORNS (mm)
PARENT	**	***	**	***	NS	***	***
Type 1	18.21	1.54	3.23	1.90	0.87	8.88	0.76
Type 3	18.07	1.47	3.00	1.70	0.83	8.07	0.63
Type 8	18.33	1.52	3.29	1.93	0.84	9.56	0.85
Type 5	20.40	1.54	3.74	2.37	0.85	10.80	1.45

B. Discriminant function analysis on seedling variables between parent types.

1. F-statistics and significance between pairs of parent types

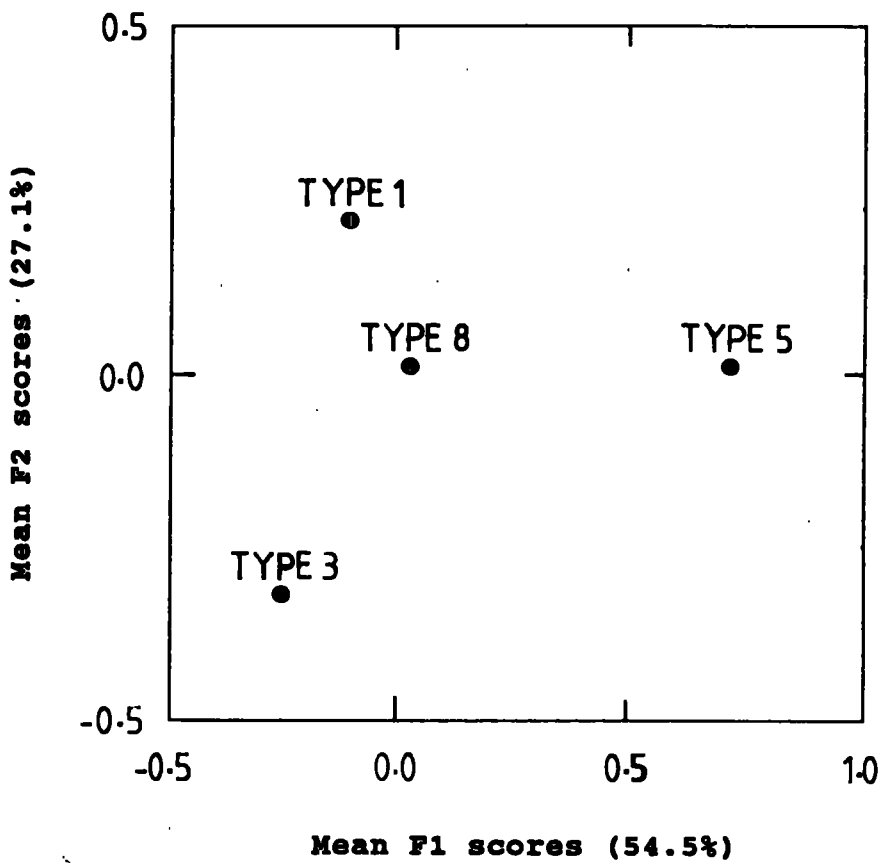
	type 1	type 3	type 8
type 3	8.521 ***		
type 8	3.437 **	8.084 ***	
type 5	12.365 ***	17.561 ***	7.373 ***

2. Standardised discriminant function coefficients

	Discriminant functions		
	1	2	3
Total variance explained (%)	54.5	27.1	18.4
HEIGHT	-0.527	0.520	-0.427
STEM DIAMETER	0.160	-1.021	0.384
LEAFLETS	-0.459	0.217	0.887
THORNS	1.038	0.440	0.636

Figure 5.5

Scatter plot of parent type mean scores for the first 2 discriminant functions (n=636 seedlings). Where figures in parentheses are the percentages of variance associated with each function.



5. Interactions between developmental, geographical and parental variation

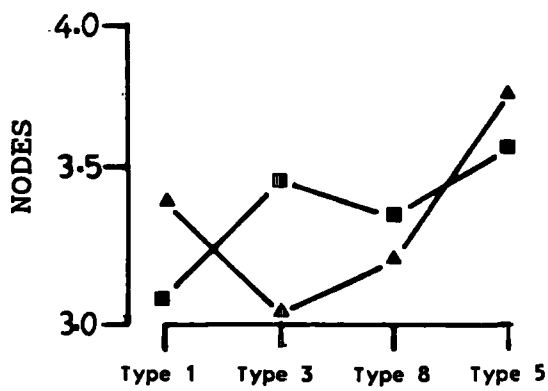
The results of two-way ANOVAs of seedling morphology between factorial pairs using seedling age, provenance origin and parent type are presented in figure 5.6, with categorical line plots of all the significant interactions. There were no significant differences in the change in morphology with time of seedlings from each provenance. The significant difference of shoot height between provenances determined by one-way ANOVA was therefore a result of the significantly taller EPZ seedlings by 7 weeks of age. In all other variables, seedling morphology between the provenances followed the whole population in not being significantly affected by their geographical origin. There was also no significant difference in the change in seedling morphology between parent types. The significant differences of the seedling variables between parent types determined by one-way ANOVAs were therefore dominated by the significant differences in the morphology of type 5 seedlings also by 7 weeks of age. These results show that the greatest morphological variation in the seedlings occurred within the first 7 weeks. This morphological homogeneity with increasing seedling age may have been in part promoted by the increasingly limiting environmental conditions inside the glasshouse.

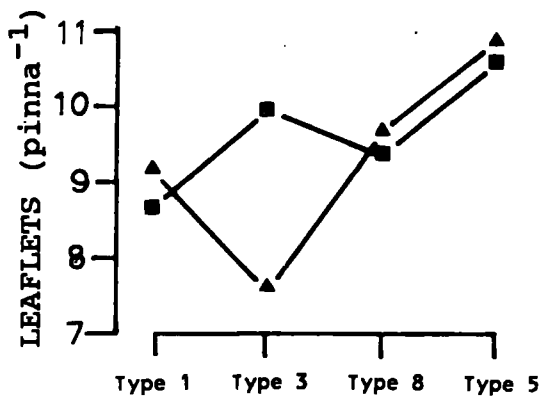
With the exception of node number, leaflets/pinna and thorn length, the seedling variables by both provenance origin and parent type were not significant. Therefore, the significant differences of shoot height between the provenances and parent types determined by the one-way ANOVAs were mainly as a result of the consistently taller type 1, 3 and 8 seedlings from the EPZ, and the taller type 5 seedlings from the CPZ. The significantly smaller stems of type 3 seedlings and the significantly larger numbers of mature leaves in type 5 seedlings determined by the one-way ANOVAs were consistent between the provenances. The significant interactions in these two-way ANOVAs were

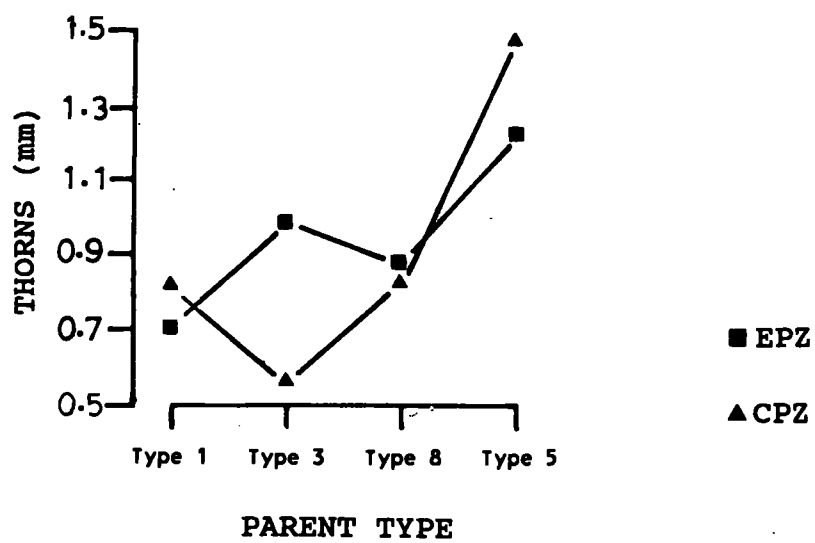
Figure 5.6

Results of two-way ANOVAs of the morphological variables by seedling age, provenance origin and parent type, with plots showing significant interactions (n=636).

	HEIGHT	STEMDIAM	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS	THORNS
AGE(weeks) & PROVENANCE	NS	NS	NS	NS	NS	NS	NS
AGE(weeks) & PARENT	NS	NS	NS	NS	NS	NS	NS
PROVENANCE & PARENT	NS	NS	*	NS	NS	***	*







mainly as a result of type 3 seedlings having more nodes, more leaflets/pinna and longer thorns when from the EPZ. Type 1 seedlings also had more nodes when from the CPZ. The significantly longer thorns in type 5 seedlings determined in the one-way ANOVA was found to be consistent between the provenances.

6. Seedlot variation in seedling morphology at 13 weeks of age

The previous sections using the complete dataset have shown that there were specific differences in the morphology of the seedlings between the provenances and between the parent types. This section examines the variation in the size and morphology of 13 week old seedlings (n=158) between the 38 seedlots. Of the standardised variables sampled from 13 week old seedlings, all except the immature leaves were highly positively correlated to each other (table 5.12a). The six correlated variables were collectively examined using principal components analysis. As the first 3 principal components accounted for 85.9% of the variation in the data, only these were examined (table 5.12b). The first principal component (F1) was the positive correlation between all six variables, and was used as an index of seedling size. The second principal component (F2) was dominated by the stem diameter in contrast to the number of leaflets/pinna, whilst the third principal component (F3) was due to both the leaflets/pinna and the stem diameter in contrast to the shoot height and thorn length.

The mean and standard error for the first principal component were determined for each seedlot (figure 5.7). Type 1 seedlings from the EPZ were the most variable in size within the seedlots. In contrast, type 5 and 8 seedlings were the least variable in size within the seedlots from both provenances. As each seedlot was sampled from a single tree, the greater within-seedlot variation of type 1 seedlings suggests that cross-pollination is more

Table 5.12

Seedlot variation in the morphology of 13 week old seedlings (n=159) for 38 seedlots.

A. Pearson's correlation coefficient half-matrix of the standardised seedling variables. All correlations are positive and highly significant at p<0.001, except where indicated.

	HEIGHT	STEMDIAM	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS	THORNS
HEIGHT	1.000						
STEMDIAM	0.314	1.000					
NODES	0.694	0.374	1.000				
MAT.LVS	0.694	0.412	0.907	1.000			
IMMAT.LVS	0.150NS	0.014NS	0.367	-0.041NS	1.000		
LEAFLETS	0.345	0.208**	0.530	0.542	0.040NS	1.000	
THORNS	0.696	0.331	0.552	0.604	0.013NS	0.414	1.000

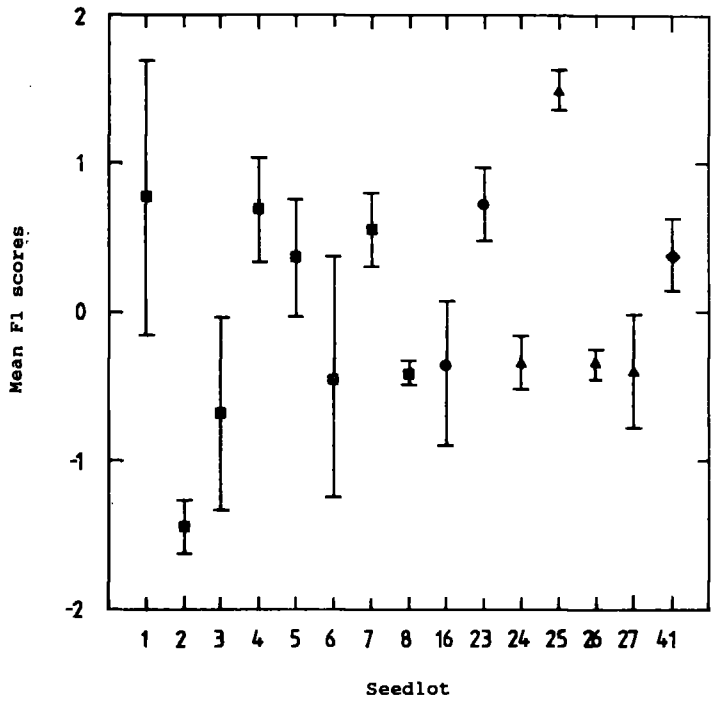
B. Score coefficients of the first 3 principal components determined by principal components analysis of 6 standardised seedling variables.

	Principal components		
	F1	F2	F3
Total variance explained (%)	60.7	13.5	11.7
HEIGHT	0.228	0.030	-0.588
STEMDIAM	0.143	-0.991	0.391
NODES	0.247	0.113	0.060
MAT.LVS	0.253	0.070	0.061
LEAFLETS	0.176	0.481	0.837
THORNS	0.215	0.019	-0.462

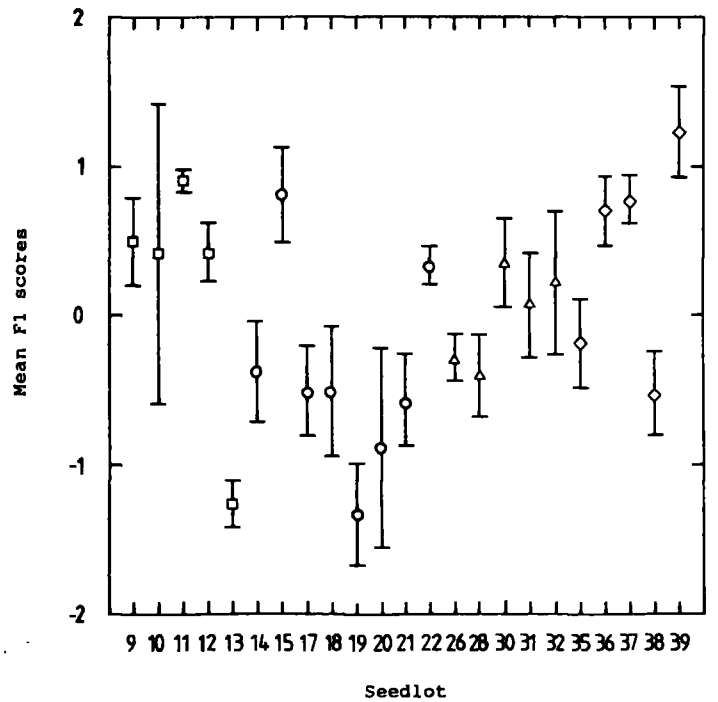
Figure 5.7

Seedling size variation between seedlots (n=38 seedlots and n=159 seedlings) at 13 weeks of age from each provenance and each parent type, using the mean scores and standard errors of the first principal component (F1).

A. Eastern Prosopis Zone (n=60)



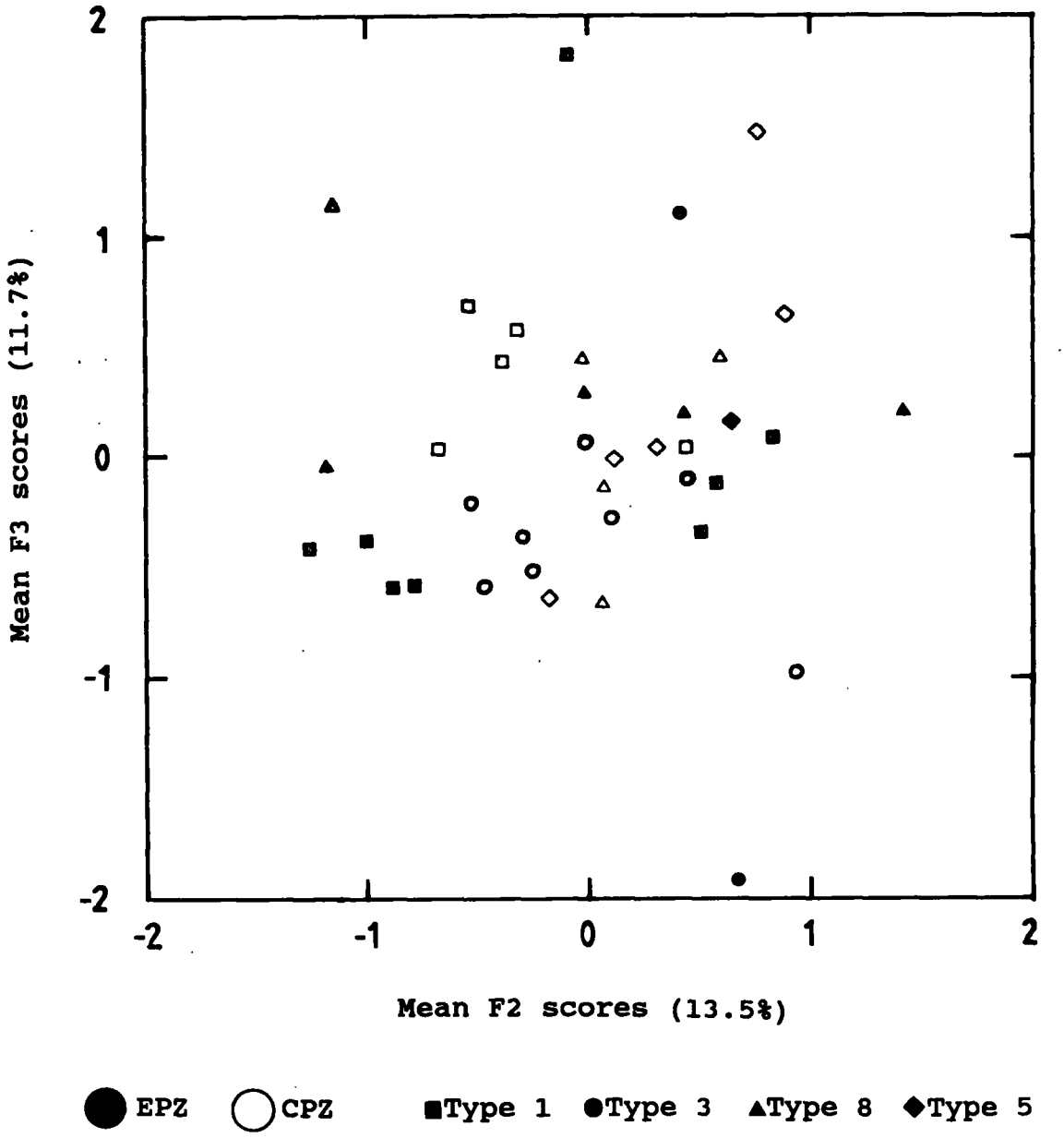
B. Central Prosopis Zone (n=99)



● EPZ ○ CPZ ■ Type 1 ● Type 3 ▲ Type 8 ◆ Type 5

Figure 5.8

Seedling morphological variation between seedlots (n=38 seedlots and n=159 seedlings) at 13 weeks of age from each provenance and each parent type, using the mean scores for the second (F2) and third (F3) principal components. Where figures in parentheses are the percentages of variance associated with each component.



common in type 1 trees. Figure 5.7 also shows some variation between seedlots of different geographical and parental origin. This suggests that genetic differences in the parent trees have been passed on to their seedlings.

The variation between the seedlots was further examined in a scatter plot of the mean scores for each seedlot for the F2 and F3 principal components (figure 5.8). This plot removes the dominating influence of seedling size so that the spatial proximity of the seedlots can be used as a measure of the morphological variation of the seedlings between the seedlots. This plot shows that the morphological variation was higher between seedlots sampled from the EPZ as a result of the greater spread of the EPZ seedlots. Two of these seedlots showed the greatest variation in seedling morphology by having the highest and lowest values of the F3 principal component. Parental origin had a greater influence on the seedlots from the CPZ, as shown by the tight clustering of type 1 and 3 seedlots. This method has allowed the early identification of morphological variation in the seedlots, such that there was greater between-seedlot variation in the EPZ and a greater parental influence in seedlots from the CPZ.

5.3.4 Salinity trial of P.cineraria

1. Analysis of results

This section presents the results of a salinity trial of P.cineraria performed under glasshouse conditions in the University of Durham Botanic Gardens (sections 5.2.3 & 5.2.5). For the controls (0% salinity) and three treatments (1% salinity, 2% salinity and 4% salinity), morphological measurements (section 5.2.6) were performed on 222 seedlings from the selected seedlot accessions at 7 weeks of age, and repeated at 9, 11 and 13 weeks of age on the survivors. A total of 597 seedlings were measured over the

trial period (see Appendix D for statistical summary). Each variable was standardised to have a mean of zero and a variance of one. Statistical analyses were performed on the standardised variables of all the seedlings, to determine the effects of salinity on the developmental, geographical, and parental variation in seedling morphology. This was followed by a multivariate analysis to determine the effects of the 1% salinity treatment on the variation in the morphology of 13 week old seedlings between the seedlot accessions. Finally, a correlation between salinity tolerance and the geographical origin of the seedlots was examined.

2. General effects of salinity on seedling morphology

Seedling survival at 4, 7, 9, 11 and 13 weeks of age in each salinity treatment was expressed as the number of survivors as a percentage of the total number of seedlings at four weeks of age (figure 5.9). In the three salinity treatments, all seedlings survived for at least three weeks after first applying the saline solutions. After this period of salt tolerance, seedling survival in 1% salinity decreased at a rate of 6% seedlings/week. In 2% and 4% salinity, seedling survival decreased at a rate of 13.5% and 25.0% seedlings/week respectively. All seedlings died after 7 weeks in 4% salinity. This early tolerance of *P.cineraria* seedlings to high salinities is comparable to a number of *Prosopis* species studied by Felker *et al*. (1981c) in a series of seedling trials, in which all species examined tolerated NaCl at 6000mgdm^{-3}, whilst *P.tamarugo* seedlings grew well in 18,000mgdm^{-3} and survived in 36,000mgdm^{-3}.

The results of one-way ANOVAs of seedling morphology by salinity treatment are presented in table 5.13, together with the mean values of the seedling variables for each categorical attribute. The significance between the mean values were examined using Tukey's multiple range test.

Figure 5.9

Salinity tolerance of glasshouse grown P.cineraria seedlings. At start of salt application (4 week old seedlings): control n=56; 1% n=50; 2% n=57; 4% n=59.

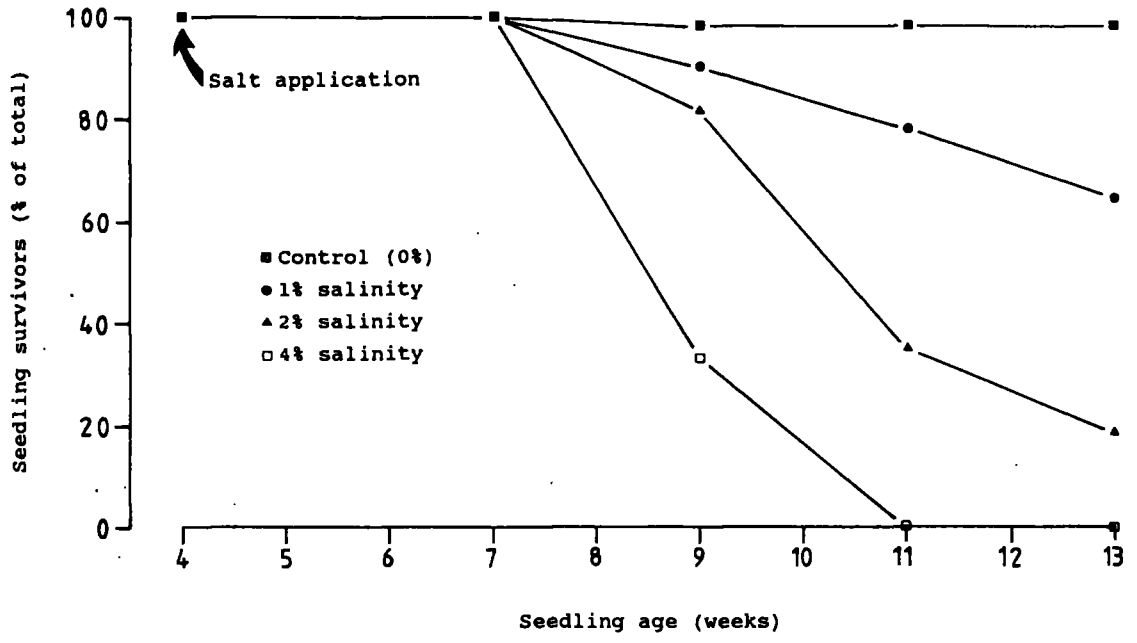


Table 5.13

Summary of treatment means and significance results of one-way ANOVAs of seedling morphology by salinity (control n=220; 1% n=164; 2% n=125; 4% n=78).

	HEIGHT (mm)	STEMDIAM (mm)	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS (pinna^{-1})	THORNS (mm)
SALINITY	***	***	***	***	***	***	**
0%	17.94	1.52	3.23	1.93	0.82	8.92	0.74
1%	16.27	1.50	2.53	1.48	0.48	7.72	0.56
2%	13.99	1.47	2.40	1.26	0.56	7.35	0.49
4%	14.36	1.43	2.27	0.77	0.63	6.56	0.38

There were significant differences in all the seedling variables between the salinity treatments ($p<0.01$), which was generally as a result of the decrease in the magnitude of the variables with increasing salinity. There were no significant differences in either the shoot height or stem diameter of seedlings between the control and 1% salinity, but these variables were significantly larger in the control than in both 2% and 4% salinity. The numbers of nodes, mature and immature leaves and leaflets/pinna were all significantly higher in the control than in the three salinity treatments. The thorn length was significantly higher in the control than in both 2% and 4% salinity, but was not significantly different between the control and 1% salinity. All variables except the mature leaves were not significantly different between 2% and 4% salinity, as a result of the large number of seedling fatalities at the higher concentrations which led to an absence of seedlings at 11 and 13 weeks in 4% salinity.

3. Salinity and developmental variation

All variables except immature leaves were highly significantly different with age (figure 5.10a), as a result of the increase in the magnitude of the variables over time. However, there were no significant differences between the shoot height, stem diameter, leaflets/pinna and thorn length between 11 and 13 week old seedlings.

The results of two-way ANOVAs of seedling morphology by both salinity treatment (control, 1% salinity and 2% salinity only due to high seed fatalities in 4% salinity) and seedling age show that there were no significant differences between each treatment in the rate of change of the variables: shoot height, stem diameter, leaflets/pinna and thorn length (figure 5.10b). Thus the significant trends of increasing in magnitude with increasing time and decreasing salinity treatment were consistent within the seedlings examined. This indicates the greatest effect of

Figure 5.10

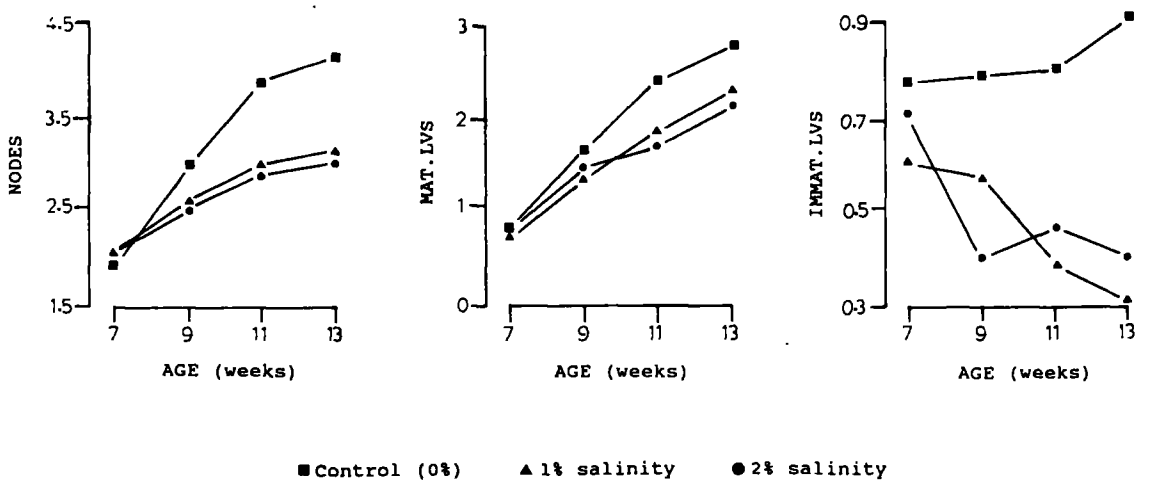
Salinity and developmental variation in seedling morphology (n=587).

A. Summary of group means and significance results of one-way ANOVAs of seedling morphology by seedling age (7 weeks n=222; 9 weeks n=160; 11 weeks n=111; 13 weeks n=94).

	HEIGHT (mm)	STEMDIAM (mm)	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS (pinna^{-1})	THORNS (mm)
AGE(weeks)	***	***	***	***	NS	***	***
7	13.12	1.42	1.98	0.82	0.72	7.37	0.24
9	15.94	1.47	2.71	1.40	0.56	7.28	0.59
11	18.54	1.55	3.33	2.12	0.61	8.82	0.86
13	20.89	1.58	3.81	2.59	0.65	9.35	1.06

B. Results of two-way ANOVAs of the morphological variables by salinity and seedling age, with plots showing significant interactions (n=509). The 4% treatment was excluded from this analysis due to 100% fatalities in 11 and 13 week old seedlings (n=509).

	HEIGHT	STEMDIAM	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS	THORNS
SALINITY & AGE	NS	NS	**	*	**	NS	NS



salinity on these variables occurred between four weeks (start of saline application) and seven weeks of age. The significant interactions of nodes and mature leaves between salinity treatment and seedling age were due to the seedlings grown in the control, which developed nodes and mature leaves at a faster rate than seedlings grown in both 1% and 2% salinity. The significant interaction of immature leaves was due to their marginal increase with age in the controls and their decrease with age in both 1% and 2% salinity.

4. Salinity and geographical variation

One-way ANOVAs of seedling morphology by provenance origin show that shoot height, node number and leaflets/pinna were significantly higher in magnitude in the EPZ seedlings (figure 5.11a). Stem diameter, mature and immature leafs and thorn length were not significantly different between the provenances. These results suggest that there exists a greater inherent salinity tolerance in the EPZ seedlings.

The results of two-way ANOVAs of seedling morphology by both salinity treatment and provenance origin show that there were no significant interactions in the variables stem diameter, node number and mature leaves (figure 5.11b). Thus the significant decreases in the magnitude of these variables with increasing salinity were consistent between the provenances, and the higher number of nodes in EPZ seedlings occurred in all the treatments. Height, leaflets/pinna and thorn length were significantly greater in EPZ seedlings mainly as a result of the larger EPZ seedlings in the control treatments. The variation of these variables between the provenances generally decreased with increasing salinity, with the exception of the shoot height of EPZ seedlings which did marginally increase between the 1% and 2% treatments. The significant interaction of immature leaves in this two-way ANOVA was a result of their

Figure 5.11

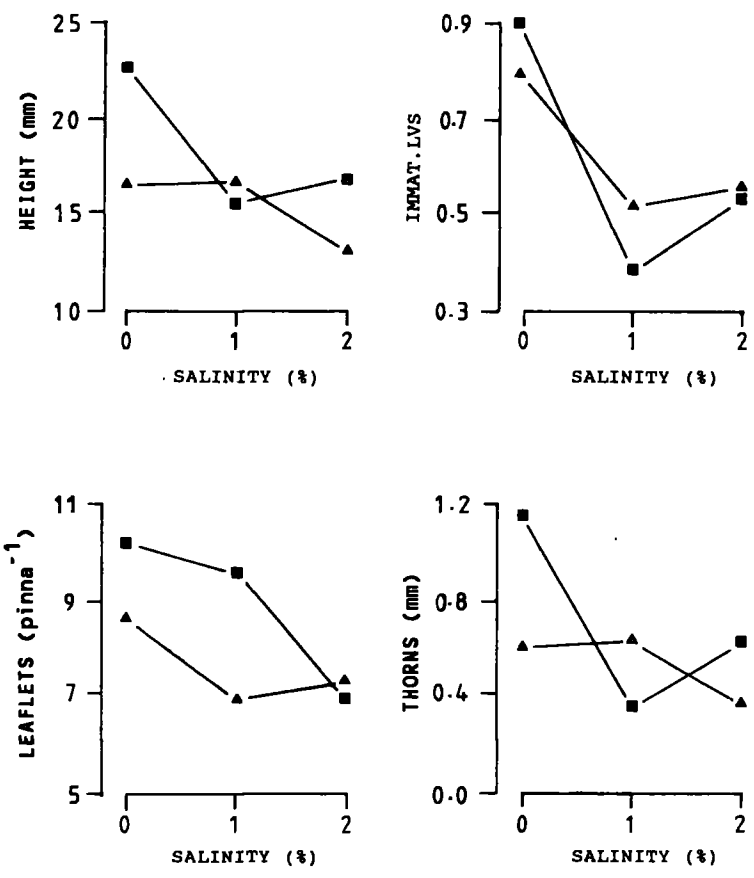
Salinity and geographical variation in seedling morphology (n=587).

A. Summary of group means and significance results of one-way ANOVAs of seedling morphology by provenance origin (EPZ n=148; CPZ n=439).

	HEIGHT (mm)	STEMDIAM (mm)	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS ($pinna^{-1}$)	THORNS (mm)
PROVENANCE	***	NS	**	NS	NS	***	NS
EPZ	18.67	1.50	2.97	1.65	0.68	8.84	0.68
CPZ	15.31	1.49	2.65	1.46	0.63	7.64	0.55

B. Results of two-way ANOVAs of the morphological variables by salinity and provenance origin, with plots showing significant interactions. The 4% treatment was excluded from this analysis due to 100% fatalities in 11 and 13 week old seedlings (n=509).

	HEIGHT	STEMDIAM	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS	THORNS
SALINITY & PROVENANCE	***	NS	NS	NS	**	**	***



lower number in CPZ seedlings grown in the 1% treatment.

5. Salinity and parental variation

All variables except immature leaves were significantly different between parent types (figure 5.12a). The significance of shoot height was due almost entirely to the taller type 8 seedlings. Stem diameters were significantly different between parent types, except for type 8 seedlings whose diameters were not significantly different to both type 1 and type 3 seedlings. The number of nodes in type 8 seedlings was generally significantly higher than all other seedling types. The significance of the mature leaves by parent type was due to the higher numbers of mature leaves in type 8 seedlings than in type 3 seedlings. The significance of leaflets/pinna was explained by the lower number of leaflets/pinna in type 3 seedlings than in both type 5 and type 8 seedlings. Thorn length was significantly different between the parent types except between type 5 seedlings and both type 1 and type 8 seedlings.

Significant interactions of two-way ANOVAs of seedling morphology between the salinity treatments and parent types were observed for all variables except immature leaves (figure 5.12b). The significantly higher numbers of immature leaves that were found in the controls than in the salinity treatments occurred in each parent type. The variables shoot height, stem diameter, mature leaves and thorn length were higher in type 8 seedlings grown in 1% salinity than in both the control and 2% salinity. These results show that type 8 seedlings were better adapted to growing in moderately saline conditions than in pure water. In contrast, most variables in type 3 seedlings were smaller than all other seedling types in the salinity treatments, with the exception of the stem diameter which was intermediate in size. The variables stem diameter, leaflets/pinna and thorn length in type 3 seedlings did

Figure 5.12

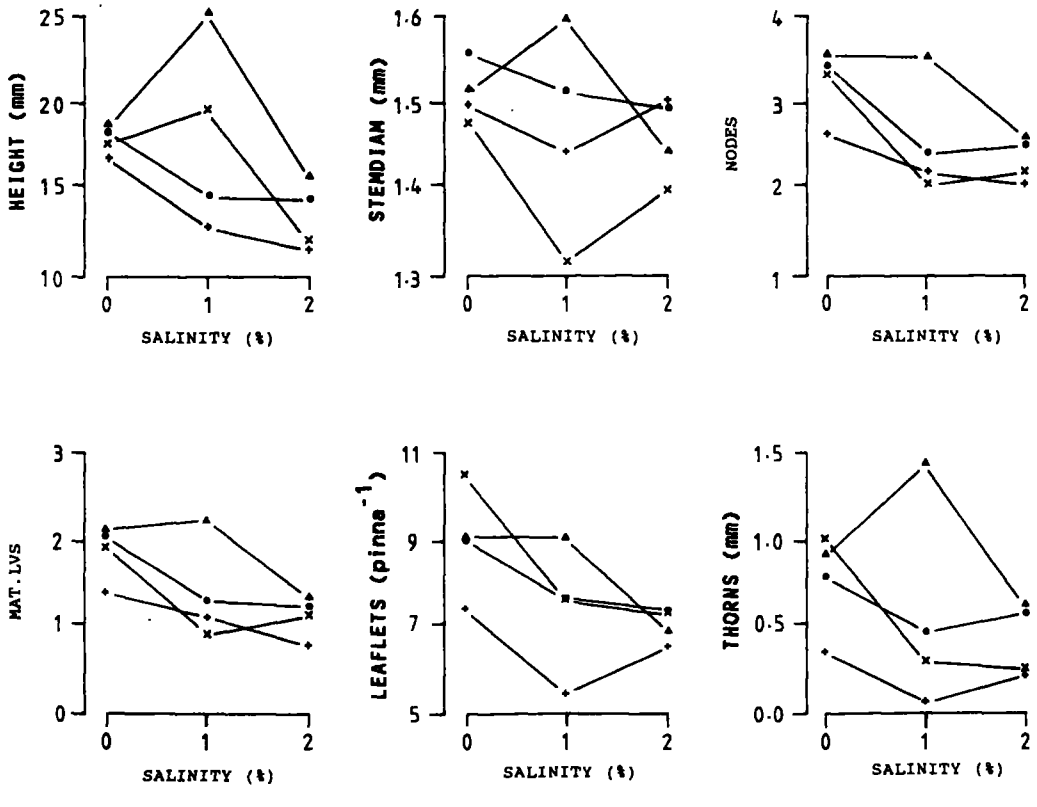
Salinity and parental variation in seedling morphology (n=587).

A. Summary of group means and significance results of one-way ANOVAs of seedling morphology by parent type (type 1 n=308; type 3 n=108; type 8 n=108; type 5 n=63).

	HEIGHT (mm)	STEMDIAM (mm)	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS ($pinna^{-1}$)	THORNS (mm)
PARENT	**	***	**	**	NS	**	***
Type 1	15.81	1.51	2.74	1.48	0.64	7.92	0.58
Type 3	14.67	1.47	2.36	1.25	0.63	6.98	0.24
Type 8	18.63	1.51	3.05	1.78	0.68	8.32	0.90
Type 5	16.19	1.41	2.78	1.60	0.64	9.02	0.66

B. Results of two-way ANOVAs of the morphological variables by salinity and parent type, with plots showing significant interactions. The 4% treatment was excluded from this analysis due to 100% fatalities in 11 and 13 week old seedlings (n=509).

	HEIGHT	STEMDIAM	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS	THORNS
SALINITY & PARENT	***	**	*	*	NS	*	**



increase in magnitude between the 1% and 2% salinity treatments, which suggests some morphological adaptations to surviving in higher salinities. Type 1 seedlings were intermediate in morphology, which decreased with increasing salinity. The variables of type 5 seedlings were generally high in the control. These decreased between the control and 1% salinity. In 2% salinity, type 5 seedlings had stunted shoots with thick stem diameters.

6. Salinity and seedlot variation

The variation in size and morphology of 13 week old seedlings grown in the controls and 1% salinity treatments between the seedlots were also examined. The 2% and 4% salinity treatments were not included in this analysis because of the extent of seedling fatalities which occurred. Severely stressed seedlings grown in 1% salinity which resulted in total leaf drop were also not included in this analysis. A Pearson's correlation coefficient half-matrix of the standardised morphological variables was determined from 79 seedlings from 9 seedlots (table 5.14a). The majority of the variables were positively correlated, with the exceptions of stem diameter by both shoot height and leaflets/pinna, and most combinations with immature leaves. A principal components analysis was performed on the correlated variables, from which the first three principal components accounted for 86.2% of the variation in the data (table 5.14b). The first principal component (F1) was used as an index of seedling size. The second principal component (F2) was dominated by the stem diameter in contrast to the number of leaflets/pinna, whilst the third principal component (F3) was dominated by the number of leaflets/pinna in contrast to the shoot height.

The means and standard errors of F1 for the controls and 1% salinity treatments in each seedlot are presented in figure 5.13, and the significance of these means between the treatments within each seedlot were determined by t-

Table 5.14

Salinity and seedlot variation in the morphology of 13 week old seedlings (n=79) for 9 seedlots between the control (n=47 seedlings) and 1% treatment (n=32 seedlings).

A. Pearson's correlation coefficient half-matrix of the standardised morphological variables. All correlations are positive and significant at p<0.001, except where indicated.

	HEIGHT	STEMDIAM	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS	THORNS
HEIGHT	1.000						
STEMDIAM	0.206NS	1.000					
NODES	0.722	0.252*	1.000				
MAT.LVS	0.677	0.292*	0.891	1.000			
IMMAT.LVS	0.362**	-0.020NS	0.562	0.214NS	1.000		
LEAFLETS	0.322**	0.117NS	0.429	0.541	0.141NS	1.000	
THORNS	0.608	0.389**	0.597	0.644	0.159NS	0.404	1.000

B. Score coefficients of the first 3 principal components determined by principal components analysis of 6 standardised seedling variables.

	Principal components		
	F1	F2	F3
Total variance explained (%)	58.6	15.6	12.0
MAT.LVS	0.263	0.128	0.034
NODES	0.255	0.143	0.269
HEIGHT	0.232	0.105	0.521
THORNS	0.230	-0.195	0.016
LEAFLETS	0.172	0.351	-0.985
STEMDIAM	0.119	-0.928	-0.271

Figure 5.13

Seedling size variation between 9 seedlots (n=79 seedlings) at 13 weeks of age grown under the control (n=47) and 1% (n=32) salinity treatments, using the mean scores and standard errors of the first principal component (F1).

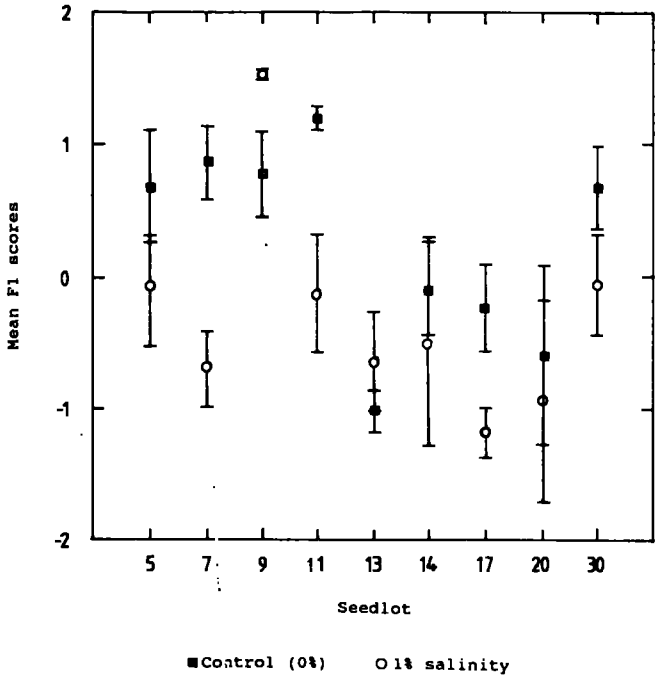
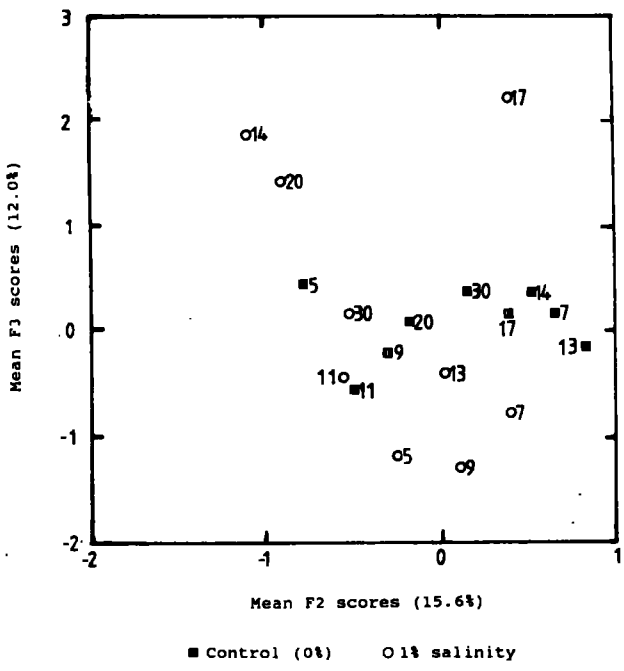


Figure 5.14

Seedling morphological variation between 9 seedlots (n=79 seedlings) at 13 weeks of age, grown under the control (n=47) and 1% (n=32) salinity treatments, using the mean scores for the second (F2) and third (F3) principal components. Where figures in parentheses are the percentages of variance associated with each component.



tests. The results show that the effect of salinity on the mean size of the seedlings in the seedlots was not consistent between the seedlots. Seedlings from Seedlots 7 and 11 in the controls were significantly larger ($p<0.05$) than the seedlings from the same seedlots in 1% salinity. There was no significant difference in the size of seedlings between the controls and 1% salinity treatments for all other seedlots. However, seedlings from Seedlots 9 and 13 were smaller in the controls than in the 1% salinity treatments, which suggests a marginally higher degree of salinity tolerance in these seedlots.

The variation in the morphology of the seedlings grown in the control and 1% salinity treatment for each seedlot was examined by plotting the mean scores of the second (F2) and third (F3) principal components (figure 5.14), which accounted for 27.6% of the variation in the data. The clustering of the controls and the spread of the 1% salinity treatments in this plot shows that salinity has increased the morphological variation of the seedlings between the seedlots. This plot also shows that the salinity-induced departures in morphology from the controls were not consistent between the seedlots. In Seedlots 5, 7 and 9, salinity increased the number of leaflets/pinna and the stem diameter and reduced the shoot height and node number. In contrast, salinity decreased the number of leaflets/pinna and increased the shoot height and stem diameter of seedlings from Seedlots 14 and 20. In seedlings from Seedlots 13 and 30, salinity reduced the leaflets/pinna and increased the stem diameter without any change in the shoot height or node number. Another salinity-induced departure in morphology from the control occurred in seedlings from Seedlot 17, in which 1% salinity increased the shoot height and node number but did not affect the leaflets/pinna or stem diameter. There was no apparent effect of 1% salinity on the morphology of seedlings from Seedlot 11, despite the significantly larger seedlings in the seedlot control.

These results show that salinity-induced variation in morphology of seedlings between the seedlots tested was high. This shows that the geographical and parental variation between the seedlots have influenced the salinity tolerance and morphological responses of the seedlings.

7. Geographical salinity tolerance of seedlot accessions

This section examines the relationship between the salinity tolerance and the geographical origin of the seedlots. Seedling survival (as a percentage of the total number of seedlings at four weeks of age) for the controls and each salinity treatment was determined for each of the seedlots in the trial (table 5.15). These data were used to rank the salinity tolerance of the seedlots tested using a salinity index. This index was determined for each salinity treatment by the following method:

$$\text{Salinity index} = \frac{(\Sigma\% \text{ survivors}) \times S}{100} \qquad \text{Equation 5.3}$$

Where $\Sigma\%$ survivors = sum of % survivors at each age

S = salinity concentration (%)

For each seedlot the sum of the salinity indices was determined and the results have been arranged in the longitudinal order in which they were sampled from the provenances (table 5.16). Also in this table, the change in the size and morphology of the seedlings grown in the control and 1% salinity treatments are also summarised. This table shows that seedlots from the central area of the CPZ produced seedlings that were either similar or larger in size than the controls, with the characteristic salinity-induced increase in the stem diameters. This suggests some geographic specificity to salinity tolerance within the CPZ. At the north and south extremes, the influence of salinity was greatest. The variation in the electrical conductance of the aquifer water across the CPZ determined from well data (Appendix E) supplied by the

Table 5.15

Seedling survival rates under the control and 3 salinity treatments (1%, 2% & 4%). At the time of salt application (4 week old seedlings): control n=56; 1% n=50; 2% n=57; 4% n=59. Seedlots from CPZ have been arranged in the longitudinal order in which they were sampled from the provenance. Where n/d = not determined.

		% SEEDLING SURVIVAL			
Seedlot accession	Salinity treatment	Sampling age (weeks) 7	9	11	13
EPZ 5	0%	100	100	100	100
	1%	100	80	80	80
	2%	100	100	0	0
	4%	100	40	0	0
EPZ 7	0%	100	100	100	100
	1%	100	100	100	100
	2%	100	67	50	17
	4%	100	43	0	0
CPZ: NORTH TO SOUTH					
17	0%	100	100	100	100
	1%	100	60	40	40
	2%	100	100	80	80
	4%	100	0	0	0
20	0%	100	100	100	100
	1%	100	100	75	50
	2%	100	67	33	33
	4%	100	0	0	0
32	0%	100	83	83	83
	1%	n/d	n/d	n/d	n/d
	2%	100	33	0	0
	4%	100	40	0	0
13	0%	100	100	100	100
	1%	100	100	83	67
	2%	100	100	60	60
	4%	100	40	0	0
9	0%	100	100	100	100
	1%	100	100	100	25
	2%	100	100	50	0
	4%	100	0	0	0
14	0%	100	100	100	100
	1%	100	100	60	60
	2%	100	100	40	0
	4%	100	33	0	0
30	0%	100	100	100	100
	1%	100	100	100	100
	2%	100	100	71	14
	4%	100	33	0	0
38	0%	100	100	100	100
	1%	n/d	n/d	n/d	n/d
	2%	100	100	50	0
	4%	100	80	0	0
11	0%	100	100	100	100
	1%	100	100	100	80
	2%	100	60	20	20
	4%	100	50	0	0

Table 5.16

Geographical variation in salinity tolerance determined by seedlot salinity index. Seedlot variation in seedling size and morphology are shown between the controls and 1% treatments. Where CON = control; INC = increase from control; DEC = decrease from control.

Seedlot accession	SALINITY INDEX 1%	2%	4%	Total	EFFECTS OF 1% SALINITY FROM CONTROL Size	Morphology
EPZ						
5	3.4	4.0	5.6	13.0	CON=1%	INC: leaflets/pinna, stem diameter DEC: height, nodes
7	4.0	4.7	5.7	14.4	CON>1%	INC: leaflets/pinna, stem diameter DEC: height, nodes
CPZ: NORTH TO SOUTH						
17	2.4	7.2	4.0	13.6	CON=1%	INC: height, nodes
20	3.3	4.7	4.0	12.0	CON=1%	INC: height, stem diameter DEC: leaflets/pinna
13	3.5	6.4	5.6	15.5	CON≤1%	INC: stem diameter DEC: leaflets/pinna
9	3.3	5.0	4.0	12.3	CON≤1%	INC: leaflets/pinna, stem diameter DEC: height, nodes
14	3.2	4.8	5.3	13.3	CON=1%	INC: height, stem diameter DEC: leaflets/pinna
30	4.0	5.7	5.3	15.0	CON=1%	INC: stem diameter DEC: leaflets/pinna
11	3.8	4.0	6.0	13.8	CON>1%	no change

Public Authority for Water Resources (Oman) shows that the conductance was highest towards the centre of this provenance. The location of the seedlot sample sites within this provenance suggests a positive correlation between the seedling salinity tolerance and the conductivity of the aquifer water. This suggests that the genotypic adaptation to saline conditions of the parent trees has been passed on to the seedlings. These results confirm those of Eshel & Waisel (1965) in which they found that the growth of P.farcta seedlings sampled from saline-adapted populations were more tolerant to high salinities than seedlings sampled from non-saline populations.

Seedlings from Seedlots 13 and 30 were the most tolerant to the salinity treatments, which shows that the increase in the stem diameter and the decrease in the leaflets/pinna of seedlings grown in 1% salinity were morphological adaptations of salinity tolerance. There appears to be a trend of increasing the leaflets/pinna and decreasing the shoot height and node number with decreasing tolerance to salinity. However, the least tolerant seedlings from Seedlot 20 were taller, with thicker stems and smaller numbers of leaflets/pinna in 1% salinity than in the control.

5.3.5 Quantitative analysis of glasshouse grown seedlings

Under glasshouse conditions in the University of Durham, seedlings grown from the general seedlot accession EPZ/1 from the EPZ were harvested at 2, 15, 33, and 44 weeks of age (section 2.10). The results of these harvests presented in table 5.17 were quantitatively analysed (section 2.12). The partitioning of dry weight between the leaves, stems and roots over the four seedling ages are summarised in figure 5.15. The proportion of the stems remained relatively constant with age, but there was an increase in the partitioning of dry matter to the roots

Table 5.17

Summary of harvest data of glasshouse grown P.cineraria seedlings (n=44).

Seedling age		Stem height (mm)	Root length (mm)	Leaf area (cm^2)	Leaf weight (g)	Stem weight (g)	Root weight (g)	Total weight (g)
2 weeks	Mean	5.000	46.667	1.333	0.010	0.002	0.005	0.018
(n=10)	S.D.	0.000	22.366	0.125	0.001	0.000	0.002	0.002
15 Weeks	Mean	32.000	170.000	3.633	0.027	0.013	0.030	0.070
(n=10)	S.D.	10.033	14.142	1.960	0.011	0.007	0.031	0.026
33 Weeks	Mean	47.500	298.750	4.128	0.030	0.013	0.104	0.147
(n=10)	S.D.	11.169	21.028	1.386	0.009	0.004	0.040	0.039
44 Weeks	Mean	66.714	254.214	3.315	0.025	0.042	0.249	0.316
(n=14)	S.D.	22.802	91.822	3.346	0.023	0.019	0.120	0.148

Figure 5.15

Dry matter partitioning in the leaves, stems and roots (as a percentage of total plant dry weight) of glasshouse grown P.cineraria seedlings (2 weeks n=10; 15 weeks n=10; 33 weeks n=10; 44 weeks n=14).

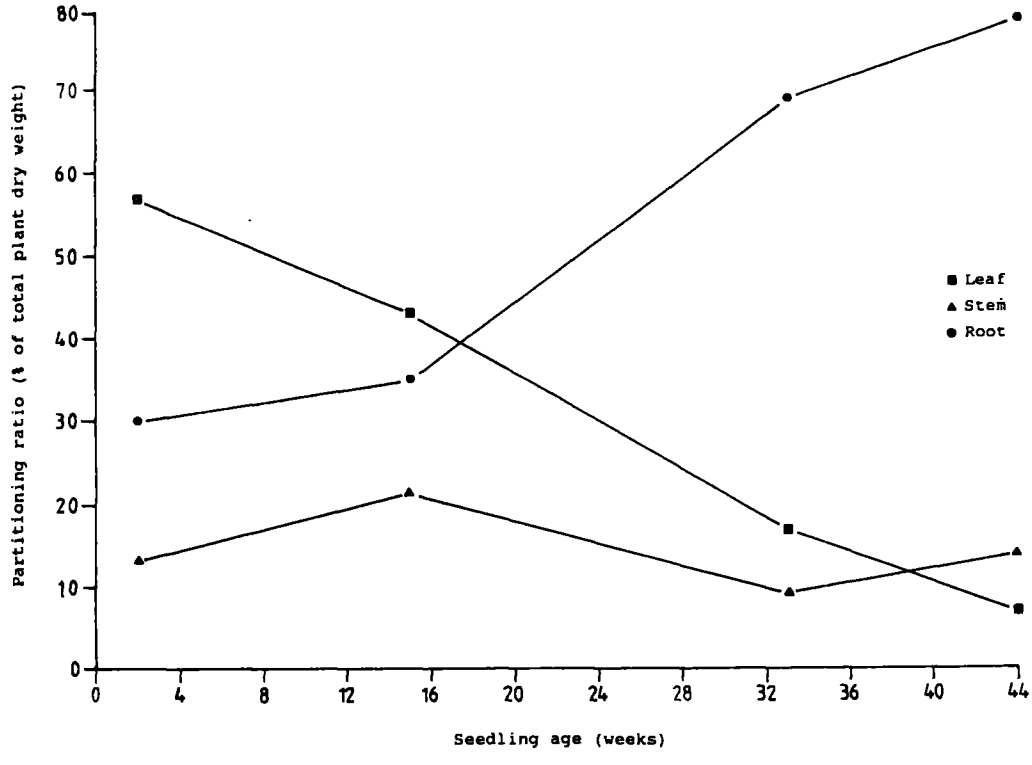


Table 5.18

Quantitative analysis of glasshouse grown seedlings (n=44).

A. Summary results of shoot/root ratio, leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR) for 2, 15, 33 and 44 week old seedlings. Where LAR in $cm^2 g^{-1}$ plant dry weight; SLA in $cm^2 g^{-1}$ leaf dry weight; and LWR in gg^{-1} plant dry weight.

Seedling age		Shoot/ root ratio	LAR	SLA	LWR
2 Weeks	Mean	2.61	76.23	133.23	0.57
(n=10)	S.D.	0.98	7.39	2.60	0.07
15 Weeks	Mean	3.75	57.36	127.64	0.43
(n=10)	S.D.	2.44	26.55	17.92	0.17
33 Weeks	Mean	0.49	30.65	136.78	0.22
(n=10)	S.D.	0.24	15.00	2.66	0.10
44 Weeks	Mean	0.28	9.73	121.60	0.07
(n=14)	S.D.	0.09	7.35	21.45	0.05

B. Summary results of mean relative growth rate (RGR), mean unit leaf rate (Emean) and mean leaf area ratio (Fmean) for the age periods 2-15 weeks, 15-33 weeks and 33-44 weeks. Where RGR in $gg^{-1}week^{-1}$; Emean in gcm^{-2}; and Fmean in $cm2g^{-1}$ plant dry weight.

Age period	RGR	Emean ($x10^{-3}$)	Fmean
2-15 Weeks	0.1045	1.746	59.84
15-33 Weeks	0.0412	1.104	37.32
33-44 Weeks	0.0696	4.141	16.81

than to the leaves with increasing age. Within the first 15 weeks of growth, the mean root and shoot dry weights were almost equal but leading to the development of long, thin tap roots and short woody stems. At 33 weeks, the root/shoot dry weight ratio increased to 2.42 with the development of just under seven times the tap root length to shoot height. By 44 weeks, the root/shoot dry weight ratio had increased to 3.61. These results are expected to be significantly higher in similar aged seedlings growing naturally in the Sharqiya, since the scarcity of water, well aerated soils and available soil nutrients are known to stimulate rapid root growth (Salisbury, 1952). This rapidly penetrating tap root will increase the chances of the seedlings reaching a more permanent subterranean water source once the temporary surface water responsible for its germination has dried out. It is also important in anchoring the seedling into the mobile soil. The lateral roots in early development are simple and small, and appear to have no function in anchorage at this stage. However, in the mature trees they form a complex web of woody roots either on the surface of the sand, or immediately below it (slide 24).

The shoot/root ratio, leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR) were determined for each seedling age (table 5.18a), and the mean relative growth rate (RGR), mean unit leaf rate (Emean) and mean leaf area ratio (Fmean) were determined for the age periods 2-15 weeks, 15-33 weeks and 33-44 weeks (table 5.18b). The mean total plant dry weights only increased from 0.018g to 0.316g between two and 44 weeks of age. There were distinct differences in the RGR of seedlings up to 44 weeks of age. Seedlings between 2-15 weeks had the highest RGR, which was mainly due to the high Fmean, so that dry matter was concentrated in the production of leaf area. As the seedlings continued to grow (15-33 weeks), the RGR dropped by a factor of more than 2.5 as a result of more than a two fold decrease in Fmean combined with a

smaller decrease in Emean. The lower net gain in dry weight suggests that the loss in leaf area production was as a result of the redistribution of assimilates into the formation of the roots. After 33 weeks of age, the RGR increased as a result of an almost four fold increase in Emean and more than a two fold decrease in Fmean. As leaf area production continued to decrease with age, the increase in the assimilation of dry matter was directed mainly towards the formation of the roots.

5.4 Conclusions and recommendations

P.cineraria seed production in the Sharqiya is variable and unpredictable. Its seeds are small, with very a hard testa which must be physically scarified to promote bulk germination. The morphological variability of the seeds is high. Specific care should be taken on collecting the morphologically different seeds in the population to ensure a minimum loss of genetic variability. The dormant seeds in the populations are the most suited to long periods of storage, whilst still maintaining moderately high levels of viability. The natural moisture content of these seeds was relatively high (8.26% by weight). The most successful method for scarifying the seeds was using abrasion by coarse-grain sandpaper.

Under artificial storage conditions, viability was highest in seeds of natural moisture content at 4°C, whilst seeds of high moisture content (13.02%) at 20°C were shown to have the lowest storage viability. Since a recommended seed moisture content of 4% optimises seed viability in a number of species tested (Harrington, 1972), the higher natural moisture content of P.cineraria seeds may have been responsible for reduced viabilities when stored at sub-zero temperatures. The unsuitable storage conditions at -20°C damaged the seed coat, which broke seed dormancy. Provided

that the seed viability is adequate for their intended utilisation, freeze treating the seeds as a form of breaking seed dormancy may prove to be a simple method for the bulk germination of seeds. The dormancy of the seeds was found to be persistent for at least 70 days exposure to moist conditions. A decrease in seed viability of approximately 10% occurred whilst the seeds were still attached to the trees.

A seed storage nomograph produced from this data for P.cineraria has allowed the identification of suitable storage conditions for seeds of known viability. This nomograph is useful in the germplasm conservation of the species, for example the protection of saline-tolerant strains of seeds. In order to preserve these seeds, the duration of time spent in storage must be calculated so that their viability does not reach a critically low level.

The vulnerable stage of regeneration by seed in the life-cycle of P.cineraria has clearly affected the successful establishment of this species in the Sharqiya. Physiological inhibition of flower and fruit production is caused by gall-forming insects, and seed production is severely reduced by seed-feeding moth and bruchid larvae. The seeds that reach maturity are physically damaged by the abrasive properties of the shifting sand, and are physically and chemically damaged when they are eaten by domestic livestock. Those seed that successfully germinate will not survive if they are buried too deep in the soil. Germinated seeds under natural conditions rapidly grow when water is available, but seedling fatalities are very high due to grazing livestock, decreasing water availability, intolerance to the canopy shade and competition by faster growing herbaceous vegetation. Factors influencing seedling survival under natural conditions can be attributed to their long tap roots which develop to reach more permanent sources of water, and their ability to grow well under full sunlight where competition by herbaceous plants is minimal.

Glasshouse trials in the University of Durham Botanic Gardens have shown that there was considerable variation in the germination of P.cineraria seeds and the plumule development of seedlings, occurring both between and within seedlot accessions. Although the rate of growth under glasshouse conditions was very slow, the range of seedling ages in which non-destructive morphological measurements were made was sufficient to demonstrate the extent of variation and how this changed with time.

The analyses have clearly separated some major differences in the seedling morphology with respect to provenance and parent origin, where type 5 seedlings were generally larger and morphologically distinct to all other seedlings, whilst type 3 seedlings showed the greatest departure in morphology. This variability in seedling growth and morphology illustrates the necessity of sampling seeds from both a wide geographical distribution and from a wide range of tree forms, in order to maximise the variability of the germplasm collection for gene conservation purposes.

Salinity trials of P.cineraria under glasshouse conditions have shown that during the early growth and development of the plant, this species was tolerant to high salinities. There was a distinct three week period of tolerance from the start of the salt application, during which the greatest salinity induced variation occurred. With increasing salinity concentration, there was an increase in seedling fatalities and an increase in the morphological homogeneity. Some seedlings were still surviving after seven weeks exposure to 4% salinity, whilst the majority of seedlings were still alive after 13 weeks exposure to 1% salinity.

The dominant effect of the 1% salinity treatment on the morphology of the most tolerant seedlings was to increase the stem diameter and decrease the number of

leaflets/pinna. With decreasing tolerance, the seedlings treated with 1% salinity generally underwent an increase in the number of leaflets/pinna and a decrease in the shoot height and node number. Seedlings of either EPZ origin or of type 5 and 8 parents were the most saline tolerant, whilst seedlings of CPZ origin or of type 3 parents were the most saline sensitive. In the CPZ, the salinity tolerance of the seedlots and their geographical distribution were tentatively shown to be correlated. This indicates a genotypic adaptation to saline conditions of the parent trees which has been passed on to the seedlings. These results support the technique of collecting seeds from habitat extremes, with the objective of sampling germplasm with genetically controlled adaptations to these extremes.

The slow seedling growth under glasshouse conditions was quantitatively assessed, such that by 44 weeks of age, the mean total plant dry weight was only 0.313g. The proportion of the stems to the whole plant weight remained relatively constant over this period, whilst the roots increased and the leaves decreased. The highest mean relative growth rate of these seedlings occurred between 2 and 15 weeks, in which time dry matter was partitioned more towards the formation of the leaves for greater photosynthetic assimilation. As the seedlings grew between 15 and 44 weeks, new dry matter was partitioned more to the formation of the roots. This strategy of dry matter partitioning can be attributed to the early development of phreatophytic growth of P.cineraria, which ensures that the plant will continue to grow after the ephemeral water responsible for its propagation has evaporated from the surface of the soil.

CHAPTER 6

SEEDLING FIELD TRIALS OF P.CINERARIA IN OMAN

6.1 Introduction

The successful reproductive regeneration of P.cineraria depends largely on the capability of individual seedlings to survive many hazards associated with the arid environment. Optimal environmental conditions will maximise the vegetative growth of the seedlings and minimise the time to reach maturity. Hence, studies on the early growth and development of P.cineraria seedlings under varying environmental conditions are relevant to understanding the strategies required for their survival into mature trees in the field.

The dominating environmental influences on seedling growth and morphology are derived from the climate and from the soil environment. The interactions between the climate and soil environment will affect the translocation, partitioning and utilisation of assimilates to the heterotrophic organs of the plant (the sinks). These sinks compete with each other for assimilates which will affect the growth strategy of the plant. If the environmental conditions increase the production of assimilates through photosynthesis, then more material may be available for translocation to the sinks. Phenotypic characters that are often easily modified by the environment are the size of the plants and individual organs, and the numbers of branches, leaves and flowers (Jones & Luchsinger, 1987).

The arid environment promotes the accumulation of assimilates in to storage organs such as the roots or crown for later utilisation when moisture conditions are more favourable to growth. Under conditions of high temperatures, high light intensities, and damage through wind or sand blast, morphological adaptations are necessary for the survival of the plant.

The most dominating factor influencing plant growth in any soil environment is nutrient availability. There are at least 16 elements that are metabolically essential to the plant which include: C, O, H, N, P, K, Ca, S, Mg, Mn, Mo, Fe, B, Cu, Zn and Cl. Except for carbon and oxygen from atmospheric CO_2 and O_2, hydrogen from water and nitrogen from diazotrophic micro-organisms, these nutrients are absorbed into the plant from the soil solution as mineral ions (Rorison & Robinson, 1986). These authors state that "the acquisition, utilisation and tolerance of these elements constitute a fundamental component of a plant's physiology and can have a profound effect upon the ecology and evolution of species and populations". When these nutrients are deficient, their availability to the plant is reduced, which may limit plant growth through physiological injury. Morpho-phenologic changes in plant growth influenced by the nutritional status of the growing medium are thought to be controlled by plant growth substances such as cytokinins and abscisic acid (Moorby & Besford, 1983).

Nutrient availability is affected by the water availability in the soil, since the rate of nutrient uptake is usually more dependent upon the rates of diffusion of ions between the bulk soil and root surfaces than the concentration of the soil ions (Rorison & Robinson, 1986). These authors identify that the potentially available soil nutrient pool consists of "the soil solution ions together with those absorbed on the solid phase that are readily exchangeable with those in solution". The amount of soil water available to the plant can be determined by the field capacity of the soil in which the roots grow (Salter & Haworth, 1961). At field capacity, the water trapped in the spaces between the particles by capillary action is the main supply of moisture to the plants (Bannister, 1986).

The physical properties of the soil environment will affect the water availability and hence nutrient

availability to the plant. As a result, there is often a strong correlation between water availability and both the primary productivity and morpho-phenologic development of desert plants (DePuit, 1979). Plant growth and partitioning of assimilates are linked to water stress, such that if water is sparse, then the variation between the root and shoot dry weights is increased during the early growth of the plant. In some arid adapted species, rapid root growth is promoted by a low water potential of the surface soil layers (Salisbury, 1952). Soil water stress reduces the activity of the shoot meristems and cell enlargement due to the reduction in the movement of assimilates to the shoot (Sosebee & Wiebe, 1971). In P.glandulosa, water stress inhibited stem elongation so that the assimilates were directed towards rapid root growth (Glendening & Paulsen, 1955), whilst water abundance promoted an increase in leaf area (Easter & Sosebee, 1975).

In addition to reducing nutrient availability, a low moisture content will often cause soil cementation which reduces root penetration, and causes root cell fatalities due to their continued exposure to desiccated conditions (Drew, 1979). Warmer soil temperatures usually enhance the translocation of assimilates to the roots (Fujiwara & Suzuki, 1961), but soil temperatures over 80°C which occur in exposed desert soils (Chapter 3) can inhibit plant growth by promoting root death.

The variation in growth and development under different environmental conditions can be examined using field trials at different locations, and using different soil treatments. The importance of this technique over glasshouse trials (Chapter 5) is that the study is performed in the field under natural conditions. This offers the advantage of studying the species natural morpho-phenologic responses to the environment, which will be the product of many inter-related abiotic and biotic factors. The biotic factors will be influenced by both

genotypic and developmental variation in the species. This technique was successfully used by Felker et al. (1981a) to study the variation in the growth of 13 Prosopis species.

The results from field trials are of both ecological and silvicultural importance by providing information on both the plant growth necessary for successful establishment of the species under arid conditions, and on the variability and plasticity of the species. Provenance field trials (Felker, 1980; Felker et al., 1981b; Felker et al., 1983) were used to screen Prosopis species for biomass production under semi-arid conditions in the United States, from which a number of species were recommended for further testing and development. Felker et al. (1984) also performed 3 different field trials in Southern California, to screen a number of Prosopis species for pod productivity. By presenting the seedlings with different environmental conditions, they found that P.velutina had the highest mean pod production of 7.2kgtree^{-1}, and that the driest irrigation treatment produced the greatest pod yield.

This chapter presents the results of multi-factorial seedling field trials of P.cineraria in Oman performed over a period of 34 weeks between November 1988 and August 1989. The experimental design was aimed at gaining the maximum information on the ecology and silviculture of P.cineraria during its early growth and development. The principal objectives of the field trials can be divided into 3 categories:

1. assessment of the early growth and morphology of P.cineraria under natural environmental conditions in Oman

2. assessment of environmental influences on P.cineraria seedling growth and morphology

3. determination of the most suitable silvicultural practices for the successful propagation of P.cineraria

To achieve these objectives, the seedlings were grown in three field trials which were subjected to different environmental conditions. In each trial, the seedlings were grown in 22 different soil treatments composed of two natural soil types with 10 soil supplements and two controls. The trial sites were specifically located in different ecological habitats contrasting in both phytogeography and environmental conditions. One trial site was located specifically within the natural range of P.cineraria near the town of Al-Kamil in the Sharqiya (AL-K trial). A second trial site in the Sultan Qaboos University (Seeb) was located in a habitat where the species is generally scattered. Two trials were set up at the university, one in full sunlight (SQU-1 trial) and the other under shade netting (SQU-2 trial) which reduced the incident sunlight by over 76%. Two natural soil types were used in this study, both of which were sampled from the Sharqiya. These included a nutrient-rich Prosopis woodland soil (WS) and a nutrient-poor dune soil (DS). The soil supplements were prepared from materials that were locally available in Oman.

The trials were established under cool, dry winter conditions in November 1988 and were maintained throughout most of the following summer. At 13 weeks of age, seedlings were harvested from 22 treatments (8 per treatment) from the SQU-1 trial. At the end of the trial period at 34 weeks of age, the shoots of 916 seedlings were harvested from all three trials, using a sample size of 16 seedlings per treatment whenever possible. From these shoots, 12 dry weight and morphological measurements were made.

As all comparisons between these variables or between the 66 treatments were not necessary, the data were divided into three subsets for separate statistical analyses. In the first analysis, the effects of the environment on seedling growth were determined by contrasting the treatments between the trial sites (SQU-1 &

AL-K). In the second analysis, the effects of shade on seedling growth were determined using treatments from the shade trial at the Sultan Qaboos University (SQU-2) and contrasting them to the equivalent treatments in the university trial under full sunlight (SQU-1). In these analyses, the size and morphology of the seedlings were used to assess seedling growth, which were determined multivariately by principal components analysis (section 2.13). This method allowed comparisons between the treatments using the majority of the variation in the data. The third analysis was performed on 13 and 34 week old seedlings sampled from SQU-1 to determine the developmental variation of seedling growth. In this analysis, the shoot dry weight was used to assess seedling growth.

In each analysis, the main effects of the climate and soil environment on seedling growth were first determined to establish null hypotheses. Departures from these null hypotheses were then used to examine the variation in seedling growth between the soil types (WS & DS) and between the soil supplements.

The results and discussion section of this chapter has been divided into 4 parts. In Part 1, the environmental differences between the trials and between the soil types are described. Parts 2 and 3 respectively describe the effects of the environment and of shade on seedling growth, and Part 4 describes the developmental variation of seedling growth. For both interpretation purposes and clarity, the soil supplements were divided into three groups, which included: NPK fertilisers; cow manure and peat; and miscellaneous supplements (water-absorbing polymer, phosphate and excess fertiliser).

6.2 Materials and methods

6.2.1 Preparation of field trials

1. Trials

The AL-K trial was set up in the Al-Kamil Tree Nursery (Forestry Section, Ministry of Agriculture and Fisheries, Oman) which was located in a Prosopis woodland near Al-Kamil in the Sharqiya. The trial was under full sunlight, protected from grazing animals and watered (under instruction) by the nursery staff. The two SQU trials were set up in the George Dew Ltd. (London, U.K.) nursery in the Sultan Qaboos University (Seeb). The SQU-1 trial was set up under full sunlight, and the SQU-2 trial was set up beneath Tildenet LS 63% shade netting (Tilder Industries Ltd., Bristol, U.K.) less than 100m from SQU-1. These trials were also protected from grazing animals and watered (under instruction) by George Dew Ltd. nursery staff.

2. Soil types

The woodland soil (WS) was sampled beneath the tree canopy to a depth of 30cm in a dense section of the Eastern Prosopis Zone (Chapter 3). The dune soil (DS) was sampled from a vegetation-free sand dune field to the East of this provenance.

3. Soil supplements

Ten soil supplements prepared from materials that were locally available in Oman (table 6.1) were applied to both soil types in the three trials. A total of 22 treatments were tested in each trial (table 6.2), which included 20 woodland and dune soil treatments with supplements and two soil type controls (no supplements). For comparative purposes, the soil supplements were divided into three groups. The objectives of the controls and the soil

Table 6.1

Materials used in the *P.cineraria* field trials in Oman.

1. Black polythene pots, 38cm high and 20cm diameter (Polythene & Plastic Products LLC., Ruwi, Oman).

2. Dried cow manure from Salalah, Oman

3. Nitrophoska NPK:15+15+15 (BSAF Aktiengesellschaft, 6700 Ludwigshafen, Federal Republic of Germany)

4. Sangral NPK:15+15+15 + trace elements (Sinclair Horticulture and Leisure Ltd., Lincoln, England)

5 Triple superphosphate

6. Floratorf 500 sphagnum peat moss (Oldenbury, Germany)

7. Alcosorb (Interlates, Agricultural Division of Allied Colloids Ltd., Skelmersdale, U.K.)

8. Sharqiya dune soil (DS)

9. Sharqiya *Prosopis* woodland soil (WS)

10. Trickle irrigation equipment (locally manufactured except where indicated, and supplied by Agricultural Materials Co. Ltd., Ruwi, Oman):

    10.1 1 inch (2.54cm) diameter uPVC pipe
    10.2 1.3cm flexible plastic drip tubing
    10.3 0.3cm flexible plastic feeder tubing
    10.4 0.5 gal/h EM-M-05 Rain bug pressure compensating emitters (Rain Bird Middle East Ltd., Sharjah, U.A.E)
    10.5 Plastic stakes

Table 6.2

Description of treatments used in the *P.cineraria* field trials, with treatment names referred to in the text and treatment labels referred to in several of the figures. Where WS = *Prosopis* woodland soil; DS = dune soil.

No.	Treatment description	Treatment name	Label for each trial SQU-1	AL-K	SQU-2
1.	Dune soil (DS) : control	DS/control	A1	C1	E1
2.	DS + NPK with trace elements (NPK+T)	DS/NPK+T	A2	C2	E2
3.	DS + NPK without trace elements (NPK-T)	DS/NPK-T	A3	C3	E3
4.	DS + CM2 + NPK+T	DS/NPK+T/CM2	A4	C4	E4
5.	DS + cow manure (CM1) (1:1 by volume)	DS/CM1	A5	C5	-
6.	DS + CM2 (2:1)	DS/CM2	A6	C6	-
7.	DS + CM3 (3:1)	DS/CM3	A7	C7	-
8.	DS + peat (ratio 1:1 by volume)	DS/peat	A8	C8	-
9.	DS + water-absorbing polymer (WAP)	DS/WAP	AW	CW	EW
10.	DS + triple superphosphate	DS/PO3	AP	CP	EP
11.	DS + excess NPK+T	DS/excess	AX	CX	EX
12.	Woodland soil (WS) : control	WS/control	B1	D1	F1
13.	WS + NPK+T	WS/NPK+T	B2	D2	F2
14.	WS + NPK-T	WS/NPK-T	B3	D3	F3
15.	WS + CM2 + NPK+T	WS/NPK+T/CM2	B4	D4	F4
16.	WS + cow manure (CM1) (1:1 by volume)	WS/CM1	B5	D5	-
17.	WS + CM2 (2:1)	WS/CM2	B6	D6	-
18.	WS + CM3 (3:1)	WS/CM3	B7	D7	-
19.	WS + peat (ratio 1:1 by volume)	WS/peat	B8	D8	-
20.	WS + WAP	WS/WAP	BW	DW	FW
21.	WS + triple superphosphate	WS/PO3	BP	DP	FP
22.	WS + excess NPK+T	WS/excess	BX	DX	FX

Table 6.3

Summary of *P.cineraria* field trial harvests. Where H1 = harvest 1; H2 = harvest 2.

Trial	Date sown	Date harvested	Seedling age Days	≈Weeks	Sampling strategies Treatments	Seedlings
SQU-1/H1	18/11/88	12-15/2/89	86-89	13	22	176
SQU-1/H2	18/11/88	13/7/89	237	34	22	352
Al-K	28/11/88	25/7/89	240	34	22	352
SQU-2	8/12/88	6/8/89	241	34	14	212

Total seedlings harvested = 1092

supplement groups are summarised below:

Controls (DS/control, WS/control)

To determine the effects of the dune and woodland soil on plant growth. These treatments were also used as controls to determine the effects of individual soil supplements on plant growth.

NPK fertilisers (NPK+T, NPK-T, NPK+T/CM2)

To determine the growth responses to synthetic NPK fertilisers with trace elements (NPK+T) and without trace elements (NPK-T), and to determine whether the NPK+T fertiliser was complemented by adding finely ground dry cow manure in a soil:manure ratio (by volume) of 2:1 (NPK+T/CM2). The NPK+T and NPK-T soil supplements per pot were prepared in the following way:

Soil supplement	Application per pot
NPK+T	2.0g nitrophoska + 1.0g sangral
NPK-T	3.0g nitrophoska

The comparison of treatments with or without trace elements was achieved using the above applications, since the NPK ratios for both nitrophoska and sangral were the same (15:15:15). These fertilisers were applied to the pots at concentrations in the upper limit recommended by the manufacturer.

Manure and peat (CM1, CM2, CM3, peat)

To determine the growth responses to cheap organic fertilisers and to changes in the physical structure of the soil. The soil types were mixed with finely ground dry cow manure in soil:manure ratios (by volume) of 1:1 (CM1), 2:1 (CM2) and 3:1 (CM3). Peat was also mixed with the soil types in a 1:1 ratio only.

Miscellaneous supplements

I. Water-absorbing polymer (WAP)

To test the benefits of applying a water-absorbing polymer to each soil type as a means of improving the efficiency of water utilisation by the plants. Following the upper limit of the manufacturer's recommended rate for dry application of alcosorb ($3kgm^{-3}$), 10g of dry alcosorb was applied per pot.

II. Abundance of triple superphosphate fertiliser (PO_3)

To test the growth responses to phosphate imbalances in the soil by applying triple superphosphate fertiliser in abundance (10.0g per pot).

III. Excess NPK+T fertiliser (excess)

To test the growth responses to fertiliser toxicity by applying NPK+T fertiliser at over 30 times the recommended rate (40.0g nitrophoska and 20.0g sangral per pot).

4. Trial design

The layout of each trial was identical, consisting of rows of parallel treatments aligned in an East-West direction. Edge effect was reduced by placing plant pots full of soil around the perimeter of each trial. Within each treatment, 16 replicate pots were arranged in a block of 4 by 4. The treatments were prepared at the George Dew nursery in the Sultan Qaboos University, where a mechanical soil mixer (Agricultural Fabrications Ltd., Sandy, U.K.) was used for mixing the soil types with the soil supplements.

5. Irrigation

The plant pots were individually supplied with equal volumes of water using a pressure compensating trickle irrigation system (slide 43). Each row of treatments was supplied with two lines of 1.3cm drip tubing. From the drip tubing, a 40cm length of 0.3cm feeder tubing fixed with Rain bug emitters was directed into each of the pots and held firm by small plastic stakes embedded in the soil. The irrigation system was attached to the main water supply of each site and operated manually using a stop tap. The trials were irrigated seven days before the seeds were sown, which allowed time to check the performance of the irrigation equipment.

6.2.2 Seedling preparation

Due to the large number of seeds to be prepared, the distances between the sites, and the time-consuming methods of expected future harvests, sowing of the trials was staggered by approximately 10 day intervals. Sowing of the trials began in the middle of November 1988 and completed in early December 1988. Germinated seeds (section 2.7) were sown four to five per pot, giving a maximum of 2240 seedlings per trial. As seed germinability (section 2.7) was estimated at less than 50% (pers. obs.), a sample of 220g of seeds (approximately 5000 seeds) was used for each trial. The pots were irrigated to approximate field capacity (section 6.2.4) every day for the first two weeks after sowing to minimise seedling fatalities, and then maintained at this level every 48 hours in the exposed trials (SQU-1 & AL-K), and twice a week in the shaded trial (SQU-2). Adjustments to the watering regimes were made to suit the changes in the climatic conditions to maintain the soil field capacity.

6.2.3 Environmental assessment

Climatological data from 1974 to 1989 for the SQU trials were obtained from a meteorological station at Seeb Airport (Ministry of Communications, Oman; Ministry of Communications, 1975), which was located less than 5km from the trials. Climatological data from 1976 to 1985 for the AL-K trial were obtained from a meteorological station at Al-Kamil (Ministry of Agriculture and Fisheries, Oman), which was located less than 1km from the trial. Monthly figures were examined for air temperature (°C), relative humidity (%), bright sunshine (hours/day), windspeed(ms^{-1}) and rainfall (mm/month). As the <u>in situ</u> collection of climatological data was not possible for the duration of the trials, the above data were used to determine the monthly variation in the climate between the trial sites.

Localised light intensities (μmol photons of photosynthetically active radiation (PAR) $s^{-1}m^{-2}$) were recorded inside and outside of the shade netting of SQU-2 using a SKP200 light meter (Skye Instruments LTD., Llandrindod Wells, U.K.). Measurements were made over a period of two days to determine the mean reduction in incident sunlight caused by the shade netting.

The water infiltration rates of a selection of soils from the field trials were determined. The infiltration rate was calculated as the time for $100cm^3$ of water applied to the surface of the soil in a $500cm^3$ glass cylinder to be completely absorbed into the soil. The field capacity of each treatment was determined using the method of Saltar & Haworth (1961). This involved the measurement of the moisture content of pre-wetted blocks of soil from which the moisture has ceased to drain.

Detailed soil chemical analyses were performed by the Department of Geography, University of Durham, U.K., whilst gross changes in the soil chemical properties were

determined using a soil test kit (section 2.5).

6.2.4 Seedling harvests

Seedlings were harvested (section 2.10) at 13 weeks from SQU-1 (Harvest 1), and at 34 weeks from all three trials (Harvest 2). The sampling strategy for each harvest (table 6.3) was as follows:

1. Harvest 1

Two pots per treatment were randomly selected in SQU-1. A total of 176 whole seedlings were harvested, 8 seedlings per treatment. Cotyledon and leaf area for each seedling were measured using an area meter (section 2.11). In addition to leaf, stem and root dry weights for each plant, cotyledon and root nodule dry weights were also determined.

2. Harvest 2

At 34 weeks of age, a total of 916 seedling shoots were harvested from the three trials. The trials were harvested in the order in which they were sown.

In both SQU-1 and Al-K, 16 shoots were harvested from 22 treatments, and up to 16 shoots from 14 treatments in SQU-2 depending on their availability in each treatment. One seedling in each of the 16 pots per treatment was selected at random and labeled. Where necessary, more than one seedling per pot was selected to make up the required sample number.

The leaf areas of three of the 16 selected seedlings of most treatments were determined using an area meter for the preparation of a leaf area calibration curve for each trial (section 2.11). Where possible the three leaf size classes (section 6.2.5) were selected from each treatment.

As the sample size for each trial was large, and the stems generally bulky to handle, it was not possible with the available equipment to immediately oven kill all harvested stems to reduce weight losses through respiration and autolysis. To enhance seedling death, intact stems were placed on sheets of paper in an open but wind-protected location and sun-dried for at least 8 hours at approximately 40°C. The stems were then transferred to the laboratory and placed on bench tops. Leaves were removed from the sun-dried plants using a blunt plastic rod that was tapped against the stem, causing the leaves to drop into a large collecting tray. Leaves were oven dried and the dry weights used to determine the leaf area from leaf area calibration curves. For each of the defoliated stems, morphological characteristics were recorded (section 6.2.5) before being sectioned into smaller pieces and oven dried for dry weight determination.

Root extractions were carried out only on three treatments in SQU-1, due to the errors caused by lost root material in the remaining treatments.

6.2.5 Seedling morphology

The morphology of seedlings sampled at 34 weeks of age from the field trials were measured using the following parameters:

1. Shoot height (cm), from the cotyledonary node to the apical meristem; HEIGHT
2. Stem diameter (cm), 0.5cm below the cotyledonary node; STEMDIAM
3. Primary branch height (cm)
4. Branch number (includes all branches >5cm); BNO
5. Diameter of longest branch (cm); BD1
6. Diameter of second longest branch (cm); BD2

7. Length of longest branch (cm); BL1

8. Length of second longest branch (cm); BL2

9. Leaf length: small (<1.5cm), medium (1.5-3.0cm), large (>3.0cm)

Mensuration of the stem diameter of the seedlings to the nearest millimetre was performed using Vernier calipers. Variables allocated with upper-case labels were used in statistical analyses.

6.3 Results and discussion

PART 1

ASSESSMENT OF THE TRIAL AND SOIL ENVIRONMENT

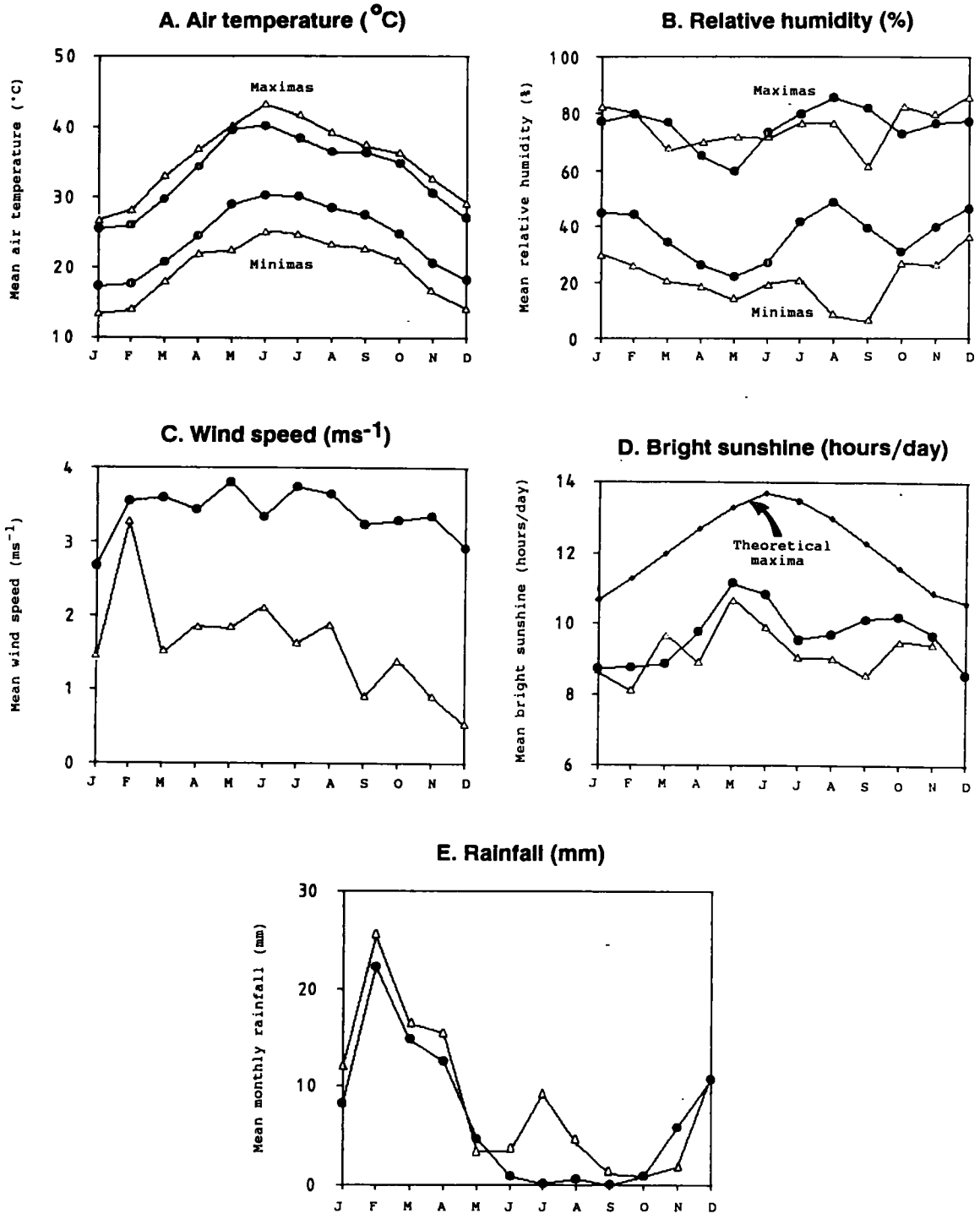
6.3.1 Environmental variation between trials

The SQU-1 and SQU-2 trials at Seeb were located less than 4km from the Batinah coast with an altitude of 15m above sea level. The Al-K trial at Al-Kamil in the Sharqiya was located over 50km from the east coast with an altitude of 105m above sea level (see figure 3.1).

The monthly variations in the climate between the trial sites are presented in figure 6.1. The mean maxima and mean minima temperatures in both sites were highest between May and August with a peak in June (figure 6.1a). The temperatures decreased between September and December and increased between January and April. The major difference between the sites was the smaller range in the mean maxima and mean minima temperatures at Seeb, which can be attributed to the greater maritime influence at this site. The highest mean maxima and lowest mean minima consistently occurred at Al-Kamil throughout the year.

Figure 6.1

Monthly climatic variation between the seedling field trial sites, from 1974 to 1989 for Seeb and from 1976 to 1985 for Al-Kamil.



The variation in the relative humidity was marginally lower at Seeb (figure 6.1b), which can also be attributed to the higher maritime influence at this site. Whilst mean maxima were approximately the same between the sites, lower mean minima occurred at Al-Kamil throughout the year.

Monthly variations in windspeed at Seeb were consistently between 2.7-3.8ms^{-1}, dominated by on-shore sea-breezes. The mean windspeeds were more variable at Al-Kamil, ranging between 0.5-3.3ms^{-1} (figure 6.1c) but with maximum windspeeds up to 20ms^{-1}, resulting in dust storms and moving sand. These winds consisted of gentle westerly or north-westerly breezes in the morning and strong easterlies and south-easterlies in the afternoon (MAF, 1988).

The longest hours of sunshine occurred in May and June at both sites (figure 6.1d), following the theoretical maxima determined by FAO (1984). The marginally shorter periods of sunshine in Al-Kamil can be attributed to cloudier conditions at this site caused by heavier occult precipitation.

The mean monthly rainfall between the sites were comparable with very dry summers from May to October, and wetter winters peaking in February and March (figure 6.1e). Marginally more rainfall did occur throughout the year at Al-Kamil. Specifically during the trials, brief and irregular periods of rainfall occurred at both sites (pers. obs.).

In both sites, the monthly variation in the climate shows that the majority of the year can be divided into a short, cool and wet winter (November to March) and a long, hot and dry summer (May to September). The climatological differences between the trial sites were dominated by the greater maritime influence on the SQU trials.

The reduction in incident sunlight beneath the shade netting of the trial SQU-2 at six sampling times over two days is shown in table 6.4. The mean reduction in light intensity over this period was more than 76%. A greater reduction in light intensity occurred in the morning and evening due to the proximity of surrounding trees and buildings. This departure from the manufacturers recommendation of 63% reduction was due to the shade netting being impregnated with dust. Associated with this shade effect was a decrease in temperature and wind speed and an increase in the immediate relative humidity. As a result of the wetter conditions beneath the shade netting, the field capacity of the soil in the pots was maintained with less than half the volume of water of the treatments in full sunlight. Associated with the shaded conditions and greater moisture availability in SQU-2 were the germination and rapid growth of the seed bank present in both the soil and the manure fertiliser. This trial required continual maintenance to reduce the competition effect of faster growing herbaceous species.

6.3.2 Physical differences between soil types

The woodland soil was loamy sand (2% coarse sand; 84% fine sand; 6% silt; 8% clay) which was brownish yellow (Munsell colour: 10YR6/6) with a low abundance of small stones and up to 30% of detritus. The dune soil was predominantly fine sand (98% fine sand; 2% silt), which was yellow (10YR7/6), with no stones and no visible detritus.

The soil infiltration rate and the soil field capacity were determined for the trial controls, the manure treatments (CM1, CM2 & CM3) and the peat treatments for both soil types (table 6.5). The infiltration of water into the woodland soil treatments was generally slower than the dune soil treatments, which was caused by anti-wetting and capping effects at the soil surface and by the sub-surface

Table 6.4

Measurement of the reduction in light intensity beneath the shade netting of the SQU-2 trial at the Sultan Qaboos University nursery between 19-20 November, 1988.

	Time	Cloud cover	Intensity ($\mu mols^{-1}m^{-2}$) Shade	Sunlight	% Reduction
Day 1	0800	clear	515	2010	74.38
	1300	clear	560	1925	70.91
	1700	<20%	185	1120	83.48
Day 2	0800	clear	178	1330	86.62
	1300	<50%	625	1950	67.95
	1700	hazy	4.1	17.0	75.88
				Mean	76.54
				S.D.	7.22

Table 6.5

Water infiltration rate and soil field capacity (FC) of some treatments used in the trials.

Soil treatment	Infiltration rate (min)	Soil field capacity (FC) (%)	FC of treatment/ FC of control
DS/control	11	14.37	1
DS/CM1	6	25.36	1.76
DS/CM2	45	23.63	1.64
DS/CM3	15	19.77	1.34
DS/peat	6	22.98	1.60
WS/control	37	18.00	1
WS/CM1	21	28.12	1.56
WS/CM2	27	25.07	1.39
WS/CM3	40	24.03	1.34
WS/peat	50	24.22	1.35

cementing of soil particles. A higher concentration of manure in both soil types generally resulted in a faster infiltration rate. This was largely due to the heterogenous range in size of insoluble particles in the manure. The greatest variation in the infiltration rate between the dune and woodland soil treatments was with the addition of peat, where there was almost a ten-fold increase in the infiltration rate in WS/peat than in DS/peat. The treatment controls had the lowest field capacities of the trials. The higher the proportion of manure in both the dune and woodland soils, the higher were their field capacities. The addition of manure to the dune soil caused a greater increase in the soil field capacity than the addition of manure to the woodland soil. The addition of peat also increased the soil field capacity in both soil types.

6.3.3 Chemical differences between soil types

Prior to the start of the trials, soils from the treatments DS/control, WS/control, DS/CM1 and WS/CM1 (see treatment nomenclature in table 6.2) were sampled for detailed chemical analysis (table 6.6). Soils from both the dune and woodland soil controls had a high carbonate content of about 35% by weight, and high levels of both calcium and magnesium. The WS/control had a higher concentration of most elements than the DS/control, but there was generally no change in the cation exchange capacity (CEC) between these treatments. There were more than 60 times more carbon, 30 times more phosphorus and double the concentration of nitrogen in the WS/control. Although there was no difference in the exchangeable calcium and sodium between the soils, there was about six times the concentration of soluble calcium ions and more than double the concentration of soluble sodium ions in the WS/control. Whilst there was double the amount of exchangeable magnesium and potassium in the WS/control than the DS/control, as soluble ions they were both about 9

Table 6.6

Chemical composition of dune and woodland soils (DS/control & WS/control) and manure treatments DS/CM1 and WS/CM1 used in the seedling trials. Analysis performed by the Department of Geography, University of Durham. Where CEC = cation exchange capacity.

TREATMENT	pH	%C	%N	Available P (ppm)	Exchangeable bases (me/100g) Ca	Mg	Na	K	Total CEC
DS/control	8.5	0.02	0.008	1.0	74.4	2.0	1.2	0.22	3.5
WS/control	7.8	1.25	0.016	32.8	74.6	3.5	1.1	0.54	3.8
DS/CM1	7.5	2.84	0.167	331.0	51.6	3.5	3.5	5.24	6.0
WS/CM1	7.4	2.69	0.179	273.0	75.1	4.9	3.3	4.91	8.5
RATIOS									
WS:DS	0.92	62.50	2.00	32.80	1.00	1.75	0.92	2.45	1.09
DS/CM1:DS	0.88	142.00	20.88	331.00	0.69	1.75	2.92	23.82	1.71
WS/CM1:WS	0.95	2.15	11.19	8.32	1.01	1.40	3.00	9.09	2.24

TREATMENT	Soluble cations (me/100g) Ca	Mg	Na	K	Soluble salts (me/dm^3) HCO_3	Cl	% CO_3	Gypsum (me/dm^3)	Specific conductance (mmhos)
DS/control	0.11	0.07	0.11	0.03	3.0	1.2	34.0	2.2	0.25
WS/control	0.65	0.65	0.27	0.26	6.4	4.0	35.5	2.0	0.55
DS/CM1	0.67	0.67	2.36	2.77	17.3	41.6	31.0	2.8	7.10
WS/CM1	1.02	1.16	2.40	3.00	17.8	45.2	29.0	2.6	3.10
RATIOS									
WS:DS	5.91	9.29	2.45	8.97	2.13	3.33	1.04	0.91	2.20
DS/CM1:DS	6.09	9.57	21.45	95.52	5.77	34.67	0.91	1.27	28.40
WS/CM1:WS	1.57	1.78	8.89	11.54	2.78	11.30	0.82	1.30	5.64

Table 6.7

Variation in the chemical composition of dune and woodland soil (DS/control & WS/control) before and after the trial, using ELE soil testing kit (section 2.5).

	Dune soil (DS) (mg/dm^3) Before	After	Ratio before:after	Woodland soil (WS) (mg/dm^3) Before	After	Ratio before:after
N	16.5	2.9	0.176	54.625	10.73	0.196
P	12	12.66	1.055	20.25	30.33	1.498
K	145	99.33	0.685	266	228	0.857
Ca	1500	1000	0.667	2375	1500	0.632
Mg	600	200	0.333	450	200	0.444
NH_4	6.2	8.8	1.419	18.45	41.66	2.258
Cl	1875	375	0.200	1187.5	375	0.316
Fe	0.07	0.08	1.143	0.2575	0.613	2.381
SO_4	113	61.66	0.546	423	88.33	0.209

times more concentrated in the WS/control. The WS/control also had more than double the amount of soluble bicarbonate and triple the amount of soluble chloride. These results show that there were major differences in the chemical composition between the soil types. As a result, the woodland soils were identified as being nutrient-rich and the dune soils as being nutrient-poor for plant growth.

There were generally no differences in the chemical composition of the soils between the treatments WS/CM1 and DS/CM1, with the exception of marginally more calcium and magnesium and marginally less phosphorus in WS/CM1. However, WS/CM1 did have less than half the conductivity of DS/CM1. The addition of manure to both dune and woodland soil in a ratio of 1:1 by volume had a dominating effect on the total chemical composition of the treatments by maximising the concentrations of the soil constituents. There was marginally less carbonate in these treatments than the respective controls, as a result of the lower volumes of sand used. The manure also greatly increased the concentration of soluble ions, particularly chloride, potassium and sodium, which accounted for the greater conductivity in the manure treatments than the respective controls. The addition of the manure to both soil types standardised their chemical composition. This allowed the study of seedling growth in physically different soils in which nutrient availability was high.

Soil from the treatments DS/control and WS/control were also sampled before the trials were started and then re-sampled when the trials were completed 34 weeks later to determine the gross changes in the chemical composition of the soil controls over the experimental growing period (table 6.7). By the end of the trial there was a decrease in the concentration of most ions in both controls, with the exception of phosphate, ammonia and iron. Phosphate marginally increased in concentration in the DS/control but increased by almost 1.5 in the WS/control. Ammonia and iron

marginally increased in the DS/control, but these ions more than doubled in concentration in the WS/control by the end of the trial. The proportional decrease in concentration of nitrate, potassium and calcium at the end of the experiment was consistent between the controls. There was a greater decrease in concentration of magnesium and chloride in the DS/control, whilst sulphate decreased by more than three times the concentration in the WS/control.

The decline in the chemical composition of the soils over the trial period can be attributed to the uptake of ions into the plant and loss through leaching from the pots. The absence of nitrate accumulation in the soil during the early growth of the seedlings suggests that the plants were utilising the available soil nitrate. This indicates that either the root nodules present in these seedlings (pers. obs.) were not actively fixing nitrogen in the presence of soil nitrates, or that the nitrate produced from active nodules complimented the nitrate absorbed from the soil solution.

PART 2

ENVIRONMENTAL EFFECTS ON SEEDLING GROWTH (SQU-1 & AL-K)

6.3.4 Statistical analysis of data

At 34 weeks of age, data collected from 704 seedlings in trials SQU-1 and AL-K were used to determine the effects of the trial environment on P.cineraria seedling growth in 44 treatments (2 soil types with 10 soil supplements and 2 controls for each trial). From each of these treatments 12 measurements were determined from 16 seedlings, which included leaf area, leaf weight and stem weight (section 6.2.4) and 9 morphological variables (section 6.2.5).

Principal components analysis was performed on all 704 seedlings, using the most highly correlated variables (table 6.8a), which were standardised to have a mean of zero and a variance of one to maximise the effectiveness of this analysis (Manly, 1986). These variables included shoot height (HEIGHT), stem diameter (STEMDIAM), branch number (BNO), the diameters (BD1 & BD2) and lengths (BL1 & BL2) of the primary branches, leaf dry weight (LEAFWT), stem dry weight (STEMWT), and the leaf area to shoot dry weight ratio (RELAREA). The latter variable was selected as a measure of the relative leaf area, rather than leaf area alone, which in most seedlings was determined from a transformation of the leaf dry weight using calibration curves (section 6.11).

The first three principal components from this analysis accounted for 84.9% of the total variation in the data and only these were examined (table 6.8b). A statistical summary of these principal components for each treatment is presented in Appendix D. The first principal component (F1) which accounted for 70.1% of the variation in the data was a result of an equal weighting between most variables in contrast to the relative leaf area (table 6.8c). In this analysis, this component described the size of the seedlings. The second principal component (F2) accounted for 8.3% of the variation in the data and was dominated by the lengths of the two primary branches and shoot height in contrast to branch number, relative leaf area, leaf weight, stem weight and stem diameter. The third principal component (F3) accounted for 6.5% of the variation in the data, and was dominated by the variables shoot height, stem diameter, stem weight and branch number in contrast to the relative leaf area and the diameters and lengths of the two primary branches. In this analysis, the F2 and F3 principal components described different aspects of seedling morphology, which as a product of the analysis were uncorrelated both to each other and to F1.

Table 6.8

Effects of trial location (SQU-1 & AL-K) on seedling morphology (n=704 seedlings).

A. Pearson's correlation coefficient half-matrix of the standardised variables. Except with relative leaf area (RELAREA), all correlations were positive and highly significant (p<0.001).

	HEIGHT	STEM DIAM	BNO	BD1	BD2	BL1	BL2	LEAFWT	STEMWT	RELAREA
HEIGHT	1.000									
STEMDIAM	0.767	1.000								
BNO	0.602	0.807	1.000							
BD1	0.528	0.651	0.560	1.000						
BD2	0.553	0.689	0.588	0.576	1.000					
BL1	0.810	0.680	0.553	0.657	0.600	1.000				
BL2	0.821	0.721	0.587	0.602	0.678	0.843	1.000			
LEAFWT	0.755	0.878	0.903	0.615	0.648	0.680	0.726	1.000		
STEMWT	0.760	0.874	0.881	0.596	0.637	0.666	0.710	0.963	1.000	
RELAREA	-0.633	-0.610	-0.436	-0.426	-0.430	-0.500	-0.508	-0.454	-0.515	1.000

B. Score coefficients for the first 3 principal components determined by principal components analysis.

	Principal components		
	F1	F2	F3
% of total variance	70.1	8.3	6.5
STEMDIAM	0.132	-0.155	0.183
LEAFWT	0.132	-0.384	0.055
STEMWT	0.131	-0.346	0.173
HEIGHT	0.124	0.314	0.207
BL2	0.123	0.321	-0.281
BL1	0.120	0.403	-0.339
BNO	0.120	-0.546	0.167
BD2	0.109	0.004	-0.422
BD1	0.105	0.093	-0.541
RELAREA	-0.092	-0.486	-0.853

C. Summary of the variable weightings to describe the functions of the first 3 principal components.

F1 = STEMDIAM + LEAFWT + STEMWT + HEIGHT + BL2 + BL1 + BNO + BD2 + BD1 - RELAREA

F2 = BL1 + BL2 + HEIGHT - BNO - RELAREA - LEAFWT - STEMWT - STEMDIAM

F3 = HEIGHT + STEMDIAM + STEMWT + BNO - RELAREA - BD1 - BD2 - BL1 - BL2

The first principal component (F1) was used to determine the significant effects of the trial environment on the variation in seedling size between combinations of treatments (section 6.3.5). The general effects of the environment on seedling size were examined by determining the significant differences in the F1 mean scores of each treatment between the two trials using independent t-tests. Specific effects of the environment on seedling size were then examined by determining the significant differences in the F1 treatment mean scores between the soil types and between the soil supplements for each trial and then comparing the significance results between the trials. The significant differences in the F1 treatment means between the two soil types were determined using independent t-tests. The significant differences in the F1 treatment means between the soil supplements were determined using one-way ANOVAs with post hoc contrasts between the controls and each of the soil supplements according to the Bonferroni procedure (section 2.13). The results of these significance tests were examined for the controls and each group of soil supplements that were identified in section 6.2.1.

The second (F2) and third (F3) principal components were used to determine the effects of the trial environment on the variation in the seedling morphology between treatments (section 6.3.6). These two components accounted for 14.8% of the variation in the data which, when combined, described the morphology of individual seedlings without the dominating effect of seedling size (F1). The treatment mean scores for each component were determined and presented as a scatter plot of F3 against F2 (see figure 6.3). In this plot, the closer the proximity of treatments the greater the morphological homogeneity of the seedlings between the treatments. Likewise, the greater the separation of treatments, the greater the heterogeneity. The morphological characteristics that were responsible for the distribution of the treatments in this plot were

identified by determining the dominant weighted variables (table 6.8c) that would be necessary to produce the four combinations of extreme scores (high and low) for both F2 and F3. The distribution of the treatments between the trials and between the soil type controls were first examined to identify the main effects of the environment on seedling morphology. Morphological departures from these main effects were then examined for each group of soil supplements.

6.3.5 Seedling size

1. Trial effects

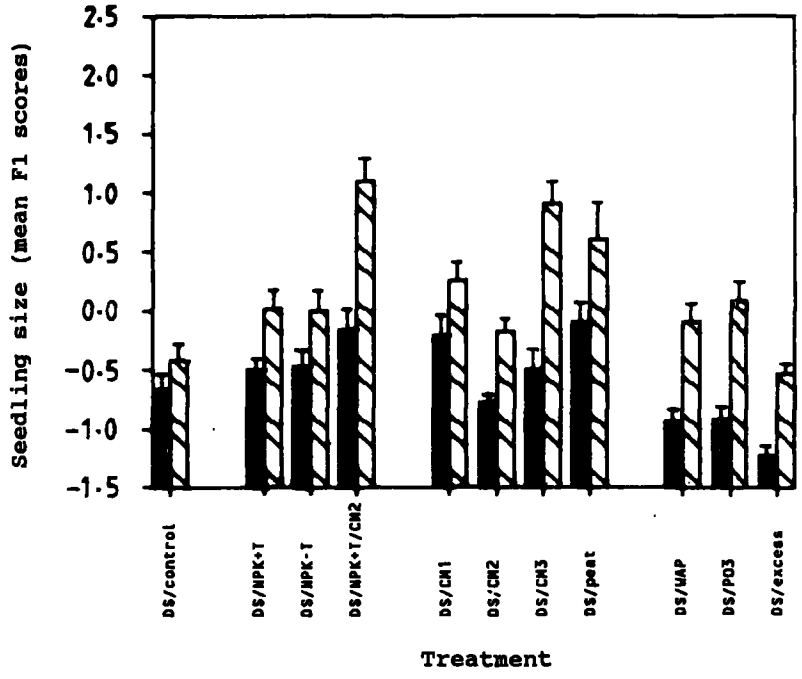
The mean F1 scores and standard errors for the 44 treatments in SQU-1 and AL-K are presented in figure 6.2. The optimal treatment in each trial in terms of seedling size (F1) was WS/NPK+T/CM2 from AL-K and WS/NPK+T from SQU-1, which produced seedlings with mean shoot dry weights of 56.36g ± 30.75 and 14.74g ± 11.79 respectively (Appendix D). With the exception of the dune soil control and the treatment DS/peat, the treatments from AL-K produced significantly larger seedlings than the equivalent treatments from SQU-1 (table 6.9). These results clearly show that over the trial period of 34 weeks, the environmental differences between SQU-1 and AL-K had a considerable effect on seedling size, such that the natural habitat of P.cineraria in the Sharqiya promoted a significantly faster seedling growth (slides 40 & 41). Therefore, a null hypothesis was used to state that seedling growth in the AL-K trial was dominated by a habitat-positive effect, whilst in the SQU-1 trial seedling growth was dominated by a habitat-negative effect.

The results also show that the soil environment presented to the seedlings grown in the dune soil control and DS/peat reduced the habitat-positive effect of the AL-K

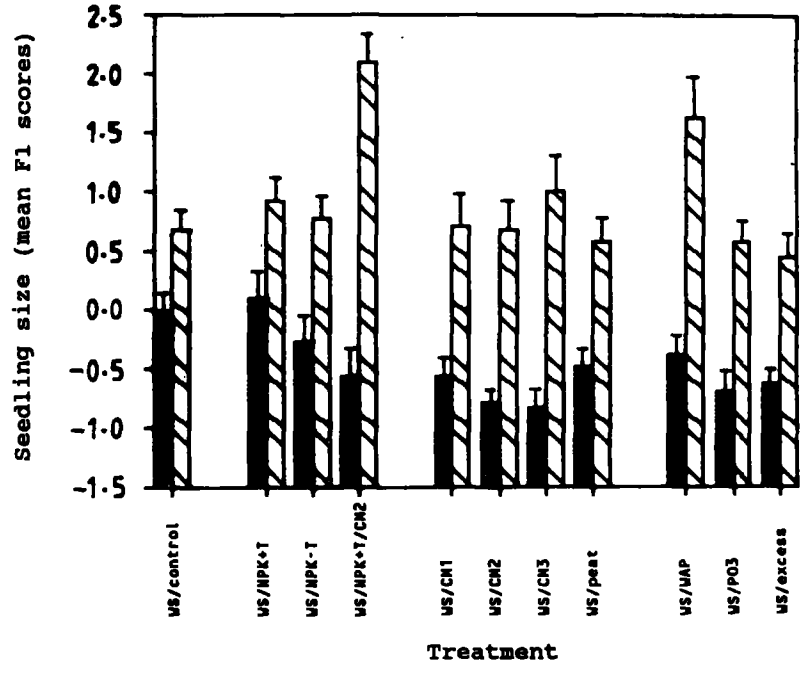
Figure 6.2

Effects of trial location (SQU-1 & AL-K) on the size of 34 week old seedlings, using the treatment mean scores and standard errors of the first principal component (F1) determined from 704 seedlings.

A. Dune soil (DS)



B. Woodland soil (WS)



SQU-1 trial AL-K trial

Table 6.9

Between trial significant differences in seedling size (F1 scores) of 34 week old seedlings (n=704) from trials SQU-1 and AL-K, using independent t-tests.

	CONTROL
DS	NS
WS	**

	Soil supplement		
	NPK+T	NPK-T	NPK+T/CM2
DS	*	*	***
WS	**	***	***

	Soil supplement			
	CM1	CM2	CM3	PEAT
DS	*	***	***	NS
WS	***	***	***	***

	Soil supplement		
	WAP	PO3	EXCESS
DS	***	***	***
WS	***	***	***

trial. Hence, the nutrient-poor soil environment in both treatments equally inhibited seedling growth in both trials as a result of nutrient deficiencies.

2. Controls

Seedlings grown in the woodland soil controls were significantly larger than the dune soil controls for both SQU-1 ($p<0.01$) and AL-K ($p<0.001$). These results show that the woodland soil had more of a positive effect on seedling size, which was independent of the different environmental effects of the trials. Therefore, a second null hypothesis was used to state that seedling growth in the nutrient-rich woodland soil was dominated by a soil-positive effect, whilst in the nutrient-poor dune soil seedling growth was dominated by a soil-negative effect.

3. NPK fertilisers (table 6.10)

In SQU-1, the significantly larger seedlings in the woodland soil than in the dune soil supplemented with NPK+T was the result of the positive effect of the woodland soil and not the supplement, as shown by the absence of any significant differences between this treatment and the WS/control. However, the supplements NPK-T and NPK+T/CM2 did not produce any significant differences in the seedling size between the soil types in this trial. Hence, under the habitat-negative effect of SQU-1, these soil supplements either reduced the positive effect of the woodland soil or reduced the negative effect of the dune soil. Since only NPK+T/CM2 applied to the dune soil produced significantly larger seedlings than its control, this suggests that the latter was predominant, showing that the increased nutrient status (due to NPK+T) and higher field capacity (due to CM2) in this treatment had the greatest effect on seedling growth. The absence of any positive effect of NPK/CM2 in the woodland soil indicates that the natural concentration of nutrients in the woodland soil without supplements was

Table 6.10

Between soil type and between soil supplement significant differences in seedling size (F1 scores) of 34 week old seedlings (n=704) in the NPK fertiliser treatments from trials SQU-1 and AL-K.

A. Between soil types using independent t-tests.

	Soil supplement		
	NPK+T	NPK-T	NPK+T/CM2
SQU-1	**	NS	NS
AL-K	**	**	**

B. Between supplements, using one-way ANOVAs and post-hoc contrasts according to the Bonferroni procedure. Where ** = p<0.001; * = p<0.005; NS = not significant at p>0.005.

	Soil supplement		
	NPK+T	NPK-T	NPK+T/CM2
SQU-1			
DS	NS	NS	*
WS	NS	NS	NS
AL-K			
DS	NS	NS	**
WS	NS	NS	**

sufficient to support the maximum seedling growth that occurred in the SQU-1 trial.

In AL-K, the soil supplements NPK+T, NPK-T and NPK+T/CM2 produced significantly larger seedlings in the woodland soil than in the dune soil. Since both NPK+T and NPK-T applied to both soil types did not produce significantly larger seedlings than their controls, these results show that the combined positive effects of AL-K and the woodland soil were greater than the individual effects of these supplements. As in SQU-1, the application of NPK+T/CM2 to dune soil reduced the negative effect of this soil type by promoting significantly larger seedlings. Under the habitat-positive effect of AL-K, this supplement enhanced the positive effect of the woodland soil, thereby producing the largest seedlings in this trial.

4. Manure and peat (table 6.11)

There were generally no significant differences in seedling size between the soil types supplemented with manure from both SQU-1 and AL-K. These results suggest that the addition of these soil supplements reduced the variation in seedling size between the soil types, which was consistent between the trials. The application of manure (CM2 & CM3) to the woodland soil in SQU-1 significantly reduced the seedling size from the control, and the application of manure (CM1 & CM3) to the dune soil in AL-K significantly increased the seedling size. These results suggest that the reduction in variation between the soil types was caused by the reduction in the positive effect of the woodland soil in SQU-1 and by the reduction in the negative effect of the dune soil in AL-K. This shows that in SQU-1 there were interactions between the woodland soil and the manure which caused an inhibitory effect on seedling growth. The habitat-negative effect of SQU-1 may have enhanced the soil surface capping, sub-surface cementing and anti-wetting properties of the woodland soil

Table 6.11

Between soil type and between soil supplement significant differences in seedling size (F1 scores) of 34 week old seedlings (n=704) in the manure and peat treatments from trials SQU-1 and AL-K.

A. Between soil types using independent t-tests

	Soil supplement			
	CM1	CM2	CM3	PEAT
SQU-1	NS	NS	NS	NS
AL-K	NS	**	NS	NS

B. Between supplements, using one-way ANOVAs and post-hoc contrasts according to the Bonferroni procedure. Where ** = p<0.001; * = p<0.005; NS = not significant at p>0.005.

	Soil supplement			
	CM1	CM2	CM3	PEAT
SQU-1				
DS	NS	NS	NS	*
WS	NS	**	**	NS
AL-K				
DS	*	NS	**	**
WS	NS	NS	NS	NS

treatments with manure (section 6.3.2) which reduced water infiltration and the transport of nutrients to the root surfaces of the seedlings. The results also show that under the habitat-positive effect of AL-K, the application of manure generally had a beneficial effect on seedling growth.

In both trials, the application of peat did not significantly affect seedling size between the soil types, but its application to dune soil significantly increased seedling size from the dune soil controls. These results suggest that the addition of peat reduced the soil-negative effect of the dune soil by increasing its field capacity, so that the low concentrations of nutrients already present became more available to the root surfaces for uptake and utilisation. Since the availability of nutrients in the WS/control under the habitat-negative effect of SQU-1 promoted almost maximum seedling growth in this trial, further increases in the field capacity of the woodland soil after adding peat therefore did not have any significant effect on seedling growth. However, under the habitat-positive effect of AL-K, the increased field capacity of woodland soil supplemented with peat which should have increased nutrient availability did not significantly affect seedling growth. This result may have been influenced by the differences in the physical properties between the soil types with peat (section 6.3.2), in which the treatment WS/peat caused a particular reduction in the infiltration of water into the soil.

5. Water-absorbing polymer, phosphate and excess fertiliser (table 6.12)

In both trials, the application of the water-absorbing polymer (WAP) produced significantly larger seedlings in the woodland soil than the dune soil. Only the application of the polymer to the woodland soil in AL-K caused a significant increase in seedling size from its control. This indicates that under faster growing conditions in AL-

Table 6.12

Between soil type and between soil supplement significant differences in seedling size (F1 scores) of 34 week old seedlings (n=704) in the treatments with water-absorbing polymer, phosphate and excess fertiliser from trials SQU-1 and AL-K.

A. Between soil types using independent t-tests

	Soil supplement		
	WAP	PO_3	EXCESS
SQU-1	**	NS	***
AL-K	***	*	***

B. Between supplements, using one-way ANOVAs and post-hoc contrasts according to the Bonferroni procedure. Where ** = p<0.001; * = p<0.005; NS = not significant at p>0.005.

	Soil supplement		
	WAP	PO_3	EXCESS
SQU-1			
DS	NS	NS	**
WS	NS	NS	NS
AL-K			
DS	NS	*	NS
WS	*	NS	NS

K, the effect of the polymer increased the availability of both the water and the naturally high concentrations of nutrients present in the woodland soil. The absence of any positive effect of the polymer when applied to the dune soil suggests this treatment had a negligible or even an inhibitory effect on seedling growth. This indicates that the polymer added to nutrient-poor soils may isolate the low concentrations of nutrients that are present in the soil solution away from the root surfaces.

The application of phosphate did not significantly affect seedling size between the soil types in SQU-1, but its application in AL-K only caused a marginally significant increase in seedling size in the woodland soil. This reduction in seedling size between the soil types was mainly caused by the reduction in the positive effect of the woodland soil, as shown by the mean F1 scores in DS/PO_3 in SQU-1, and the significant increase in seedling size when this supplement was applied to the dune soil in AL-K. The supplementary levels of phosphate added to the already high levels of natural phosphate in the woodland soil (section 6.3.3) suggests that this marginally inhibited growth was a response to phosphate imbalances in the soil.

The potential negative effect of fertiliser toxicity in the treatments supplemented with excess fertiliser did not reduce the positive effect of the woodland soil, as shown by the highly significantly larger seedlings in the woodland soil than the dune soil in both trials. Only the application of excess fertiliser to the dune soil in SQU-1 caused a significant decrease in seedling size. These results suggest that components in the woodland soil specifically reduced the effect of fertiliser toxicity to the seedlings, which was independent of the different environmental effects of both trials.

The application of phosphate and excess fertiliser did not cause large variations in seedling size,

particularly when these supplements were added to the woodland soil. These results clearly demonstrate the tolerance of P.cineraria seedlings to nutrient imbalances and fertiliser toxicity in the soil. This resistance to stressed soil conditions supports the results of the glasshouse salinity trial described in Chapter 5, in which a particularly high salinity tolerance was identified in P.cineraria seedlings.

6.3.6 Seedling morphology

1. Dominant morphological characteristics in the analysis

A scatter plot of the treatment mean scores of the principal components F3 against F2 for the 44 treatments in SQU-1 and AL-K is presented in figure 6.3. The morphological characteristics that were responsible for the distribution of these treatments are summarised below:

Principal component scores		Dominant morphological characteristics
F2	F3	
1. HIGH	HIGH	Tall
2. HIGH	LOW	Long primary branches with a low branch number. This describes a primary-branching morphology.
3. LOW	HIGH	Many branches with shortest primary branches with thick stems (diameter and weight). This describes a multiple-branching morphology.
4. LOW	LOW	High relative leaf areas

For comparative purposes, separate plots were prepared for the controls and the three groups of soil supplements.

2. Trial effects

The distribution of the treatment means in figure 6.3 clearly shows that most of the variation in seedling morphology between the trials was accounted for by the variation in the branching morphology. In SQU-1, the habitat-negative effect on seedling growth promoted a primary-branching morphology, whilst the habitat-positive effect of AL-K promoted a multiple-branching morphology. The main effects of the trials are summarised in table 6.13.

3. Controls (figure 6.4)

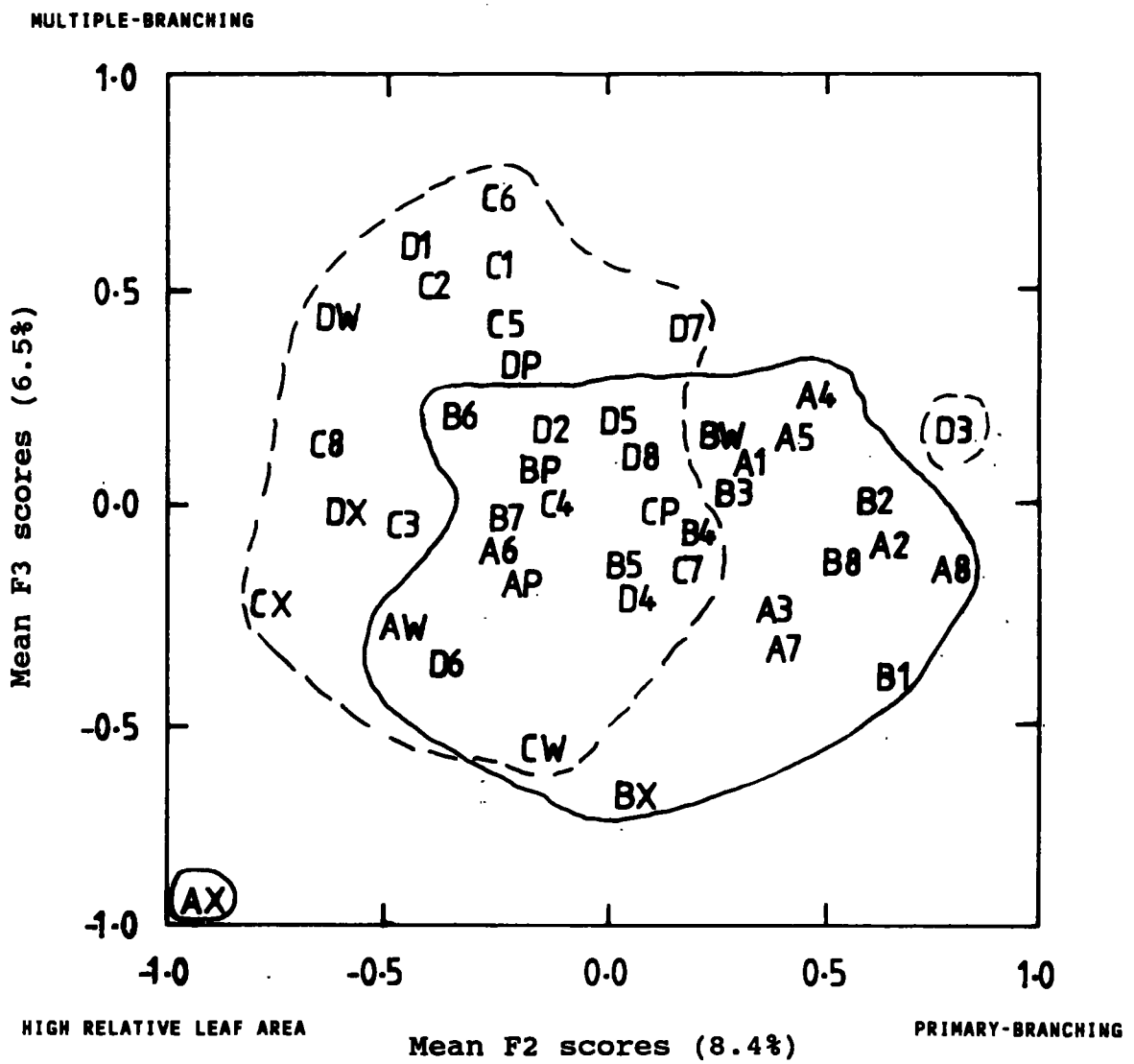
In SQU-1, seedlings in the woodland soil control (B1) had a higher primary-branching morphology than seedlings in the dune soil control (A1), but both controls produced seedlings that were intermediate in height and relative leaf area. These results show that under the habitat-negative effect of the SQU-1 trial, the main effect of the woodland soil was to promote primary-branching, whilst the main effect of the dune soil was to promote an increase in multiple-branching. In contrast, there were no morphological differences between the soil types in AL-K (C1 & D1) so that the seedlings in both controls were predominantly multiple-branched. These results show that under the habitat-positive effect of AL-K, the main effect of both soil types was to enhance the multiple-branching effect of this trial. The main effects of each soil type are also summarised in table 6.13.

4. NPK fertilisers (figure 6.5)

The treatments with NPK+T, NPK-T and NPK+T/CM2 from SQU-1 were more clustered than the same treatments from AL-K. This shows that the combined effects of SQU-1 and these supplements reduced the morphological variation between the soil types. This reduction was greatest in the treatments

Figure 6.3

Effects of trial location (SQU-1 & AL-K) on the morphological variation of 34 week old seedlings, using the treatment mean scores of the second (F2) and third (F3) principal components determined from 704 seedlings. Where figures in parentheses are the percentages of variance associated with each component.



——— SQU-1 treatments — — — AL-K treatments

A1	DS/control	B1	WS/control	C1	DS/control	D1	WS/control

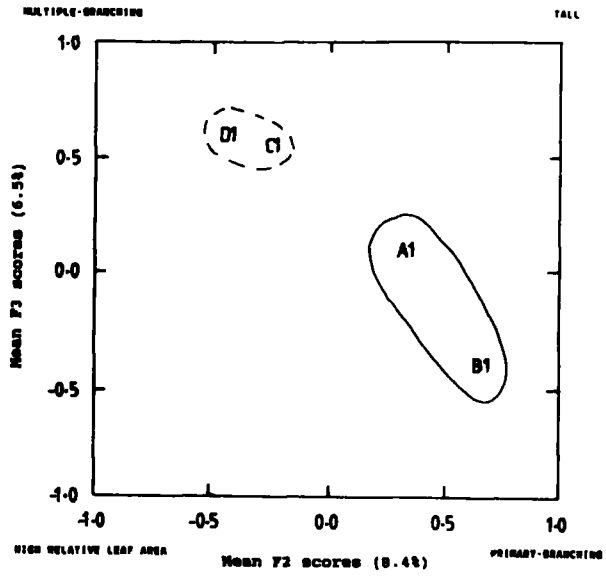
Table 6.13

Summary of the main effects of trials (SQU-1 and AL-K) and soil types (dune soil and woodland soil) on the variation in the morphology of P.cineraria seedlings determined by principal components analysis.

	SQU-1	AL-K
Trial effects	High primary-branching	High multiple-branching
	Intermediate relative leaf area and height	
Dune soil effects	Increase in multiple-branching	High multiple-branching
	Intermediate relative leaf area and height	
Woodland soil effects	High primary-branching	High multiple-branching
	Intermediate relative leaf area and height	

Figure 6.4

Effects of trial location (SQU-1 & AL-K) on the morphological variation of 34 week old seedlings grown in the treatment controls (no supplements). Plot redrawn from figure 6.3.

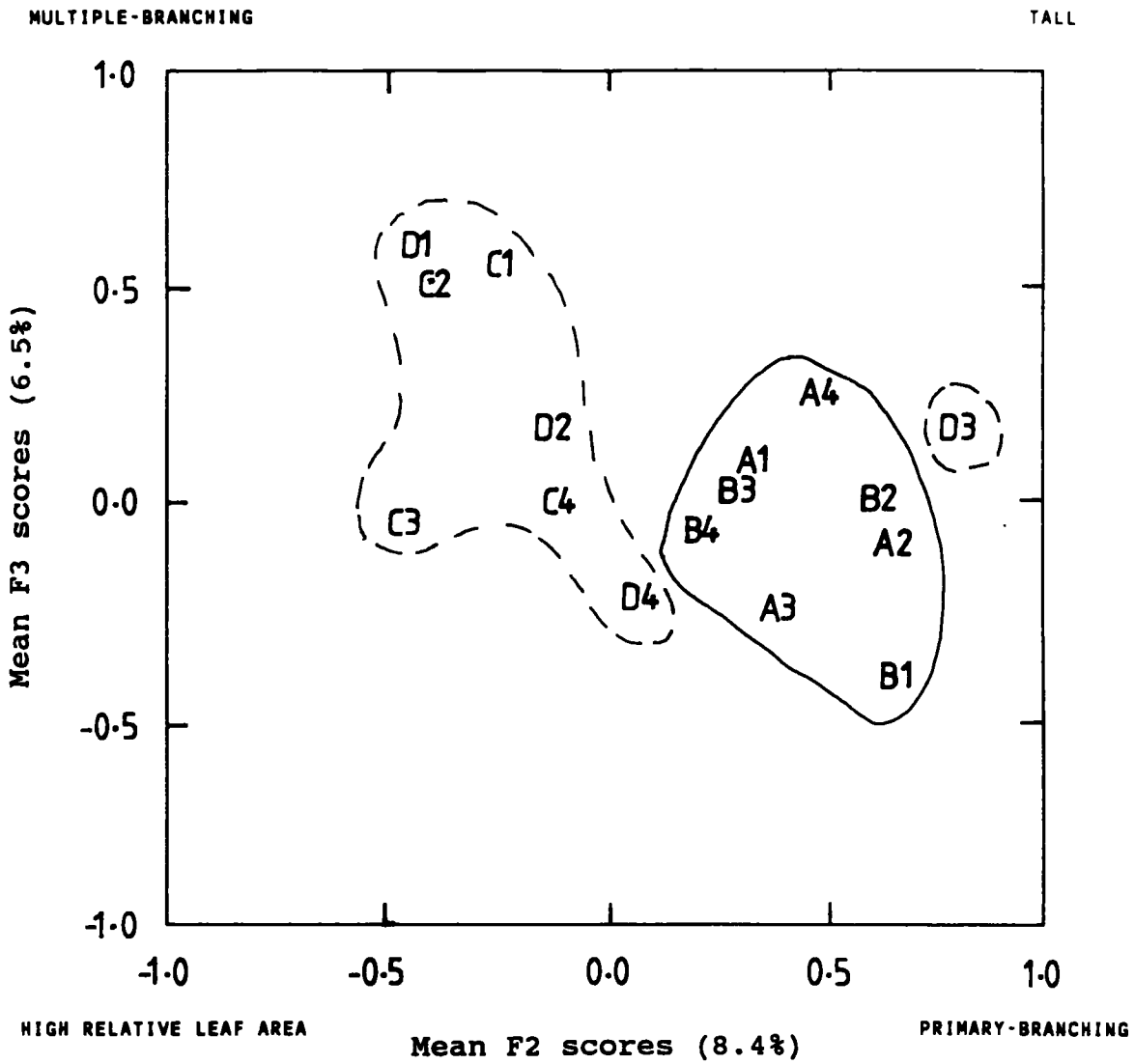


——— SQU-1 treatments — — — AL-K treatments

A1 DS/control B1 WS/control C1 DS/control D1 WS/control

Figure 6.5

Effects of trial location (SQU-1 & AL-K) on the morphological variation of 34 week old seedlings grown in treatments supplemented with NPK fertilisers (NPK+T, NPK-T & NPK+T/CM2). Plot redrawn from figure 6.3.



——— SQU-1 treatments — — — AL-K treatments

A1	DS/control	B1	WS/control	C1	DS/control	D1	WS/control
A2	DS/NPK+T	B2	WS/NPK+T	C2	DS/NPK+T	D2	WS/NPK+T
A3	DS/NPK-T	B3	WS/NPK-T	C3	DS/NPK-T	D3	WS/NPK-T
A4	DS/NPK+T/CM2	B4	WS/NPK+T/CM2	C4	DS/NPK+T/CM2	D4	WS/NPK+T/CM2

supplemented with NPK+T (A2 & B2), which suggests that the high nutrient status provided by this fertiliser had a similar influence on seedling morphology in both soil types. The habitat-negative effect of SQU-1 on these treatments also reduced morphological departures from the controls, although their application to the dune soil marginally increased primary-branching, whereas their application to the woodland soil marginally increased multiple-branching.

In AL-K, the greater morphological variation between the soil types supplemented with these fertilisers was dominated by the departure from the main effects of both soil types with the supplement NPK-T (C3 & D3). The application of NPK-T to the woodland soil (D3) increased the primary-branching and shoot height, whilst its application to the dune soil (C3) increased the relative leaf area and reduced the shoot height. The absence of trace elements in NPK-T caused departures in the morphology of the seedlings, which may be attributed to increased trace element deficiencies in the nutrient-demanding faster growth of AL-K. Whilst the application of NPK+T to the dune soil (C2) in this trial did not cause any departures in the seedling morphology from the trial controls, its application to the woodland soil (D2) did increase primary-branching.

There was only marginal variation in the morphology of seedlings grown in the treatments supplemented with NPK+T/CM2 between the trials and between the soil types (A4, B4, C4 & D4). These seedlings were dominated by a primary branching morphology, and were intermediate in both shoot height and relative leaf area. This nutrient-rich supplement which caused significant increases in seedling size in the dune soil in SQU-1 and in both soil types in AL-K (section 6.3.4) also dominated the morphological development of the seedlings.

In SQU-1, the application of this supplement to the dune soil in SQU-1 (A4) did not affect seedling morphology, whilst its application to the woodland soil (B4) increased the multiple-branching of the seedlings. In contrast, the application of this treatment to both soil types in AL-K (C4 & D4) increased the primary-branching morphology of the seedlings, particularly when added to the woodland soil.

5. Manure and peat (figure 6.6)

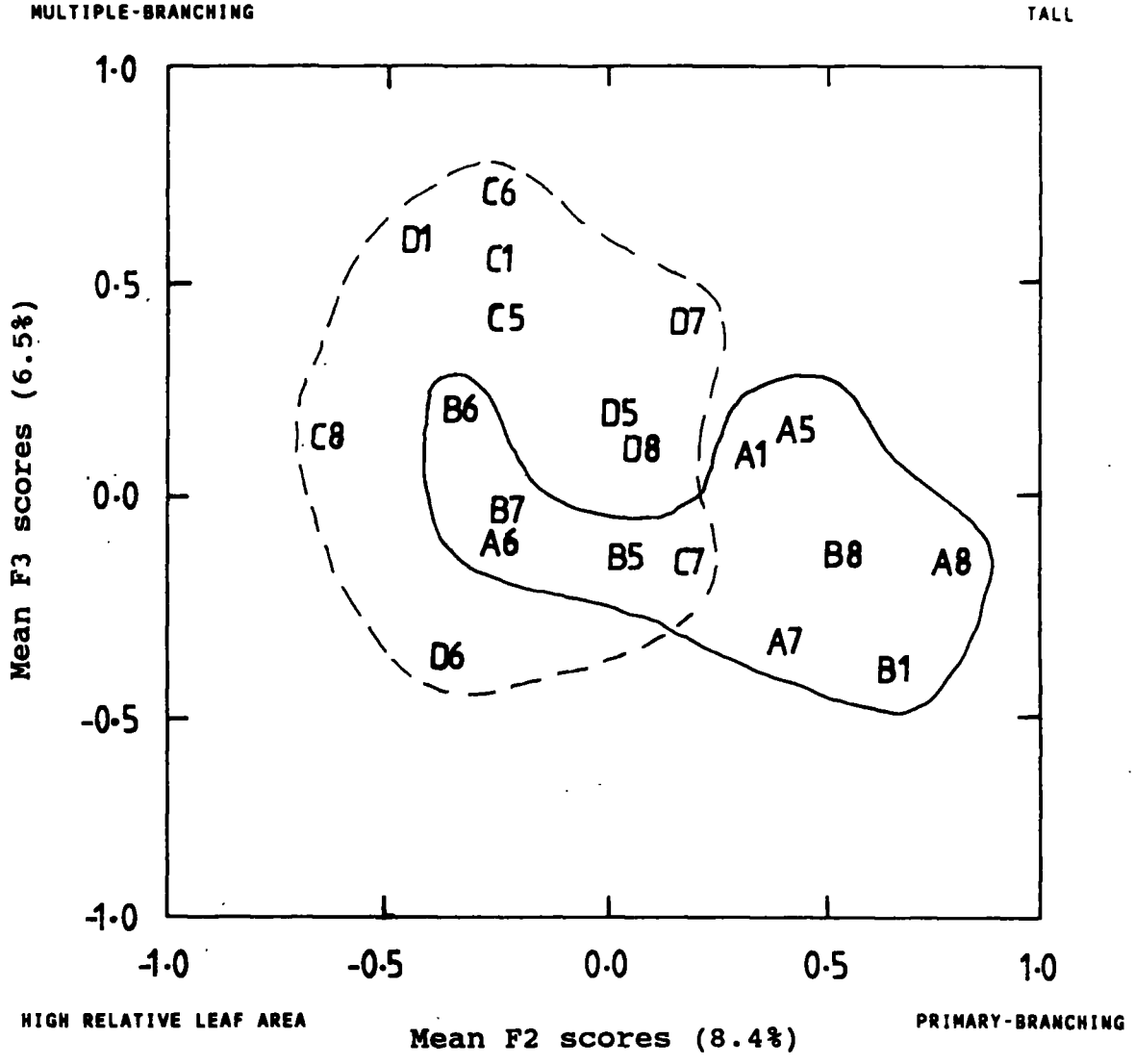
The chemical and physical effects of the three manure concentrations on the seedling morphology between the trials were variable. The main difference between the trials was the greater variation in seedling morphology in AL-K than in SQU-1. This variation may also have been enhanced by the habitat-positive effect of AL-K in which faster seedling growth was promoted.

In SQU-1, the variation in seedling morphology was higher when the manure was applied to the dune soil than the woodland soil. When added to the dune soil, the manure generally increased the relative leaf area with no change in the primary-branching morphology. This departure from the main effect of the dune soil did not occur when the highest manure concentration of CM1 (A4) was applied. The application of manure to the woodland soil increased the multiple-branching morphology and stem size of the seedlings. The seedlings in these treatments were homogenous in morphology, and comparable to many seedlings in the AL-K trial.

In AL-K, the highest manure concentrations of CM1 (C5) and CM2 (C6) added to the dune soil did not cause any departures in the morphology of the seedlings, but the lowest manure concentration of CM3 (C7) in this soil reduced multiple-branching, such that the seedlings were of comparable morphology to those in the SQU-1 trial. Whilst the application of manure to the woodland soil in this

Figure 6.6

Effects of trial location (SQU-1 & AL-K) on the morphological variation of 34 week old seedlings grown in treatments supplemented with manure and peat (CM1, CM2, CM3 & peat). Plot redrawn from figure 6.3.



——— SQU-1 treatments — — — AL-K treatments

A1	DS/control	B1	WS/control	C1	DS/control	D1	WS/control
A5	DS/CM1	B5	WS/CM1	C5	DS/CM1	D5	WS/CM1
A6	DS/CM2	B6	WS/CM2	C6	DS/CM2	D6	WS/CM2
A7	DS/CM3	B7	WS/CM3	C7	DS/CM3	D7	WS/CM3
A8	DS/peat	B8	WS/peat	C8	DS/peat	D8	WS/peat

trial also decreased multiple-branching, the lowest manure concentrations of CM2 (D6) and CM3 (D7) promoted further departure from the main effect of the woodland soil. The treatment WS/CM2 (D6) produced short seedlings with high relative leaf areas, whilst the opposite occurred in the treatment WS/CM3 (D7) which produced tall seedlings with low relative leaf areas.

The use of the supplement of peat in the SQU-1 trial (A8 & B8) did not cause any departures from the main effects of both the trial or the soil types. Whilst the application of peat to dune soil significantly increased the seedling size (section 6.3.4), this greater seedling growth did not have any effect on the seedling morphology. The differences in the physical properties of the treatments DS/peat and WS/peat (section 6.3.2) in this trial also did not effect the way in which dry matter accumulated in the shoot sinks.

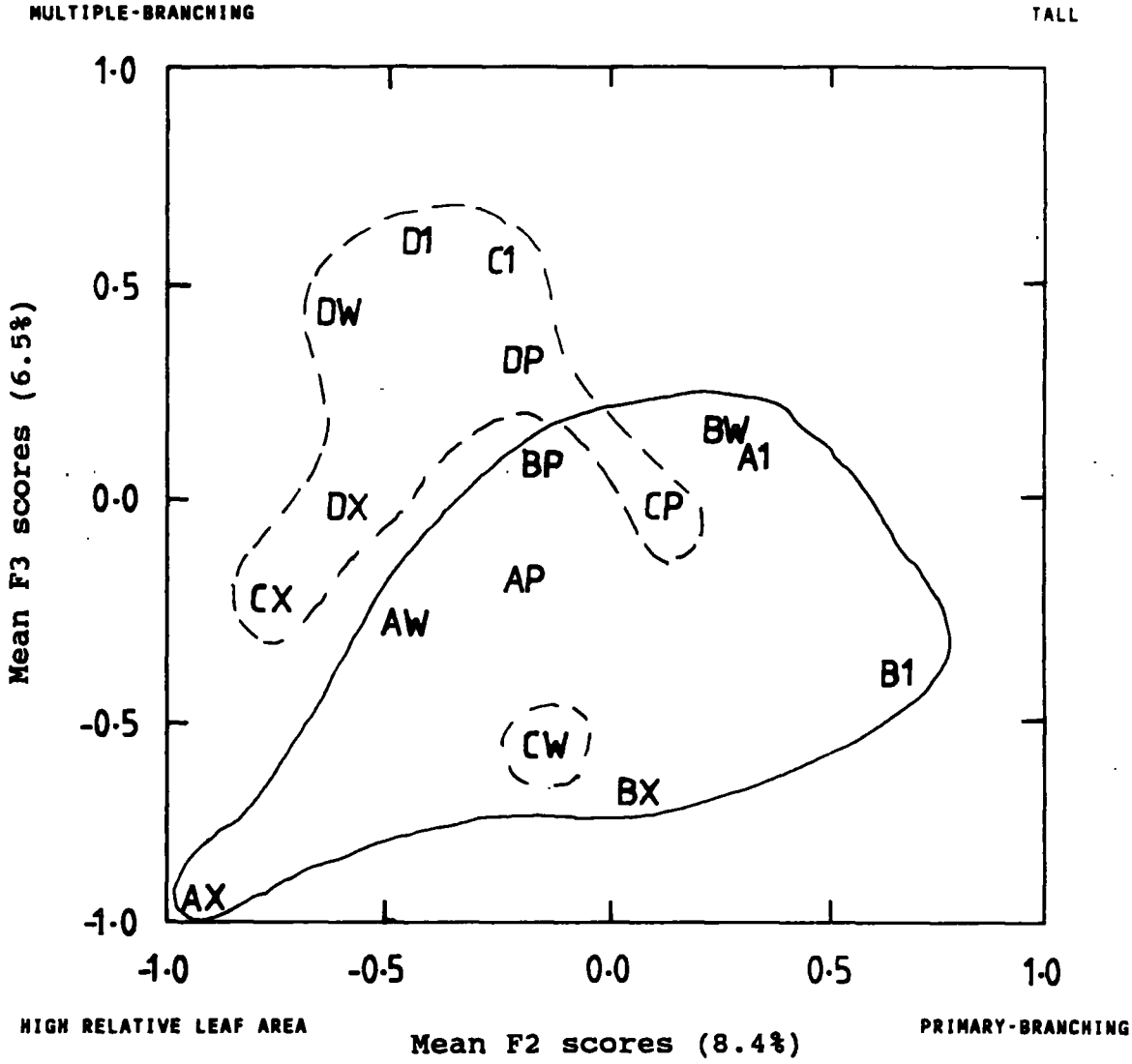
There was a greater departure from the main effects of the trial and soil types when peat was used in the AL-K trial (C8 & D8). This departure involved a decrease in the multiple-branching morphology in the woodland soil (D8), and a marginal increase in the relative leaf area in the dune soil (C8). An increase in the relative leaf area of seedlings grown in the dune soil with peat may have been partly responsible for the significantly larger seedlings in this treatment than the dune soil control (section 6.3.4). This indicates that the higher field capacity of DS/peat than the control promoted greater leaf development. That this did not occur when peat was applied to the woodland soil may be the result of the differences in the physical properties of WS/peat and DS/peat.

6. Water-absorbing polymer, phosphate and excess fertiliser (figure 6.7)

The effects of these supplements caused a greater variation in the morphology of seedlings in SQU-1 than AL-

Figure 6.7

Effects of trial location (SQU-1 & AL-K) on the morphological variation of 34 week old seedlings grown in treatments supplemented with water-absorbing polymer (WAP), phosphate (PO_3) and excess fertiliser (excess). Plot redrawn from figure 6.3.



——— SQU-1 treatments — — — AL-K treatments

A1	DS/control	B1	WS/control	C1	DS/control	D1	WS/control
AW	DS/WAP	BW	WS/WAP	CW	DS/WAP	DW	WS/WAP
AP	DS/PO3	BP	WS/PO3	CP	DS/PO3	DP	WS/PO3
AX	DS/excess	BX	WS/excess	CX	DS/excess	DX	WS/excess

K, and also caused departures from the main effect of each trial and each soil type.

In both SQU-1 and AL-K, the application of the water-absorbing polymer (WAP) to dune soil (AW & CW) greatly increased the relative leaf area and decreased the shoot height of the seedlings. These results suggest that the nutrient-limiting effect of this polymer in dune soil (section 6.3.4) influenced the partitioning of dry matter more into the leaves than the stem. As water availability was high in this treatment due to the presence of the polymer, the larger leaf areas may have promoted higher transpiration rates in these seedlings. Since a higher transpiration rate would increase the bulk flow of the nutrient solution to the root surfaces, it is suggested that the increase in the leaf area was a morphological response for maximising the uptake of nutrients present at low concentrations in the soil solution. This hypothesis was supported by the absence of any departures in the relative leaf areas of seedlings grown in the nutrient-rich woodland soil in both trials. The application of this polymer to the woodland soil in SQU-1 (BW) did reduce the primary-branching morphology, resulting in morphological homogeneity between these seedlings and those grown in the dune soil control (A1).

The application of phosphate (AP, BP, CP & DP) reduced the variation in the seedling morphology between the trials and between the soil types. The seedlings produced by these treatments were intermediate in the branching form, relative leaf area and shoot height. Hence, phosphate had a dominating effect on the seedling morphology, by reducing the primary-branching effect of SQU-1, and reducing the multiple-branching effect of AL-K.

Excess fertiliser added to both soil types in both trials (AX, BX, CX & DX) distinctly caused an increase in the relative leaf area and a decrease in the height of the

seedlings. This morphological departure was greatest when this supplement was added to the dune soil in both trials (AX & CX), but particularly in SQU-1 (AX). The smaller increases in the relative leaf area and the smaller decreases in shoot height in the woodland soil than in the dune soil supports the hypothesis presented in section 6.3.4 that components in the woodland soil reduced the sensitivity of the seedlings to fertilizer toxicity.

Since the application of excess fertiliser to both soil types in both trials did not cause any significant differences in the seedling size from the controls (section 6.3.4), these departures in the morphology of the seedlings were caused predominantly by changes in the partitioning of dry matter between the leaf and stem sinks. It is suggested that the increased leaf area was a growth response to reduce the effect of fertiliser toxicity, by accumulating excess ions taken up by the plant into extra leaf sinks which are eventually removed when the leaves are dropped.

PART 3

SHADE EFFECTS ON SEEDLING GROWTH (SQU-1 & SQU-2)

6.3.7 Statistical analysis of data

At 34 weeks of age, the same 12 measurements used in Part 2 were performed on 212 seedlings in 14 treatments (2 soil types with 6 soil supplements and 2 controls) in the shaded trial SQU-2 (see table 6.2). A sample size of 16 seedlings was used in most treatments, but in five treatments a smaller sample size (12-15 seedlings) was necessary due to their availability. The treatments supplemented with manure (CM1, CM2 & CM3) and with peat were rejected from this analysis because of high seedling fatalities resulting in too few seedlings for statistical

interpretation. These 14 treatments sampled in SQU-2 were compared to the equivalent treatments in SQU-1 (n=224 seedlings) to determine the effect of shade on the variation in the growth of P.cineraria seedlings.

Using the same statistical methods described in Part 2 (section 6.3.4), a principal components analysis of 10 standardised highly correlated variables (table 6.14a) was performed on the 436 seedlings sampled from SQU-1 and SQU-2. The first three components of this analysis accounted for 82.7% of the variation in the data and only these were examined (table 6.14b). A statistical summary of these principal components for each treatment are presented in Appendix D.

The first principal component (F1), which accounted for 66.5% of the variation in the data, was a result of an equal weighting between most variables in contrast to the relative leaf area (table 6.14c). As in Part 2, this principal component described the size of the seedlings, and was used to determine the significant treatment variations in seedling size between the trials, between the soil types and between the soil supplements and their controls.

The second principal component (F2) accounted for 10.3% of the variation in the data and was a result of the shoot height, relative leaf area, leaf and stem weights and the lengths of the two primary branches in contrast to the diameters of the two primary branches and the stem. The third principal component accounted for 5.9% of the variation in the data and was a result of the relationship between the diameter of the longest primary branch, the relative leaf area and the lengths of the two primary branches in contrast to the stem diameter, shoot height and number of branches. The F2 and F3 principal components, which accounted for 16.2% of the variation in the data were used to determine the main effects of the trials and

Table 6.14

Effects of trial shade (SQU-1 & SQU-2) on seedling morphology (n=436 seedlings).

A. Pearson's correlation coefficient half-matrix of the standardised variables. Except with relative leaf area (RELAREA), all correlations were positive and highly significant (p<0.001).

	HEIGHT	STEM DIAM	BNO	BD1	BD2	BL1	BL2	LEAFWT	STEMWT	RELAREA
HEIGHT	1.000									
STEMDIAM	0.513	1.000								
BNO	0.444	0.759	1.000							
BD1	0.206	0.571	0.474	1.000						
BD2	0.339	0.837	0.700	0.597	1.000					
BL1	0.590	0.699	0.615	0.558	0.713	1.000				
BL2	0.608	0.718	0.652	0.472	0.802	0.815	1.000			
LEAFWT	0.626	0.801	0.771	0.494	0.694	0.722	0.746	1.000		
STEMWT	0.617	0.796	0.719	0.480	0.689	0.708	0.704	0.959	1.000	
RELAREA	-0.297	-0.726	-0.506	-0.484	-0.657	-0.457	-0.477	-0.455	-0.463	1.000

B. Score coefficients for the first 3 principal components determined by principal components analysis.

	Principal components		
	F1	F2	F3
% of total variance	66.5	10.3	5.9
STEMDIAM	0.138	-0.142	-0.329
LEAFWT	0.136	0.223	0.004
STEMWT	0.134	0.217	-0.034
BD2	0.131	-0.272	0.012
BL2	0.131	0.132	0.213
BL1	0.128	0.113	0.461
BNO	0.124	-0.016	-0.188
RELAREA	-0.101	0.461	0.764
BD1	0.097	-0.442	0.819
HEIGHT	0.096	0.581	-0.189

C. Summary of the variable weightings to describe the functions of the first 3 principal components.

F1 = STEMDIAM + LEAFWT + STEMWT + BD2 + BL2 + BL1 + BNO + BD1 + HEIGHT - RELAREA

F2 = HEIGHT + RELAREA + LEAFWT + STEMWT + BL2 + BL1 - BD1 - BD2 - STEMDIAM

F3 = BD1 + RELAREA + BL1 + BL2 - STEMDIAM - HEIGHT - BNO

the soil type controls on the variation in the seedling morphology. Morphological departures from these main effects were then examined for two groups of soil supplements.

6.3.8 Seedling size

1. Trial effects

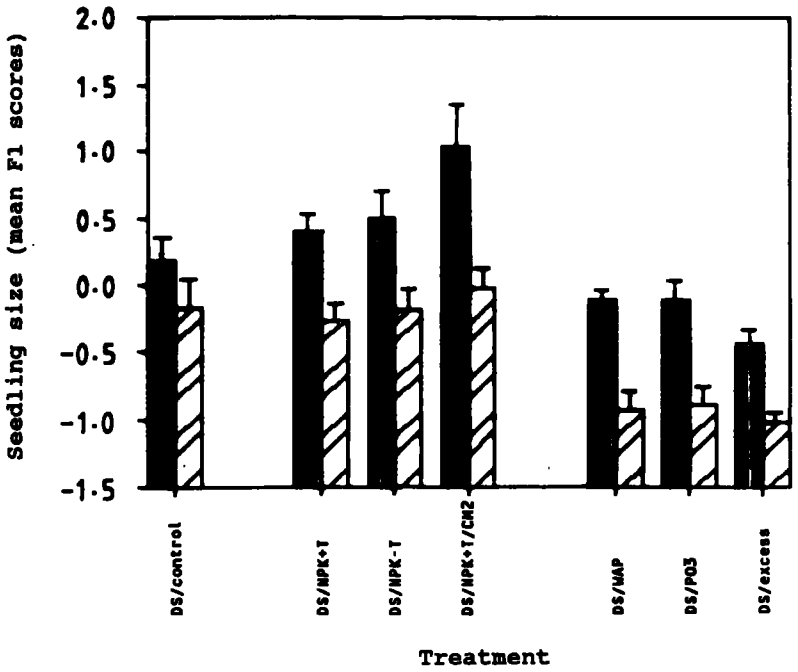
The mean F1 scores and standard errors for the 28 treatments in SQU-1 and SQU-2 are presented in figure 6.8. The optimal treatment in SQU-2 in terms of seedling size (F1) was DS/NPK+T/CM2, which had a mean shoot dry weight of 4.47g ± 2.36 and was only 30.3% of the mean shoot weight of the optimal treatment in SQU-1 (WS/NPK+T). In all treatments except the dune soil control, the seedlings were significantly larger in SQU-1 than in SQU-2 (table 6.15). These results show that the shade and associated environmental variables of SQU-2 had a greater habitat-negative effect on seedling growth than the habitat effect of SQU-1 (slides 40 & 42). Therefore, a null hypothesis was used to state that the shade effect in SQU-2 trial had a negative effect on seedling growth.

The seedlings grown in the dune soil in both SQU-1 and AL-K were comparable in size to seedlings grown in dune soil under the shade of SQU-2. These results clearly show that the negative effect of shade did not increase the negative effects of nutrient deficiencies in the dune soil. This indicates that the wetter environment of the dune soil promoted by the shade maximised the availability of the low concentrations of *in situ* soil nutrients, resulting in seedlings of comparable size to those grown in the dune soil under full sunlight.

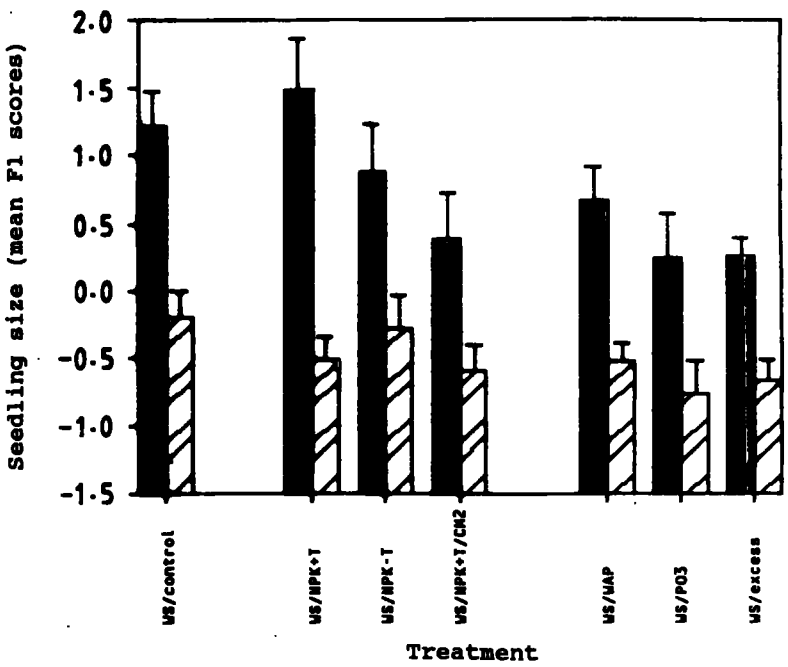
Figure 6.8

Effects of trial shade (SQU-1 & SQU-1) on the size of 34 week old seedlings, using the treatment mean scores and standard errors of the first principal component (F1) determined from 433 seedlings.

A. Dune soil (DS)



B. Woodland soil (WS)



SQU-1 trial SQU-2 trial

Table 6.15

Between trial significant differences in seedling size (F1 scores) of 34 week old seedlings (n=436) from trials SQU-1 and SQU-2, using independent t-tests.

	CONTROL
DS	NS
WS	***

	Soil supplement		
	NPK+T	NPK-T	NPK+T/CM2
DS	**	*	**
WS	***	*	*

	Soil supplement		
	WAP	PO3	EXCESS
DS	***	***	***
WS	***	*	***

2. Controls

There were no significant differences in seedling size between the woodland and dune soils in the shade trial, compared to the trial in full sunlight which produced significantly larger seedlings in the woodland soil ($p<0.01$). Since there was a significant reduction in seedling size in the woodland soil between SQU-1 and SQU-2, these results show that the shade effect of SQU-2 reduced the soil-positive effect of the woodland soil, resulting in the significant reduction of seedling growth.

These results indicate that the combined inhibitory effects of shade and woodland soil were largely responsible for the failure of P.cineraria seedlings to survive beneath the tree canopy of the fenced plots in the EPZ (Chapter 5). Since the woodland soil that was sampled from beneath the tree canopy promoted the growth of seedlings under full sunlight (SQU-1 & AL-K), the results show that the woodland soil had an allelopathic effect on seedling growth only when under shade conditions. It is suggested that the properties of the woodland soil have influenced the growth and development of the Prosopis woodland habitat in the following way. Under the canopy shade the woodland soil will have inhibited seedling growth to prevent plant competition between the parent and its progeny. In contrast, under full sunlight the woodland soil will have promoted seedling regeneration, thereby causing the colonisation of both the woodland margins and the between-clump gaps.

3. NPK fertilisers (table 6.16)

The application of the three NPK fertiliser supplements in the shade trial produced smaller seedlings in the woodland soil than in the dune soil, although only NPK+T/CM2 was significant. Whilst these NPK fertilisers did not cause any significant differences in seedling size from

Table 6.16

Between soil type and between soil supplement significant differences in seedling size (F1 scores) of 34 week old seedlings (n=436) in the NPK fertiliser treatments from trials SQU-1 and SQU-2.

A. Between soil types using independent t-tests.

	Soil supplement		
	NPK+T	NPK-T	NPK+T/CM2
SQU-1	**	NS	NS
SQU-2	NS	NS	*

B. Between supplements, using one-way ANOVAs and post-hoc contrasts according to the Bonferroni procedure. Where ** = p<0.001; * = p<0.005; NS = not significant at p>0.005.

	Soil supplement		
	NPK+T	NPK-T	NPK+T/CM2
SQU-1			
DS	NS	NS	*
WS	NS	NS	NS
SQU-2			
DS	NS	NS	NS
WS	NS	NS	NS

the controls for both soil types under the shade, the results suggest that the NPK fertilisers enhanced the allelopathic effect of the woodland soil, especially when the NPK fertiliser was supplemented with manure. In the wetter environmental conditions of this trial, the increased soil field capacity by the manure in the treatment WS/NPK+T/CM2 produced a nutrient-rich saturated soil environment that was inhibitory to seedling growth, possibly in response to the development of soil anoxia. Soil anoxia may also have contributed to the poor performance of seedlings in the treatments supplemented with manure or peat.

4. Water-absorbing polymer, phosphate and excess fertiliser (table 6.17)

Despite the wetter environmental conditions in SQU-2 than in SQU-1, the application of the water-absorbing polymer (WAP) produced marginally significantly larger seedlings in the woodland soil than in the dune soil. This result suggests that the polymer in this moisture-rich environment physically prevented the woodland soil from becoming saturated with water. Whilst there were no significant differences in seedling size between the treatments WS/WAP and the WS/control, the application of this polymer to the dune soil produced significantly smaller seedlings. As in SQU-1, but to a greater extent, this result shows that the shade effect of SQU-2 enhanced the nutrient-limiting effect of WAP when this supplement was applied to the nutrient-poor dune soil.

Under shade, the application of phosphate did not significantly affect seedling size between the soil types, whilst the application of excess fertiliser only marginally significantly increased seedling size in the woodland soil. Since both supplements applied to the dune soil under shade caused a significant reduction in seedling size from the control, these results show that despite the allelopathic effect of the woodland soil under shade

Table 6.17

Between soil type and between soil supplement significant differences in seedling size (F1 scores) of 34 week old seedlings (n=436) in the treatments with water-absorbing polymer, phosphate and excess fertiliser from trials SQU-1 and SQU-2.

A. Between soil types using independent t-tests

	Soil supplement		
	WAP	PO_3	EXCESS
SQU-1	**	NS	***
SQU-2	*	NS	*

B. Between supplements, using one-way ANOVAs and post-hoc contrasts according to the Bonferroni procedure. Where ** = p<0.001; * = p<0.005; NS = not significant at p>0.005.

	Soil supplement		
	WAP	PO_3	EXCESS
SQU-1			
DS	NS	NS	**
WS	NS	NS	NS
SQU-2			
DS	**	**	**
WS	NS	NS	NS

conditions, the woodland soil continued to reduce the negative effects of these soil supplements on seedling growth. The results also show that the negative effect of shade promoted a greater sensitivity to phosphate imbalances and fertiliser toxicity of seedlings grown in the dune soil.

6.3.9 Seedling morphology

1. Dominant morphological characteristics in the analysis

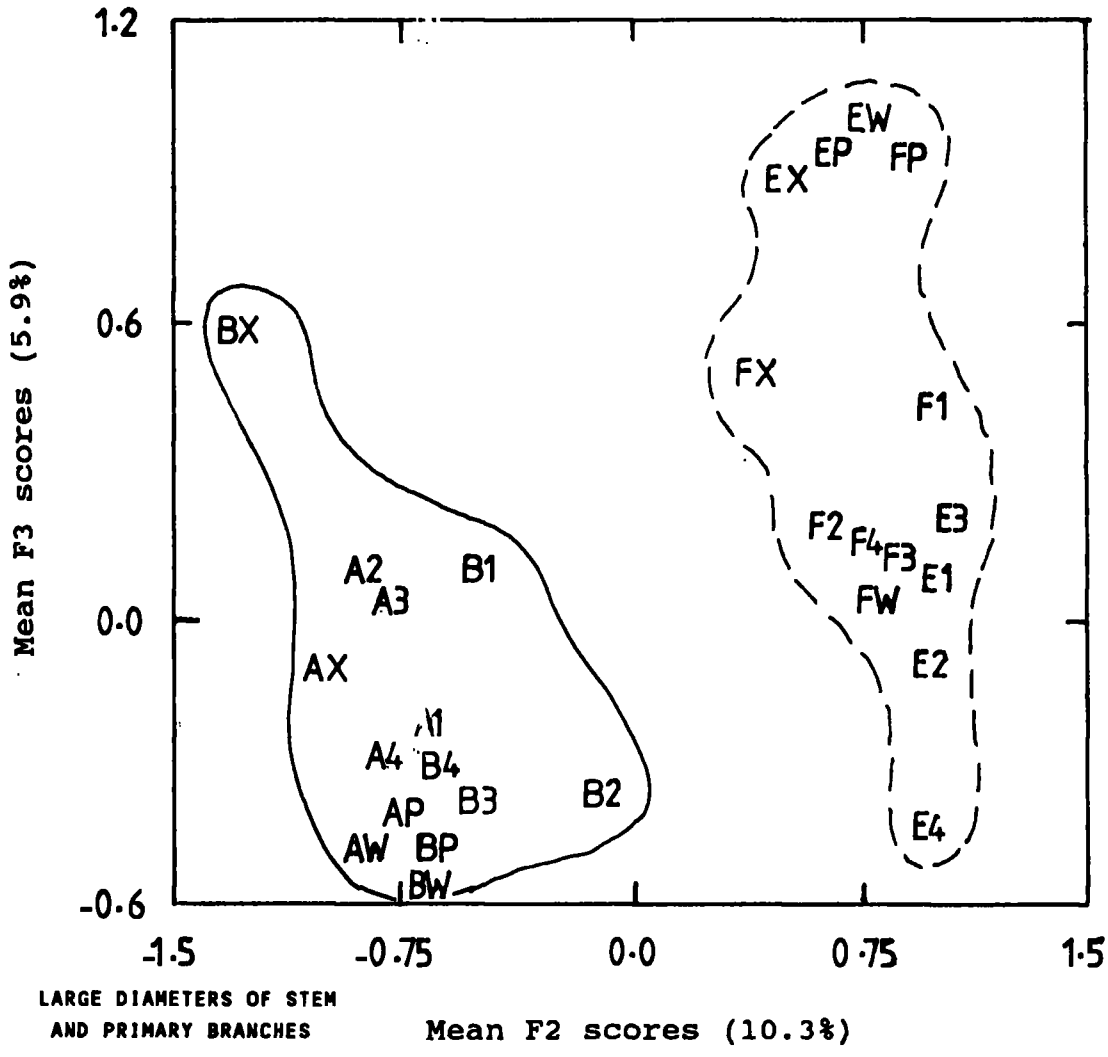
A scatter plot of the treatment mean scores of the principal components F3 against F2 for the 28 treatments in SQU-1 and SQU-2 is presented in figure 6.9. The morphological characteristics that were responsible for the distribution of these treatments are summarised below:

Principal component scores		Dominant morphological characteristics
F2	F3	
1. HIGH	HIGH	High relative leaf areas and long primary branches
2. HIGH	LOW	Tall
3. LOW	HIGH	Large diameter of the longest primary branch
4. LOW	LOW	Large stem and primary branch diameters

For comparative purposes, separate plots were prepared for the controls and the two groups of soil supplements.

Figure 6.9

Effects of trial shade (SQU-1 & SQU-2) on the morphological variation of 34 week old seedlings, using the treatment mean scores for the second (F2) and third (F3) principal components determined from 436 seedlings. Where figures in parentheses are the percentages of variance associated with each component.



——— SQU-1 treatments — — — SQU-2 treatments

A1 DS/control B1 WS/control E1 DS/control F1 WS/control

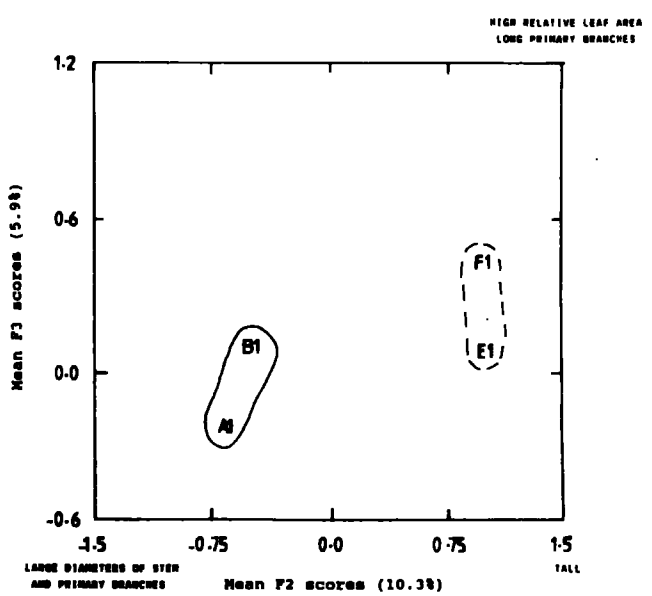
Table 6.18

Summary of the main effects of trials (SQU-1 and SQU-2) and soil types (dune soil and woodland soil) on the variation in the morphology of *P.cineraria* seedlings determined by principal components analysis.

	SQU-1	SQU-2
Trial effects	Large stem diameters	High relative leaf area
	Large primary branch diameters	Long primary branches
		Tall
Dune soil effects	Same as for trial	Same as for trial
		Increase in height
Woodland soil effects	Same as for trial	Same as for trial
		Increase in relative leaf area

Figure 6.10

Effects of trial shade (SQU-1 & SQU-2) on the morphological variation of 34 week old seedlings grown in the treatment controls (no supplements). Plot redrawn from figure 6.9.



——— SQU-1 treatments — — — SQU-2 treatments

A1 DS/control B1 WS/control E1 DS/control F1 WS/control

2. Trial effects

The distribution of the treatments in figure 6.9 clearly shows that the dominating morphological effect of shade intolerance in all treatments was to produce taller seedlings with higher relative leaf areas and longer primary branches than the seedlings grown under full sunlight. Hence, the main effect of SQU-2 was in the promotion of an etiolated shoot, where the leaf area and shoot height have been increased to maximise the capture of light for photosynthesis to sustain growth rates necessary for survival. The main effect of SQU-1 in this analysis was the promotion of large diameters of the stem and primary branches. The main effects of the trials on seedling morphology are summarised in table 6.18.

3. Controls (figure 6.10)

The main effect of each soil type was the same as the main effect of the trial which they were from (see table 6.18). However, there was some marginal morphological variation between the soil types in each trial. Under shaded conditions, the seedlings in the dune soil (E1) were marginally taller with a lower relative leaf area than the seedlings in the woodland soil (F1). This indicates a difference in the survival response of the seedlings to shade conditions between the soil types. The nutrient-poor dune soil promoted the partitioning of more dry matter into the stems to gain height, compared to the nutrient-rich woodland soil which promoted the transfer of more dry matter into the leaves for increasing the leaf area. The allelopathic effect of the woodland soil under shade (section 6.3.8) may have promoted this deviation in morphology. The morphological variation between the soil types under full sunlight in SQU-1 described in the section 6.3.6 was brought out in this analysis as a marginal increase in the stem and primary branch diameters in the dune soil than in the woodland soil.

4. NPK fertilisers (figure 6.11)

The treatments with the soil supplements NPK+T (E2 & F2) and NPK-T (E3 & F3) under the shade of SQU-2 produced seedlings with a lower variation in morphology than the equivalent treatments from SQU-1. This shows that the combination of the shade effect of SQU-2 and the treatment effect of these fertilisers reduced the variation in seedling morphology between the soil types. The seedlings in these treatments were morphologically similar to the seedlings in the DS/control (E1), which suggests that the application of both these fertilisers promoted the partitioning of more dry matter into gaining shoot height.

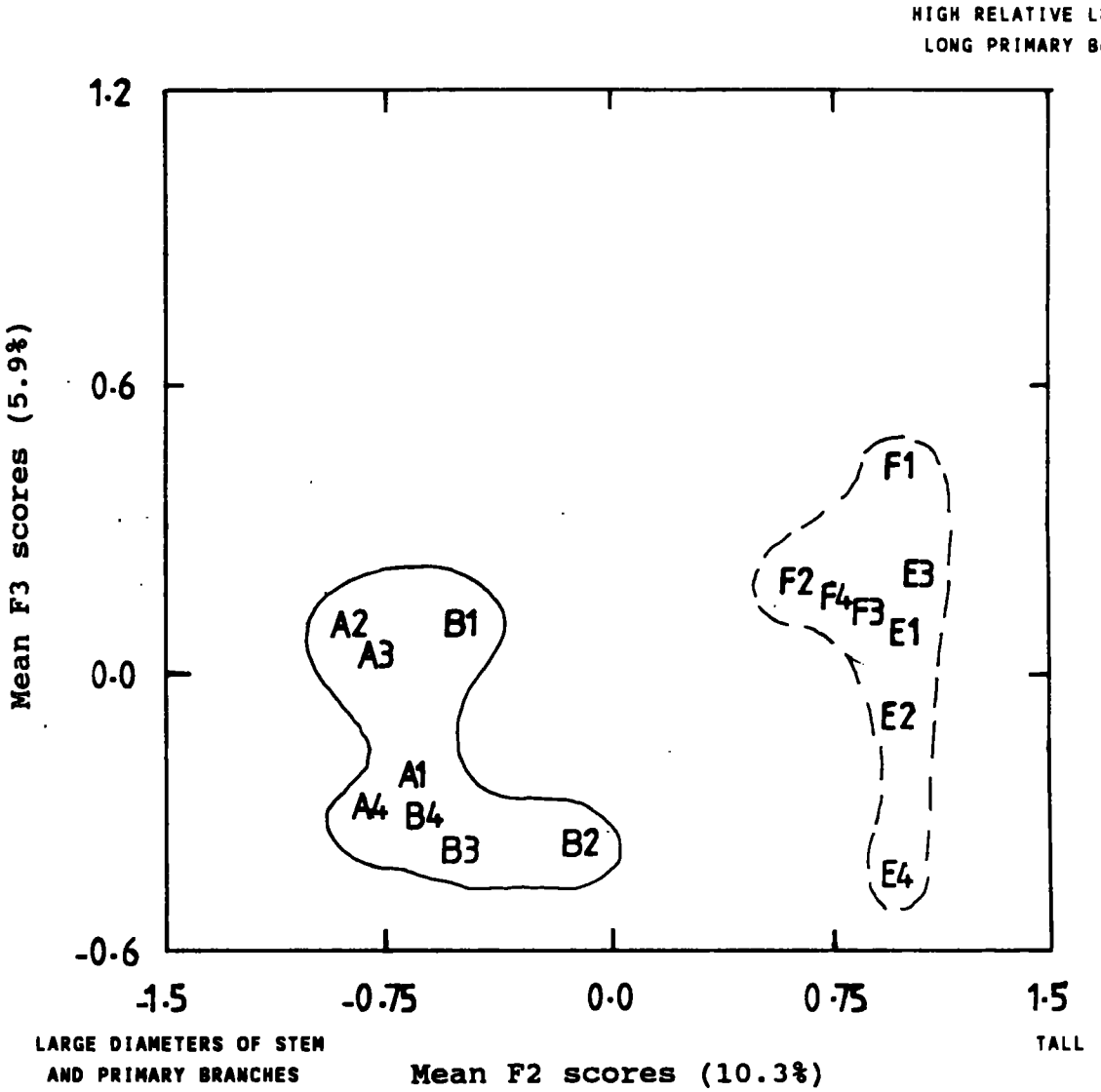
The greatest departure in morphology under shade occurred when NPK+T/CM2 was applied to the dune soil (E4). This treatment resulted in the development of seedlings which were the tallest and had the largest stem and primary branch diameters of all other treatments in this trial. Since the application of this supplement to the dune soil did not cause a significant increase in seedling size in the dune soil compared to the control (section 6.3.8), this shows that the combined effects of shade and this supplement promoted a change in the partitioning strategy in the shoot sinks, resulting in the accumulation of more dry matter in the stems.

5. Water absorbing polymer, phosphate and excess fertiliser (figure 6.12)

Under shade, the application of the water-absorbing polymer (WAP) to the dune soil (EW) caused a large departure in the morphology from the controls, whilst its application to the woodland soil (FW) only had a marginal effect on morphology. The hypothesis that seedlings grown in dune soil supplemented with this polymer increased their leaf area to encourage higher transpiration rates to maximise nutrient uptake in impoverished soils (section 6.3.6) can also be applied to the same treatment under

Figure 6.11

Effects of trial shade (SQU-1 & SQU-1) on the morphological variation of 34 week old seedlings grown in treatments supplemented with NPK fertilisers (NPK+T, NPK-T & NPK+T/CM2). Plot redrawn from figure 6.9.

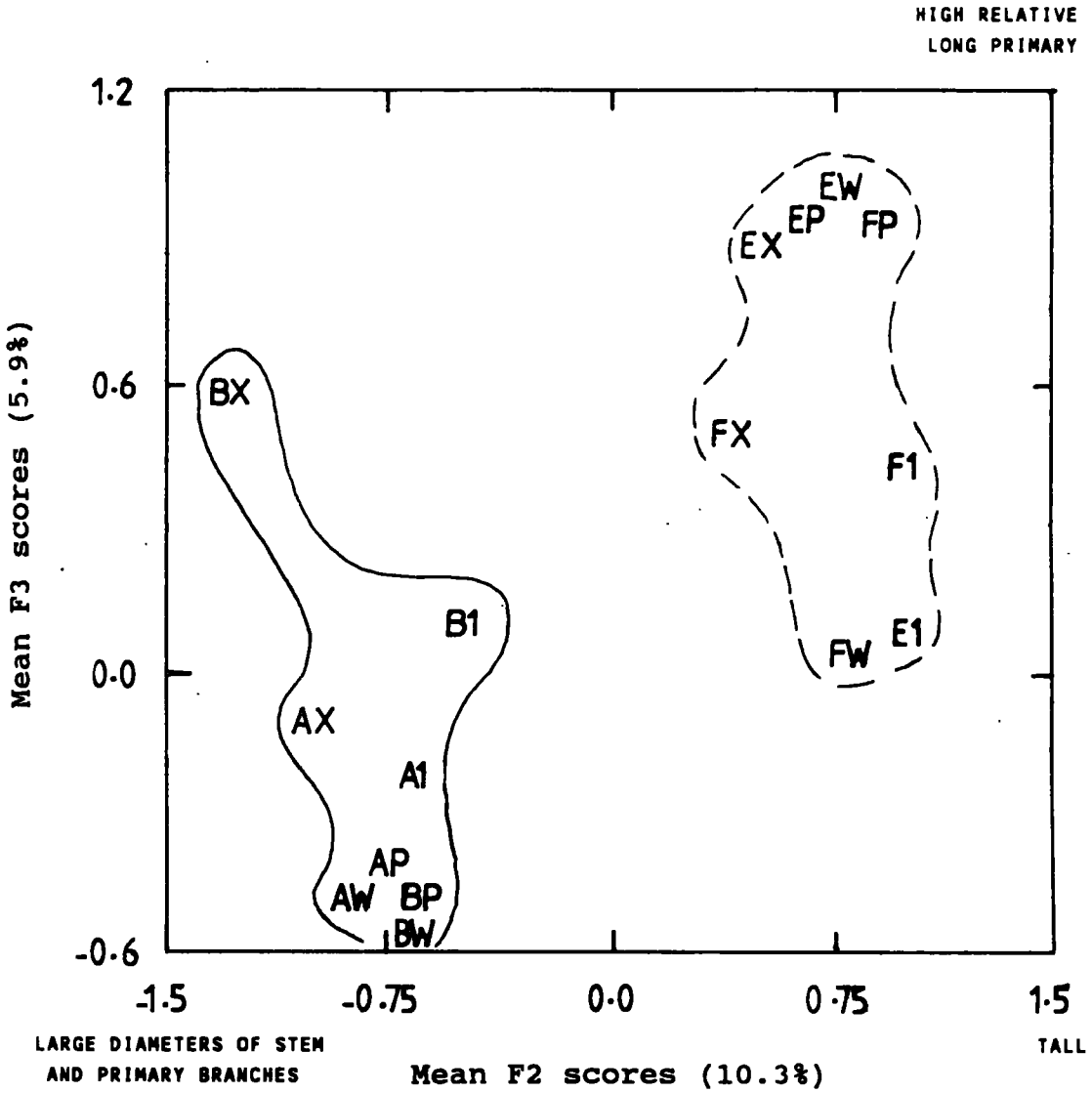


——— SQU-1 treatments — — — SQU-2 treatments

A1	DS/control	B1	WS/control	E1	DS/control	F1	WS/control
A2	DS/NPK+T	B2	WS/NPK+T	E2	DS/NPK+T	F2	WS/NPK+T
A3	DS/NPK-T	B3	WS/NPK-T	E3	DS/NPK-T	F3	WS/NPK-T
A4	DS/NPK+T/CM2	B4	WS/NPK+T/CM2	E4	DS/NPK+T/CM2	F4	WS/NPK+T/CM2

Figure 6.12

Effects of trial shade (SQU-1 & SQU-2) on the morphological variation of 34 week old seedlings grown in treatments supplemented with water-absorbing polymer (WAP), phosphate (PO_3) and excess fertiliser (excess). Plot redrawn from figure 6.9.



——— SQU-1 treatments

A1	DS/control	B1	WS/control
AW	DS/WAP	BW	WS/WAP
AP	DS/PO3	BP	WS/PO3
AX	DS/excess	BX	WS/excess

— — — SQU-2 treatments

E1	DS/control	F1	WS/control
EW	DS/WAP	FW	WS/WAP
EP	DS/PO3	FP	WS/PO3
EX	DS/excess	FX	WS/excess

shade. In this case, the wetter soil environment under shade promoted the highest relative leaf area of all treatments in this trial. These results also show that the reduction in saturation of soils by the polymer under shade only caused a marginal variation in seedling morphology when grown in the nutrient-rich woodland soil.

As in SQU-1, the application of phosphate reduced the variation between the soil types in SQU-2 (EP & FP). However, this treatment in both soil types under shade caused large morphological departures from the controls, resulting in the development of seedlings of comparable morphology to the seedlings in the treatments DS/WAP (EW) and DS/excess (EX). These results suggest that promotion of leaf area under shaded conditions was enhanced by the application of phosphate in both soil types and by excess fertiliser in dune soil. Under these conditions, it is suggested that the seedlings have developed unusually large leaf areas in order to maximise the capture of light for photosynthesis, and to minimise the effects of phosphate imbalances and fertiliser toxicity by providing extra leaf-sinks for the isolation and probable removal of unwanted ions from the plants (section 6.3.6).

The applications of the water-absorbing polymer and excess fertiliser to the woodland soil under shade (FW & FX) only caused marginal departures from the main effect of the woodland soil control (F1). Despite the combined negative effects of shade (including saturated soils), fertiliser toxicity and woodland soil allelopathy, the soil-positive effect of the woodland soil increased morphological homogeneity.

PART 4

DEVELOPMENTAL VARIATION IN SEEDLING GROWTH (13 & 34 WEEKS)

6.3.10 Statistical analysis of data

Developmental variation in the shoot dry weight and the leaf and stem partitioning ratios (as a percentage of the shoot dry weight) of P.cineraria seedlings at 13 weeks of age (Harvest 1) and 34 weeks of age (Harvest 2) in SQU-1 were examined from 22 treatments (2 soil types with 10 soil supplements and 2 controls) in the SQU-1 trial. From each of these treatments, 8 seedlings were harvested at 13 weeks of age (n=176), and 16 shoots were harvested at 34 weeks of age (n=352).

A full quantitative analysis of seedling growth (section 2.10) was performed on three treatments (DS/control, DS/excess & WS/excess) from the SQU-1 trial between 13 and 34 weeks of age. This analysis was not performed on all other treatments due to the difficulty of extracting the roots of 34 week old seedlings.

Shoot dry weight was used to study the effect of the soil environment (soil type and soil supplement) on the developmental variation of the seedlings from the 22 treatments in SQU-1. For each seedling age, the significance of the shoot weights between the soil types and between the soil supplements and their controls were determined using independent t-tests and one-way ANOVAs with post hoc contrasts according to the Bonferroni procedure. For the controls and each group of soil supplements identified in section 6.2.1, the results of these significance tests were then compared between the seedling ages.

6.3.11 Developmental variation between 13 & 34 week old seedlings

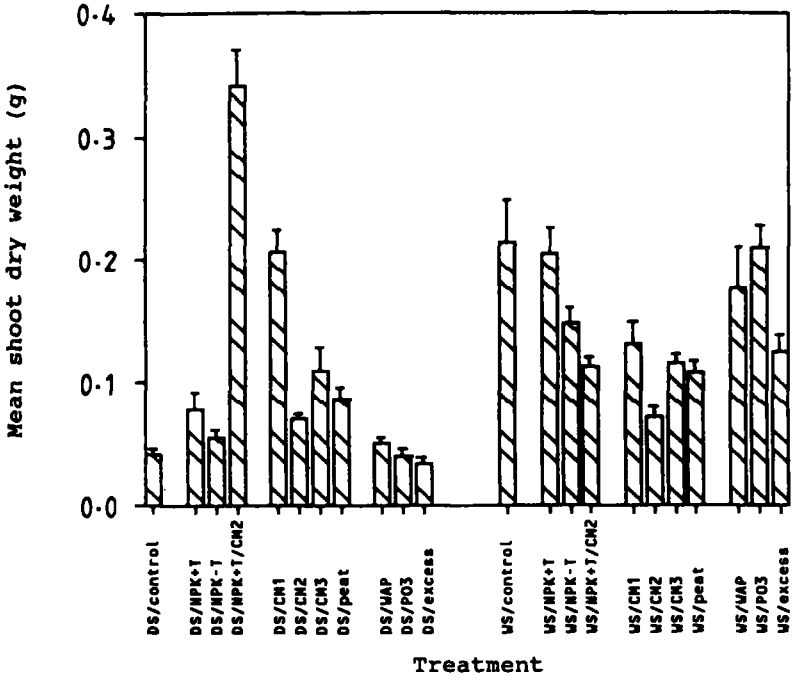
The treatment means and standard errors for the shoot dry weight for both seedling ages are shown in figure 6.13, and a statistical summary of the treatments is presented in Appendix D. The optimal treatment at 13 weeks of age was DS/NPK+T/CM2 with a mean total plant weight of 0.74g ± 0.15 and a mean shoot weight of 0.34g ± 0.09. By 34 weeks the optimal treatment was WS/NPK+T with a mean shoot weight of 14.74g ± 11.79. These results show that the seedling growth between 13 and 34 weeks of age was considerably greater than the seedling growth up to 13 weeks of age. The faster seedling growth between 13 and 34 weeks of age can be attributed to the summer environmental conditions (section 6.3.1) which occurred during this growth period. This suggests that in addition to developmental variation in growth between the two seedling ages, seedlings up to 13 weeks of age were also the product of winter-growth, whilst seedlings between 13 and 34 weeks of age were also the product of summer-growth.

The changes in the partitioning strategy of dry matter in the shoots between 13 and 34 weeks of age are presented in figure 6.14. In both seedling ages, the heavier the shoots the greater the partitioning of dry matter occurred in the stems than in the leaves. The developmental and seasonal variation between 13 and 34 week old seedlings resulted in the greater partitioning of dry matter into the stems than the leaves for the majority of seedlings at 34 weeks of age. The 13 week old seedlings showed a greater variation in the shoot partitioning strategy between the leaves and stems, but this decreased in the treatments with mean shoot weights above approximately 0.14g. Under the environmental conditions of the SQU-1 trial, this value represented a threshold shoot weight, after which proportionally more assimilates were translocated to the stems in order to provide structural support to their

Figure 6.13

Shoot dry weight treatment means and standard errors of 13 week old (n=176) and 34 week old (n=352) seedlings from trial SQU-1.

A. 13 week old seedlings



B. 34 week old seedlings

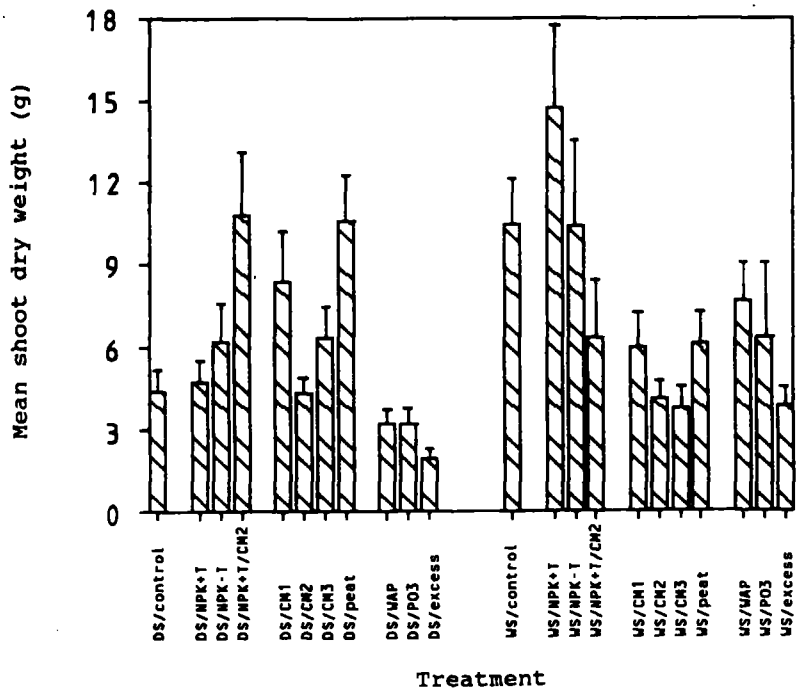
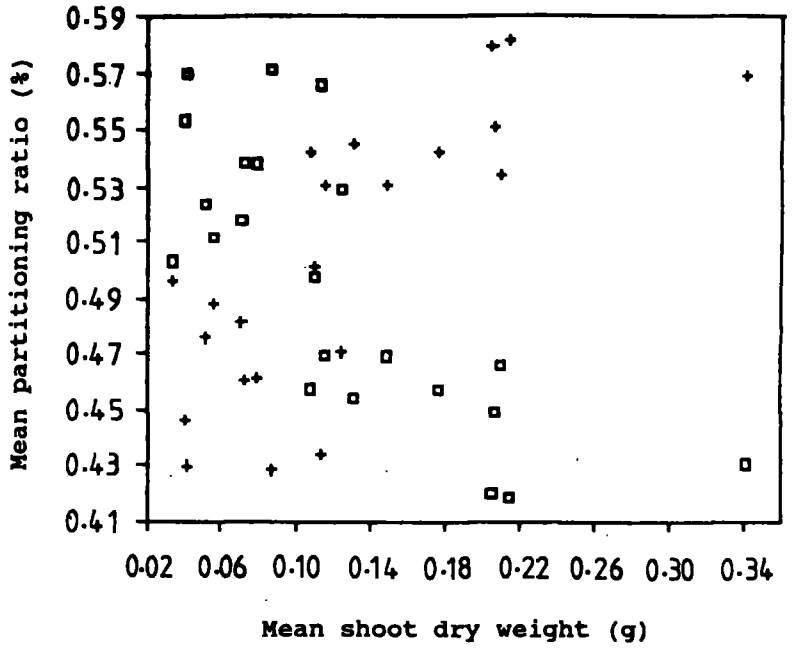


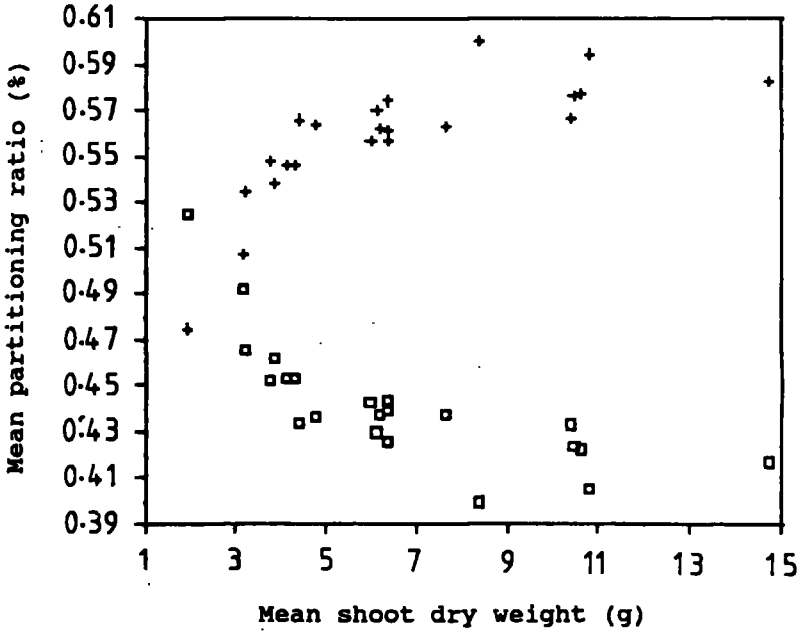
Figure 6.14

Scatter plots of treatment means for the leaf and stem partitioning ratios (as a percentage of shoot dry weight) against treatment mean shoot dry weights for 13 week old (n=176) and 34 week old (n=352) seedlings from trial SQU-1.

A. 13 week old seedlings



B. 34 week old seedlings



□ Leaf + Stem

photosynthetic apparatus. The greater the positive influence of the treatment in promoting shoot growth, the faster the seedlings reached this threshold shoot weight.

The results of a quantitative analysis of seedling growth performed on the treatments DS/control, DS/excess & WS/excess from the SQU-1 trial between 13 and 34 weeks of age are presented in table 6.19a, and the significant differences of the harvest variables between the seedling ages are presented in table 6.19b. In these treatments, leaf area, partitioning weights, total plant weight, leaf weight ratio (LWR), shoot weight ratio (SWR) and the shoot/root ratio were significantly higher in 34 week old seedlings, whilst the root weight ratio (RWR) and specific leaf area (SLA) were significantly higher in 13 week old seedlings. These results show that the partitioning of dry matter was directed more to the roots during the early growth in the winter, and more to the stems and leaves during the later growth in the summer. Rapid root growth immediately after seed germination would increase the survival of the seedlings by the formation of adventitious tap roots into the soil in search of more permanent sources of moisture. At some point between 13 and 34 weeks of age, an increase in the development of the stems (cross-sectional area) occurs for structural support, and an increase in the production of leaves occurs to meet the increased metabolic requirements of the plants.

The significant reduction in the SLA with age was consistent in the seedlings for each of the three treatments. This suggests a developmental variation of the leaves towards more efficient photosynthetic activity. This may have been influenced by the increase in the temperature and daylength during the summer as a morphological adaptation to reducing water loss through transpiration. The LARs of seedlings in the treatments DS/control and DS/excess were significantly higher at 34 weeks, but were not significantly different in the seedlings grown in the

Table 6.19

Quantitative analysis of 13 week old seedlings (n=8 per treatment) and 34 week old seedlings (n=16 per treatment) grown in the treatments DS/control (DS), DS/excess (DS/ex) and WS/excess (WS/ex) from trial SQU-1.

A. Summary data of seedling harvests, and dry matter partitioning ratios.

		Leaf area (cm^2)	Leaf weight (g)	Stem weight (g)	Root weight (g)	Total weight (g)	Shoot/ root ratio	LAR	SLA	LWR	SWR	RWR
1. 13 WEEKS												
DS	Mean	3.5	0.024	0.018	0.143	0.189	0.37	18.89	146.57	0.13	0.10	0.74
	S.D.	1.4	0.009	0.005	0.065	0.072	0.14	4.47	41.67	0.03	0.02	0.07
DS/ex	Mean	2.6	0.016	0.017	0.094	0.130	0.40	20.72	158.27	0.13	0.13	0.72
	S.D.	0.5	0.003	0.006	0.033	0.038	0.11	4.29	18.85	0.02	0.03	0.05
WS/ex	Mean	6.9	0.064	0.061	0.169	0.299	0.82	25.16	108.71	0.23	0.20	0.55
	S.D.	1.7	0.017	0.030	0.075	0.118	0.15	6.50	9.07	0.05	0.02	0.04
2. 34 WEEKS												
DS	Mean	171.9	1.833	2.561	2.183	6.577	1.94	26.28	95.95	0.28	0.37	0.36
	S.D.	86.9	0.964	1.584	0.891	3.278	0.66	2.53	9.42	0.03	0.07	0.08
DS/ex	Mean	98.9	0.995	1.047	1.169	3.106	1.75	35.92	108.46	0.33	0.30	0.38
	S.D.	60.8	0.679	0.805	0.828	2.147	0.54	10.80	17.70	0.05	0.05	0.07
WS/ex	Mean	159.3	1.676	2.176	1.978	5.840	2.01	29.70	96.91	0.31	0.35	0.34
	S.D.	83.1	0.950	1.397	1.093	3.372	0.48	4.90	4.08	0.05	0.03	0.05

B. Significance results of harvest variables and dry matter partitioning ratios between 13 & 34 week old seedlings for each treatment, using independent t-tests.

Treatment	Leaf area	Leaf weight	Stem weight	Root weight	Total weight	Shoot/ root ratio	LAR	SLA	LWR	SWR	RWR
DS/control	***	***	***	***	***	***	***	***	***	***	***
DS/excess	***	***	***	***	***	***	**	***	***	***	***
WS/excess	***	***	***	***	***	***	NS	**	**	***	***

treatment WS/excess. These results show that nutrient deficiency in the treatment DS/control and fertiliser toxicity in the treatment DS/excess had a significant effect on the production of leaf area by the seedlings. These results confirm that the soil-positive effect of the woodland soil reduced the negative effect of excess fertiliser on seedling growth.

There were minimal variations in the RGR determined for each treatment, which are summarised below:

	Treatment		
	DS/control	DS/excess	WS/excess
Relative growth rate (RGR) ($gg^{-1}week^{-1}$)	0.169	0.151	0.142
Mean unit leaf rate (Emean) (gcm^{-2} $x10^{-3}$)	7.034	5.354	5.435
Mean leaf area ratio (Fmean) (cm^2g^{-1} plant dry weight)	24.030	28.230	26.030

These results show that the soil-negative effect of the dune soil and the negative effect of excess fertiliser on plant growth produced seedlings with similar RGRs. There was variation in both the mean unit leaf rate (Emean) and the mean leaf area ratio (Fmean) between the three treatments. Seedlings in the DS/control had the highest Emean but the lowest Fmean of the three treatments, in contrast to seedlings in DS/excess which had the highest Fmean and lowest Emean. These results show that the effect of excess fertiliser in the dune soil caused a decrease in the photosynthetic efficiency of the leaves to produce dry matter but increased the relative area of the leaves per seedling. The seedlings in WS/excess had a marginally lower Fmean and a marginally higher Emean than the seedlings in DS/excess. This shows that the woodland soil promoted the development of more photosynthetically efficient leaves, which allowed the production of less leaf area to achieve a similar RGR.

6.3.12 Environmental effects on developmental variation

1. Controls

The shoot dry weight of seedlings grown in the woodland soil controls for both seedling ages were significantly heavier than the dune soil controls. These results show that in the absence of supplements, the soil-positive effect of the woodland soil promoted shoot growth throughout the trial period. The long-term positive effect of the woodland soil did marginally decrease, as shown by the reduction in significance from $p<0.001$ at 13 weeks of age to $p<0.01$ at 34 weeks of age.

2. NPK fertilisers (table 6.20)

The shoot weights of 13 week old seedlings grown with the supplements NPK+T and NPK-T were significantly heavier in the woodland soil than in the dune soil. By 34 weeks of age, only the supplement NPK+T produced significantly larger shoots in the woodland soil. Since both NPK fertilisers did not significantly increase the shoot weights when applied to both soil types at both seedling ages, these results show that the larger shoots were promoted by the positive effect of the woodland soil rather than the effects of the individual NPK fertilisers. However, prolonged exposure to NPK-T during the hotter summer months increased the decline in the long-term positive effect of the woodland soil, perhaps caused by an increase in the negative effect of trace element deficiencies.

When manure was added with the NPK+T fertiliser (NPK+T/CM2), this resulted in the production of significantly heavier shoots in the dune soil than in the woodland soil at 13 weeks of age but this significance between the soil types was lost by 34 weeks of age. The application of this supplement to the dune soil caused a

Table 6.20

Between soil type and between soil supplement significant differences in seedling size (F1 scores) of 13 week old seedlings (n=176) and 34 week old seedlings (n=352) grown in the NPK fertiliser treatments from trial SQU-1.

A. Between soil types using independent t-tests.

	Soil supplement		
	NPK+T	NPK-T	NPK+T/CM2
13 WEEKS	***	***	***
34 WEEKS	**	NS	NS

B. Between supplements, using one-way ANOVAs and post-hoc contrasts according to the Bonferroni procedure. Where ** = p<0.001; * = p<0.005; NS = not significant at p>0.005.

	Soil supplement		
	NPK+T	NPK-T	NPK+T/CM2
Dune soil (DS)			
13 WEEKS	NS	NS	**
34 WEEKS	NS	NS	**
Woodland soil (WS)			
13 WEEKS	NS	NS	**
34 WEEKS	NS	NS	NS

significant increase in the shoot weight from the DS/control for both 13 and 34 week old seedlings, but in contrast this supplement inhibited shoot growth in the woodland soil at 13 weeks of age, but had no effect by 34 weeks of age. These results show that the supplement NPK+T/CM2 reduced the early positive effect of the woodland soil, but this supplement effect decreased with time. This can be attributed to the hotter summer conditions which produced seedlings of comparable weight because the nutrients in both soil types were in concentrations that did not limit shoot growth. The absence of any soil-positive effect of the woodland soil during the early growth of the shoots suggests that the cumulative effect of the nutrient-rich woodland soil with both the NPK fertiliser and manure produced a soil environment toxic to the seedlings. This was probably enhanced by the higher soil moisture content caused by the wetter winter months which increased the root exposure to these nutrients.

3. Manure and peat (table 6.21)

The application of manure generally did not affect the shoot weight between the soil types for both seedling ages because of the dominating chemical and physical effects of the manure when applied to these natural soils (sections 6.3.2 & 6.3.3). At 13 weeks of age, the application of manure to the dune soil generally caused a significant increase in the shoot weights, whilst its application to the woodland soil caused a significant decrease in the shoot weights. These results show that during the early growth of the seedlings, manure stimulated shoot growth in the dune soil but inhibited shoot growth in the woodland soil. The absence of a soil-positive effect of the woodland soil on 13 week old seedlings can also be attributed to early exposure to nutrient imbalances and nutrient toxicity which have been enhanced by both the physical and chemical properties of the manure. By 34 weeks of age, the manure did not significantly promote shoot growth in both soil

Table 6.21

Between soil type and between soil supplement significant differences in seedling size (F1 scores) of 13 week old seedlings (n=176) and 34 week old seedlings (n=352) grown in the manure and peat treatments from trial SQU-1.

A. Between soil types using independent t-tests.

	Soil supplement			
	CM1	CM2	CM3	PEAT
13 WEEKS	*	NS	NS	NS
34 WEEKS	NS	NS	NS	*

B. Between supplements, using one-way ANOVAs and post-hoc contrasts according to the Bonferroni procedure. Where ** = p<0.001; * = p<0.005; NS = not significant at p>0.005.

	Soil supplement			
	CM1	CM2	CM3	PEAT
Dune soil (DS)				
13 WEEKS	**	NS	*	NS
34 WEEKS	NS	NS	NS	**
Woodland soil (WS)				
13 WEEKS	*	**	**	**
34 WEEKS	NS	NS	NS	NS

types, probably as a result of competition from weeds and changes in the physical properties of the soil mixture affecting the bulk flow of water and dissolved nutrients.

At 13 weeks of age, the shoot weights of seedlings in the peat treatments were not significantly different between the soil types, but by 34 weeks of age the presence of this supplement produced significantly heavier seedlings in the dune soil than in the woodland soil. The application of peat to the woodland soil significantly reduced the shoot weight of 13 week old seedlings. Since peat did not contribute to the chemical status of the woodland soil, these results show that the slower infiltration of water in WS/peat than in DS/peat (section 6.3.3) was primarily responsible for the absence of any soil-positive effect of the woodland soil during the early growth of the seedlings. The absence of any significant effect of peat applied to dune soil on shoot growth of 13 week old seedlings suggests that the wetter winter conditions during the early growth produced similar physical soil environments between the DS/control and DS/peat. As temperatures increased during the summer, the treatment DS/peat with its high soil field capacity would maintain a better soil water status than the DS/control, thereby maximising the availability of the low concentrations of soil nutrients.

4. Water-absorbing polymer, phosphate and excess fertiliser (table 6.22)

The shoot weights of seedlings grown in the woodland soils supplemented with the water-absorbing polymer (WAP) for both seedling ages were significantly heavier than the equivalent dune soil treatments. Since the treatments with the polymer did not significantly increase shoot weights from the controls for both soil types at both seedling ages, this shows that the soil-positive effect of the woodland soil had a greater influence on shoot growth throughout the trial period than the effect of the polymer.

Table 6.22

Between soil type and between soil supplement significant differences in seedling size (F1 scores) of 13 week old seedlings (n=176) and 34 week old seedlings (n=352) grown in the treatments with water-absorbing polymer, phosphate and excess fertiliser from trial SQU-1.

A. Between soil types using independent t-tests

	Soil supplement		
	WAP	PO_3	EXCESS
13 WEEKS	**	***	***
34 WEEKS	**	NS	*

B. Between supplements, using one-way ANOVAs and post-hoc contrasts according to the Bonferroni procedure. Where ** = p<0.001; * = p<0.005; NS = not significant at p>0.005.

	Soil supplement		
	WAP	PO_3	EXCESS
Dune soil (DS)			
13 WEEKS	NS	NS	NS
34 WEEKS	NS	NS	NS
Woodland soil (WS)			
13 WEEKS	NS	NS	*
34 WEEKS	NS	NS	NS

However, the same significant levels ($p<0.01$) for both seedling ages between the soil types with this polymer suggest that this supplement maintained the variation between the soil types throughout the trial by preventing the decline in the long-term positive effect of the woodland soil.

The treatments supplemented with phosphate produced significantly larger shoots at 13 weeks in the woodland soil than in the dune soil, but these treatments were not significantly different between the soil types by 34 weeks. Since the application of this supplement to both soil types at both ages did not cause any significant differences in the shoot weights, these results show that the main effect of phosphate was in promoting the decline in the long-term positive effect of the woodland soil on shoot growth during the trial.

The significantly lower shoot weights of seedlings grown in the dune soil than in the woodland soil with excess fertiliser for both seedling ages shows that the soil-positive effect of the woodland soil in reducing fertiliser toxicity occurred throughout the trial period. The negative effect of excess fertiliser when added to the woodland soil was greater at 13 weeks than at 34 weeks, which suggests that the effect of the woodland soil in reducing fertiliser toxicity did marginally increase with time. Excess fertiliser applied to the dune soil did not cause any significant differences in the shoot growth of both 13 and 34 week old seedlings, which shows that the soil-negative effect of the dune soil was consistently greater than the negative effect of fertiliser toxicity.

6.4 Conclusions and recommendations

The results of the multi-factorial field trials in Oman have provided information on the following:

1. variation in seedling growth and development
2. silvicultural techniques
3. seedling nutritional requirements including tolerance to nutrient deficiency and toxicity
4. morphological modifications induced by the environment and by physiological injury.

The effects of the three experimental factors (trial, soil type and soil supplement) on the growth and morphology of P.cineraria seedlings are summarised below.

6.4.1 Trial effects

The results have shown that in the majority of treatments tested (20 out of 22), seedling growth was significantly higher in the AL-K trial than the SQU-1 trial. Climatic factors influencing faster growth in Al-Kamil included marginally higher temperatures, and marginally higher rainfall, which were promoted by the inter-tropical convergence (kharif monsoon) over the South of Oman (Warren, 1988a) and a lower maritime influence. These habitat-positive environmental conditions may have been responsible for the development and maintenance of the Prosopis woodlands in the Sharqiya (Chapter 3).

The faster growth in AL-K generally had the effect of producing seedlings that were dominated by a multiple-branching morphology to support the foliage necessary for high rates of photosynthetic assimilation. Where slower seedling growth occurred in SQU-1, the relative leaf area

was more dominant, supported generally by a primary-branching morphology. Thus the seedlings in these field trials have gone through a distinct shift in dry matter partitioning from the production of more leaf area to the development of cross-sectional area and multiple branches. The time taken for the seedlings to change their partitioning strategy was affected in different ways by interactions between the climate and the soil environment.

The negative effect of shade on seedling growth resulted in the majority of treatments (13 out of 14) in the SQU-2 trial having significantly smaller seedlings than the equivalent treatments under full sunlight in the SQU-1 trial. Reduction in light intensity by over 76% promoted etiolated growth, resulting in a significant reduction in the size of the seedlings in most of the treatments. Shade therefore affected the rate of photosynthesis and the translocation of assimilates to the shoot sinks. The major morphological responses to limited light were the production of an increased leaf area and greater shoot elongation. Assimilates that were produced were specifically translocated into sinks for the manufacture of leaves in order to maximise the capture of light in the mature leaves, and into the stem for gaining shoot height. The wetter conditions under shade had a tendency to produce soil anoxia, which had a detrimental effect on both the growth and morphology of the seedlings.

These results have shown that the greatest variation in seedling growth and morphology was induced by the environmental differences between the trial locations. For optimal growth and successful propagation of P.cineraria, efforts should be made to select sites in habitats where this species is naturally distributed. During the winter, the seedlings are light demanding, so that shade protection during the early growth of P.cineraria is both unnecessary and detrimental to the plant.

6.4.2 Soil type effects

Under full sunlight (SQU-1 & AL-K), the nutrient-rich woodland soil generally promoted superior seedling growth, particularly under the habitat-positive effects of the AL-K trial. This soil-positive effect of the woodland soil was maintained throughout the trial period, but did marginally decline with time. The greater nutrient availability in the woodland soil than the dune soil can be attributed to nutrient cycling occurring in the Prosopis woodlands, which was absent in the vegetation-free dune field. Prosopis-specific soil rhizobia and nutrient concentrations may have promoted seedling growth in the woodland soil.

The higher organic content of the woodland soil did marginally reduce the advantages of using this soil under full sunlight, which included soil surface anti-wetting and capping and sub-surface cementing of soil particles. These tended to reduce water availability to the roots, which inhibited early seedling growth in a number of treatments through reduced nutrient availability. These physical properties can be attributed to the organic material present in the woodland soil.

In many of the treatments the nutrient-rich woodland soil eventually produced large seedlings which were morphologically distinct from those grown in the dune soil. The dune soil generally inhibited growth through nutrient deficiency after prolonged periods of growth, particularly in the AL-K trial where the growth rates were high. This nutrient-deficient effect of the dune soil was generally more dominant than the effects of the habitat differences between the trials. In treatments in woodland soil where the nutrients were not limiting to seedling growth, this soil type promoted differentiation in the branching morphology between the trials, so that primary branching was enhanced in SQU-1 and multiple branching was enhanced in AL-K.

The negative effects of shade on seedling growth reduced the soil-positive effects of the woodland soil in many treatments. The wetter environmental conditions under shade promoted the development of saturated soils, and the growth of shade-tolerant weeds. Shade also promoted an allelopathic effect on seedling growth as a means of reducing plant competition between the parent and its progeny. In this way seedling regeneration is inhibited beneath the parent tree canopy, but is promoted under full sunlight along the woodland margins or in the between-clump gaps.

Seedling morphology between the soil types was dominated by the negative effect of shade. However, the results have indicated that the morphological response in maximising the capture of light under shade was different between the soil types. In the dune soil, this response was to gain height, whilst in the woodland soil it was to increase the leaf area.

The differences in the chemical and physical properties between the soil types have greatly affected the growth and morphology of P.cineraria seedlings. The quality of the soil medium will therefore heavily influence the growth of the plant. The nutrient concentrations in the dune and woodland soils can be used respectively as indicators of nutrient deficiency and nutrient abundance for this species. This will allow the selection of suitable soils for seedling propagation under nursery conditions, and the selection of suitable soils in specific sites for successful transplantation of the species.

6.4.3 Soil supplement effects

The majority of the supplements in both soil types in all three trials produced seedlings that were not significantly different in size to the seedlings in the

respective controls. These results have shown that the effects of the habitat and/or soil type had greater influences on seedling growth than the effects of the individual soil supplements. In many treatments, the main effects of the soil supplements were in the maintenance or the decline in the long-term positive effect of the woodland soil. Seedlings at 13 weeks of age were generally more sensitive to the soil supplements than at 34 weeks of age, particularly in the woodland soil treatments that were already rich in nutrients.

The soil-positive effects of the woodland soil in all three trials did reduce the morphological variation of the seedlings in response to supplements that were potentially detrimental to growth. These results demonstrate the advantages of using the woodland soil to produce seedlings of morphological homogeneity. Since the early growth of the seedlings can influence the eventual morphology of the mature tree, an early control of the seedling morphology using the woodland soil will minimise the variation incurred through the course of their artificial propagation. This silvicultural technique would ensure that important morphological characteristics such as multi-purpose properties that are passed from the parent to the seeds are not lost in the new progeny.

The effects of the individual soil supplements on seedling growth and morphology are summarised below.

1. NPK fertilisers (NPK+T, NPK-T & NPK+T/CM2)

The application NPK fertiliser with trace elements (NPK+T) to both soil types from the trials under full sunlight (SQU-1 & AL-K) had the effect of producing larger seedlings than the application of fertiliser without trace elements (NPK-T). Manure complemented this fertiliser (NPK+T/CM2), particularly under the habitat-positive effects of AL-K in which the seedlings required

supplementary nutrients to support their rapid growth.

Under full sunlight, the application of these soil supplements caused some morphological departures from the main effects of the trials and the soil types. The morphological characteristics of these particular seedlings can be used as indicators of seedling growth of P.cineraria under high nutrient availability. These indicators can then be used to assess the nutrient status of seedlings grown in the field, so that modifications can be made to ensure optimal growth under the prevailing environmental conditions of the particular site.

The dominating effect of shade reduced the positive effects of these soil supplements on seedling growth. This has shown that the application of these supplements to treatments under shaded conditions in winter will not promote seedling growth.

2. Manure and peat (CM1, CM2, CM3 & peat)

The application of manure under some conditions positively influenced seedling growth by promoting nutrient availability. However, in other conditions the application of manure inhibited growth due primarily to nutrient toxicity. The cumulative abiotic and biotic effects of manure have been responsible for the way in which the assimilates were manufactured, translocated and utilised in the plant. Abiotic factors included surface capping, sub-surface cementing and both nutrient deficiency and nutrient toxicity. Severe soil packing may also have limited root growth by inhibiting root penetration into the soil. The high conductivity of the soils with manure suggests that the forage in which the animals were eating were high in salts. Serious consideration should be given to the application of manure to already poor quality soils. Biotic factors included plant competition by weeds for nutrients and space and possibly by pathogens such as

nematodes and disease associated with the manure.

The addition of manure to sandy soil had the immediate effect of increasing the soil field capacity and increasing the rate of water infiltration into the soil due to the heterogeneous size of the manure particles. This would increase the availability of essential nutrients to the plant. The concentration of manure was significant in influencing the size and morphology of the seedlings. The lowest concentration of manure (CM3) added to dune soil significantly increased seedling size from the dune soil control. The combination of improved chemical and physical properties of this soil mixture enhanced seedling growth. Increasing proportions of manure to both soil types generally did not effect seedling size from the respective controls, although there were indications that the highest manure concentrations marginally reduced seedling size as the physical properties in the treatment deteriorated.

The effect of manure on seedling size was different between SQU-1 and AL-K, since in SQU-1 the size of the seedlings was positively correlated to the manure concentration, whilst in AL-K it was negatively correlated. Under the habitat-positive effect of AL-K, the higher concentrations of manure limited seedling growth. This has shown that since nutrients were not limiting to growth, the physical properties of the soil mixture were responsible for these results. Increases in the organic content did increase the capping effect at the soil surface which may have reduced the volume of water reaching the roots causing desiccation and death at the sites of nutrient uptake.

The addition of manure had a particular effect on the morphology of seedlings. These supplements produced seedlings with a primary-branching morphology and a low relative leaf area.

The result have shown that there were more disadvantages than advantages in using manure. As well as inhibiting shoot growth, the manure also affected the early morphology of the seedlings. This may have a detrimental effect later on in the development of the plant.

Like the addition of manure, peat was found to be useful by increasing the soil field capacity of the sandy soils. However, the physical interaction of peat with components in the woodland soil particularly reduced the rate of infiltration of water into the soil mixture.

The addition of peat to the dune soil from SQU-1 had an early effect on seedling morphology, promoting the development of the primary branches and relatively large leaf areas in 13 week old seedlings. This treatment had a late effect on seedling growth, perhaps by gradually increasing the field capacity of the soil from repeated irrigation so that nutrients became more available to the root surfaces. Under the more favourable growing conditions of AL-K, the addition of peat to both soil types promoted the development of a multiple branching morphology.

3. Water-absorbing polymer, phosphate and excess fertiliser

In the nutrient-poor dune soil, the application of the water-absorbing polymer (WAP) inhibited seedling growth, whilst in the nutrient-rich woodland soil it promoted seedling growth. These results have shown that whilst increasing the efficiency of water utilisation in sandy soils, this polymer only promoted seedling growth when the soil environment was rich in nutrients. Environmental differences between the trials did enhance the effects of this polymer on seedling growth, such that the combination of this polymer with the positive effects of AL-K and the woodland soil produced some of the largest seedlings of the field trials. As a means of promoting seedling growth and increasing the efficiency of water utilisation by the

plants, this polymer should only be added to soils that are rich in nutrients.

The combination of shade and this polymer had the effect of reducing seedling growth, although it did tend to reduce soil saturation. The results have indicated that a morphological response to nutrient deficiency in moist soils was to increase the leaf area of the plant. In this way, a higher transpiration rate would increase the flow of soil nutrients towards the root surfaces for uptake.

The application of both phosphate and excess fertiliser did not generally cause significant reductions in the size of seedlings, which has shown the degree of tolerance of P.cineraria seedlings to saline conditions. This early tolerance of these seedlings to 30 times the recommended concentration of NPK+T fertiliser was comparable to the results of salinity trials performed under glasshouse conditions (Chapter 5). However, the application of these supplements did affect seedling morphology, by promoting high relative leaf areas both under full sunlight and under shade. This response was suggested to be a morphological adaptation to nutrient imbalances and fertiliser toxicity, by translocating un-wanted ions to leaf sinks which are removed from the plant when the leaves are dropped.

CHAPTER 7

SUMMARY CONCLUSIONS AND RECOMMENDATIONS

7.1 Summary conclusions

7.1.1 The woodland habitat

The Prosopis woodlands in the Sharqiya are typical desert thorn forests, in that they exist as isolated pockets of ecologically rich habitats in an environment predominantly consisting of open sandy desert plains. There are differences between the woodland provenances with respect to their structure and topography. Trees both between and within provenances are highly variable in density, size and morphology.

Survival strategies of the mature tree in the Sharqiya have been determined from the structure of the existing woodlands. The survival responses of P.cineraria from sand accumulation can be summarised into those that form clumps, those that are naturally protected and those that are resistant to change. These responses are either through vertical or lateral vegetative growth. Specifically, the penetration of the megadunes of the sand sea into the western margin of the Eastern Prosopis Zone suggests that the clumps have been formed primarily by vertical vegetative growth of submerged single trees. This response to sand encroachment has been suggested as being a major factor in the present distribution of the Prosopis woodlands. This strategy also indicates that these relic woodlands are remnants of the original woodlands that were present over 12000 years ago during the last pluvial period.

The woodland soils are alkaline with a higher nutrient availability than soils from the adjacent open plains. The presence of the Prosopis woodlands in arid conditions support the 'islands of fertility' concept of Garcia-Moya &

McKell (1970). These trees increase nutrient availability in the canopy soil, particularly nitrate, phosphate and carbon. This has been widely reported in many Prosopis species, but results presented in this thesis have also shown that P.cineraria also reduces the salinity of the canopy soil.

The cumulative effect of available nutrients, low salinity, shade, cool temperatures and a moist micro-climate beneath the tree canopy has resulted in the development of the understorey habitat with species not necessarily adapted to arid conditions. This has resulted in almost double the floral diversity in the Prosopis woodlands than the surrounding open plains. The understorey vegetation was divided into seven communities, predominantly made up of ephemeral species. Species diversity was enhanced in the woodlands by the zonation of plants along gradients of varying light intensity between the canopy shade and the between-clump gaps.

The Prosopis woodlands support an abundance of fauna. High insect diversity in the woodlands was attributed to the supply of food and micro-habitats by the trees and the understorey vegetation. This has attracted many insectivorous animals in to the woodlands, including reptiles and birds. These animals may have a function in the life-cycle of the tree as pollinators and vectors for seed dispersal. The ecological richness of this habitat has encouraged wildlife to thrive in conditions in which they would not normally be found. The woodlands represent corridors for the colonisation of the desert plains and allow species to extend their natural range. The woodlands also are important habitats for passage migrant birds.

The results presented in this thesis have shown that P.cineraria in the Sharqiya is a very important multi-purpose tree, particularly for providing fodder, fuelwood and shade protection. As a successful multi-purpose tree in

areas of low biological productivity, this has led to the inevitable over-exploitation of the Prosopis woodlands in Oman, resulting in the decline in the condition and stability of the habitat. The man-made factors responsible for the present poor condition and deforestation of the Prosopis woodlands in the Sharqiya have been shown to be:

1. un-controlled felling of trees
2. over-lopping of trees
3. destruction of woodland margins fronting mobile dune-fields
4. sand encroachment and tree inundation
5. over-grazing by goats and sheep
6. increasing numbers of livestock and size of herds
7. disturbance of understorey vegetation and soil surface structure by the trampling of livestock and by vehicles
8. declining traditional management and utilisation of the woodland resources
9. increasing numbers of people and permanent settlements in the woodlands
10. accumulation of non-biodegradable rubbish
11. increasing density of feral animals that compete with the indigenous arboreal wildlife
12. increasing entrepreneurial exploitation of the woodland resources by both resident and non-resident people in the woodlands.

The recovery of the Prosopis woodlands from over-exploitation has been limited, due mainly to the reduction in the reproductive regeneration of trees from seed.

Factors that have reduced recent reproductive regeneration include:

1. seed infestation by insects
2. physiological inhibition of seed production through infestation
3. regional variation in pest species density and diversity
4. destructive utilisation of pods and seeds by generalist feeders
5. low seed viability
6. physical damage of seeds by local environmental conditions
7. germination and death of deeply buried seeds
8. absence of P.cineraria seed bank in the soil
9. absence of obvious seed dispersal vectors
10. seed and seedling destruction by grazing animals
11. intolerance of young seedlings to canopy shade and allelopathic influences
12. changes in growth strategies induced by disturbance of the fragile soil architecture
13. plant competition by faster growing and more drought tolerant herbaceous and shrubby understorey species.

The results have shown that the survival of the Prosopis woodlands of the Sharqiya is tenuous. The fragile structure of the woodlands has prevented their ability to recover from un-inhibited over-grazing and un-controlled exploitation of their multiple resources. Irreversible damage to some parts of the Prosopis woodlands in the

Sharqiya will become inevitable, unless steps are immediately taken to control the present exploitation of these habitats and implement planting programmes in deforested areas.

7.1.2 The mature trees

P.cineraria in the Sharqiya is a typical phreatophyte, with roots going down to a depth of at least 18m and probably over 60m. This access to the aquifer would fulfill the water requirements of the tree and explain the absence of direct competition for surface water between the tree and the abundant understorey vegetation. The dependence upon aquifer water has allowed the species to grow, maintain abundant foliage, and produce seeds in continuous drought conditions when most other vegetation types have died back or been forced into dormancy.

The morphology of the mature trees in the Prosopis woodlands of the Sharqiya was shown to be highly variable, with the field identification of 13 distinct morphotypes. The most abundant morphotypes were shown to be highly significantly different in their morphology. This morphological variation was found to be due to phenotypic plasticity between some morphotypes and due to genotypic variation in others.

Morphological variation was greatest in areas of shifting sand dunes, particularly along the margins of the sand sea. This variation was attributed to the vertical and lateral vegetative regeneration of the trees in response to sand encroachment. Where the rate of sand encroachment was greater than the vegetative regeneration of the trees, the morphological variation was also attributed to the trees in various degrees of submergence in sand. Trees that survived sand encroachment were either solitary large trees, or clumped small trees. Solitary trees were generally

homogenous in morphology and in healthy condition. Trees in clumps where heterogenous in morphology and in generally poor condition. The greater the distance between the soil surface and the aquifer caused by sand encroachment has reduced the phreatophytic capacity of trees in clumps.

Greatest genetic variation of trees was found between the provenances, rather than between trees within each provenance. Provenance genetic variation may be attributed to their biologically isolated distribution and to natural genetic drift. The further the trees were geographically apart, the greater were their variation in both the genotype and phenotype. Although there were no significant differences in the overall size of the trees between the Sharqiya provenances, there were some distinct morphological differences. This variation may have been promoted by the environmental differences either side of the sand sea.

Multivariate methods were used to classify trees in to morphologically homogenous groups. Five groups were identified between the provenances, and six groups within the transects in the Eastern Prosopis Zone. The multi-purpose properties of these groups were assessed, in which a number of groups satisfied the basic requirements of fodder, fuelwood and shade protection. Other groups were potentially useful in environmental protection and the provision of multi-purpose products such as building materials, fence posts and tool implements. The extensive variation in the morphology of P.cineraria in the Sharqiya has therefore enhanced the multi-purpose properties of this species.

The utilisation of the most superior multi-purpose trees identified in the Sharqiya will require the sampling of seeds for future testing in field trials. These trials can be used to determine whether the multi-purpose characteristics of a selected tree are genotypic in origin

or are a phenotypic response to the environment in which the tree has grown.

The reproductive development of trees in the Eastern Prosopis Zone influenced the canopy morphology, by promoting the relocation of photosynthates from the leaves into the production of the pods. The lush canopy of these trees was suggested to be a signal in attracting ovipositing insects to the tree. High seed infestation of trees in the Central Prosopis Zone also influenced the canopy morphology, by reducing the foliage condition and causing defoliation. This was attributed to the higher species diversity of insect pests in this provenance.

7.1.3 Seeds and seedling establishment

The morphological variability of the seeds was found to be high, resulting in the identification of six morphologically distinct groups. This variation may have influenced the considerable variation in the germination rate of the seeds and the plumule development of the seedlings in the glasshouse trials in Durham. The frequency of seed dormancy was high in seedlot accessions from the Sharqiya. The most effective method of breaking seed dormancy was by scarification using coarse sand paper.

P.cineraria seed viability was highest when the seeds were collected from the tree, which reduced seed death and the degree of infestation by insects. The optimum storage condition tested for P.cineraria seeds was at 4°C using seeds with a natural moisture content of 8.26%. At this temperature and moisture content, the seed viability will be reduced by half after a storage period of approximately five years. The lowest viability occurred in seeds of high moisture content (13.02%) stored at 20°C. The storage temperature of -20°C damaged the seed coat and promoted fungal infection during their germination.

Seed dormancy was persistent for at least 70 days exposure to moist conditions. Seed dormancy was broken when seeds were stored at -20°C, and may prove a simple method for the bulk germination of seeds. The results of these studies on seed storage viability were used to produce a seed storage nomograph for P.cineraria (figure 5.3).

Despite the absence of reproductive regeneration in the Prosopis woodlands of the Sharqiya for reasons described in section 7.1.1, factors influencing the natural regeneration of P.cineraria from seeds have been shown to be:

1. areas of readily available moisture, especially along wadis and in areas of shallow aquifers or temporary surface water from heavy rainfall for the germination of seeds buried near the surface
2. species-specific climate and soil environment
3. sandy substrate for rapid root penetration
4. rapidly penetrating root during early growth to reach more permanent subterranean water
5. viable dormant seeds that will only germinate after repeated soaking, ensuring that germination occurs in areas of abundant water
6. tolerance of young seedlings to full sunlight and to highly saline soils
7. anchoring properties of roots in shifting sand dunes.

The propagation of P.cineraria will be more successful if the silvicultural techniques that are used mimic the conditions that enhance natural regeneration.

7.1.4 Glasshouse trials in Durham

1. General growth responses

The seedlings under glasshouse conditions were very slow growing. The highest growth rates occurred in the first 15 weeks from germination, where dry matter was directed towards the formation of abundant leaves, short stems and long thin tap roots. Between 15 and 44 weeks there was an increasing partitioning of dry matter from the leaves to the further development of the roots. Seedlings that have successfully established will have benefited from a large endosperm in the seeds which allows the rapid growth of the roots at the expense of the shoots to find permanent water.

2. Ecotypic variation

Variation in seedling growth and morphology under glasshouse conditions was found between the EPZ and CPZ provenances and between the parent morphotypes. The results have shown that even in the early growth of this species, considerable variation in the morphology of the plants occurred. The variation between the seedlots suggests some genetic differences, whilst the variation within each seedlot suggests cross-pollination. The results have emphasised the importance of performing seed collections from a wide geographic area and from extremes of habitats for the genetic conservation of the species (Ford-Lloyd & Jackson, 1986).

3. Salinity tolerance

During the early growth and development of the seedlings, the results have shown that P.cineraria is tolerant to high salinities. For the first three weeks of the salinity treatments (1%, 2% and 4% salinities), there were no seedling fatalities. Some seedlings were still

alive after seven weeks exposure to 4% salinity, whilst the majority of the seedlings were still alive after 13 weeks exposure to 1% salinity. This high salinity tolerance improves the potential of an already excellent multi-purpose tree species for its utilisation in the social forestry of degraded and over-irrigated soils.

Salinity influenced seedling growth by generally decreasing the size of the seedlings and increasing their morphological homogeneity. The salinity tolerance of the seedlings was found to be dependent upon the source of the seeds, which included both their geographical origin and their parent type. As a result, a number of seedlots collected from the Sharqiya were identified as producing seedlings that were particularly saline tolerant.

7.1.5 Field trials in Oman

The development of P.cineraria seedlings up to 34 weeks of age in the field trials in Oman occurred in three distinct phases:

1. Immediately following epigeal germination the translocation of assimilates to the below-ground sinks resulted in the elongation of the roots.

2. An increase in the leaf area in which assimilates were directed towards increasing the photosynthetic capacity of the plant. The seedlings were dominated by a primary-branching morphology.

3. After a threshold shoot weight was reached the assimilates were directed more into increasing the cross-sectional area of the shoot, resulting in the development of a multiple-branching morphology.

The complex interactions between the climate and the soil environment have affected the lengths of each growth

phase which in turn has affected the size and morphological variability of the seedlings. Factors promoting seedling variation included:

1. climatic differences between the trials
2. nutrient availability
3. water availability
4. soil chemical interactions
5. physical structure of the soil
6. plant competition within and between species
7. soil allelopathy
8. soil anoxia
9. genetic variability of the seeds.

The faster seedling growth in most treatments between 13 and 34 weeks of age occurred in summer when the mean air temperatures were highest. The results have shown that by sowing in winter, the plants will respond positively to increases in temperature during the summer. The hot summer temperatures promoted fast seedling growth, particularly when nutrients were not limiting.

1. Trials

The climate in the Sharqiya where P.cineraria is naturally distributed provided the most favourable conditions for seedling growth and development in most treatments tested. This has indicated that the species-specific habitat in the Sharqiya has influenced the ontogeny of the Prosopis woodlands. The faster seedling growth in Al-Kamil produced seedlings dominated by a multiple-branching morphology to support the foliage necessary for high rates of photosynthetic assimilation.

Where slower seedling growth occurred at Seeb, the leaf area productivity was more dominant, supported generally by a primary-branching morphology.

P.cineraria seedlings were shown to be intolerant to shade, to the extent that a 76% reduction in light intensity caused a significant reduction in seedling size in most of the treatments. Shade promoted an etiolated growth to maximise the capture of light for photosynthetic assimilation. This growth was characterised by an increase in the leaf area and an increase in stem elongation.

2. Soil types

The differences in the chemical and physical properties between the dune and woodland soils have had some significant effects on the early growth and morphology of P.cineraria seedlings. The dune soil generally inhibited growth through nutrient deficiency, particularly when the seedlings were grown under optimal climatic conditions.

In many of the treatments the nutrient-rich woodland soil eventually produced large seedlings which were morphologically distinct from those grown in the nutrient-poor dune soil. The woodland soil promoted the development of a multiple-branching morphology and generally reduced the morphological heterogeneity between seedlings. The woodland soil promoted the early seedling growth (13 weeks of age) and reduced the effects of phosphate imbalances and fertiliser toxicity. The positive effects of the woodland soil on seedling growth were attributed to species-specific soil physical and chemical properties.

The woodland soil under shade produced an allelopathic effect on seedling growth. Under natural conditions, this property of the woodland soil ensures the growth of the woodland habitat, by inhibiting seedling regeneration under the shade of the parent tree canopy, and by promoting

seedling regeneration along the woodland margins and the between-clump gaps.

The chemical composition of the woodland soil represents the soil nutrient status that will promote the healthy growth of P.cineraria seedlings. In contrast, the nutrient status of the dune soil will result in poor seedling growth.

3. Soil supplements

The field trials have shown that the effects of the trials and the soil types were greater on seedling growth and morphology than the effects of the individual soil supplements. Hence, maximum P.cineraria seedling growth can be achieved without additional soil supplements if care is taken in selecting suitable sites and species-specific soils.

Some soil supplements did affect the size and morphology of the seedlings. The application of NPK fertiliser generally promoted seedling growth resulting in large seedlings with a multiple-branching morphology, particularly in the trial where climatic conditions were optimal for growth. The morphology of these seedlings can be used as indicators of optimal growth of this species when grown under natural conditions.

The addition of manure to sandy soil generally increased nutrient availability by increasing the soil field capacity. However, the high organic content of the soil environment with manure often inhibited seedling growth. This was attributed to soil surface capping and anti-wetting and sub-surface cementing which reduced both water and nutrient availability and prevented the penetration of the roots into the soil. Seeds present in the manure germinated under moist conditions, which resulted in plant competition. Soils with manure had a

tendency to become water-logged, which promoted the development of soil anoxia. The high concentrations of nutrients and salts in the manure may have also affected seedling growth through nutrient toxicity and salinity stress.

The application of peat also increased the field capacity of the soil. This supplement in the dune soil promoted seedling growth by making the low concentrations of nutrients more available to the root surfaces of the seedlings. This supplement reduced the positive effects of the woodland soil by preventing the penetration of water into the soil.

The water-absorbing polymer produced very large seedlings when added to the nutrient-rich woodland soil by increasing both the efficiency of water utilisation and the availability of the nutrients. However, this polymer in the nutrient-poor dune soil inhibited growth by reducing nutrient availability to the root surfaces of the seedlings. The morphological response of the seedlings to nutrient-deficient conditions was to increase the leaf area of the seedlings. It has been suggested that in a moisture-rich soil environment, this was an adaptation by the plant to increase transpiration in order to increase the bulk movement of the soil solution to the root surfaces to maximise nutrient uptake. The polymer added to sandy soil under shade prevented soil saturation, and also prevented soil-surface anti-wetting and capping and sub-surface cementing.

Phosphate fertiliser generally promoted seedling growth by enhancing the development of multiple branches when grown under favourable climatic conditions. However, under some conditions phosphate did have a detrimental effect on growth, which was attributed to phosphate imbalances in the soil.

The salinity tolerance of P.cineraria resulted in the limited effect of excess fertiliser on the size of the seedlings. However, this treatment did affect the seedling morphology by promoting the highest relative leaf areas of all treatments in the field trials. It has been suggested that the increased leaf area was a morphological response to excess fertiliser, by isolating the toxic effects of unwanted ions into leaf sinks which can then be removed from the plant when the leaves are dropped.

7.1.6 Comparisons of seedling growth in Durham and Oman

There was a considerable difference between the growth of seedlings in the glasshouse accession trial in Durham and in the field trials in Oman. In Durham, the mean shoot dry weight of 34 week old seedlings was only 0.043g ± 0.013. In Oman, the mean shoot dry weight was highest in woodland soil supplemented with NPK+T/CM2 in the AL-K trial (56.36g ± 30.75), and lowest in the dune soil with excess fertiliser under the shade of the SQU-2 trial (0.95g ± 0.40). These results have shown that the mean shoot dry weights of 34 week old seedlings in Oman were greater than the same aged seedlings in Durham by a factor of between 22-1300. This emphasises the necessity of studying plant growth both in their natural environment and in conditions in which the plant species is to be propagated.

Saline or nutrient toxic soils in both the salinity trial in Durham and the field trials in Oman promoted the development of leaf area. This suggests a specific morphological aclimation which allows the seedlings to survive in these types of soil environments.

7.2 Recommendations

Specific recommendations determined from work presented in this thesis are summarised below. These have been divided into two parts, the conservation and research of P.cineraria in Oman (section 7.2.1), and silvicultural methods required for the successful reafforestation of this species in Oman (section 7.2.2).

7.2.1 Conservation and research

1. Woodland conservation

1.1 Identify areas of over-exploitation for immediate rigorous conservation management practices. Efforts should be concentrated on the margins fronting the sand sea or areas of rapid sand movement encroaching arable land or permanent settlements.

1.2 Map accurately the distribution of the Prosopis woodlands throughout Oman.

1.3 Identify and implement management techniques needed to improve the condition of the woodlands. These should should include:

I. air-layering of P.cineraria using the methods of Rawat et al. (1985), for the management of isolated woodlands where the logistics and infrastructure necessary for re-planting with seedlings are not available;

II. controlled lopping of P.cineraria, such as annually and only in winter to increase both the fodder production and the growth of this species (Srivastava, 1978; Sharma & Gupta, 1981).

1.4 Assess the environmental impact of deforestation on soil fertility, vegetation establishment and sand encroachment, following the methods of:

I. Tiedemann & Klemmmedson (1986) on the long-term effects of P.juliflora removal on the soil characteristics;

II. Gadzia & Ludwig (1983) on the influence of Prosopis trees in the process of dune building.

1.5 Continue up-dating the flora and fauna systematic lists presented in this thesis.

1.6 Determine the seasonal invertebrate and vertebrate seed infestation pressures on seed regeneration.

1.7 Determine the suitability of seeds, pods and leaves as fodder for livestock in Oman.

1.8 Examine the potential role of the bedu in the conservation and management of the woodlands.

1.9 Provide educational information on the needs of protecting the woodland environment.

1.10 Update and implement the draft forestry policy prepared by the Forestry Section, Ministry of Agriculture and Fisheries (Lawton, 1987).

2. Genetic conservation

2.1 Perform more seed collections throughout Oman.

2.2 Collect seeds from extreme habitats, particularly from areas of high salinity for the selection of salinity tolerant strains.

2.3 Collect seeds from multi-purpose trees for the selection of multi-purpose strains.

2.4 Collect seeds from trees that are high seed yielders and are low in insect infestation for the selection of high yielding and insect resistant strains.

2.5 Collect seeds off the tree immediately after seed maturation to minimise the degree of seed infestation by insects.

2.6 Care should be taken in collecting the morphologically different seeds in the population, as a means of minimising the loss of genetic variability.

2.7 Perform a detailed investigation of the P.cineraria genome in the Sharqiya and determine how this relates to other provenances in Oman and in other countries. The genetic variation should be analysed using more than one isoenzyme system and a higher resolution PAGE technique.

2.8 Determine the genotypic control of the mature tree phenotype to identify specific characteristics that are transmitted by seed.

2.9 Perform a phenological study of flowering and fruiting for predicting optimum times for sampling seeds.

2.10 Develop methods for propagating selected strains, such as micro-propagation and cuttings.

2.11 Establish a permanent P.cineraria database and seed bank in Oman.

3. Silviculture and seedling growth

3.1 Establish field trials in Oman with seeds collected from trees identified as being multi-purpose, salinity or drought tolerant, high seed yielding and resistant to insect infestation, to determine whether these traits are genotypic or phenotypic in origin.

3.2 Establish field trials throughout Oman to determine the reafforestation potential of P.cineraria in different habitats and environmental conditions.

3.3 Perform collaborative studies on P.cineraria with international research stations, to include seed collections and provenance trials.

3.4 Determine practical and efficient watering strategies for optimal plant growth.

3.5 Determine the water relations of the seedlings to maximise the efficiency of water utilisation.

3.6 Determine the effects of rhizobia and mycorrhiza inoculation on seedling growth.

3.7 Determine the physiological adaptations to nutrient deficiency and fertiliser toxicity, which should include a mineral analysis of leaves from seedlings grown in high salinity soils.

7.2.2 Silvicultural methods

1. Seeds and seedling propagation

1.1 Long term storage of important seed accessions should be performed using naturally dried seeds stored at 4°C in hermetically sealed containers after being surface sterilised with 5% sodium hypochlorite for five minutes.

1.2 If optimal storage conditions are not available, then the viability of the seeds stored under a particular set of conditions must be calculated using the P.cineraria seed nomograph presented in Chapter 5 (figure 5.3) to determine when the seeds must be removed from storage and used before too many have lost their viability.

1.3 Use the floatation method for the bulk extraction of seeds from the pods (section 2.6).

1.4 Prior to germination, scarify all seeds using coarse sand paper to break seed dormancy (section 2.6).

1.5 Imbibe scarified seeds in fresh water for 18 hours at approximately 20°C, then place seeds between wet filter paper and store in the dark at the same temperature for 48 hours.

1.6 Select only germinated seeds with emerged radicles and sow to a depth of 5mm with the radicles orientated down into the soil.

1.8 Germinate and sow seeds during the winter so that the seedlings can acclimatise to the environment before the onset of the summer, which will reduce fatalities and maximise growth during the hotter summer temperatures.

2. Selection and preparation of reafforestation sites

2.1 For optimal P.cineraria seedling growth, select areas where the species occurs naturally. This will reduce the dependency of seedlings on additional soil supplements.

2.2 Select sandy sites that overlay permanent aquifers. The shallower the aquifer the greater the chances the seedlings will reach maturity and the lesser the dependence on imported water.

2.3 Analyse the physical and chemical properties of the soils at the selected sites before planting.

2.4 The chemical composition of the Prosopis woodland soil should be used as a reference for assessing the suitability of soil at the site for seedling growth.

2.5 The salinity tolerance of P.cineraria seedlings makes it a suitable species for the reafforestation of sites with saline and degraded soils.

2.6 In saline sites, dig plant pits deeper than 40cm to remove the highly saline surface soil and reduce the rooting distance to moist soil horizons.

2.7 In vegetation-free sandy sites, supplements must be added to the soil for healthy seedling growth.

3. Soil environment for seedling propagation

3.1 Use the species-specific Prosopis woodland soil for propagating the seedlings.

3.2 Use the woodland soil for reducing the toxic effect of saline soils.

3.3 Use the woodland soil for promoting morphological homogeneity of the seedlings, in order to retain, through to maturity, important morphological attributes identified in the parent trees.

3.4 The disadvantages of using the woodland soil include: anti-wetting and surface capping due to a high organic content; competition by herbaceous species germinated from the soil seed bank; water-logging causing soil anoxia; and allelopathy when the soil is used under shaded conditions.

3.5 To promote seedling growth, supplement nutrient-poor soils with NPK fertilisers with trace elements. The morphology of these seedlings can be used as indicators of optimal growth.

3.6 The absence of trace elements in the NPK-T fertiliser and the presence of manure in NPK+T/CM2 generally will reduce the positive effects of the NPK fertiliser.

3.7 The application of just triple superphosphate fertiliser can be inhibitory to seedling growth as a result of phosphate imbalances in the soil.

3.8 Considerable thought should be given to the use of cow manure as a cheap untreated organic fertiliser. This supplement generally had a detrimental effect on seedling growth and morphology.

3.9 Due to the high concentrations of salts found in the manure, this supplement should not be used in already saline or degraded soils.

3.10 There are several benefits in applying manure to sandy soils, which include increasing both the soil field capacity and the soil nutrients.

3.11 If manure is used, labour must be required to: weed; prevent soil surface anti-wetting and capping; prevent sub-surface cementing; and check for infection, disease and soil anoxia.

3.12 Peat in dune soil increases the soil field capacity which increases the nutrient availability to the plants. However, interactions between peat and woodland soil is detrimental to seedling growth.

3.13 The water-absorbing polymer greatly improves the growth of seedlings in conditions where nutrients are not limiting, and maximises the utilisation of the available water. However, this treatment should on no account be applied directly to natural soils with low nutrients as this will inhibit seedling growth by physically reducing nutrient availability to the plant.

3.14 The water-absorbing polymer reduces water-logging and prevents soil anoxia. This polymer should be applied to seedlings that are grown in over-irrigated soils, such as in plant pits irrigated by flooding.

4. Assessment of growth of transplanted seedlings

4.1 Regularly monitor seedling growth using non-destructive mensuration methods described in sections 5.2.6 and 6.2.5 and continue through to maturity using the mensuration methods described in section 4.2.1.

4.2 The nutrient status of the site soil can be assessed by observing the period of time for P.cineraria seedlings to start multiple-branching.

4.3 Evidence of abnormal seedling growth can be detected by observing the morphological development of the transplanted seedlings. The development of stunted seedlings with high relative leaf areas has been suggested to be a morphological response to either nutrient deficiency or fertiliser toxicity.

4.4 If establishing plants in winter, do not plant under shade as this will be detrimental to seedling growth by promoting etiolation.

7.3 Future of P.cineraria in Oman

The results of this research have clearly shown that as a multi-purpose morphologically variable leguminous tree, P.cineraria forms unique woodland habitats that are an important ecological resource both to man and to wildlife. Since the Prosopis woodlands of Oman are a national heritage, recommendations have been given in this thesis on the protection of the existing Prosopis woodlands and the propagation of new woodland cover. The results have also shown that P.cineraria is ideally suited for utilisation in future social forestry programmes in Oman, particularly in sandy areas or where the species is naturally distributed.

Many of the Prosopis woodlands in Oman are relict and are often in particularly poor condition. To the people and wildlife that depend upon the multiple resources provided by these woodlands, their immediate management is essential. If the exploitation of these woodlands continues at the rate observed during the period of study, then large areas will become deforested in the next two decades. The over-exploitation of these woodlands in sandy areas will inevitably promote the process of desertification and the multiple hazards associated with the increase in desert areas. The complete removal of Prosopis woodland cover will have a severe effect on the surrounding environment, which in turn will reduce the chances of successful reafforestation in the future.

The Prosopis woodland of Oman are often distributed in areas where the benefits of modernisation are rarely felt. The management and controlled exploitation of these woodlands will ensure that people can continue to live and prosper in these areas. The principal multi-purpose properties of the Prosopis woodlands were identified as being fodder, fuelwood and shade protection. These properties were exploited by man in the past using traditional methods that sustained the woodlands. However, during the present period of economic prosperity in Oman promoted by its oil reserves, the Prosopis woodlands are being heavily over-exploited. The importance of the Prosopis woodlands to man will be significantly increased in the future when Oman's reliance on its revenue from oil is reduced. This stresses the necessity to immediately design and implement the conservation management of the Prosopis woodlands, to ensure that the woodlands continue to provide their multi-purpose properties in the future.

The results in this thesis have clearly shown that there are many advantages in the utilisation of P.cineraria in future forestry programmes in Oman. As an indigenous species which is both genotypically and phenotypically adapted to the specific

environmental conditions of Oman, the silvicultural methodology necessary for its propagation is simple to perform and can be inexpensive to implement. Established forestry plots will survive for long periods of time, requiring minimal periods of dependency on water and maintenance facilities. These woodlands will provide a range of multi-purpose properties to the local people who are already familiar with this species. Their knowledge of the traditional methods of woodland management will ensure the long-term survival of the newly forested areas. Specifically, P.cineraria is ideally suited for the development of fuelwood and fodder plantations, shelter belts, and the improvement and stabilisation of soil. It also can be used in areas of degraded or saline soils which are unsuitable for agriculture. Since mature P.cineraria does not appear to compete directly with surface vegetation for moisture and soil nutrients, this species is potentially suitable for use in future agro-forestry practises.

Forestry in Oman is in its infancy, but in the last several years interest in the management of the existing woodlands and the propagation of new woodland cover has increased. To date, three forestry sites have been established in Northern Omân by the Ministry of Agriculture and Fisheries as pilot projects to investigate the silvicultural requirements necessary for the long-term establishment of forests in Oman. These pilot study areas have concentrated on using the indigenous tree species of Oman. A number of additional forestry programmes are currently in the planning stage. These programmes should incorporate species trials to test the performance of both native and exotic species, and provenance trials to test the variability of growth of individual species. To ensure that the forestry plots survive for long periods of time, these plots should be planted with a minimum number of well documented indigenous trees. This will also allow the comparison between the indigenous and exotic species under the specific environmental conditions in which they are grown.

The accumulation of information on P.cineraria and other tree species in Oman must be continued in order to maximise the utilisation of the land that has been allocated for forestry in this country. As a pioneer study of P.cineraria in Oman, this thesis used a multi-disciplinary approach to gather relevant information on the species. A similar approach can also be applied to other tree species that need to be tested in Oman.

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APPENDICES

APPENDIX A

PROSOPIS CINERARIA SLIDE REFERENCE COLLECTION

Photography was used extensively as a method of recording observations whilst working in the field (section 3.2.1). Relevant photographs were used to build up a reference collection of slides for P.cineraria in Oman. Slides rather than plates have been presented in this collection for three reasons:

1. The quality and colour of the photographs are higher in slide form.

2. Slides are more accessible for future utilisation by the Ministry of Agriculture and Fisheries (Oman) and the Office of the Conservation Advisor (Diwan, Oman), the joint sponsors of this thesis.

3. In slide form, more photographs can be viewed at any one time, which is often necessary for comparative purposes.

The slides in this reference collection have been arranged in order by subject for easy access. These subjects incorporate:

A. Wahiba Sands
B. Prosopis woodlands
C. Regeneration and tree clumps
D. Woodland ecology
E. Multi-purpose properties of P.cineraria
F. Utilisation and over-exploitation of the Prosopis woodlands
G. Morphological variation in mature P.cineraria
H. Voucher specimens of P.cineraria from the Sharqiya
I. Seedling field trials in Oman

For more detailed descriptions of the slides, refer to the relevant chapters of this thesis in which the slides have been cited. With the exception of slide 39 (Janet Allison), these slides were taken by the author.

PROSOPIS CINERARIA SLIDE REFERENCE COLLECTION

SLIDES 1 TO 15

PROSOPIS CINERARIA SLIDE REFERENCE COLLECTION

SLIDES 16 TO 30

PROSOPIS CINERARIA SLIDE REFERENCE COLLECTION

SLIDES 31 TO 45

APPENDIX B

BOTANICAL NAMES OF *PROSOPIS* SPECIES USED IN THE TEXT

1. *Prosopis cineraria* (L.) Druce
2. *Prosopis farcta* (Solander ex Russell) Macbride
3. *Prosopis koelziana* Burkart
4. *Prosopis africana* (Guill., Pere. & Rich.) Taubert
5. *Prosopis tamarugo* F. Philippi
6. *Prosopis kuntzei* Harms
7. *Prosopis ruscifolia* Grisebach
8. *Prosopis pallida* (Humboldt & Bonpland ex Willdenow) H.B.K.
9. *Prosopis articulata* S. Watson
10. *Prosopis chilensis* (Molina) Stuntz
11. *Prosopis juliflora* (Swartz) D.C.
12. *Prosopis nigra* (Grisebach) Hieronymus
13. *Prosopis flexuosa* D.C.
14. *Prosopis glandulosa* Torrey
15. *Prosopis alba* Grisebach
16. *Prosopis velutina* Wooton

From Burkart (1976).

APPENDIX C

PROSOPIS CINERARIA SEED DATA BANK

Seeds from 103 accessions of P.cineraria collected in Oman were stored under suitable conditions, as a reference seed bank. Data collected from each accession was centralised into a data bank, following the recommendations of the International Board of Plant Genetic Resources (IPBGR, 1983). The format of the seed data bank included the following parameters:

A. DATABASE FORMAT

1. Accession data
1.1 Accession number
1.2 Donor name
1.3 Donor identification number
1.4 Acquisition date
1.5 Accession size

2. Collection data
2.1 Collector's number
2.2 Collecting institute
2.3 Date of collection
2.4 Country of collection
2.5 Province/State
2.6 Location of collecting site
2.7 Easting of collection site
2.8 Northing of collection site
2.10 Number of trees sampled
2.11 Photographs
2.12 Herbarium specimen

3. Characterisation data
3.1 Tree height or mean tree height
3.2 Tree girth at breast height or mean tree girth
3.3 Flowers present
3.4 Mean pod length
3.5 Mean number of seeds per pod
3.6 Extent of seed infestation (%)
3.7 Pest species
3.8 Parasitic flora
3.9 Habitat description
3.10 Soil type
3.11 Climatic conditions
3.12 Associated plant species

4. Evaluation data

Additional information on the site and on specific traits of the trees such as disease and drought resistance.

B. SUMMARY DATA OF P.CINERARIA SEED ACCESSIONS COLLECTED

				SEED DATA			TREE DATA			
Accession	UTM Grid Reference		Mean pod	Mean	Infestation	Tree	Girth	Canopy	Canopy
number	/code	Easting	Northing	length(cm)	seeds/pod	(%)	height(m)	(m)	shade(%)	diam(m)
1	1-2-1	740331	2425425	10.95	3.90	35.00	10.00	1.60	70.00	9.00
2	1-3-1	739474	2401460	7.45	2.70	48.08	8.00	0.50	80.00	6.00
3	1-3-2	739474	2401460	8.39	6.90	19.15	7.00	0.66	75.00	5.00
4	1-3-3	739474	2401460	8.86	4.00	68.25	7.00	0.67	80.00	5.00
5	1-3-4	739474	2401460	8.15	4.90	27.94	5.00	0.59	50.00	3.50
6	4-1-1	733745	2385573	12.70	6.00	15.49	6.00	0.64	30.00	
7	4-1-2	733745	2385573	10.45	4.10	37.68	6.00	0.68	30.00	
8	4-1-3	733745	2385573	14.75	3.90	55.17	6.00	0.00	25.00	
9	4-1-4	733745	2385573	14.18	2.64	67.78	6.50	0.59	20.00	
10	4-1-5	733745	2385573	11.60	5.10	32.89	6.50	1.07	35.00	
11	4-1-6	733745	2385573	11.10	3.40	39.29	6.00	0.71	15.00	
12	4-1-7	733745	2385573	17.25	8.10	28.95	6.50	0.93	15.00	
13	4-1-8	733745	2385573	14.73	7.00	22.22	6.00	0.84	20.00	
14	4-1-9	733745	2385573	15.40	7.30	27.72	5.50	0.59	20.00	
15	4-1-10	733745	2385573	13.55	5.30	39.08	7.00	0.57	20.00	
16	4-1-11	733745	2385573	14.85	7.20	14.29	6.00	0.68	30.00	
17	4-1-12	733745	2385573	15.60	9.30	5.10	5.50	0.00	20.00	
18	4-1-13	733745	2385573	15.60	7.20	38.98	6.00	0.00	30.00	
19	4-1-14	733745	2385573	12.15	4.90	30.00	7.75	1.30	40.00	
20	4-1-15	733745	2385573	11.70	2.20	68.57	7.00	0.00	45.00	
21	4-1-16	733745	2385573	15.30	7.90	15.05	7.50	0.71	25.00	
22	5-1-1	739780	2405698	13.50	5.60	44.55	10.00	2.56	70.00	12.00
22	6-1-1	738656	2397272	10.65	2.80	42.86	7.50	1.50	50.00	6.00
23	6-1-2	738656	2397272	11.35	3.30	21.43	8.00	1.32	40.00	7.00
24	6-1-3	738656	2397272	13.20	5.20	34.18	8.00		30.00	10.00
25	6-1-4	738656	2397272	9.90	3.70	28.85	7.50	1.09	30.00	8.00
26	6-2-1	737539	2401104	12.80	5.50	39.56	5.00	0.70	60.00	
27	6-2-2	737539	2401104	12.40	1.80	74.63	5.50	0.82	65.00	
28	6-3-1	738337	2401250	13.00	2.30	35.90	10.00		50.00	
29	7-1-1	739428	2409972	11.70	5.60	8.20	6.50	0.58	60.00	5.00
30	7-1-2	739428	2409972	8.50	2.00	16.67	7.50	0.87	60.00	7.00
31	7-1-3	739428	2409972	11.80	3.30	46.77	7.50	0.79	80.00	7.00
32	7-2-1	740124	2410119	14.50	6.30	16.00	9.00		60.00	8.00
33	7-3-1	740194	2410740	12.15	6.10	22.78	8.50		50.00	10.00
34	7-3-2	740194	2410740	11.15	6.20	16.22	8.00		55.00	8.00
35	7-4-1	738709	2417395	11.70	1.90	36.67	5.00	0.60	50.00	4.00
36	7-4-2	738709	2417395	10.25	1.30	58.06	8.50	1.23	60.00	6.00
37	7-4-3	738709	2417395	10.00	1.20	50.00	7.50	0.81	60.00	5.00
38	8-1-1	736036	2430518	8.70	1.10	60.00	7.00	0.83	90.00	5.00
39	8-1-2	736036	2430518	9.20	2.30	32.35	6.50	0.69	90.00	4.50
40	8-1-3	736036	2430518	5.90	0.78	50.00	6.00	0.52	75.00	4.00
41	8-1-4	736036	2430518	8.85	2.40	42.86	6.50	0.59	75.00	4.00
42	8-2-1	728223	2442698	10.15	3.90	45.07	12.00	2.12	80.00	10.00
43	9-1-1	738565	2396963	9.25	3.60	10.00	9.50	0.88	40.00	9.00
44	10-1-1	738255	2396883	11.45	4.80	11.11	8.00	1.10	45.00	8.00
45	10-1-2	738255	2396883	9.50	4.30	2.27	7.00	0.86	40.00	4.00
46	10-2-1	737921	2396456	13.00	9.30	8.11	7.50	0.94	30.00	6.00
47	10-3-1	735033	2396621	7.80	6.10	11.59	9.50	0.87	40.00	9.00
48	10-4-1	734916	2394780	14.80	9.10	13.33	7.50	0.94	50.00	6.50
49	10-4-2	734916	2394780	14.05	9.20	7.07	7.00	0.59	50.00	3.00
50	10-4-3	734916	2394780	13.75	5.00	53.27	7.50	0.94	35.00	5.00

	Accession number/code	UTM Grid Reference Easting	Northing	SEED DATA Mean pod length(cm)	Mean seeds/pod	Infestation (%)	TREE DATA Tree height(m)	Girth (m)	Canopy shade(%)	Canopy diam(m)
51	10-4-4	734916	2394780	13.70	7.80	29.09	7.50	0.93	40.00	6.00
52	2-1.1.1	670825	2389289	15.25	5.40	55.00	9.50		40.00	10.00
53	2-1.2.1	670675	2388222	12.95	3.90	45.07	6.50	0.53	60.00	4.00
54	2-1.2.2	670675	2388222	14.75	7.90	24.04	7.50		50.00	6.00
55	2-1.2.3	670675	2388222	15.15	7.90	24.76	6.50		50.00	5.00
56	2-1.2.4	670675	2388222	13.60	5.60	30.00	6.50	0.52	40.00	4.00
57	2-2.1.1	669814	2385113	13.55	4.40	34.33	7.50	1.04	60.00	5.50
58	2-2.1.2	669814	2385113	11.35	4.60	29.23	6.50	0.60	60.00	4.50
59	2-2.2.1	673216	2373697	10.40	4.50	49.44	7.00	1.13	60.00	7.00
60	2-2.3.1	673154	2372076	11.75	2.10	32.26	6.50	0.84	65.00	6.50
61	2-2.4.1	672421	2370424	11.30	3.60	55.00	7.50		40.00	8.50
62	2-2.5.1	673221	2383771	13.00	3.60	62.86	9.50	1.00	60.00	7.00
63	2-2.5.2	673221	2383771	11.43	6.70	37.33				
64	2-3.1.1	670385	2358917	11.90	6.20	38.00	6.00	0.90	75.00	4.50
65	2-3.2.1	669582	2357651	13.45	2.20	72.50	7.00	0.90	40.00	6.00
66	2-3.2.2	669582	2357651	12.95	2.30	78.10	7.00	0.85	35.00	8.00
67	2-3.2.3	669582	2357651	15.20	3.80	66.07	7.00		40.00	6.00
68	2-3.3.1	668912	2355607	16.25	8.20	50.30	5.50	0.69	45.00	5.00
69	2-3.4.1	689944	2355253	12.00	2.50	78.45	5.00	0.94	30.00	5.50
70	2-3.5.1	667139	2352056	13.25	5.10	61.36	5.50	0.94	70.00	4.00
71	2-4.1.1	663255	2400947	16.20	8.10	31.36	7.50	0.90	80.00	5.00
72	2-4.1.2	663255	2400947	15.40	8.40	22.94	9.50	1.13	80.00	6.00
73	2-4.2.1	662227	2403608	11.45	2.60	63.38	7.50		70.00	5.00
74	2-4.3.1	660726	2406740	13.60	4.50	37.50	8.50		80.00	9.00
75	2-4.3.2	660726	2406740	13.25	3.30	50.00	8.00	0.53	70.00	8.50
76	2-4.4.1	660350	2408123	8.05	1.40	50.00	5.50	0.75	50.00	2.50
77	2-4.4.2	660350	2408123	8.50	1.20	62.50	5.50	0.58	50.00	4.50
78	2-4.4.3	660350	2408123	6.90	1.20	47.83	6.50	0.95	50.00	5.00
79	2-4.4.4	660350	2408123	7.70	1.70	29.17	7.50	0.95	50.00	6.00
80	2-4.4.5	660350	2408123	7.10	1.70	45.16	7.00	0.79	60.00	5.00
81	2-4.4.6	660350	2408123	8.05	1.50	55.88	5.00	0.93	60.00	3.00
82	2-4.4.7	660350	2408123	8.50	2.50	30.56	7.50	0.90	60.00	5.00
83	2-4.4.8	660350	2408123	9.00	1.70	50.00	8.50	0.65	70.00	7.00
84	2-4.4.9	660350	2408123	8.40	2.20	45.00	6.50	0.52	65.00	4.50
85	2-6.1.1	655446	2417865	12.09	4.09	43.04	6.00	0.74	60.00	3.50
86	2-7.1.1	660450	2345150	12.00	2.20	77.08	8.50	1.41	60.00	7.50
87	2-8.1.1			11.05	3.20	58.44	8.00	1.50	50.00	8.50
88	2-8.2.1			14.00	4.33	65.18	7.00	1.08	50.00	7.00
89	2-9-1.1	285385		7.40	4.90	28.99	7.50	1.16	60.00	5.50
90	3-1.1.1			9.40	2.40	64.18	6.00	0.50	55.00	4.50
91	3-2.1.1			12.55	2.70	64.00	8.50	1.28	45.00	7.50
92	3.3.1.1			10.60	5.30	44.79	7.50	0.99	90.00	5.00
93	3-3.2.2			16.90	13.00	8.45	10.50	1.16	95.00	5.00
94	4-1.1.1			14.80	8.00	23.08	9.50	2.65	55.00	11.00
95	4-1.2.2			12.50	5.30	18.46	10.50	2.00	70.00	9.50
96	4-2.1.1	743859	2418158	11.05	5.50	21.43	11.00		70.00	12.00
97	4-2.1.2	743859	2418158	7.28	1.33	0.00	7.00	1.10	80.00	7.00
98	4-2.1.3	743859	2418158	9.22	2.70	0.00	11.00	1.25	80.00	9.00
99	4-2.1.4	743859	2418158	10.25	2.60	7.14	9.00	1.27	80.00	10.00
100	4-2.1.5	743859	2418158	12.15	5.00	29.58	6.00	1.36	70.00	6.00
101	EPZ/1	Eastern Prosopis Zone provenance collection (No. 1)								
102	EPZ/2	Eastern Prosopis Zone provenance collection (No. 2)								
103	CPZ/1	Central Prosopis Zone provenance collection (No. 1)								

The P.cineraria seed accessions used in this thesis include:

1. 38 accessions sampled from individual trees in the glasshouse accession trial (Chapter 5);

2. seven accessions sampled from individual trees in the glasshouse salinity trial (Chapter 5);

3. EPZ/1 provenance accession, randomly sampled from over 100 trees throughout the EPZ. These seeds were used to examine the genetic variation in the provenance (Chapter 4), the morphological variation of the seeds (Chapter 5) and the seed source for the seedling field trials in Oman (Chapter 6).

APPENDIX D

SUMMARY OF DATA NOT PRESENTED IN CHAPTERS 3, 4, 5 AND 6.

CHAPTER 3 DATA

1. Summary of chemical composition ($mgdm^{-3}$) of *Prosopis* woodland soils (section 3.3.2), using the soil analysis method described in section 2.5.

	N	P	NH_4	Fe	EC	pH
Mean	31.56	15.49	5.47	0.22	1265.56	8.29
S.D.	46.56	8.54	6.70	0.25	1838.67	0.55
Minimum	0.90	5.00	0.00	0.00	123.00	7.11
Maximum	288.00	50.00	46.00	1.05	8320.00	9.27
N	63	63	63	63	52	52

	K	Ca	Mg	Cl	SO_4
Mean	434.48	2484.13	323.91	1730.16	864.97
S.D.	220.96	1670.16	140.16	2930.43	1269.36
Minimum	71.00	1000.00	100.00	125.00	0.00
Maximum	1160.00	8000.00	600.00	15000.00	5850.00
N	63	63	46	63	63

2. Summary of tree distances (d) and girth at breast height (GBH) for each transect (T1-T5; T1W-T5W) in the Eastern *Prosopis* Zone (EPZ), sampled by the point centred quarter method (PCQM) and wandering-quarter method (WQM) (section 3.3.3).

A. PCQM data

	T1		T2		T3		T4		T5	
	d (m)	GBH (cm)	d (m)	GBH (cm)	d (m)	GBH (cm)	d (m)	GBH (cm)	d (m)	GBH (cm)
Mean	11.2	85.2	22.6	68.8	13.3	75.2	21.3	67.7	15.8	61.3
S.D.	7.9	29.2	20.4	21.4	10.4	37.3	39.1	34.8	12.7	27.0
Minimum	0.9	31.0	3.0	20.0	1.5	32.0	2.0	13.0	2.0	26.0
Maximum	31.5	188.0	72.3	120.0	42.5	202.0	167.0	171.0	57.0	148.0
N	76	76	48	48	40	40	32	32	24	24

B. WQM data

	T1W		T2W		T3W		T4W		T5W	
	d (m)	GBH (cm)	d (m)	GBH (cm)	d (m)	GBH (cm)	d (m)	GBH (cm)	d (m)	GBH (cm)
Mean	10.0	80.1	17.6	76.3	8.5	66.6	10.9	59.0	6.7	50.8
S.D.	8.0	31.3	22.6	22.6	5.6	21.0	19.9	28.9	6.5	17.4
Minimum	0.4	31.0	1.0	40.0	0.4	30.0	0.2	14.0	0.5	18.0
Maximum	48.0	250.0	135.0	132.0	21.5	125.0	133.0	170.0	29.0	100.0
N	184	184	72	72	92	92	104	104	83	83

CHAPTER 4 DATA

1. Summary of tree mensuration variables (sections 4.3.1 to 4.3.5).

A. Continuous variables

	HEIGHT (m)	CRODIAM (m)	GIRTH (cm)	BRANCH.HT (m)	SHADE (%)	ROOT.HT (m)	ROOT.SPREAD (m)
Mean	5.904	4.407	78.994	1.821	51.430	0.050	0.207
S.D.	1.654	2.095	32.754	1.080	23.260	0.227	0.715
Minimum	1.200	0.800	13.000	0.000	0.000	0.000	0.000
Maximum	12.000	12.000	256.000	5.000	95.000	2.000	5.000
N	321	291	315	321	321	321	321

B. Categorical variables

CROSHAPE (N=321)

Attribute	N	Percent
Sphere	156	50.16
Dome	77	24.76
Spindle	22	7.07
Irregular	56	18.01

STEMTYPE (N=321)

Attribute	N	Percent
Erect	132	41.12
Leaning	90	28.04
Twining	99	30.84

BRANTYPE (N=321)

Attribute	N	Percent
Divergent	286	89.10
Non-divergent	35	10.90

FOLIAGE (N=321)

Attribute	N	Percent
Poor	104	32.40
Medium	147	45.79
Good	70	21.81

HABIT (N=321)

Attribute	N	Percent
Solitary	153	47.66
Clump	130	40.50
Solitary/clump	38	11.84

ROOTYPE (N=321)

Attribute	N	Percent
None	283	88.16
Lateral	13	4.05
Enlarged base	25	7.79

SUCKERS (N=321)

Attribute	N	Percent
No	295	91.90
Yes	26	8.10

FRUIT (N=321)

Attribute	N	Percent
No	201	62.62
Yes	120	37.38

2. Summary of legume variables for the Eastern Prosopis Zone and Central Prosopis Zone (section 4.3.6).

	Eastern Prosopis Zone			Central Prosopis Zone		
	PODLENGTH (mm)	VIABSEED (per pod)	INFESTATION (%)	PODLENGTH (mm)	VIABSEED (per pod)	INFESTATION (%)
Mean	11.80	4.68	33.29	11.90	3.97	47.59
S.D.	2.50	2.34	18.12	2.72	2.24	16.08
Minimum	5.90	0.80	2.27	6.90	1.20	22.94
Maximum	17.30	9.30	74.65	16.30	8.40	78.45
N (x10 pods)	54	54	54	32	32	32

CHAPTER 5 DATA

1. Summary of data from the P.cineraria glasshouse accession trial in Durham, U.K. (section 5.3.3).

	HEIGHT (mm)	STEMDIAM (mm)	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS (per pinna)	THORNS (mm)
Mean	18.518	1.514	3.258	1.921	0.850	9.111	0.848
S.D.	8.479	0.154	1.409	1.230	0.518	2.687	0.922
Minimum	5.000	0.900	0.000	0.000	0.000	0.000	0.000
Maximum	68.000	2.400	8.000	5.500	2.000	14.000	3.300
N	636	636	636	636	636	636	636

2. Summary of data from the P.cineraria glasshouse salinity trial in Durham, U.K. (section 5.3.4).

	HEIGHT (mm)	STEMDIAM (mm)	NODES	MAT.LVS	IMMAT.LVS	LEAFLETS (per pinna)	THORNS (mm)
Mean	16.157	1.490	2.728	1.507	0.644	7.939	0.586
S.D.	7.400	0.142	1.279	1.116	0.539	3.351	0.751
Minimum	5.000	0.500	0.000	0.000	0.000	0.000	0.000
Maximum	41.000	2.000	7.000	5.500	2.500	14.000	3.000
N	587	587	587	587	587	587	587

CHAPTER 6 DATA

PART 2

Environmental effects (SQU-1 & AL-K) on the size (F1) and morphology (F2 & F3) of 34 week old seedlings, using principal components analysis performed on 10 continuous variables measured from 704 seedlings. Treatment means and standard deviations of these first three principal components are summarised below (n=16 seedlings per treatment).

		SQU-1			AL-K		
		F1	F2	F3	F1	F2	F3
1. DS/control	Mean	-0.657	0.358	0.114	-0.414	-0.241	0.535
	S.D.	0.492	1.004	0.947	0.458	0.461	0.898
2. DS/NPK+T	Mean	-0.491	0.611	-0.132	0.017	-0.310	0.500
	S.D.	0.409	0.821	0.495	0.661	0.749	0.772
3. DS/NPK-T	Mean	-0.473	0.395	-0.250	-0.001	-0.472	-0.058
	S.D.	0.574	0.990	0.991	0.640	0.846	0.883
4. DS/NPK+T/CM2	Mean	-0.154	0.476	0.243	1.099	-0.085	0.007
	S.D.	0.747	0.775	0.952	0.793	0.956	1.049
5. DS/CM1	Mean	-0.211	0.437	0.140	0.269	-0.220	0.411
	S.D.	0.650	0.744	0.917	0.609	0.784	0.772
6. DS/CM2	Mean	-0.770	-0.196	-0.092	-0.180	-0.222	0.673
	S.D.	0.322	0.566	0.774	0.407	0.425	0.534
7. DS/CM3	Mean	-0.501	0.412	-0.302	0.901	0.217	-0.125
	S.D.	0.658	1.033	0.732	0.622	0.694	1.135
8. DS/peat	Mean	-0.090	0.779	-0.169	0.597	-0.629	0.133
	S.D.	0.579	0.793	0.871	1.242	1.776	0.838
9. DS/WAP	Mean	-0.931	-0.427	-0.314	-0.091	-0.168	-0.559
	S.D.	0.231	0.528	0.589	0.575	0.600	0.741
10. DS/PO3	Mean	-0.913	-0.174	-0.135	0.080	0.159	0.009
	S.D.	0.438	0.928	0.701	0.551	0.530	0.917
11. DS/excess	Mean	-1.231	-1.126	-1.091	-0.530	-0.729	-0.229
	S.D.	0.296	0.919	2.188	0.374	0.517	0.634
12. WS/control	Mean	-0.021	0.686	-0.393	0.684	-0.377	0.589
	S.D.	0.633	0.877	0.663	0.701	0.602	1.075
13. WS/NPK+T	Mean	0.106	0.559	0.011	0.922	-0.102	0.155
	S.D.	0.902	0.774	0.869	0.692	0.975	1.014
14. WS/NPK-T	Mean	-0.273	0.329	0.081	0.785	0.799	0.161
	S.D.	0.847	0.907	0.693	0.624	1.010	0.693
15. WS/NPK+T/CM2	Mean	-0.570	0.208	0.002	2.104	0.064	-0.165
	S.D.	0.816	1.158	1.038	1.063	1.661	1.074
16. WS/CM1	Mean	-0.563	0.048	-0.119	0.720	0.034	0.162
	S.D.	0.533	0.746	0.880	1.051	0.892	0.770
17. WS/CM2	Mean	-0.785	-0.283	0.185	0.686	-0.333	-0.368
	S.D.	0.395	0.605	0.998	0.902	0.959	1.758
18. WS/CM3	Mean	-0.840	-0.173	-0.013	1.001	0.224	0.394
	S.D.	0.451	0.752	0.839	1.224	0.933	0.801
19. WS/peat	Mean	-0.475	0.545	-0.160	0.589	0.092	0.148
	S.D.	0.570	1.013	0.652	0.761	1.194	0.872
20. WS/WAP	Mean	-0.385	0.293	0.158	1.628	-0.603	0.450
	S.D.	0.620	0.948	0.607	1.370	2.050	0.832
21. WS/PO3	Mean	-0.695	-0.064	0.077	0.587	-0.089	0.381
	S.D.	0.722	0.504	0.595	0.718	0.896	0.882
22. WS/excess	Mean	-0.628	0.077	-0.696	0.448	-0.581	-0.014
	S.D.	0.534	0.867	1.813	0.775	0.737	0.760

PART 3

Shade effects (SQU-1 & SQU-2) on the size (F1) and morphology (F2 & F3) of 34 week old seedlings, using principal components analysis performed on 10 continuous variables measured from 436 seedlings. Sample size, treatment means and standard deviations of these first three principal components are summarised below.

		SQU-1			SQU-2		
		F1	F2	F3	F1	F2	F3
1. DS/control	N	16	16	16	16	16	16
	Mean	0.181	-0.581	-0.285	-0.173	0.885	-0.021
	S.D.	0.633	0.496	0.619	0.711	0.383	0.950
2. DS/NPK+T	N	16	16	16	16	16	16
	Mean	0.394	-0.781	0.044	-0.270	0.889	-0.148
	S.D.	0.531	0.728	0.479	0.524	0.325	0.866
3. DS/NPK-T	N	16	16	16	16	16	16
	Mean	0.497	-0.703	-0.008	-0.187	0.974	0.077
	S.D.	0.817	0.691	0.778	0.590	0.404	0.635
4. DS/NPK+T/CM2	N	16	16	16	16	16	16
	Mean	1.035	-0.653	-0.299	-0.034	0.903	-0.555
	S.D.	1.172	0.883	0.850	0.485	0.524	0.735
5. DS/WAP	N	16	16	16	16	16	16
	Mean	-0.111	-0.770	-0.493	-0.939	0.668	0.953
	S.D.	0.307	0.417	0.445	0.484	0.268	0.570
6. DS/PO3	N	16	16	16	14	14	14
	Mean	-0.120	-0.633	-0.442	-0.887	0.568	0.893
	S.D.	0.581	0.428	0.583	0.418	0.304	0.759
7. DS/excess	N	16	16	16	16	16	16
	Mean	-0.444	-0.929	-0.143	-1.021	0.417	0.828
		0.410	0.485	0.853	0.253	0.312	0.862
8. WS/control	N	16	16	16	16	16	16
	Mean	1.210	-0.401	0.045	-0.200	0.920	0.354
	S.D.	0.966	0.685	0.539	0.647	0.414	0.540
9. WS/NPK+T	N	16	16	16	16	16	16
	Mean	1.488	-0.043	-0.400	-0.512	0.577	0.073
	S.D.	1.458	1.005	0.809	0.595	0.485	0.903
10. WS/NPK-T	N	16	16	16	12	12	12
	Mean	0.871	-0.427	-0.412	-0.291	0.763	-0.016
	S.D.	1.401	1.315	0.469	0.849	0.408	0.927
11. WS/NPK+T/CM2	N	16	16	16	15	15	15
	Mean	0.377	-0.542	-0.361	-0.596	0.691	0.031
	S.D.	1.234	1.144	1.014	0.680	0.400	0.687
12. WS/WAP	N	16	16	16	16	16	16
	Mean	0.665	-0.582	-0.595	-0.526	0.714	-0.040
	S.D.	0.881	0.802	0.691	0.486	0.418	0.592
13. WS/PO3	N	16	16	16	12	12	12
	Mean	0.243	-0.596	-0.491	-0.771	0.843	0.871
	S.D.	1.191	0.956	0.432	0.809	0.529	0.901
14. WS/excess	N	16	16	16	13	13	13
	Mean	0.252	-1.417	0.491	-0.665	0.293	0.389
	S.D.	0.613	1.408	2.795	0.518	0.356	0.859

PART 4

Developmental variation in seedling growth between 13 and 34 week old seedlings from the SQU-1 trial. Summary of harvest data for each seedling age. Where Cot. = cotyledon.

A. 13 week old seedlings (n=8 per treatment)

Treatment		Cot. area (cm^2)	Cot. weight (g)	Leaf area (cm^2)	Leaf weight (g)	Stem weight (g)	Root weight (g)	Nodule weight (g)	Total weight (g)
1. DS/control	Mean	0.4	0.004	3.5	0.024	0.018	0.138	0.005	0.189
	S.D.	0.6	0.006	1.4	0.009	0.005	0.060	0.007	0.072
2. DS/NPK+T	Mean	0.3	0.003	6.3	0.043	0.036	0.177	0.002	0.260
	S.D.	0.6	0.005	3.5	0.023	0.016	0.064	0.003	0.087
3. DS/NPK-T	Mean	2.6	0.013	4.3	0.029	0.027	0.186	0.005	0.251
	S.D.	1.4	0.004	1.4	0.011	0.010	0.065	0.007	0.082
4. DS/NPK+T/CM2	Mean	1.0	0.012	14.1	0.143	0.199	0.396	0.0	0.740
	S.D.	0.0	0.003	1.0	0.022	0.073	0.083	0.0	0.151
5. DS/CM1	Mean	1.4	0.014	10.3	0.090	0.117	0.204	0.0	0.412
	S.D.	0.0	0.000	2.0	0.022	0.044	0.043	0.0	0.098
6. DS/CM2	Mean	1.3	0.012	5.2	0.037	0.034	0.094	0.0	0.171
	S.D.	0.3	0.006	1.4	0.009	0.008	0.051	0.0	0.064
7. DS/CM3	Mean	0.0	0.000	7.0	0.054	0.056	0.127	0.0	0.237
	S.D.	0.0	0.000	3.2	0.028	0.035	0.062	0.0	0.117
8. DS/peat	Mean	0.0	0.0	6.6	0.050	0.037	0.117	0.012	0.213
	S.D.	0.0	0.0	2.3	0.018	0.013	0.031	0.006	0.049
9. DS/WAP	Mean	0.8	0.007	3.8	0.028	0.024	0.146	0.016	0.205
	S.D.	0.0	0.002	1.2	0.010	0.007	0.051	0.008	0.062
10. DS/PO3	Mean	0.0	0.0	0.0	0.022	0.018	0.117	0.005	0.161
	S.D.	0.0	0.0	0.0	0.008	0.007	0.033	0.002	0.041
11. DS/excess	Mean	1.2	0.009	2.6	0.016	0.017	0.094	0.0	0.130
	S.D.	0.4	0.004	0.5	0.003	0.006	0.033	0.0	0.038
12. WS/control	Mean	0.0	0.0	12.1	0.090	0.124	0.238	0.0	0.452
	S.D.	0.0	0.0	5.0	0.043	0.054	0.118	0.0	0.212
13. WS/NPK+T	Mean	0.0	0.0	9.8	0.085	0.120	0.247	0.006	0.455
	S.D.	0.0	0.0	2.6	0.022	0.038	0.092	0.002	0.141
14. WS/NPK-T	Mean	1.6	0.013	8.2	0.069	0.080	0.210	0.003	0.361
	S.D.	0.0	0.000	2.3	0.022	0.029	0.082	0.003	0.113
15. WS/NPK+T/CM2	Mean	2.2	0.026	6.6	0.064	0.050	0.138	0.001	0.255
	S.D.	0.0	0.000	1.6	0.014	0.018	0.044	0.000	0.050
16. WS/CM1	Mean	1.3	0.015	5.7	0.058	0.073	0.116	0.006	0.256
	S.D.	0.4	0.005	1.7	0.024	0.033	0.049	0.005	0.094
17. WS/CM2	Mean	0.0	0.0	4.7	0.037	0.035	0.123	0.0	0.196
	S.D.	0.0	0.0	1.3	0.009	0.020	0.043	0.0	0.065
18. WS/CM3	Mean	0.0	0.0	5.8	0.053	0.063	0.139	0.016	0.263
	S.D.	0.0	0.0	0.9	0.012	0.019	0.050	0.007	0.061
19. WS/peat	Mean	1.8	0.014	5.3	0.050	0.059	0.144	0.0	0.254
	S.D.	0.0	0.000	1.4	0.012	0.016	0.055	0.0	0.082
20. WS/WAP	Mean	2.1	0.027	8.4	0.087	0.091	0.325	0.003	0.506
	S.D.	0.0	0.000	4.9	0.052	0.038	0.161	0.000	0.249
21. WS/PO3	Mean	0.0	0.0	8.9	0.095	0.115	0.254	0.0	0.464
	S.D.	0.0	0.0	1.6	0.019	0.041	0.056	0.0	0.107
22. WS/excess	Mean	1.9	0.018	6.9	0.064	0.061	0.169	0.0	0.299
	S.D.	0.6	0.005	1.7	0.017	0.030	0.075	0.0	0.118

B. 34 week old seedlings (n=16 per treatment). Where n/d = not determined.

Treatment		SQU-1 Shoot weight (g)	AL-K Shoot weight (g)	SQU-2 Shoot weight (g)
1. DS/control	Mean	4.394	9.538	4.029
	S.D.	2.531	6.601	2.399
2. DS/NPK+T	Mean	4.770	16.469	3.865
	S.D.	2.915	12.699	1.964
3. DS/NPK-T	Mean	6.209	14.914	3.896
	S.D.	5.264	10.924	2.352
4. DS/NPK+T/CM2	Mean	10.821	31.121	4.465
	S.D.	8.452	14.810	2.361
5. DS/CM1	Mean	8.367	18.800	n/d
	S.D.	7.729	11.839	
6. DS/CM2	Mean	4.325	11.365	n/d
	S.D.	2.052	4.786	
7. DS/CM3	Mean	6.348	24.418	n/d
	S.D.	4.508	10.629	
8. DS/peat	Mean	10.619	25.439	n/d
	S.D.	6.254	26.470	
9. DS/WAP	Mean	3.183	13.183	1.340
	S.D.	1.487	7.016	0.940
10. DS/PO3	Mean	3.234	15.945	1.332
	S.D.	1.979	7.313	1.023
11. DS/excess	Mean	2.042	9.245	0.954
	S.D.	1.449	5.266	0.399
12. WS/control	Mean	10.464	27.571	3.995
	S.D.	6.063	13.170	2.962
13. WS/NPK+T	Mean	14.736	29.667	2.612
	S.D.	11.789	13.169	2.134
14. WS/NPK-T	Mean	10.390	23.925	3.372
	S.D.	11.985	11.774	2.783
15. WS/NPK+T/CM2	Mean	6.382	56.364	2.494
	S.D.	7.892	30.749	2.354
16. WS/CM1	Mean	5.981	26.633	n/d
	S.D.	4.385	21.139	
17. WS/CM2	Mean	4.139	25.947	n/d
	S.D.	2.387	18.452	
18. WS/CM3	Mean	3.759	32.979	n/d
	S.D.	2.465	24.498	
19. WS/peat	Mean	6.118	25.573	n/d
	S.D.	3.940	16.385	
20. WS/WAP	Mean	7.667	48.455	2.466
	S.D.	5.107	34.191	1.541
21. WS/PO3	Mean	6.375	24.018	2.263
	S.D.	10.573	13.832	2.195
22. WS/excess	Mean	3.852	23.085	1.553
	S.D.	2.319	15.771	1.159

APPENDIX E

WELL WATER DATA FROM BORE HOLES IN THE CENTRAL *PROSOPIS* ZONE

Well	ION Cl	SO_4	Ca	Na	Mg	Total	pH	Source of water
SW4	3094.50*	2700.00	929.86	2060.00	405.98	9382.12	7.75	aeolianite
	32.98@	28.78	9.91	21.96	4.33			
SW2	9433.50	3650.00	761.52	5840.00	590.73	20460.05	6.15	siltstone
	46.37	17.75	3.70	28.40	2.87			
SW6	6581.00	3500.00	444.89	4840.00	700.13	16323.26	8.87	aeolianite
	40.32	21.44	2.73	29.65	4.29			
SW1	2017.90	980.00	102.20	1330.00	138.57	4721.91	6.47	sand
	42.73	20.75	2.16	28.17	2.93			
SW5	16868.00	5500.00	717.43	12000.00	1293.29	36789.88	8.72	siltstone
	45.85	14.95	1.95	32.62	3.52			
W6	1129.97	937.50	122.00	1070.00	103.16	3605.24	7.71	alluvium
	31.34	26.00	3.38	29.68	2.86			
SW3	17941.50	5500.00	1318.63	12300.00	741.46	38034.78	5.88	siltstone
	47.17	14.46	3.47	32.34	1.95			
Mean Ratio by wt.	40.97	20.59	3.90	28.97	3.25			

Data from Public Authority for Water Resources (Oman) and Jones *et al*. (1988). Where * = $mgdm^{-3}$; @ = % of total ions.